10-10-2017

The North American Quails, Partridges, and Pheasants

Paul A. Johnsgard

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The North American Quails, Partridges, and Pheasants

Their Biology and Behavior

Paul A. Johnsgard

This book documents the biology of six species of New World quails that are native to North America north of Mexico (mountain, scaled, Gambel's, California, and Montezuma quails, and the northern bobwhite), three introduced Old World partridges (chukar, Himalayan snowcock, and gray partridge), and the introduced common (ring-necked) pheasant. Collectively, quails, partridges, and pheasants range throughout all of the continental United States and the Canadian provinces. Two of the species, the northern bobwhite and ring-necked pheasant, are the most economically important of all North American upland game birds. All of the species are hunted extensively for sport and are highly popular with naturalists, birders, and other outdoor enthusiasts.

The New World quails and Old World partridges share many basic aspects of social and reproductive behavior, such as gathering during nonbreeding periods into small, usually closely related coveys. They also all exhibit prolonged monogamous pair-bonding, biparental brood care, reduced sexual dimorphism in adult plumages and body mass, and a high diversity of vocalizations associated with covey, family, and pair interactions. As relatively small species with high mortality rates, they have evolved rapid periods to sexual maturity, unusually large clutch sizes that are among the largest of all birds, and pairings that regularly attempt to renest following nest failures.

By comparison, the ring-necked pheasant is one of the Old World pheasants, which form less cohesive and less tightly structured flocks and have evolved nonmonogamous (polygynous or promiscuous) breeding strategies. Adult pheasants exhibit strong sexual dimorphism in plumage, body mass, and sexual behavior. Adult males have sharp tarsal spurs that are used during fights when establishing dominance status, and they perform some of the most spectacular sexual advertisement displays of all birds. Clutch sizes average considerably smaller than those of quails and partridges, whereas brooding durations and durations to sexual maturity are longer.

The book totals more than 85,000 words and includes about 1,100 literature citations, 29 pages of drawings, 27 photos, and 11 maps. Together with an earlier volume on grouse, it completes a survey of the biology and behavior of all 19 native and introduced species of North American quails, partridges, and pheasants.

Photos, back: Montezuma quail, male; *front:* Gambel's quail, male

Zea Books • Lincoln, Nebraska

ISBN: 978-1-60962-117-9 doi: 10.13014/K2G15Z1P

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Their Biology and Behavior

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School of Biological Sciences
University of Nebraska–Lincoln

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Abstract

This book documents the biology of six species of New World quails that are native to North America north of Mexico (mountain, scaled, Gambel's, California, and Montezuma quails, and the northern bobwhite), three introduced Old World partridges (chukar, Himalayan snowcock, and gray partridge), and the introduced common (ring-necked) pheasant. Collectively, quails, partridges, and pheasants range throughout all of the continental United States and the Canadian provinces. Two of the species, the northern bobwhite and ring-necked pheasant, are the most economically important of all North American upland game birds. All of the species are hunted extensively for sport and are highly popular with naturalists, birders, and other outdoor enthusiasts.

Biologically, the nearly 200 species of New World quails and Old World partridges share many basic aspects of social and reproductive behavior, such as gathering during nonbreeding periods into small, usually closely related coveys. They also all exhibit prolonged monogamous pair-bonding and biparental brood care lasting up to one or more months. These adaptations have resulted in the group's evolution of reduced sexual dimorphism in adult plumages and body mass, and a high diversity of vocalizations associated with covey, family, and pair interactions. As relatively small species with high mortality rates, they have evolved rapid periods to sexual maturity, unusually large clutch sizes that are among the largest of all birds, and pairings that regularly attempt to renest following nest failures. Males might participate at times in incubation, or at least will take over incubation duties if their mate is lost.

By comparison, the ring-necked pheasant is one of the Old World pheasants, a group of about 50 species that are variably larger and heavier than quails and partridges, with adults weighing up to five kilograms (in peafowl). Pheasants form less cohesive and less tightly structured flocks than quails and partridges, and have evolved nonmonogamous (polygynous or promiscuous) breeding strategies. Among adult pheasants the sexes exhibit strong sexual dimorphism in plumage, body mass, and sexual behavior, and adult male pheasants have sharp tarsal spurs that are used during fights when establishing relative male dominance status.

Male pheasants also perform some of the most spectacular sexual advertisement displays of all birds, which serve to attract and fertilize multiple females. During such displays, males exhibit these conspicuous feathers and colorful facial skin, often while performing dramatic posturing and vocalizing, or producing related sounds such as wing-flapping or foot-stamping. Clutch sizes in pheasants average considerably smaller than those of quails and partridges, whereas brooding durations average longer. Durations to sexual maturity also average longer than in quails and partridges, and in some large species may require up to at least three years.

The book totals more than 85,000 words, and includes about 1,100 literature citations, 29 pages of drawings, 25 photos, and 11 maps. Together with an earlier volume on grouse, it completes a survey of the biology and behavior of all 19 native and introduced species of North American quails, partridges, and pheasants.

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ISBN: 978-1-60962-117-9

doi: 10.13014/K2G15Z1P

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Contents

List of Maps	4
List of Figures	4
List of Photographs	5
Preface.	6
 I. Introduction to the North American Quails, Partridges, and Pheasants	7
 II. Species Accounts	12
Family Odontophoridae: New World Quails	12
Mountain Quail, <i>Oreortyx pictus</i>	16
Scaled Quail, <i>Callipepla squamata</i>	25
Gambel's Quail, <i>Callipepla gambelii</i>	32
California Quail, <i>Callipepla californica</i>	40
Northern Bobwhite, <i>Colinus virginianus</i>	49
Montezuma Quail, <i>Cyrtonyx montezumae</i>	62
Family Phasianidae: Pheasants, Partridges, and Relatives	71
Tribe Perdicipini: Old World Partridges and Relatives	71
Chukar, <i>Alectoris chukar</i>	72
Himalayan Snowcock, <i>Tetraogallus himalayensis</i>	81
Gray Partridge, <i>Perdix perdix</i>	87
Tribe Phasianini: Pheasants and Their Relatives.	97
Ring-necked Pheasant, <i>Phasianus colchicus</i>	98
 III. References	109
<i>The Birds of North America</i>	109
World, National, Regional, and Local Surveys	109
Monographs: Distribution and Biology of Galliformes	112
General Taxonomic and Taxon-Based Studies	112
Genetic and Evolutionary Studies.	113
Multiple-Taxon Studies	114
Dual-Species and Hybrid Studies	115
Single-Species Studies	116
Mountain Quail.	116
Scaled Quail	116
Gambel's Quail	117
California Quail.	118
Northern Bobwhite	120
Masked Bobwhite.	123
Montezuma Quail.	124
Himalayan Snowcock	124
Chukar and <i>Alectoris</i> Partridges	125
Gray Partridge	126
Ring-necked Pheasant.	127

Maps

1.	Distribution of major native plant communities in North and Central America	8
2.	Residential distribution of the mountain quail.	17
3.	Residential distribution of the scaled quail	26
4.	Residential distribution of the Gambel's quail	33
5.	Residential distribution of the California quail.	41
6.	Residential distribution of the northern bobwhite	51
7.	Residential distribution of the Montezuma quail.	63
8.	Introduced North American distribution of the chukar	73
9.	Introduced North American distribution of the Himalayan snowcock	81
10.	Introduced North American distribution of the gray partridge	88
11.	Introduced North American distribution of the ring-necked pheasant.	99

Figures

1.	External topography of galliform birds.	9
2.	Beak and leg characteristics of quails, partridges, and pheasants	9
3.	Partridge and pheasant social behavior	10
4.	Display postures of male New World quails.	13
5.	Vocalization sonograms of New World quails	14
6.	Male New World quails and hybrids (head profiles)	15
7.	Mountain quail, adult male	18
8.	Mountain quail, adult male in flight	19
9.	Scaled quail, adult male	29
10.	Gambel's quail, adult male.	35
11.	California quail, adult pair	43
12.	Northern bobwhite, adult pair	52
13.	Northern bobwhite, adult male in flight	53
14.	Northern bobwhite, adult male frontal throat	55
15.	Montezuma quail, adult male	64
16.	Montezuma quail and ferruginous pygmy-owl	65
17.	Chukar, adult walking	74
18.	Chukar social behavior	77
19.	Himalayan snowcock, adult male	82
20.	Gray partridge, adult at rest	89
21.	Gray partridge, adult landing.	90
22.	Gray partridge social behavior	93
23.	Ring-necked pheasant, adult male walking	100
24.	Ring-necked pheasant male social behavior	101
25.	Ring-necked pheasant social behavior.	102
26.	Green pheasant social behavior	103

Photographs

1.	Mountain quail, male	22
2.	Mountain quail, male crowing	23
3.	Barred quail and scaled quail.	31
4.	Gambel's quail, male	36
5.	Gambel's quail, female	37
6.	Gambel's quail, pair	39
7.	California quail, male crouching	44
8.	California quail, male	45
9.	California quail, male dozing	47
10.	Northern bobwhite, alert male	56
11.	Northern bobwhite, male	57
12.	Northern bobwhite, pair.	59
13.	Montezuma quail, male	66
14.	Montezuma quail, male	67
15.	Montezuma quail, female and male	69
16.	Chukar, adult	78
17.	Chukar, adult walking	79
18.	Himalayan snowcock, adult male	83
19.	Himalayan snowcock, male calling	84
20.	Gray partridge, adult	94
21.	Gray partridge, adult	95
22.	Ring-necked pheasant, male hiding in grass	104
23.	Ring-necked pheasant, male portrait	105
24.	Ring-necked pheasant, adult females	106
25.	Ring-necked pheasant, male	107

Preface

This volume is the last of seven works that are intended to summarize the ecology and behavior of nearly all the major North American game birds. Five of these volumes survey all 55 species of North American waterfowl (Family Anatidae) known to breed or have bred in North America, or have historically been reliably reported from North America, operationally defined here as comprising the continental United States and Canada as well as Greenland and other Arctic islands (Johnsgard, 2016a, 2016c, 2016d, 2017a, 2017b). A sixth volume summarizes the ecology and behavior of the 12 species of North American grouse (Johnsgard, 2016b). The present volume similarly documents the biology of all five species of New World quails (Family Odontophoridae) and four species of successfully introduced pheasant-like birds (Family Phasianidae), including three Old World partridges (Tribe Perdicini) and one introduced pheasant (Tribe Phasianini).

All of these volumes are largely based on, and are primarily updated versions of, books I wrote more than four decades ago on the grouse and quails of North America (Johnsgard, 1973), the waterfowl of North America (Johnsgard, 1975a, 1975b), and several associated titles (Johnsgard, 1975a, 1986, 1988, 2002). Collectively these seven volumes comprise approximately 500,000 words, contain over 5,500 literature references, and include nearly 700 maps, photos, drawings, and sketches, all of which are my own.

As indicated in the earlier volumes of this series, in writing and revising these books I have relied a great deal on a variety of university, municipal, and private libraries as well as many natural history museums. I received personal help and advice from biologists, ornithologists, ecologists, aviculturists, librarians, editors, curators, and friends. I have also relied on some now nearly forgotten foreign guides, bush pilots, and others in whom, at various times, I have trusted my life.

There is no way I can possibly thank everyone who has helped me on these endeavors. However, as with my previous monographs already placed in the UNL DigitalCommons, I owe yet another huge debt of gratitude to Paul Royster, coordinator of Scholarly Communications for the University of Nebraska–Lincoln Libraries and publisher of Zea Books, for accepting and seeing this project through to publication and, together with his sharp-eyed, ever-cheerful editor, Linnea Fredrickson, for producing such a splendid book.

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Lincoln, Nebraska

I. Introduction to the North American Quails, Partridges, and Pheasants

All of the North American native grouse and quails and the introduced partridges and pheasants share a number of anatomical traits that are the basis for their common inclusion within the order Galliformes—thus, they are collectively called “gallinaceous birds” or “galliforms.” They are also often referred to by hunters as “upland game birds,” together with some doves, pigeons, and sometimes cranes.

Among the common traits of galliforms are fowl-like beaks and four toes. In nearly all the North American galliforms the hind toe is elevated and quite short, and thus is ill-adapted for perching. All the species have 10 primary (outer) flight feathers, 13 to 21 secondary (inner) flight feathers, and 12 to 22 tail feathers (rectrices). A large crop is present, associated with the largely granivorous (seed-eating) behavior of most quails and the more generally herbivorous (leaf-eating) diets of grouse.

The egg colors of galliform birds range from pastel or earth tones (buff, cream, olive, etc.) to white, with darker spotting prevalent among those species having nonwhite eggs. The very simple nest is built on the ground, and incubation is by the females alone, or rarely, by both sexes (in some quails and partridges). The young are down-covered and precocial at hatching, and are usually able to fly short distances in less than two weeks. They are cared for by the female (in most pheasants and grouse) or by both parents (in quails and partridges).

The geographic distribution of the gallinaceous birds of North America is closely associated with the geography of the region’s natural plant communities or major ecosystems (Map 1). Because nearly all galliform species are highly sedentary, there is usually a close correlation between a species’ overall range and its preferred climatically and botanically defined habitats.

Most of the species described in this book are members of the very large family Phasianidae, which includes not only 50 pheasants and pheasant-like birds of the world but also more than 130 species of partridges and some related forms variously known as francolins or spurfowl and other vernacular names. Some of the smaller members of this family are also called “quails” and, like “partridges,” it is a descriptor of no taxonomic significance. Thus, 20-plus species of galliform birds native to the New World are variously called quails, wood-quails, and tree-quails and are not currently believed to be close relatives of the Old World quails. They are now considered by many authorities to constitute a separate family, the Odontophoridae, so named for their diagnostic slightly irregular (“toothed”) edges of their lower mandibles.

The technical nomenclature and taxonomic sequence of all the species discussed in this book closely follow the current nomenclature of the seventh edition of the American Ornithologists’ Union’s *Check-list of North American Birds* (AOU, 1998), with supplements through 2017. However, two supra-generic categories used here are slightly modified to conform with my earlier taxonomic treatments of the Phasianidae (Johnsgard, 1986, 1989). Thus, the subfamily Phasianinae is here recognized

as two tribes, to distinguish the pheasant-like forms (Phasianini) from the Old World partridge-like species (Perdicini), following an earlier treatment by Jean Delacour (1961; 1977). There is, however, increasing doubt as to whether these two groups are monophyletic (Crowe et al., 2006; Wang et al., 2013), such as the bamboo-partridge (*Bambusicola*) possibly being a sister-group of the junglefowl (*Gallus*), traditionally considered as part of the pheasant lineage, and the gray partridges (*Perdix* spp.) being aligned with the gallo-pheasants, the core group of pheasants including *Phasianus*, *Syrnaticus*, *Chrysolophus*, *Crossoptilon*, and *Catreus*.

Finally, following long-standing practice of the American Ornithologists’ Union, and as noted earlier, the New World quails are here recognized as a separate family Odontophoridae, rather than being considered as part of the family Phasianidae. Various studies suggest that this group, like the cracids (*Cracidae*) and the turkeys (*Meleagrididae*), is quite isolated and may represent a basal evolutionary position among the galliform birds (Sibley and Monroe, 1990; Dimcheff et al., 2002). The resulting arrangement of higher taxonomic categories, the included genera, and the number of species that are documented in this book are as follows:

Order Galliformes: Gallinaceous Birds

Family Odontophoridae: New World Quails

Oreortyx: mountain quail (1 sp.)

Colinus: bobwhites (1 sp.)

Callipepla: crested quails (3 spp.)

Cyrtonyx: Montezuma quail (1 sp.)

Family Phasianidae: Pheasants and Allies

Subfamily Phasianinae: Pheasants and Partridges

Tribe Perdicini: Old World Partridges, Francolins, and Quails

Alectoris: rock partridges (1 sp.)

Tetraogallus: snowcocks (1 sp.)

Perdix: gray partridges (1 sp.)

Tribe Phasianini: Pheasants, Junglefowl, and Peafowl

Phasianus: typical pheasants (1 sp.)

The New World Quails (Family Odontophoridae)

The New World quails can be distinguished from the grouse and their Old World partridge and pheasant relatives by the fact that they are relatively small (less than 250 grams in North American species), their nostrils are unfeathered, and the edge of the lower mandible is slightly irregular in profile (the basis for their Latinized family name Odontophoridae, meaning “tooth-bearing”). There are 13 to 16 secondaries, 10 to 14 rectrices, and the tarsi are neither feathered nor are tarsal spurs present in males. Although their hind toes are short and ill-adapted for

Map 1. Distribution of major native plant communities in North and Central America

Fig. 1. External topography and nomenclature of galliform birds, including protocol for numbering flight feathers.

perching, their legs are relatively long and adapted for running, and in some genera (*Cyrtonyx*, *Odontophorus*) the toes and claws are long, curved, and especially adapted for digging (*Cyrtonyx* means "bent claw"). The beak is short and the upper maxilla decurved and stout. The rounded nostrils are exposed but are partly covered and protected by a horny shelf-like operculum. The comparative head, leg, and foot traits of New World quails and Old World partridges are illustrated in Figure 2.

The number of outer flight feathers (primaries) total 10 in all the New World quails, as well as in all other species of galliform birds. Clark (1899) reported that in at least all the United States species of New World quails, the longest primary is the sixth (counting outwardly from the outermost secondary). According to Clark (1899), the number of secondaries is 14 in the Montezuma and scaled quails, 14 to 15 in bobwhites, 15 to 16 in the crested quails ("*Lophortyx*"), and 16 in the mountain quail. In all of these species the secondaries grade gradually into the scapulars and proximal wing coverts, and thus become very difficult to count accurately (Ohmart, 1967). The arrangement of the larger wing feathers and other important plumage features of New World quails are shown in Figure 1.

Many of the New World species of quails bear elaborate crests that may be similar or different in the sexes. These insert in a distinctive arrangement on the crown. In the mountain

Fig. 2. Beak and leg characteristics of (A, B) New World quail (toothed mandible, unspurred tarsus), (C, D) Old World partridge (untoothed mandible, rudimentary tarsal spur), and (E) male pheasant (spurred tarsus).

quail this very long crest is made up of two feathers, whereas in "*Lophortyx*" (meaning "crested quail") six to nine are present. Although the scaled quail lacks such a conspicuous crest, it too has an arrangement of shorter crest feathers similar to that found in the typically crested species (Ohmart, 1967).

All New World quails are seasonally monogamous, and although males only rarely aid in incubation, the pair-bond usually lasts at least until hatching, the males often remaining to participate in brood care. All quails are gregarious, and typically gather in coveys at all times except during nesting. The majority of the 27 species of New World quails are tropically distributed, and many are forest dwellers, but a few are adapted to life in very arid environments having little or no surface water.

Although in their ecology and behavior the New World quails closely resemble the Old World partridges, several taxonomic studies (e.g., Holman, 1961; Sibley and Monroe, 1990; Kimball et al., 1999; Armstrong, Braun, and Kimball, 2001), have supported the position that the New World quails should be accorded a family-level distinction from the Old World quail, partridges, and pheasants. That position is adopted in this book. Other major suprageneric groupings and evolutionary relationships that I proposed in 1986 and retained here have received general support from Dyke, Gulas, and Crowe (2003), based on both genetic and structural evidence.

The Old World Partridges and Pheasants (Subfamily Phasianinae)

The Old World partridges and pheasants are a large and diverse assemblage of birds totaling nearly 200 species. They range in size from tiny sparrow-sized birds (sometimes weighing less than 50 grams) in coturnix quails (*Coturnix*), to the stately and familiar peafowl (*Pavo*), which might weigh up to about 5 kilograms. This entire diverse assemblage is often divided taxonomically into about 150 partridge-like species (Tribe Perdicipini) and about 50 pheasant-like species (Tribe Phasianini), a classification followed here.

Although long classified as part of the partridge side of the partridge-pheasant taxonomic divide, males of several African species of francolins (*Francolinus*) have sharp tarsal spurs (sometimes two per leg), as do three species of Asian spurfowl (*Gallus*) and two bamboo-partridges (*Bambusicola*). Their reproductive biologies are still incompletely studied, but at least in *Bambusicola* the genetic evidence suggests a phyletic link with the junglefowl and thus with the pheasant assemblages (Akishinomiya et al., 1995). Among adults of many partridges, including rock partridges (*Alectoris*), the tarsi of males have a rounded bony enlargement that apparently represent rudimentary spurs (Fig. 2). Such situations illustrate the questionable taxonomic significance of the behavioral divide that has traditionally separated partridges from pheasants (Crowe et al., 1992; Kimball et al., 1999), or at least may expose the limited taxonomic value of sexually significant traits such as spurs and mating systems. More genetic work will probably need to be done to finally define and separate the partridges from the pheasants, if indeed it is ever possible.

Like the New World quails, at least most Old World partridges are monogamous. Thus, males establish and defend breeding territories that are shared with their mates, remain with their mates through incubation, and often share in brood rearing. The Perdicipini also includes three Old World partridges that have been successfully introduced into North America. They differ from the New World quails in being larger in adult body mass and in lacking indentations on the cutting edges of the lower mandible.

The largest species of the partridge group are the snowcocks. They are heavy-bodied species (up to 3 kilograms) occurring in alpine habitats from the Caucasus to Tibet and Mongolia, but one species has been successfully introduced into North America. Snowcocks are strong fliers, having long, broad wings and long, rounded tails. The sexes are alike or only slightly dimorphic and, like rock partridges, adult males have blunt tarsal spurs.

The Old World partridges and their relatives thus almost seamlessly grade anatomically and structurally into the typical pheasants (Tribe Phasianini). This assemblage of about 50 species includes such morphologically diverse groups as the core or typical gallopheasants (*Phasianus*, *Syrmaticus*, etc.), the junglefowl ancestors of domestic poultry (*Gallus*), the peafowl and peacock-pheasants (*Pavo*, *Afropavo*, and *Polyplectron*), and the distinctive and evidently quite isolated tragopans (*Tragopan*) (Johnsgard, 1986).

Clutch sizes in pheasants average considerably smaller than those of quails and partridges, whereas brooding durations average longer, especially in larger species. Durations to sexual maturity in pheasants also average longer than in quails and partridges. In some very large species, such as peafowl, maturity may

Fig. 3. Partridge and pheasant social behavior, including (A) tidbitting by chukar, (B) waltzing by chukar, (C) lateral display by gray partridge, (D) precopulatory posture by gray partridge, and (E) lateral wing display by ring-necked pheasant.

require up to at least three years, and male plumage traits may continue to become more elaborate until at least the fifth year.

The pheasants also differ from both quails and partridges by being more sexually dimorphic in both adult plumage and body mass. In the great majority of pheasant species the mating system is polygamous, the males often attracting harem-like groups of females, while in other species promiscuous mating occurs within mixed-sex flocks.

Among pheasants, male mating rights are determined by individually variable social male dominance, with the social ranking usually dictated by "peck-orders" resulting from the outcomes of individual threats and fights. Adult pheasant males all have tarsal spurs that provide effective weapons during such hostile encounters. Over the bird's prime years of physical fitness, the tarsal spurs reach a maximum in length, sharpness, and relative fighting effectiveness.

Male pheasants and other family members such as junglefowl and peafowl are also among the most ornately and colorfully plumaged of all birds. Few if any other species have evolved more extensively iridescent plumages than have pheasants, and males of the spectacularly plumaged crested argus, *Rheinartia*

ocellata, display the longest tail feathers of all the more than ten thousand bird species. Because male pheasants are thus wholly involved in activities related to achieving successful mating, all the responsibilities associated with nesting and brooding fall on the females.

Only one pheasant species has been successfully introduced into North America, the ring-necked (common) pheasant, although numerous introduction efforts have been attempted with many other species. One of these is the Japanese green pheasant, which was successfully introduced into Hawaii. The green pheasant also has been released into the Maryland-Delaware region, where it reportedly has hybridized with local ring-necked pheasants. The two species have so many shared traits that I concluded (Johnsgard, 1988) that *versicolor* should be classified within a collective pheasant superspecies, as indicated by the parenthetic inclusion of *colchicus* in its Latin name, *Phasianus (colchicus) versicolor*.

A less closely related species, the Reeve's pheasant (*Syrmatiscus reevesi*), was unsuccessfully introduced into Ohio (Knoder, 1955), and several other attempted pheasant introductions have likewise been failures. For detailed descriptions of all the other species of pheasants, partridges, and quails of the world, see my earlier books on these groups (Johnsgard, 1986, 1988, 1999).

Grouse and Ptarmigans (Subfamily Tetraoninae)

Although not included in this book, but comparably documented elsewhere (Johnsgard, 2016), the grouse are a group of closely related Northern Hemisphere galliforms. Grouse share many structural traits with quails, partridge, and pheasants, the most obvious differences being associated with their adaptations to arctic and alpine breeding distributions. All grouse can be characterized by the fact that they have feathered-over nostrils, which helps to restrict heat loss, and also have dense feathering on their lower legs (tarsi) that extends at least to the base of their toes. Among three Arctic-adapted species (ptarmigans), this feathering extends to the tips of the toes in winter, thus also conserving heat. In all other grouse species, the toes are not feathered, but some species develop unique marginal comb-like extensions during winter that increase the surface area and thereby probably provide snowshoe-like support for walking over snow.

In contrast to quails and partridges, most grouse species are polygamous or promiscuous, although the three ptarmigan species (*Ptarmigan*) are variably monogamous. Grouse are also not normally so gregarious as quails and partridges, but during fall and winter some high-latitude species that migrate considerable distances may form large flocks. In association with their usual polygamous or promiscuous mating, male grouse often are highly dimorphic in their behavioral traits related to breeding. Some are also quite sexually dimorphic in overall body mass, although sexual plumage differences are sometimes slight.

Dimcheff, Drovetski, and Mindell (2002) judged the divergence time of ancestral grouse from other early Phasianidae at 27 million years ago. For detailed descriptions of all the species of the world's grouse, see my earlier book on this group (Johnsgard, 1983).

Other North American Galliform Birds

In addition to the groups just described, two other native galliform groups are represented in the North American avifauna. One of these is represented by the wild turkey (*Meleagris gallopavo*), the largest of all galliforms. Because of several unique structural traits related to the turkey's large size, mast-centered diet, and promiscuous mating strategy, it—together with a related Mexican species (*Meleagris ocellata*)—have long been separated taxonomically as a distinct family (Meleagrididae).

Using mitochondrial evidence, Dimcheff, Drovetski, and Mindell (2002) judged a divergence date of 27 million years ago for the separation of *Meleagris* from other early pheasants. Other recent evidence suggests turkeys are indeed quite isolated genetically from the pheasant family, so the wild turkey has been excluded from this book.

Finally, a distinctive group of relatively arboreal galliform birds occurs in South and Central America, with a single species, the plain chachalaca (*Ortalis vetula*) reaching extreme southern Texas (Delacour and Amadon, 2004). This anatomically divergent galliform group (Family Cracidae) is evidently quite distantly related to all other North American galliforms (Prager and Wilson, 1976), and Dimcheff, Drovetski, and Mindell (2002) judged that the Cracidae occupy a basal evolutionary branch in the Galliformes. For these reasons the cracids have also been excluded from consideration in this book.

II. Species Accounts

Family Odontophoridae: New World Quails

Gambel's quail, adult male

Reproductive Biology of the New World Quails

The reproductive potential of any animal species is a compound result of numerous behavioral and physiological characteristics, most of which can be considered species-typical. These include such things as the time required to attain reproductive maturity, the number of nesting or reneating attempts per year once maturity is attained, the number of eggs laid per breeding attempt, and the number of years adults may remain reproductively active. These traits place an upper limit on the reproductive potential of a species, which is never actually attained. Rather, the actual rate of increase will only approach the reproductive potential, being limited by such things as the incidence of non-breeding; the mortality rates of adults; decreased hatching success resulting from infertility, predation, or nest abandonment; relative rearing success; incidence of reneating and clutch sizes of reneats; and similar factors that affect reproductive efficiency.

The relative involvement of the male in protecting the nest or the young may also influence hatching or rearing success. Among those species in which the male does not participate in nesting behavior, the relative degree of monogamy, polygamy, or promiscuity may strongly influence the reproductive ecology and population genetics of the species. Although many of these considerations will be treated under the accounts of the individual species, a general comparison of the grouse and quail groups as a whole are worth considering here, to see if any general trends can be detected.

In the absence of evidence to the contrary, it must be assumed that all native quail species mature during their first year. This maturation is indicated by the apparent absence of non-breeding females during favorable years under natural conditions, known regular breeding by females still carrying juvenal outer primaries, and consistent breeding under captive conditions of birds less than a year old. Bobwhites reared in captivity usually attain sexual maturity at 139 to 185 days under lighted conditions (Baldini, Roberts, and Kirkpatrick, 1952), and scaled quail have laid fertile eggs in my laboratory within 160 days after hatching. My graduate students and I have also regularly obtained breeding from yearlings of all the other quail species we have maintained in captivity.

Extensive nonbreeding during unfavorable years is apparently much more prevalent among quails than grouse, at least among the more northerly species of quails. Mountain quail may not nest at all in very dry years (Leopold, 1959). The same applies to scaled quail; precipitation occurring during the current spring and summer seems to be the most important influence on this species (Campbell, 1968). Little or no rainfall during the preceding winter and spring reduces the overall nesting success of the California quail (Hungerford, 1964). The same may apply to northern bobwhites (Lehmann, 1946).

Fig. 4. Male display postures of New World quails, including scaled quail's pay-cos call and head-throw call (top), Gambel's quail's meah call (middle left), California quail's squil call (middle right), and northern bobwhite's bob-white call (bottom left) and forward threat display (bottom right) (Johnsgard, 1973).

Fig. 5. Vocalization sonograms of New World quails (Note: "Harlequin quail" = Montezuma quail)

Fig. 6. Male head sketches of New World quails and hybrid combinations

Mountain Quail

Oreortyx pictus (Douglas) 1829

Other Vernacular Names

Codorniz de montana, mountain partridge, painted quail, plumed quail, San Pedro quail

Range

Resident in the western United States from southern Washington and western Idaho (Columbia River valley east) to western Nevada and south through western Oregon and California (Cascades, Sierra Nevada, and coastal ranges) to northern Baja California. Also introduced in western Washington (Puget Sound) and Vancouver Island, where the latter has since apparently become extirpated (Davidson et al., 2012).

Subspecies

(ex AOU *Check-list*, 1957)

- O. p. pictus* (Douglas): Sierra mountain quail. Resident in mountain regions of extreme western Nevada west to the west side of the Cascade Range in southern Washington and south to the Sierra Nevada and inner coastal ranges of California. Note: Taxonomic confusion exists over type localities and the proper application of the epithets *pictus* and *plumiferus* (Browning, 1977).
- O. p. plumiferus* Gould: Coast mountain quail. Resident from southwestern Washington south through northwestern Oregon and adjacent Idaho to northwestern San Luis Obispo County, California. Also introduced in southern Vancouver Island, British Columbia, where it is now probably extirpated.
- O. p. eremophila* van Rossem: Desert mountain quail. Resident in the mountains of southern and west central California in the Sierra Nevada south to about the Baja California boundary, and in extreme southwestern Nevada.
- O. p. russelli* Miller: Pallid mountain quail. Resident in the Little San Bernadino Mountains in Riverside and San Bernadino Counties, California.
- O. p. confinis* Anthony: San Pedro mountain quail. Resident in northern Baja California in the Sierra Juarez and Sierra San Pedro Martir.

Measurements

Folded wing: Males (*p. picta*), 125–140 mm, ave. of 26, 131.8 mm; females 125–135 mm., ave. of 16, 129.2 mm (Ridgway & Friedmann, 1946).

Tail: Males (*p. picta*), 73–84 mm, ave. of 26, 81.7 mm; females 71–79 mm, ave. of 75.6 mm (Ridgway & Friedmann, 1946).

Weight (mass): Males, ave. of 30, 235 g (8.2 oz.), females, ave. of 24, 230 g (8.2 oz.) (Johnsgard, 1975a). Males, ave. of 45, 244.7 g, females, ave. of 24, 230 g (Gutiérrez and Delehanty, 1999).

Identification

Adults are 10.6 to 11.5 inches long. The sexes are very similar in appearance. This relatively large western quail differs from all others in that both sexes have straight, narrow, and blackish crests composed of only two feathers, which appear with the juvenal plumage. The throat is chestnut, edged with black, and this is separated from the slate gray chest, neck, and head by a white line. Otherwise the birds are plain olive gray on the back, wings, and tail. The flanks are a rich, dark brown with conspicuous vertically oriented black and white bars.

Field Marks

The slender plumes and boldly patterned flanks serve to identify mountain quail without difficulty. The California quail occurs in some of the same regions, but it has a shorter, curved, “comma” shaped crest and dull brown flanks that are narrowly streaked with white. A loud, clear, whistled *quee-ark* or *plu-ark* is the advertising call of the male during spring.

Age and Sex Criteria

Females have slightly shorter and browner plumes than males (average of 12 is 58 mm with a maximum of 66 mm, as compared to a minimum of 66 mm and an average of 72 mm in 12 males). Ormiston (1966) reported that nine adult females averaged 62.1 mm and ten males averaged 85.3 mm in crest length, but this difference was not statistically significant. McLean (1930) reported that in addition to having a longer crest, the male is more brightly colored beneath, and the gray of the hind-neck is more sharply defined than that of the female. Schlotthauer (1967) likewise noted that in females the brown back color extends to the top of the head, while in males the back of the neck is grayish blue. F. E. Strange (pers. comm.) believed that the neck color is the most reliable criterion, but it has limited use with dark coastal birds.

Immatures have buff-tipped greater upper primary coverts, as compared with the uniformly gray coverts in adults (van Rossem, 1925). The two outer primaries are more pointed and frayed than the inner primaries.

Juveniles have dull fuscous crest feathers (under 60 mm) of which the terminal third is banded with tawny drab (Ridgway and Friedmann, 1946), and they have whitish chins surrounded by dark gray throats.

Downy young of this species are quite distinct from *Callipepla* downies and approach *Colinus* in some respects. Besides being slightly larger than any of these, mountain quail downies exhibit more whitish tones, especially on the sides of the head and body and particularly just below the chestnut crown. The black-bordered chestnut color is also present on the back as a mid-dorsal stripe, which in *Callipepla* is a pale buff or dull mummy brown. A second blackish stripe, separated from the mid-dorsal

stripe by a white line, occurs above the legs, and black is also evident on the upper neck region. There is a large blackish mark extending from the rear of the eye to the ear region, where it expands considerably in size.

Distribution and Habitat

The mountain quail is perhaps the most temperate-adapted of any of the species inasmuch as it is the only United States quail species that barely extends its range into Mexico, and thus is limited to the extreme northern part of the Baja peninsula. It is larger than the *Callipepla* species of the arid lowlands, although it does not quite reach the body size of *Dendrortyx*, the endemic montane Mexican tree quails ("wood-partridges" in the AOU *Check-List*). Nevertheless, it occupies a comparable climatic zone, being found in dense brush, in coniferous forests, around the edges of mountain meadows, and sometimes on fairly high crests (Leopold, 1959).

During the breeding season the vertical distribution of *pictus* and *eremophila* in California is from about 1,500–2,000 feet to 9,500–10,000 feet, although the coastal form *palmeri* occurs only up to 5,600 feet (Grinnell and Miller, 1944). The habitats of these three subspecies in California include brushy mountainsides, particularly those covered with chaparral vegetation, such as manzanita, snowbush, chinquapin, and similar broad-leaved hardwoods. Coniferous forest edges, open forests, or forests disturbed by logging or fires provide additional habitat for this species.

McLean (1930) stated that the Sierra form of mountain quail is most often associated with white-leaved and mariposa manzanita (*Arctostaphylos vicida* and *A. mariposa*), often dropping down in winter to the chamise (*Adenostoma fasciculatum*) zone. However, the coastal form (*palmeri*) is generally found in the dense undergrowth of the redwood (*Sequoia sempervirens*) belt.

The desert mountain quail (*eremophila*) extends its breeding range into sage, pinyon, and juniper vegetation where water is available locally (Grinnell and Miller, 1944), and the vertical range of mountain quail in the Sierra Nevada mountains extends lower on desert-facing slopes than on those that are moister (Sumner and Dixon, 1953). Sumner and Dixon indicated that brushy areas of California black oak (*Quercus kelloggii*) and ponderosa pine (*Pinus ponderosa*) are favored breeding habitats, and the lower blue oak (*Q. douglasii*) zone is used in winter.

In Washington, where the species was introduced in the late 1800s, it inhabits brushy burns and clearings, brushy canyon thickets, and areas near farms and woodland borders (Jewett et al., 1953). The Washington population is generally declining, with the remaining core centered in Mason, Knapp, and northeastern Grays Harbor Counties (Wahl, Tweit, and Mlodinow, 2005). In Oregon the coastal race likewise inhabits cutover lands and edges of clearings in the humid forest zone, while the interior race is found in more open country (Gabrielson and Jewett, 1940).

The species was introduced into British Columbia in the 1870s and 1880s and may be extirpated from its only location on Vancouver Island, where it was once fairly common but has not been seen in recent years (Davidson et al., 2015). In western Idaho the mountain quail may or may not be native, but it probably occurs along the lower parts of several river systems, including the Snake, Boise, Clearwater, and Salmon (Ormiston, 1966). It also

Map 2. Residential distribution of the mountain quail as of the 1970s. Recent (2011–15) denser populations (averaging 3–10 birds per Breeding Bird Survey route) are stippled.

historically occurred sparsely in the northern and western parts of Nevada (Gullion and Christensen, 1957), possibly also representing introduced stock.

Populations and Hunting

Few estimates of population densities of mountain quail have been made. Edminster (1954) cited California research indicating an early spring density of one bird per three acres following a winter of high survival, and near water densities up to one bird per two acres occurred. In areas where the average covey size is relatively high (11 birds), the late summer and fall density of birds may reach one bird per five acres (Pittman-Robertson Quarterly, April 1950, p. 136).

A 2004 estimate of the species' total North American population was 160,000 (Rich et al., 2004), all of which was north of Mexico. Data from the North American Breeding Bird Survey for the period 1966–2015 indicate that this species underwent a survey-wide decline of 0.59 percent annually for the period 1966–2015, and 4.26 percent annually for the period 2005–2015 (Sauer et al., 2017).

Fig. 7. Mountain quail, adult male

In 1975, I (Johnsgard, 1975a) estimated that 375,000 mountain quail were then being shot annually in the United States, plus a few in Canada, based on data from individual states and provinces. In 2016 mountain quail were legally hunted in California, Nevada, Oregon, and Washington. Some statewide hunter kill estimates were: California (2014–15), 119,000; Oregon (average, 1994–2015), 28,000; and Washington (including unknown numbers of bobwhite and California quails, 2014–15), 80,500.

Habitat Requirements

Winter habitat of the mountain quail typically consists of mixed brush and herbs, with the brushy species including such plants as manzanita, scrub oaks, chamise (*Adenostoma*), Fremont silktassel (*Garrya*) and other species (Edminster, 1954). Edminster judged that snow cover was not usually important in winter

survival, since the bird can use shrubs and trees for sources of food when herbaceous vegetation is covered. Snow may, however, be important in the northern parts of the range or set an upper altitudinal limit for winter survival in mountainous country. In a winter of unusually cold weather and heavy snowfall, no noticeable decrease in wintering quail was seen in two California study areas (*Pittman-Robertson Quarterly*, July 1949, p. 307).

In spring, the birds return to their breeding habitats and seek out suitable nesting areas. Edminster (1954) indicated that the birds prefer moderately open brush and tree cover on slopes. Woody cover shading from one-quarter to one-half of the ground was regarded as being best for nesting and roosting. Where the mountain quail nests in desert habitats, it is often associated with such woody plants as juniper (*Juniperus*), thornbush (*Lycium*), black brush (*Coleogyne*), and desert apricot (*Prunus*)

Fig. 8. Mountain quail, adult male in flight

(*Pittman-Robertson Quarterly*, October 1948, p. 408). In desert areas the availability and distribution of water are probably important; the birds are apparently restricted to remaining no more than a mile from water (*Pittman-Robertson Quarterly*, January 1948, p. 11). Rather than fly, they try to escape danger by running uphill on hillsides of at least a 20-degree slope.

Nesting cover in various parts of the California range varies greatly as to plant species, but most such cover contains large shrubs, trees, or both, usually in dense growth. Mixtures of trees and shrubs may be more valuable than either alone, perhaps because of decreased density in the shrub layer. Small trees are more useful than large for roosting, and the mast from trees such as ponderosa pine, firs, and oaks provides important food. Roads in unusually dense cover provide useful clearings where dusting occurs and where young birds can dry out and warm up early in the morning (*Pittman-Robertson Quarterly*,

October 1949, p. 459). Nesting areas may possibly be selected on the basis of abundant green plant food, which often occurs on flatlands adjacent to wooded hills (*Pittman-Robertson Quarterly*, October 1948, p. 408).

In the central Sierra Nevada, nesting occurs both in the foothill chaparral belt and also at high elevations near timberline. The foothill nesting population is a sedentary population, whereas the timberline nesting population moves upward every year from the foothills through a heavily vegetated forest zone where few quail nest. Birds nesting in higher elevations evidently are much more dependent on available free water than are the foothill nesters; their nests are usually no more than a few hundred yards from it, and they frequently visit watering places. However, the foothill residents may nest more than a mile from water and not visit watering places until after the young are hatched (*Pittman-Robertson Quarterly*, October 1949, p. 459).

Since chicks require water soon after hatching; its availability is an important aspect of brooding cover. Insects and succulent green vegetation are also likely to be abundant near water, as well as shady cover and safe roosting places. Miller and Stebbins (1964) never found adults more than a mile, or young more than half a mile, from water in the Joshua Tree National Monument, and usually they were much closer. They also knew of no nesting success except near springs. Edminster (1954) judged that few broods were raised more than a quarter mile from a source of water. Ormiston (1966) likewise considered free water to be an essential part of mountain quail habitat in Idaho.

Fall habitat needs of the mountain quail include suitable food sources. Edminster (1954) noted that oak-pine stands provide important mast sources, on which the birds feed until the weather forces them to lower elevations. In the western Sierra Nevada range, the birds were found in stands of ponderosa pine, California black oak (*Quercus kelloggii*), and mountain misery (*Chamaebatia*) during September, and by early October they were seen in a variety of associations of mixed conifers, oak, and chaparral vegetation where water was commonly present (*Pittman-Robertson Quarterly*, April 1950, p. 136).

Food and Foraging Behavior

Most of the limited data on mountain quail foods comes from fall collections, such as the analysis by Yocom and Harris (1952). Of 33 quail from Washington that they analyzed, smooth sumac (*Rhus*) fruits and seeds comprised nearly a quarter of the diet. Other important sources of fruits included hackberry (*Celtis*), serviceberry (*Amelanchier*), grape (*Vitis*), gooseberry (*Ribes*), manzanitas, nightshade (*Solanum*), elder (*Sambucus*), Christmas berry (*Photinia*), and snowberry (*Symphoricarpos*). Tree seeds, including those of various pines, Douglas-fir (*Pseudotsuga*), and black locust (*Robinia*) are consumed, as well as acorns and a host of legume and other weed seeds (Edminster, 1954). Tubers and roots are also used to some extent for fall foods and may compose about 10 percent of the early fall diet, but they are not eaten much at other times of the year.

Winter foods of the mountain quail consist of acorns and seeds of a diverse array (Martin, Zim, and Nelson, 1951). In addition to acorn meats, pine seeds and greens may also be taken in fall and winter (*Pittman-Robertson Quarterly*, April 1948, p. 165).

As greens become available in late winter and spring, they are heavily utilized and may make up 25 to 40 percent of their diet. Leaves and, later on, buds and flowers are used through the summer, and collectively they compose about a quarter of the annual diet. The yearly average of food from animal sources is only about 3 to 5 percent, with fruit, mast, and seeds making up most of the remainder of the total food intake (Edminster, 1954).

Judd (1905a) provided an analysis of foods from the crops of 23 mountain quail collected in California, of which only 3 percent by volume came from animal sources. Legumes, weeds, and grasses totaled 47 percent, grain 18 percent, fruit 8 percent, and seeds and other miscellaneous vegetation the remaining 24 percent.

One thorough study on mountain quail foods was that of Ormiston (1966), which was based on 48 adult samples collected from spring to fall, along with 12 samples from young birds. During the spring, two early-maturing annual herbs, chickweed (*Holosteum*) and microsteris (*Microsteris*), were the most important

foods, with the birds consuming the developing seed heads. Chickweed and blue-eyed Mary (*Collinsia*) seed heads were found in May samples, and barley (*Hordeum*) occurred in large quantities in one May sample. Underground bulblets of fringe-cup (*Lithophragma*) were found in May samples and evidently became increasingly important in late summer and early fall, when they made up nearly half of the sample volumes. Seeds of grasses, hawthorn (*Crataegus*), pines, and sweet clover (*Melilotus*) were also important fall food sources. Large weedy species such as thistles (*Cirsium*), ragweed (*Ambrosia*), and teasel (*Dipsacus*) provided important fall seed sources as well.

Foods of young mountain quail collected by Ormiston contained only 7.5 percent animal matter. Lahnum (1944) reported that 20 percent of the food contents of 10 young quail was of insect origin, so it would seem that a surprisingly small amount of the food taken by young quail is of animal matter. Flower heads of chickweed and miner's lettuce (*Claytonia*) were the major foods of chicks under a week old, while older chicks began to consume fringe-cup bulblets and the seeds of miner's lettuce and various woody plant species. By the time the chicks were eight weeks old, they were feeding largely on the dry seeds of various herbaceous species and also continuing to feed on fringe-cup.

By fall, with the ripening of the acorn crop in California, the birds once again began to concentrate on it. Miller and Stebbins (1964) described how unripe acorns are shelled by the mountain quail. At the green base, where the shell is still soft, the bird opens a hole and tears or cuts away enough of the rest of the covering to extract the meat. Quite possibly the birds pull such green acorns from the trees before they would normally fall to the ground.

Mobility and Movements

The unique vertical migration of the mountain quail is no doubt a reflection of the fact that it breeds at higher elevations and in an associated cooler climate than do any of the other North American quail species in the United States. The migratory movements are fairly leisurely and are normally undertaken on foot, although the birds will sometimes fly across canyons (Leopold, 1959). On the west Sierra Nevada slope the total migratory movement may be 20 miles or more (*Pittman-Robertson Quarterly*, January 1951, p. 9).

While in the wintering habitat, daily movements are not great; one study indicated that the maximum was about 1,000 yards per day, and the minimum about 400 yards, as the birds moved from roosting and loafing areas under scrub oaks to forage in low brush (*Pittman-Robertson Quarterly*, January 1948, p. 11).

By late February, movement back to the breeding areas begins, with the coveys remaining intact until the nesting range is reached. At this time the males become intolerant of one another and dispersion of pairs occurs.

Ormiston (1966) found that during the summer, daily movements were limited and did not exceed half a mile unless the birds were disturbed. In his study area in Idaho he found little evidence of major seasonal movements, with marked birds remaining within a one-square-mile area at all seasons. The longest move recorded for any marked individual was about one mile, including a 700-foot movement upslope. Sumner and Dixon (1953) observed surprisingly long flights of about half a mile by disturbed birds, while Miller and Stebbins (1964) saw a bird fly 150 yards upslope at a 25-degree angle.

There is also little movement in the summer during brood-rearing. Ormiston (1966) noted that when birds were young, coveys remained in a two- or three-acre area for several days at a time. However, there was a gradual movement toward areas of available water. In late July of 1947, several thousand mountain quail concentrated at Jackass Spring in the Panamint Mountains of Inyo County, California.

A similar but smaller concentration occurred at various springs in Joshua Tree National Monument the same month, with a minimum of 730 birds at 12 watering points, or an average of 60.8 birds per spring. When a small amount of rain fell in August, the birds immediately left the springs and were later found two to three miles from water, feeding on new plant growth produced by the rain. Banded birds were seen from one to five miles away from the point of banding during August and September (*Pittman-Robertson Quarterly*, January 1948, p. 11). In succeeding years, birds often return to the same water hole. Of 17 banded birds observed at watering holes a year after banding, most were at the same water hole and none was more than a mile away from the point of banding. Only about 10 percent of the birds banded one summer were seen the following summer (*Pittman-Robertson Quarterly*, October 1948, p. 408).

Mountain quail probably need to visit water sources only once a day because they can hold up to 12 cc of water in their crops (*Pittman-Robertson Quarterly*, January 1948, p. 11). In the Jackass Spring area, such watering usually occurred after 10:00 a.m., and most usage was near noon. However, in other areas, the birds were seen to come in at all hours of the day but especially during early morning. Ormiston (1966) noted that coveys were usually found near streams between 8:00 and 10:00 a.m., and after they finished drinking they fed, dusted, and finally moved to heavy cover to spend the hottest part of the day. A second period of feeding occurred from late afternoon until just before dark, when the birds went to roost in heavy cover, probably on the ground.

Miller and Stebbins (1964) reported a similar late afternoon visit to water holes during late summer. The birds would arrive on foot in coveys of six to twenty, walking single file, and approach the spring with great caution. When frightened the birds invariably move uphill, preferring to run than fly unless the cover is unusually open.

In the Sierras the movement back down the mountains toward the winter habitat starts in late August or early September, and by the first of October the birds are usually gone from elevations above 5,000 feet, regardless of the weather conditions that might be prevailing (Bent, 1932).

Vocal Signals

The unmated male announcement call is undoubtedly the best known of the mountain quail vocalizations. Miller and Stebbins (1964) noted that the male's whistled call might also occasionally be heard in October from birds in flocks, which might be a reflection of a fall resurgence of sexual activity. An important covey maintenance call is the assembly or rally call, used to reunite separated birds. This is a loud *cle-cle-cle* or *kow-kow-kow* series of notes (Miller and Stebbins, 1964; McLean, 1930), which are quite distinctly different from the brief assembly calls of *Callipepla* or *Colinus* and more closely approach the repeated call

notes of *Philortyx*. The alarm note is a *scree* (Miller and Stebbins, 1964), or a shrill *t-t-t-r-r-r-r-rt* (Haskin, in Bent, 1932), rapidly delivered in a sharp crescendo and accented like a barnyard fowl's cackle. See Figure 5 for a sample sonogram. Sonograms of four of the species' vocalizations were provided by Gutiérrez and Delehanty (1999).

A variety of other calls have been described as associated with enemy avoidance. The male is said to utter a shrill *quaih-quaih* while performing distraction displays (Bendire, 1892). The call of the female with young that stimulates them to "freeze" is a nasal *keel-err* and a hen-like *kut, kut, kut*, while a low *whew, whew, whew* is uttered as they rush for cover (Hoffman, 1927). When in the hand, the distress call of both sexes is a loud, repeated *psieuw*.

Social and Reproductive Behavior

As in all New World quail, the covey forms the basis of the social group for nearly the entire year. Except where drought conditions cause other groupings, most coveys are probably basically family groups. In the Sierra Nevada, covey size has been reported to average seven birds, and in the San Gabriel Mountains five birds represented an average covey size (*Pittman-Robertson Quarterly*, April 1950, p. 136).

The average of 21 coveys from late summer through winter at Joshua Tree National Monument was 9.1 birds and ranged from 3 to 20 (Miller and Stebbins, 1964). Coveys consisting of family groups would be expected to average a pair and up to perhaps as many as ten young. Broods probably averaged about five in well-grown broods, assuming a 50 percent loss of young. Unsuccessful adults probably join such family groups, thus increasing their numbers. In unusually dry years, little or no nesting occurs, and at such times fairly large coveys consisting entirely of adults may be seen in early summer (Leopold, 1959).

In California the mating season begins in March at low elevations, or early April higher in the mountains, and mate selection occurs while the birds are still in coveys (McLean, 1930). The onset of mating may be recognized by the location call of unmated males, which is usually uttered from a prominent stump, rock, or branch in a break in the woody cover. This call, a clear whistle that drops slightly in pitch toward the end, sounds like *quee-ark, kyork, queerk*, or *plu-ark* and can sometimes be heard for three-quarters of a mile (McLean, 1930).

In one California study, male crowing was first heard on February 20, and the first pair was seen February 26. By March 6, a total of seven pairs had been located, but some coveys were still present. These coveys all broke up by the end of March (*Pittman-Robertson Quarterly*, July 1949, p. 307). As males become antagonistic toward one another, the population spreads out, with a nesting pair occupying from 5 to 50 acres (*Pittman-Robertson Quarterly*, January 1950, p. 10).

Grinnell and Storer (1924) indicated an average interval between calls of about 6 to 7 seconds, and a recorded series in the Cornell University Laboratory of Ornithology Library of Natural Sounds averaged 8.5 seconds apart over a 6.7-minute period. The head is quickly thrust upward and thrown back and the crest suddenly erected as each call is uttered. Although the call, or a whistled imitation of it, may stimulate other males to respond (Dawson, 1923), it should not be regarded as a territorial proclamation signal. Rather, as in the other New World quails, it simply

Mountain quail, male

represents the announcement of the location of an unmated male, to which available females might be attracted.

As for several other quails, pair formation has not been described adequately, but Delehanty (1997) provided some details. One frequent display is the stand/crouch display, in which one subordinate bird crouches while the dominant bird stands above its head and neck at a perpendicular angle, apparently displaying its throat-patch, flank barring, and breast to the crouching bird below. This display ceases after the crouching bird emits a "crouch-whistle."

Another display is the lateral display, during which the bird's contour feathers are raised to the point that the feathers look scaled. There is also a "smooth lateral display," in which the male raises the contour feathers of his neck, breast, and flank while drooping his barred flank feathers, sometimes thus promenading before the female for more than 30 minutes. Other common displays include tidbitting and a fanning of the wings and tail by the male, a running in semicircles before the female with one or both wings and the tail fanned (Gutiérrez and Delehanty,

1999), and extending the legs, ruffling the flank feathers, fanning the tail, and tilting the body downward until the beak almost touches the ground (Stokes and Williams, 1971).

The strong similarity in the sexes would suggest that sexual recognition in this species may be more difficult than in the genera *Callipepla* or *Colinus*, and one might expect that initial male responses to females would be largely aggressive. The striking flank markings would suggest that lateral displays are important visual signals, and a male hybrid mountain × California quail in my collection had a strongly developed frontal display (without wing-spreading) that exhibited its throat markings very well.

Copulation usually occurs after a male approaches the female from behind. Copulation might be preceded or followed by reciprocally performed stand/crouch displays and accompanying whistles (Gutiérrez and Delehanty, 1999).

April is the nesting period in Joshua Tree National Monument (Miller and Stebbins, 1964), with a probable average hatching date in 1948 of May 7 (*Pittman-Robertson Quarterly*, October 1948, p. 408). However, in the central Sierras, nesting occurs

Mountain quail, male crowing

from mid-June to mid-July (*Pittman-Robertson Quarterly*, January 1948, p. 10).

The average clutch size of 11 nests was 10 eggs in one study done in the Sierras (*Pittman-Robertson Quarterly*, January 1948, p. 10). Grinnell, Bryant, and Storer (1918) summarized early literature references on clutch sizes of this species and added their own observations. If two clutches of 19 and 22 eggs are excluded as being the probable result of two females, the average clutch size for 29 clutches would be 8.7 eggs. A few of the smaller clutch records were probably of incomplete clutches; thus 9 to 10 eggs would seem to be a typical clutch size for mountain quail. A sample of 29 California clutches averaged 9.9 eggs (Miller, 1959), while 13 Idaho clutches averaged 12.0 (Heekin et al., 1994).

Nests are usually well concealed, often being placed under fallen pine branches, amid weeds or shrubs at the base of large trees, beside large rocks in the shade of shrubs, or in masses of shrubby vegetation (Bent, 1932). Of 63 nests, 35 were under shrubs, 14 were against logs, 6 were against rocks, 4 were under brush piles, 2 were under tree limbs, and 2 were in grass (Gutiérrez and Delehanty, 1999). Nests are usually located near paths or roads, and are probably always within a few hundred yards of water.

The incubation period is 24 to 25 days. The male takes an active role in nest and brood defense and will perform distraction displays, such as feigning injury (Bendire, 1892). Males also regularly exhibit brood patches (Miller and Stebbins, 1964), indicating that they might assist with incubation, particularly if the female dies.

Nesting success data are few. In one study, 10 of 13 clutches hatched successfully (Heekin et al., 1994). One California study indicated that a single adult of either sex led most broods (*Pittman-Robertson Quarterly*, October 1948, p. 408), but broods tended by both adults averaged larger than those with only one present. One California study indicated that 8 of 14 nests under observation were successful, and the hatching success of the eggs in successful nests was 95.8 percent (*Pittman-Robertson Quarterly*, January 1948, p. 10).

So far, there is no evidence that two broods are ever normally raised by mountain quail, although unsuccessful pairs will often make a second or even a third attempt to nest (Leopold, 1959). However, there is some evidence that the male may incubate the first clutch, allowing the female to lay and incubate a second one. In desert habitats reproductive success is strongly correlated with rainfall; during dry years virtually no reproduction occurs. Percentages of young in the fall population varies greatly, from 0.5 percent to 93.1 percent during five years of study in the Mojave Desert (Delehanty, 1997). Data on life expectancy and mortality rates are still lacking.

Evolutionary Relationships

Holman (1961) regarded the scaled quail as the nearest relative of the mountain quail, with somewhat lesser affinities to the other crested quails ("*Lophortyx*") and to the bobwhites. Certainly the occurrence of wild hybrids between the mountain and California quail would imply a moderately close relationship between these two species, but I would suggest that *Oreortyx* was derived from a pre-*Callipepla* ancestor prior to the separation of gene pools into the currently extant species. It would seem likely that *Oreortyx* developed in the mountains of southwestern North America in a semiarid woodland or chaparral habitat after being isolated from stock adapted to more arid habitat, such as that of the Gambel's quail. Apparently the mountain quail had a considerably more widespread distribution in pre-Columbian times, since its remains have been found in cave deposits of New Mexico (Howard and Miller, 1933).

Using an "electrophoretic clock," Gutiérrez et al. (1983) estimated that *Oreortyx* separated from its contemporary relatives about 12.6 million years ago, and that *Callipepla squamosa* split off about 2.8 million years ago, *Colinus* about 7 million years ago, and ancestral *C. gambelli* and *C. californica* were separated about 190,000 years ago, the two becoming isolated during the Wisconsinian glaciation.

Scaled Quail

Callipepla squamata (Vigors) 1830

Other Vernacular Names

Blue quail, blue racer quail, codorniz azul, codorniz escamosa, cottontop quail, Mexican quail, scaled partridge, top-knot quail, zollin

Range

Resident from southern Arizona, northern New Mexico, eastern Colorado, and southwestern Kansas south to central Mexico. Introduced into central Washington and eastern Nevada. Some range contractions have occurred in the past century, including a retraction westward of its eastern range limits in Texas (Oberholser, 1974).

Subspecies

(ex AOU *Check-list*, 1957)

- C. s. squamata*: Mexican scaled quail. Resident in Mexico from northern Sonora and Tamaulipas south to the Valley of Mexico.
- C. s. pallida* Brewster: Arizona scaled quail. Resident from northern Sonora and Chihuahua north to Arizona, New Mexico, Colorado, Kansas, Oklahoma, and western Texas; introduced into central Washington (Yakima and Grant Counties) and Nevada (Elko, Nye, and White Pine Counties).
- C. s. castanogastris* Brewster: Chestnut-bellied scaled quail. Resident in southern Texas south through Tamaulipas, Nuevo Leon, and eastern Coahuila, Mexico.

Measurements

Folded wing: Males (*C. s. squamata*), 113–121 mm, ave. of 10, 116.9 mm; females 111–120 mm, ave. of 11, 115.4 mm (Ridgway & Friedmann, 1946).

Tail: Males (*C. s. squamata*), 75–90 mm, ave. of 10, 84.9 mm; females 75–88 mm, ave. of 11, 81.7 mm (Ridgway & Friedmann, 1946).

Weight (mass): Males, ave. of 143, 191 g (6.7 oz.); females, ave. of 132, 177 g (6.2 oz.) (Johnsgard, 1975a).

Identification

Adults are 10 to 12 inches long. The sexes are very similar in plumage. Scaled quail have a predominantly bluish gray coloration (thus “blue quail”) and are extensively marked on the back, breast, and abdomen with blackish “scaly” markings. The crest is bushy, varying in color from buff in females to more whitish in males. Otherwise, the head is light grayish brown; the lower back, wings, and tail are brownish gray to gray; and the flanks are grayish to brownish with lighter shaft markings. Males of one race (*castanogastris*) have chestnut abdomen coloration similar to that of male California quail.

Field Marks

The “cottontop” crest is often visible from some distance, and the generally grayish coloration of the species sets it apart from all other quail in the arid grasslands where they occur. Scaled quail are usually reluctant to fly, preferring to run rather than remain hidden. The distinctive *pey-cos* location calls (stronger in males) will often reveal the presence of scaled quail in an area. The barred quail (*Philortyx fasciata*) is very similar in plumage to the scaled quail (see color plate), and has a nearly adjacent but nonoverlapping range in southwestern Mexico (Jalisco to Guerrero).

Age and Sex Criteria

Females may be distinguished from adult males by their less conspicuous crests (male crests average 40.6 mm, females 36.8 mm) and by the dark brown shaft-streaks on the sides of the face and the throat, as compared with the unstreaked pearly gray to white coloration of the male in this area (Wallmo, 1956a).

Immatures of both sexes have buff-tipped greater upper primary coverts associated with the first seven primaries.

Juveniles have poorly developed crests, central tail feathers with much cross-barring of darker and whitish coloration (Ridgway and Friedmann, 1946), and whitish shaft-streaks on the upper parts. They are quite similar to juvenile California quail but are paler and more streaked, and they are grayer below, mottled with dull white (Dwight, 1900).

Downy young differ from those of elegant quail (*C. douglasii*) by their considerably paler lower back and upper leg coloration and from California and Gambel's quail young by their grayer overall body tone, with yellow or cinnamon-buff tints limited mostly to the head area. The two pale lines delimiting the darker middorsal stripe in scaled quail downies are nearly white rather than being buffy or cinnamon as in Gambel's and California quail.

Distribution and Habitat

The geographic distribution of the scaled quail more or less conforms to the Chihuahuan desert and adjacent desert grasslands, just as the distribution of the Gambel's quail centers on the Sonoran desert. The southern limit of the Chihuahuan desert extends approximately to the southern limits of San Luis Potosi (Leopold, 1959; Jaeger, 1957), whereas the scaled quail is common as far south as Hidalgo in locally arid habitats lying in the rain shadow of the Sierra Madre Oriental. This area represents the southern limit of natural mesquite (*Prosopis*) grassland, but Leopold (1959) believed that the extension of the scaled quail's range farther southward to the Valley of Mexico has been brought about by the clearing of the pine-oak forest, overgrazing, and farming with the resulting formation of a secondary desert habitat.

Map 3. Residential distribution of the scaled quail as of the 1970s. Recent denser populations (averaging 1–3 birds per Breeding Bird Survey route, 2011–15) are stippled.

Leopold reported that in Mexico the bird thrives best where there is a combination of annual weeds, some shrubby or spiny ground cover, and available surface water. The natural desert habitats best provide this combination of characteristics; the secondary deserts just mentioned, as well as the more extreme creosote bush deserts, support only relatively low populations. Dixon (1959) pointed out that the scaled quail was reported in all of four different studies of Chihuahuan desert birds and also occurred in a study of Tamaulipan thorn scrub habitat in south central Texas.

In Texas the scaled quail occurs in the Panhandle and trans-Pecos area eastward to the western parts of the Edwards Plateau and southeastward locally to McMullen and Hidalgo Counties. Its range is largely complementary to that of the bobwhite (McCabe, 1954), although a slight amount of range overlap does occur. Hamilton (1962) noted that the scaled quail is typically found in mesquite or juniper savanna habitats, whereas the bobwhite typically occurs in scrub oak woodland, riparian woodland, or juniper-oak woodland.

Scaled quail in Texas prefer calcareous soils having a combination of grass and brush and cannot survive where heavy

woody cover is lacking (Texas Game, Parks and Oyster Commission, 1945). The chestnut-bellied race in southern Texas has some habitat preferences that differ from those of the Arizona race. It is typically found in thorn-scrub vegetation on caliche (calcium soil) ridges, or in riparian lowlands, rather than in open grasslands having a low percentage (10–15 percent) of shrubs (Silvy, Robertson, and Whisenant, 2007).

During the breeding season, the Arizona race of scaled quail is also found on open mesquite grassland and farming land, while the chestnut-bellied scaled quail prefers open prickly-pear cactus (*Opuntia*) flats. The winter habitats are around ranches, creek bottoms, and canyons in the case of the Arizona race, while the chestnut-bellied race prefers gravelly hills covered with black brush (*Acacia*). Scaled quail are primarily found in the open grasslands of southeastern Arizona, with the largest populations in the Silver Springs Valley, near Oracle Junction, and in the Altar Valley foothills (Engel-Wilson and Kuvlesky, 2002).

In Oklahoma the scaled quail is common only in Cimarron County, but it also occurs less commonly in 16 other western Oklahoma counties. Of 70 reports of scaled quail occurrence as to habitat type in Oklahoma, 47 percent were in sand sagebrush (*A. filifolia*) habitats, 21 percent in short grass–high plains habitat, 13 percent on mesquite grassland, 10 percent on mixed-grass prairies, and the remaining 9 percent on shinnery oak, post oak–black oak, and tallgrass prairies (Schemnitz, 1959).

The range of the scaled quail in Kansas is extremely limited, and it is found locally south and west of Pawnee County in the southwestern part of the state (Johnston, 1964). It occurs in roughly the same areas as the lesser prairie chicken, namely where sandy soils occur along the Cimarron and Arkansas Rivers and a combination of grasses and sagebrush predominate (Baker, 1953).

In Colorado the species extends along the Arkansas and Cimarron river basins from the Kansas and Oklahoma borders on the east and the New Mexico border on the south, westward to the foothills of the front ranges of the Rocky Mountains (Hoffman, 1965). Its altitudinal range in the state is mainly from 3,400 feet to 7,000 feet, but it has been found as high as 8,000 feet.

Based on observed quail usage, the most important habitat type in eastern Colorado is the sand sagebrush community on sandy soils, which in Hoffman's study accounted for more than 40 percent of the quail observed. The second most important habitat type is dense cholla cactus and/or yucca grassland, an overgrazed shortgrass community in which the cactus or yucca has developed into thick stands. The third most important habitat type is the pinyon pine (*Pinus edulis*) and juniper (*Juniperus*) woodland community, which is typically found on stony soils and rocky outcrops. All other natural and agriculturally modified habitats were of considerably less value to scaled quail, judging from numbers observed (Hoffman, 1965).

In New Mexico the scaled quail extends over most of the non-forested areas of the state up to an elevation of at least 6,990 feet, and its range is largely coextensive with those of mesquite, blue chaparral (*Condalia*), and cholla cactus (Ligon, 1961).

In Arizona the scaled quail occurs only in the southeastern part of the state, where it is associated with grassland vegetation. It is replaced by the Gambel's quail wherever the grasses have been replaced by mesquite and cholla cactus as a result of overgrazing (Phillips, Marshall, and Monson, 1964). As a result, the scaled quail's range in that state may have decreased considerably in recent decades.

In central Washington state the species has been introduced and is well established in Yakima County and also in the eroded basalt scablands below the potholes of Grant County. There the birds are fairly common in the dense sagebrush (*Artemisia tridentata*) and grass habitats. Birds in Nevada use a similar sage-shadscale (*Atriplex*) habitat, where they have been introduced in several eastern counties and now appear to be well established (Tsukamota, 1970).

Populations and Hunting

Densities of this species probably vary greatly in different habitats, and even in the same habitats during different years. In southern Texas, concentrations of about one bird per acre were reported on areas as large as 200,000 acres during 1940 and 1941 (Texas Game, Fish and Oyster Commission, 1945). Studies by Hoffman (1965) indicated lower scaled quail populations averaging only about ten birds per square mile, or one per 64 acres.

At the northern edge of its range in Colorado, Figge (1946) reported a winter population of 333 scaled quail on 8,960 acres, or one bird per 27 acres. Winter covey counts by Schemnitz (1961) in Oklahoma indicated that the population density on an overall acreage basis on his study area was one quail per 12.9 acres, but if only occupied ranges were considered, the density was 0.84 acre per bird. By the same consideration of using only occupied range, Wallmo (1956b) found an average winter density of one quail per 10.1 acres. These figures simply point out the great locational and probably yearly differences to be expected in quail populations occupying desert or other habitats that are often marginal for survival.

A 2004 estimate of the species' total North American population was 1.2 million (Rich et al., 2004), 50 percent of which was in the United States and Canada. Church et al. (1993) noted that North American Breeding Bird Survey data indicated that the continental population of scaled quail declined 3.8 percent annually from 1966 to 1991, with the rate of decline 8.2 percent annually between 1982 and 1991. Data from the Breeding Bird Survey for the period 1966–2015 indicate that this species underwent a survey-wide decline of 1.21 percent annually for the period 2005–2015 (Sauer et al., 2017).

In 1975 I (Johnsgard, 1975a) estimated that 3.6 million scaled quail were then being shot annually in the United States, including 2 million from Texas alone. In 2016 scaled quail were legally hunted in the following six states: Arizona, Colorado, Nevada, New Mexico, Oklahoma, and Texas. Some statewide hunter kill estimates are: Texas (2014–15), 22,000 (plus part of a mixed-species bobwhite-scaled quail kill of 65,000), and New Mexico (2014–15), 17,000.

Habitat Requirements

Habitat usage and requirements of the scaled quail have been well analyzed by Schemnitz (1961), whose work provides the basis for the following summary. During winter, quail fed in soapweed (*Yucca*) or soapweed-sand sage pastures, weed patches, or grain stubble fields during the early morning, then moved to resting cover, often consisting of human-made structures or piles of brush. Escape cover consisted of soapweed, soapweed-sandsage-grassland habitat, or heavier cover, depending on degree of disturbance.

Artificial structures not only served as protective shelter but also were usually associated with food plants in the form of weedy herbaceous plants. Midday periods were spent in the shade of tree cactus (*Opuntia*) plants. Wallmo (1956b, 1957) emphasized the importance of midday shade and loafing cover and noted that night roosting cover must not be so dense or thick that it prevents easy movements by the birds. Schemnitz (1964) also pointed out that scaled quail cover should provide overhead protection but opportunities for ground-level movement because the species typically runs when disturbed. In contrast, the bobwhite, which more often “freezes” when disturbed, inhabits heavier woodland and brush habitats.

During the spring the birds moved from the heavier cover associated with winter areas to less dense cover, perhaps because of a seasonally lower hawk population. Soapweed and sand sage continued to be used for resting purposes, along with annual forbs and grasses. The nesting cover (based on 50 nests) consisted of a variety of forb or shrub cover types, with two-thirds of the nests being found under dead Russian thistle (*Salsola*), machinery and junk, or mixed forbs and soapweed. Russell (1932) suggested similar nest-site requirements. He found 16 of 23 New Mexican nests in Russian thistle, forbs, soapweed, Johnson grass (*Sorghum*), or under overhanging rocks. Schemnitz (1964) found that grassy situations provided nesting cover for only 3 of the 50 nests. During the summer, the birds studied by Schemnitz foraged in fairly exposed grassland areas and loafed under soapweed clumps, where dry sandy soil was usually available for dusting.

Considering usage by life-form of the habitat, Schemnitz found that the habitats dominated by shrubs 3 to 20 feet high contributed the majority (54 percent) of more than 2,000 flush observations of scaled quail, with human-created cover providing about 30 percent, and the remaining 17 percent more or less equally divided among forb clumps, cropland, and open grassland. In pinyon-juniper ranges, skunkbush (*Rhus*), tree cactus, and dense soapweed provided favored shrub cover types; in short-grass habitats skunkbush was used most heavily; and on sand sage habitats a combination of dense soapweed and sand sage represented the major shrub cover type used by scaled quail. Skunkbush and artificial structures are used throughout the year by scaled quail for cover, and where they are available they received a total usage that was far in excess of their relative availability on the habitat. On the other hand, croplands and open grasslands were used much less frequently than their availability might have suggested.

The importance of available water as a habitat requirement for scaled quail is somewhat controversial. Wallmo (1956b, 1957) questioned its importance and noted that he had observed coveys from as far as 3 to 7 miles from water during his studies. However, Schemnitz (1961) never observed quail farther than 1.25 miles from water and, furthermore, found that they were distributed closer to water sources than a random distribution pattern would dictate. However, food or cover distributions might also be positively correlated with water distribution, and thus a direct relationship between the occurrence of water and quail cannot be positively stated. The water requirements of the scaled quail have not been as intensively studied as those of other southwestern quail, but some early observations (Vorhies, 1929) suggest that the birds can survive well without free water.

Food and Foraging Behavior

Apparently the usage of insect food by the scaled quail varies considerably in different areas or years, with some studies (Martin, Zim, and Nelson, 1951; Texas Game, Fish and Oyster Commission, 1945; Bailey, 1928) indicating that up to 30 percent of the total food may be of this source, while other persons (Wallmo, 1956b; Kelso, 1937; Schemnitz, 1961) indicate that 7 percent or less of the food may be of animal origin.

Studies in Texas (Texas Game, Fish and Oyster Commission, 1945) indicate that in the plains area of northwestern Texas weed and grass seeds are eaten extensively, while the chestnut-bellied scaled quail of south Texas relies heavily on seeds of woody plants (Lehmann and Ward, 1941). The two most important of these seed sources are elbowbrush (*Forestiera*) and cat's-claw (*Acacia*). Similarly in the trans-Pecos area the Mexican huisache (*Acacia*) is an important food, and on the lower plains and panhandle areas the seeds of mesquite and hackberry (*Celtis*) are relatively frequently taken. Mesquite is also used by birds on the Edwards Plateau, together with the seeds of sennabeans (*Vigna*) and weedy herbs (*Amaranthus* and *Solanum*).

The study by Schemnitz (1961) provides comparable information on scaled quail food usage in pinyon-juniper and sand sage-grassland communities. In this area tree fruits are of minor importance, and of the 20 leading foods, 13 were seeds of annual and perennial forbs, 2 were agricultural grains, 2 were insects, and the remaining 3 were grass seeds, tree fruits, and leafy materials. A variety of weedy forbs, such as pigweed (*Amaranthus*), Russian thistle, sunflower (*Helianthus*), and ragweed (*Ambrosia*) made up the majority of winter foods. Sorghum grain was the only distinctly preferred food among the cultivated grains, and grass seeds were likewise little utilized.

In contrast to the Gambel's quail, for which herbaceous legumes are a staple food source, only one species (*Psoralea*) was found to be an important food in Oklahoma. However, leguminous forbs such as lupines (*Lupinus*), locoweed (*Astragalus*), and deervetches (*Lotus*) have been reported in Texas foods. Schemnitz found a surprising diversity of foods consumed, with up to as many as 24 food types in one crop, which he considered a desirable foraging adaptation and one that might help support a relatively high bird population.

Schemnitz noted that scaled quail typically foraged from daybreak to about 10:00 a.m. and again from about 4:00 p.m. to dark, varying somewhat with the season and the temperature. Although the birds sometimes foraged during rain, they usually did not feed during snowstorms but waited until the snow had ceased falling. When the snow was fairly deep the birds perched in trees up to 25 feet above the ground, where they could reach the seeds of hackberry, skunkbush, and juniper.

Mobility and Movements

The only major study of scaled quail home ranges and movements to date is that of Schemnitz (1961), which is the basis for the following discussion. In the winter, scaled quail gather in fairly large flocks that may number up to 100 or more birds. By marking individual birds, Schemnitz estimated that the average size of a winter home range in 1954–55 was 52.3 acres, but ten such home ranges varied from 24 to 84 acres. During the following winter the average estimated home range was slightly larger (69.5 acres) for the same home ranges, and all ten of the home ranges studied the previous year were again occupied.

These winter coveys averaged about 30 birds during the two winter periods, ranging from 7 to 150; generally larger coveys were present in the sand sage-grassland habitats than in short-grass or pinyon-juniper habitats.

The maximum diameter of a winter home range found by Schemnitz was 1 mile, or less than an estimated 1.5-mile cruising radius reported by Figge (1946) for Colorado birds, and the 0.75-mile ranging distance from winter roosting sites estimated by Russell (1932) for New Mexico. Wallmo (1956b) found that winter coveys had ranges averaging about 450 acres and restricted their daily movements to areas within 160 acres.

Schemnitz found only a limited amount of cover shifting among the winter coveys, a situation reported earlier by Wallmo (1956b). However, winter home ranges generally overlapped only slightly or not at all, and thus opportunities for covey mixing were rather limited.

Winter home ranges were not distinct from but rather part of the larger summer home ranges. The summer home ranges of three coveys studied by Schemnitz were 720, 1,220, and 2,180 acres, but within these larger areas individual pairs probably occupied fairly small home ranges. Studies of individual birds marked on their winter ranges and seen again during the summer indicated movements of from as little as none to as much as 2.75 miles from the winter range. In the case of three pairs, the birds returned with their brood to the winter home range occupied the year previously.

Although scaled quail are not generally considered highly mobile, one documented case of apparent mass dispersal during late fall and winter has been established. Campbell and Harris (1965), while banding more than 2,000 birds during the years 1960 and 1964, found that during the late part of 1961 and early 1962 a substantial population dispersal occurred. This dispersal involved both sexes and adult as well as immature birds. Thirteen banded birds were known to have moved at least 10 miles or more, and a maximum movement of 60 miles was found for one subadult male. The movements did not have any clear directional tendencies and probably should be interpreted as population dispersal rather than possible migration.

Vocal Signals

Surprisingly little has been written on the vocalizations of the scaled quail. The best-known call is the separation call, used by individuals separated from their covey as well as by both sexes when visually separated from their mates. This is a two-syllable, nasal call *pe-cos'* or *pey-cos'*, with both syllables having the same, uniform pitch, although the second syllable is of longer duration and somewhat greater amplitude. The two syllables have sharp starting points that are two-fifths of a second apart, and the call is repeated several times at intervals of about one second. Males that are unmated will respond to the playback of female *pey-cos* calls by approaching the recorder during the breeding season (Levy, Levy, and Bishop, 1966), which provides a census method for male populations. It is not yet established whether mated males can differentially distinguish the separation calls of their mates from those of other females, as is known to occur in Gambel's and California quails. See Figure 5 for sample sonograms.

The announcement call of an unmated male is a single-note, slightly nasal whistle, which Schemnitz (1961) described as a *whock* whistle and Wallmo (1956b) called a *squawk* or *kwook*.

Fig. 9. Scaled quail, adult male

This is usually uttered from a conspicuous calling point and is probably uttered during the entire period that unmated males are in reproductive condition, as has been proven for the corresponding call in Gambel's quail. Wallmo (1956b) heard it only in males, probably only those that were unmated.

Wallmo (1956b), who described the separation or "gathering" call as a *chin-tang'* or *chuk-ching'*, indicated that the group alarm note is similar but more excited and rapid, sounding like *chink-thank'-a*. Bendire (1892) also indicated the same similarity in these two calls. When birds were removed from traps, they sometimes uttered a fright call, *tsing*. This call is very much like the down-slurred distress calls of other New World quails.

So far only a single type of male-to-male aggressive call has been noted in my laboratory. When confronted with other males (or a mirror), paired males utter a strong series of nasal calls, each of which is associated with a rapid and vigorous head-throw (Fig. 3), with the bill being raised to the vertical and the head drawn well backward. Up to seven or more of these are given in rapid sequence at intervals approximately one-half

second apart. The female also uncommonly performs a version, weaker both in relative movement and sound amplitude, of the same display under conditions of disturbance, but this does not occur with predictable regularity as it does in males. In both the releasing situation and its sound characteristics the "head-throw" call is clearly homologous to the *squill* of the California quail and the *meah* of the Gambel's quail, and male hybrids of the scaled quail and each of these species regularly perform intermediate calls and postures in this situation.

Strangely, the scaled quail apparently lacks any, or at most has very poorly developed, aggressive calls that correspond to the *wit-wit* and *wit-WUT* calls of these two species, thus the scaled quail's head-throws are neither preceded by nor alternated with other threat calls, as is the typical situation in the Gambel's and California quails. Likewise the scaled quail apparently almost lacks the typically repeated soft *chip* sounds made by these species in situations of mild alarm, with the head-throw call or a variant of it serving to keep the covey together as they retreat through the brush.

Daniel Hatch (pers. comm.) noted that about a third of the birds he heard calling in this situation uttered the head-throw call (males?), another third produced *chip'* and *chip-eee'* calls, and the remainder uttered only a *chip-eee'* note. Bendire (1892) described this call as a *chip-churr* sound. He also noted that when chased by a hawk the birds uttered a guttural *oom-oom-oom*; I have not had an opportunity to hear the response of this species to avian predators.

Laboratory-produced hybrids between the scaled quail and bobwhite produced a call that was intermediate between the *pey-cos* and the *hoy, hoy-poo* complex when placed in a situation that would elicit separation calls. The male call that is uttered in male-to-male aggressive situations lacks a definite head-throw component but acoustically appears to be intermediate between the head-throw call and the bobwhite's caterwaul call.

The total adult vocal repertoire of the scaled quail is thus a surprisingly limited one, which includes an unmated male announcement call, a separation call used by both sexes, an agonistic call that is largely but not entirely typical of males, an alarm *chip* note that is probably used by both sexes, an avian predator call, and a distress call. Wallmo (1956b) mentioned hearing various "conversational" or contact notes that might be added to this list, and doubtless one or more parental calls also occur. I have not heard calling by either sex during copulation, and the tidbitting display of males to females is likewise silent. It would thus seem unlikely that more than ten call-types are present in the scaled quail, or far fewer than have been found to occur in the bobwhite.

Social and Reproductive Behavior

The fairly large winter coveys of scaled quail remain intact until the males begin to come into reproductive condition, and the combination of increasing male aggression toward other males and the separation of paired birds from the coveys gradually cause the dissolution. Schemnitz (1961) noted that in Oklahoma this breakup of winter coveys began to occur shortly after the period from March 1 to April 15, which was marked by male fighting and intolerance among mated pairs. He reported the first *whock* call of unmated males on April 13, and the earliest copulation that he observed was on April 5. Nests, however, were not found until early May, a rather surprisingly late date for a desert-nesting bird.

Leopold (1959) reported that in Mexico most nesting occurs from June through August, pointing out that it is during this time that the summer rains usually fall, resulting in an abundance of water, insects, and succulent foods. This long nesting period, which extends into September or even October as far north as Oklahoma, no doubt is an adaptation to allow nesting during the most favorable period, or possible renesting attempts if initial efforts are unsuccessful.

Nests are usually located under shrubs or some other protected and shady site, and a fairly large clutch is typical. They are often located on a flat or an open ridge and frequently situated in a clump of grass or at the base of a cactus or shrub. Common cover plants in Texas include javelina bush (*Condalia*), tobosa grass (*Hilaria*), yucca (*Yucca*), and prickly pear (*Opuntia*) (Lerich, 2002; Rollins, 2000).

Wallmo (1956b) estimated that 14 eggs is an average clutch size based on personal observations and literature sources, and Schemnitz (1961) reported a similar average clutch size of 12.7 eggs. Male scaled quail evidently share in incubation less

regularly than do bobwhite males; Schemnitz noted only one definite case and the presence of a second bird in the vicinity of the nest for only six of 50 nest locations. Incubation requires from 22 to 23 days, although a 21-day incubation period has been commonly estimated.

There is evidence that males normally take over the care of the first clutch, which would enable the female to begin a second one, although at least two cases of males sharing incubation or taking over after the death of its mates are known. Recent work indicates that persistent renesting frequently occurs following clutch loss, and that multiple brooding has also been documented (Evans, 1997; Rollins, 2000; Brennen, 2007). Wallmo (1956b) reported one such case in which the male raised the first brood while the female began laying again.

Available data summarized by Schemnitz (1961) indicated a low average hatching success of scaled quail, generally under 20 percent. However, four other studies summarized by Brennen (2007) indicated nest success rates of less than 25 percent, 44 percent, 64 percent, 71 percent, and 83 percent. Schemnitz reported that causes of nest failures have included human activities (38.9 percent), depredation (25 percent), abandonment (19 percent), weather (2.8 percent), and unknown (13 percent).

A low hatching success, together with a high adult mortality rate would suggest that persistent renesting or possibly double brooding would be the only way that populations might be maintained. Average brood sizes in Oklahoma were apparently fairly high (7.8 to 11.5 young), but the percentage of adults without broods ranged from 38 to 70 during the three years of Schemnitz's study. Other more recent indications of low brood survival rates in scaled quail include those of Evans (1997) and Pleasant (2003).

Similarly, Hoffman (1965) reported an overall average brood size of 8.7 young for a six-year period, and an average young-to-adult ratio of 2.8 to 1 during the same period based on these brood counts. Schemnitz reported a very similar juvenile-to-adult ratio of 2.86 to 1 (74.1 percent juveniles) for fall hunter samples. This would suggest that each adult pair must have averaged 5 to 6 young that were raised to the November to January hunting season, which could hardly be possible if roughly 50 percent of the adults were unsuccessful nesters and only a single brood was raised by successful breeders.

During extremely dry summers, little or no successful nesting occurs in quail, and the birds may not even attempt to nest. Leopold (1959) attributed this behavior to a possible weakening of the adults because of the resultant poor diet, a reduced hatching success of eggs because of the lack of moisture, or reduced food and water supplies for the developing chicks and consequent high chick mortality.

As the chicks mature, the broods gradually become organized into larger covey units. During trend-route counts from July to early September in Colorado, the covey sizes seen averaged about 11 to 17 birds (Hoffman, 1965). Later area-covey counts made from mid-November to the early winter period provided yearly average covey sizes of 17 to 23 birds, suggesting a gradual merging of broods in late fall to form the fairly large winter coveys that are typical of this species. Wallmo (1956b) noted that 7 fall coveys averaged 38.7 birds, while by spring the average size of 12 coveys observed during two different years had been reduced to 18.8 and 21.7 birds.

Barred quail adult (left) and scaled quail adult (right)

As for other quail, survival rates of the scaled quail are low. In a hunted New Mexico population, immature females had a 10.9 percent annual survival rate and males 17.6 percent, whereas adult females had a 25 percent survival rate and adult males 36.4 percent. The influence of hunting on scaled quail populations is evidently very low (Campbell et al., 1973).

Evolutionary Relationships

Even if *Lophortyx* were not merged with *Callipepla* there could be no question that the Gambel's, California, and also the elegant quail are the nearest relatives of the scaled quail, and the lack of a distinctively colored and elongated crest in this species is of no taxonomic significance beyond the species level. It is difficult to judge with which of these three species the scaled quail has the greatest affinities, but the elegant quail bears an interesting allopatric relationship to the scaled quail.

One might readily imagine that speciation of these two quails occurred following isolation from a common ancestral type by the Sierra Madre Occidental mountains. Both species are desert-adapted and dependent on the presence of shrubby or brushy vegetation in relatively scattered (for the scaled quail)

or continuous (for the elegant quail) groupings. Both also have strong similarities in their vocalizations, their downy young, and their general plumage patterns; although differences in adult plumages do occur, they are not any greater than between those of the scaled and the California or Gambel's quails. However, the only known hybrids between the scaled and elegant quail have apparently been sterile (Banks and Walker, 1964), whereas at least a limited degree of hybrid fertility exists between the scaled quail and both the Gambel's and California quails.

There is apparently also a partial sterility barrier between the scaled quail and both the barred quail and the bobwhite quail, with female hybrids representing these crosses apparently either laying no eggs (scaled $\times$ barred) or laying abnormally small ones (scaled $\times$ bobwhite). One might presume therefore that the scaled quail does not provide a definite "link" between the crested quails (*Callipepla*) and *Colinus*, nor between these species and the Mexican barred quail (*Philortyx fasciatus*). For these reasons, and the very weak morphological criteria for separating *Callipepla* from "*Lophortyx*," it seems most reasonable to consider the scaled quail and the three crested quails as a close-knit evolutionary unit.

Gambel's Quail

Callipepla gambelii (Gambel) 1843

Other Vernacular Names

Arizona quail, codorniz de Gambel, desert quail, Olanthe quail

Range

From southern Nevada, southern Utah, and western Colorado south to northeastern Baja California, central Sonora, northwestern Chihuahua, and western Texas.

Subspecies

(ex AOU *Check-list*, 1957)

- C. g. gambelii*: Southwestern Gambel's quail. Resident from southern Utah and southern Nevada south to the Colorado and Mojave deserts and northeastern Baja California. Introduced in north-central Idaho (Lemhi Valley).
- C. g. fulvipectus* Nelson: Fulvous-breasted Gambel's quail. Resident in north-central to southwestern Sonora and probably north to southeastern Arizona and southwestern New Mexico.
- C. g. sana* (Mearns): Colorado Gambel's quail. Resident in western Colorado in the drainage areas of the Rio Grande and the Uncompahgre and Gunnison Rivers.
- C. g. ignoscens* (Friedmann): Texas Gambel's quail. Resident of desert areas in southern New Mexico and extreme western Texas from El Paso to southeastern Terrell County.

Measurements

Folded wing: Males (*C. g. gambelii*), 108–122 mm, ave. of 56, 112.1 mm; females 105–118 mm, ave. of 41, 112.1 mm (Ridgway & Friedmann, 1946).

Tail: Males (*C. g. gambelii*), 91–107 mm, ave. of 41, 96.3 mm; females, 83–102 mm, ave. of 41, 94.2 mm (Ridgway & Friedmann, 1946).

Weight (mass): Males, ave. of 390, 161 g; females, ave. of 337 birds, 156 g (Johnsgard, 1975a). Males (*C. g. gambelii*) ave. of 185, 169.3 g, females, ave. of 108, 167.3 g (Gorsuch, 1934).

Identification

Adults are 9.5 to 11 inches long. The sexes are different in appearance. This southwestern quail has a blackish, forward-tilting, teardrop-shaped crest, as in the California quail, but it completely lacks the scaly patterning of the underparts typical of the latter. Some scaly patterning is evident on the back of the neck of males, but this is ill-defined. Male Gambel's quail also have a black forehead and reddish-brown crown coloration, and both sexes have more rufescent brown flank coloration than occurs in the California quail. Otherwise the birds are generally grayish brown to brown on the upperparts and tail and have buffy underparts that may be streaked with brown (females) or have an extensive black area on the abdomen (males).

Males also have the characteristic black throat pattern that is lacking in females.

Field Marks

Generally limited to desert regions of the southwest, Gambel's quail can be identified in the field by the combination of "teardrop" crests and unscaled underparts. The rich reddish-brown flanks of both sexes are visible at considerable distances, and at close range the reddish crown color of males and the black mottling of their underparts may be evident. This species' calls are similar to those of the California quail but are less metallic and more nasal. The distinctive location call consists of occasionally repeated *chi-ca-go-go* notes (occasionally California quail will also add a fourth syllable to their location call).

Age and Sex Criteria

Females have dark brown rather than black crests and lack black throats. Immatures have mostly buff-tipped greater upper primary coverts, which are carried for the first year (Leopold, 1939). The outer two primaries may be somewhat more pointed and frayed than the inner primaries in immature birds.

Juveniles resemble females but have dull brown crests and broad bands of pale cinnamon buff above the eyes. They are very similar to California quail of this age except the nape feathers lack dusky borders and are uniformly gray with more distinct shaft-streaks (Dwight, 1900).

Downy young of this species cannot be easily distinguished from California quail of the same age, but they are perhaps in general slightly paler and less yellowish in tone overall. The pale spinal stripe is somewhat tinged with darker streaks in the Gambel's quail, whereas in the California quail it is a slightly brighter buff. Furthermore, the downy California quail generally has less sepia brown and more buffy on the forewing than do the Gambel's and scaled quails.

Distribution and Habitat

A detailed analysis of the range and habitat of the Gambel's quail has been made by Gullion (1960). No major changes in ranges have occurred since that time, and his review of the species' distribution by states is still relevant. He found that the species is found in three major climatic and habitat types. One of these is the mesquite (*Prosopis*), saltbush (*Atriplex*), tamarisk (*Tamarix*), and desert thorn (*Lycium*) shrub associations of desert valleys from Texas west to southern California, Nevada, Utah, and northern Mexico. These areas have similar altitudinal ranges, low annual precipitation totals, and mild winter temperatures.

Especially in the western part of its range, this species also occurs in upland desert habitats, particularly where a fairly uniform desert vegetation is dominated by cat's-claw (*Acacia*), creosote bush (*Larrea*), desert thorn, skunkbush (*Rhus*), yuccas (*Yucca*), burroweed (*Franseria*), and prickly pear (*Opuntia*).

This habitat type occurs on the Mohave Desert region of Arizona, California, and Nevada, and to a reduced extent in arid lands of southwestern New Mexico and Utah. The habitat's altitudinal range is from 3,000 to 4,500 feet, and winter temperatures average considerably above freezing. Although precipitation averages more than in the valley habitats, it is still only from about 3 to 9 inches. Birds in this upland habitat exhibit greater population fluctuations than is typical of lowland habitats, depending on annual productivity. Winter precipitation variation is one of the most important factors regulating their population changes.

In Arizona the Gambel's quail is the mostly widely distributed quail species, and Arizona supports the species' largest US population. They require more woody vegetation than the other US quails and have increased with the increase of shrub invasion as a result of overgrazing (Engel-Wilson and Kuvlesky, 2002).

In addition to these two warm desert habitats, the species also occurs in the Colorado River basin areas of New Mexico, Colorado, and Utah and as an isolated population in the Lemhi Valley, Idaho, all of which are subjected to considerably colder temperatures. The vegetation here is essentially that of the Great Basin desert, with such shrubs as greasewood (*Sarcobatus*), rabbit brush (*Chrysothamnus*), skunkbush (*Rhus*), saltbush (*Atriplex*), and sagebrush (*Artemisia*) being almost universally present. These habitats and climates are marginal for the Gambel's quail, and at least in some areas the presence of food in the form of agricultural crops such as alfalfa may be critical for survival. Gullion also suggested that such populations are marginal where snowfall exceeds 20 inches or where at least an inch of snow is on the ground for more than about 40 days a year. Where the northern population survives best, the winter precipitation totals are normally quite low, usually well below 50 percent of the total annual precipitation.

Population Density and Hunting

Breeding populations of the Gambel's quail have not been intensively studied as to population densities. Hensley (1954), in studying the birds of desert habitats in Arizona, estimated that the average number of breeding quail pairs per 100 acres—on 210 total acres of study areas—was 6, or 1 pair per 16.6 acres. However, based on one study area of 70 acres, he had an estimated maximum population of 12 pairs per 100 acres, or 1 pair per 8 acres.

In a study of the breeding bird population of a cholla cactus (*Opuntia*), palo verde (*Cercidium*), and saguaro (*Cereus*) desert community in Arizona, an estimate of 20 territorial male quail per 100 acres has been made (*Audubon Field Notes* 19:610–611, 1965), or presumably 1 pair per 5 acres. Also, Hensley (1954) reported that 4 pairs of Gambel's quail occupied a mountain canyon study area measuring 25 by 800 yards (4.1 acres), suggesting that under favorable conditions a population density of at least one bird per acre may sometimes occur. Gullion (1962) reported that an estimated total of 472 quail were present on a 777-acre study area in Nevada, or one bird per 1.6 acres. This total apparently referred to a late winter population.

A 2004 estimate of the species' total North American population was 1.8 million (Rich et al., 2004), 60 percent of which was in the United States and Canada. Data from the North American Breeding Bird Survey for the period 1966–2015 indicate that this species underwent a range-wide decline of 0.30 percent annually for the period 1966–2015, and 2.25 percent annually for the period 2005–2015 (Sauer et al., 2017).

Map 4. Residential distribution of the Gambel's quail as of the 1970s. Recent (2011–2015) denser populations (averaging 10–30 birds per Breeding Bird Survey route) are stippled.

In 1975 I (Johnsgard, 1975a) estimated that 1.3 million Gambel's quail were being shot annually in the United States, based on data from individual states. In 2016 Gambel's quail were legally hunted in the following states: Arizona, California, Colorado, Nevada, New Mexico, Texas, and Utah, as well as Hawaii. Some recent estimated state-wide US hunter kill estimates are: California (2014–15) 38,000; Nevada (average, 2006–15), 16,000; and New Mexico (2014–15), 5,800.

Habitat Requirements

Gullion (1960) has suggested several biotic and physical environmental features that may represent limiting factors for Gambel's quail. Soils having good populations are residual soils of decomposed granite in the uplands of Nevada; such soils support a relatively luxuriant and diversified vegetation. Transported soils of river bottoms also support luxuriant shrub growth and high quail populations. Populations are also highest where January temperatures do not drop below 40°F; additionally, as mentioned earlier, winter snow cover is probably an important limiting factor in northern marginal populations. However, the Colorado race of

Gambel's quail is known to survive winter temperatures as low as -8°F in New Mexico, the Texas race of Gambel's quail occurs in areas having minimum winter temperatures of -5°F , and in Utah and Idaho the introduced race *gambelii* have survived temperatures of approximately -40°F .

Although lowland populations of Gambel's quail depend on subsurface moisture that may originate several hundred miles away, upland populations evidently require winter precipitation of more than five inches (Gullion, 1960). This amount, of course, is not a reflection of drinking water needs but the effects of the precipitation on vegetational growth. Swank and Gallizioli (1954) considered December to April in Arizona to be the most critical months for precipitation, and Gullion (1960) correlated quail populations with the precipitation totals of the preceding October to March. Apparently winter germination and growth of green plants is vital to the breeding success of this species, possibly because of its effect on vitamin A storage in potential breeding birds (Hungerford, 1964).

Raitt and Ohmart (1968) reported that in New Mexico the fall productivity index based on age ratios was closely correlated with amounts of precipitation during the preceding May and June rather than those of the previous fall, winter, or early spring, indicating a lack of strict dependency on such winter rainfall. They suggested that the effects of irrigation or a winter climate that permits an accumulation of soil moisture might account for this apparent difference in climatic correlation.

The importance of free water for drinking purposes by Gambel's quail is not completely clear. Gullion (1960) believed that where a combination of high humidity and fleshy plants occurs, the birds can live an entire lifetime without drinking water. Hungerford (1960) concluded that water catchments were nonessential in southern Arizona, where moist succulent plant foods are normally available. However, on desert uplands, such as in Nevada, there may be a critical period for moisture from about mid-June to mid-July, when succulent spring annuals have dried up and summer thunderstorms have not yet occurred. During such times, if succulent plants are not available, artificial watering structures may be quite important to the species (Gullion, 1960).

Miller and Stebbins (1964) reported that in Joshua Tree National Monument the Gambel's quail occurs primarily in the vicinity of springs, and the greatest distance from water which they have recorded for this species was 1.5 miles at a time when succulent vegetation was widespread. Most coveys probably stay within a mile of water when it is needed.

Nesting cover requirements for the Gambel's quail are simple, consisting of desert shrubs or trees, with the primary requirement apparently being a source of shade from the midday sun (Bent, 1932). Brooding requirements no doubt include brushy escape cover, shade for resting, and foraging sites where insects and small green plant growth is readily available. Grit sources and dusting locations are readily available in desert habitats.

Food and Foraging Behavior

In common with the California quail, the Gambel's quail relies very little on animal sources of food, adults taking perhaps as little as 0.5 percent of their annual food from this source (Judd, 1905a), with a maximum usage of 12 to 13 percent during spring and summer (Martin et al., 1951). Otherwise, the birds rely predominantly on the foliage and seeds of a large array of plants.

Judd's analysis (1905a) of 28 food samples from Arizona and Utah indicated that virtually no fruit material is consumed and

only a very small amount of cultivated grains (3.9 percent of annual total). Rather, leafy materials, mainly legumes, and seeds of a variety of species made up more than 95 percent of the total sample, with these two food categories totaling 31.9 and 63.7 percent respectively by volume. Legume seeds alone made up 21.2 percent of the total food material, especially those of alfalfa and bur clover (*Medicago* spp.). Gullion (1960, 1966) noted that at least 91 species of plants are consumed by Gambel's quail in southern Nevada, but the availability of species representing only three groups—namely deer vetch (*Lotus* spp.), filaree (*Erodium*), and a few herbaceous legumes (*Astragalus* and *Lupinus*)—determines the abundance of Gambel's quail in this area.

Hungerford (1962) examined the seasonal variations in food consumed by Gambel's quail in southeastern Arizona, based on the study of 221 samples. He found that various legumes (*Lotus*, *Lupinus*, *Mimosa*, *Prosopis*) were the most important food sources, with their leaves, flowers, and seeds all being consumed. Filaree seeds and flowers were a highly preferred food source as well. On a yearly basis, seeds made up 60.7 percent of the diet and were important foods throughout the year.

Considering only life-form of food sources, forbs were most important, making up 54.2 percent of the annual diet; shrubs were second, totaling 31.8 percent; and grasses, animal foods, and unknown plants made up the remaining amount. During spring, a high 1:1 ratio of succulent to nonsucculent plants was present, while during fall and winter this ratio dropped to about 1:2. Apparently these succulent food sources, during dry periods or in areas where free water is not normally available, provide important sources of moisture and are highly important aspects of the quail's ecology.

A study by Campbell (1957) on the fall foods of the Gambel's quail in New Mexico provides an additional index of the diverse food usage of this species. Of 57 crops studied, all had seeds and/or fruits present, and collectively 87 plant species representing 27 different families were present in the crops. However, foods representing 22 species of plants accounted for more than 90 percent of the sample volume, including 5 species of legumes, 4 composites, 4 grasses, and 3 chenopods. Campbell concluded that the flexibility in foraging behavior of Gambel's quail in utilizing so many different food sources helped to explain its success in agricultural areas, where the vegetational complex is quite different from that prevailing in undisturbed desert habitats.

Kuvlesky, DeMaso, and Hobson (2007) summarized food items from a large variety of studies in Arizona, New Mexico, and Nevada, which totaled 40 taxa of plants, especially legumes and their seeds, and 8 invertebrate taxa. The seeds, leaves, and flowers of mesquite are notably important throughout the year, and the seeds of annual and perennial forbs, mast, and green vegetation are major food components (Schemnitz, Dye, and Cardenas, 1997).

Mobility and Movements

The movements and social organization of Gambel's quail coveys have been studied by Gullion (1962) in Nevada on a 777-acre area of thorn shrub vegetation. A total of 24 coveys were present on the area, ranging from 3 to 40 birds and averaging 12.5. An estimated total of 472 birds were present, of which 217 banded birds were used to establish covey organization and movements. There were three major areas of use on the study area, with some overlapping of home ranges. The home ranges of ten coveys spanned from 19 to 95 acres, averaging about 35.7 acres per covey. No clear correlation occurred between covey

Fig. 10. Gambel's quail, adult male

size and size of home range, with the largest covey (22 birds) having a 95-acre range, the second largest (21 birds), a 37-acre range, and a still smaller covey an intermediate range.

During the winter, covey movements appeared to be erratic. From late December to the following April, the ten coveys ranged over areas with diameters from 1,500 to 4,200 feet, averaging 2,340 feet. One covey of 22 birds consisted of at least four subgroups and moved about over a 63-acre area, then all moved into a new area 2,200 feet away. After staying in the new area for at least ten days, the covey disappeared from the study area, with a few of the birds eventually returning to the location where they were originally trapped.

Seasonal variations in covey movements were considerable and influenced by the age composition of the coveys, with coveys composed of adults moving considerably farther than did brood coveys. During the winter period of December through late January, 5 adult coveys moved an average of 103 feet per day, while 13 brood coveys averaged 63 feet per day. The movements increased in late January and early February, with average daily movements of 264 feet for adults and 131 feet for broods. During late March and early April there was a considerable prenesting shuffle, with coveys actively moving about, and the five adult coveys averaged 1,029 feet per day during this time. However, after about the first week of April, most of the coveys became sedentary, with the exception of a few new

arrivals on the study area.

Individual movements of 3 birds during periods between late morning and midafternoon ranged from 400 to 1,250 feet, while the movements of 42 banded birds over 24-hour periods averaged 755 feet but were as much as 2,800 feet. One male moved at least 2,400 feet in a 48-hour period and another male at least 3,800 feet in 96 hours. A third male moved 4.7 miles between April and November, and a fourth male moved 5 to 6 miles between late April and October. The longest recorded movement was by an adult female, which moved 6.5 miles from the banding site in somewhat over two years; she was at least 4.5 years old when she was killed.

No definite fall dispersal pattern for single quail could be established, but a spring dispersal pattern was clearly evident. This dispersal, which consisted of covey shifting, was performed mostly by young males, plus a few young females. Although the evidence was not clear, major dispersals over long distances probably involved entire coveys rather than individual birds.

Vocal Signal

The most complete analysis of vocalizations of the Gambel's quail is that of Ellis and Stokes (1966), which is followed here. They grouped the species' calls into those associated with group activity, feeding relationships, responses to enemies, and

Gambel's quail, male

agonistic and sexual phases of reproductive behavior. See Figure 5 for sample sonograms.

Calls important in integrating covey activity are the basic contact *took!* note, a conversational *ut-growl*, and the location call. The contact note is uttered by both sexes and carries only a short distance. It occurs at all times of the day but is especially associated with foraging. A similar call, the *ut-growl*, is the same note with an added trill and is especially prevalent when the birds find food or water after being deprived of them.

The location or separation call is a four-noted *ka-KAA-ka-ka* (also interpreted as *cow-COW-cow-cow* or *chi-CA-go-go*) and is produced by birds when separated from their mate or covey. Both sexes produce the same call, but sufficient individual variation occurs in the call (which is the most acoustically complex as to cadence and amplitude characteristics) that individual recognition is typical. Visually isolated birds keep in contact by use of this call, and males can distinguish the location call of their mates from those of other females.

Ellis and Stokes mentioned no specific food calls, nor have I heard any. Evidently paired males do show or pick up food particles in front of their females, a display ("tidbitting") that is widespread in galliform birds, but Ellis and Stokes did not notice any associated calling. However, Prosski (1970) did hear vocalizations in this situation.

Several calls are associated with responses to enemies. The most typical alarm note of Gambel's quail, as well as other

Callipepla species, is a repeated *chip-chip-chip* as the birds investigate any disturbance during moderate alarm or curiosity. When thoroughly frightened and rushing for cover, a bird utters a raucous *squawk* followed by a series of *chip* notes, or the two kinds of calls may be alternated. The *squawk* note is both louder and more prolonged than the chip sounds, but they probably intergrade with one another. During times when the birds are being held in the hand, they usually utter loud, down-slurred distress *kee-OW!* notes, repeated almost indefinitely at intervals of about one-half second. Both sexes use the call, but individuals vary in the ease with which the call can be elicited from them.

The reproductive phase of sexual behavior has several associated calls. One of the most important of these is the *kaa* or *cow* call, already discussed in the section on social and reproductive behavior. Another is the location or separation call, *ka-KAA-ka-ka*, uttered by members of a pair whenever they are visually separated. Ellis and Stokes noted that during copulation the female, and probably also the male, uttered a series of short squealing calls. When an unpaired male is displaying toward a female, he faces her and utters a series of *wit-WUT* aggressive notes that are the same as those heard when two males are threatening one another. At this time the head is bobbed somewhat, causing the erect plumes to vibrate, and the bird stands in an erect posture.

During aggressive encounters between two males, the same *wit-WUT* call is uttered, often alternated with pecking movements or actual attacks. In such situations the calling may be

Gambel's quail, female

almost continuous as the birds face one another, seemingly unwilling to attack or retreat. After a varying number of such threats and attacks, one of the birds typically utters a cat-like *meah* call, at the same time lifting his beak almost to a vertical position. This call is no doubt homologous to the *squill* of the California quail but is both more prolonged and much slower in the associated head movements. This call usually stimulates the other male to respond in the same fashion and generally leads to a termination of the encounter.

Observations on the vocalizations of a male hybrid bobwhite $\times$ Gambel's quail (Proski, 1970) allows for the establishment of some probable vocalization homologies between these genera. The announcement call of the unpaired male bobwhite is a whistled *bob-white!* (Stokes, 1967). The hybrid's call was a similar two-note call, but the two notes were virtually identical in volume and frequency characteristics, sounding something like *cow-COW!*

The separation call of the male hybrid was apparently the same call as the male's announcement call, whereas in the bobwhite two calls (*hoy-poo* and *hoy*) serve this purpose. The calls are also used in agonistic situations by male bobwhites.

Two calls were produced in agonistic situations by the hybrid male, a two-noted *porquoi* and a growling *ker-ra-wa* call. Typically he would begin with a number of *ker-ra-wa* calls, followed by several *porquoi* notes. The *ker-ra-wa* calls sonographically most resemble the *hoy-poo* calls of the bobwhite, while the second note of the *porquoi* approached the *meah* in its acoustic

characteristics. No sounds resembling the Gambel's quail's *wit-WUT* call were produced.

The hybrids also produced chipping alarm calls, hand-held distress calls, contact calls, tidbitting calls, and copulation calls, all of which were comparable to those of both parental species, since interspecific differences are generally not great in these calls.

It is of interest that in this group of quails the male call that is used to announce the location of unmated males (thus also communicating information on species, sex, and reproductive state) is a simple one-syllable note in at least three species (Gambel's, scaled, and California quails). However, the call used by both sexes to announce the location of a bird separated from its mate and serving both for individual recognition and for homing purposes consists of two notes in elegant and scaled quail, three in California quail, or four in Gambel's quail—varying in cadence, pitch, and loudness but all having similar harmonic characteristics. In the Gambel's and California quails the male announcement call is, in effect, a single note "excerpt" from the longer location call, while in the scaled quail the male's announcement note more closely approaches a pure whistle. This distinction between a harmonic-rich location call and a nearly harmonic-free whistle for a male announcement call is even greater in the bobwhite. The bobwhite also seemingly has a greater number of agonistic calls than do the species of *Callipepla*, and in general its acoustic communication system appears to be more complex.

The Gambel's quail apparently has two basic male agonistic

calls, one of which (the *wit-WUT*) is used during sexual display toward females and aggressive encounters with other males, and the other (the *meah*) which is used only toward other males and apparently serves to break off aggressive encounters. Similarly the California quail has two calls, the *wip-wip*, which serves the same function as the Gambel's *wit-WUT*, and the *squill*, which occurs during high-intensity male-to-male threat. In contrast, the scaled quail seems to lack a call comparable to the *wip-wip* or *wit-WUT*, and the head-throw call is performed by both sexes in agonistic situations, although it is used predominantly by males.

Again, the bobwhite is the most complex in its agonistic vocabulary. Both sexes use the *hoy* and *hoy-poo* calls in agonistic situations, and two additional calls, the *squee* and "caterwaul," are largely but not entirely characteristic of the males (Stokes, 1967). The *hoy*, *hoy-poo*, and "caterwaul" calls seem to represent one intergrading motivational complex, while the *squee* call has a different seasonal and contextual occurrence. Thus a certain vocal duality is present, but it is difficult to judge possible homologies in these calls. One might only imagine that the evolutionary trend has been from a situation (as in the scaled quail) in which both sexes perform a common call in an agonistic situation to one (as in Gambel's and California quail) in which the male has separate vocal signals for male-to-male situations and male-to-female situations, and finally (as in bobwhite), to a condition in which both sexes have a complex intergrading series of calls associated with varying agonistic situations.

Ellis and Stokes (1966) list a total of ten call-types for the Gambel's quail, of which at least seven are common to both sexes, two occur only in males, and one (the copulation call) occurs in the female and possibly also the male. Stokes's analysis (1967) of the bobwhite's vocalizations indicated a considerably larger number of vocalizations, but the intergrading qualities of many of the calls make a strict numerical comparison impossible.

Social and Reproductive Behavior

Gullion's (1962) study indicated that coveys of Gambel's quail consist basically of family units of 5 to 7 birds or their aggregates (9–13, 17–22). Winter coveys might consist either of such combined broods or of varying numbers of nonbreeder adults. Although some overlapping of home ranges of coveys does occur, there is considerable covey fidelity, with little of the covey exchange that has been reported for other species of quail. Such covey exchange that Gullion found (20 of 217 birds) occurred mostly during the prenesting shuffle, with only five birds shifting during the earlier winter period.

The study by Raitt and Ohmart (1966) in southern New Mexico provides one of the best analyses of seasonal variations in social behavior that is available for the Gambel's quail. During late winter, pair formation and increased hostility among males begins to cause the dissolution of coveys, which in New Mexico begins in March. The process of pair formation is a subtle one, which apparently occurs over a prolonged period of contact. Raitt and Ohmart thought that chases of females by males, during which they uttered explosive high-pitched notes together with longer and lower-pitched, softer notes, might be associated with pair formation under natural conditions.

Such chases rarely if ever occur in captive birds that have been held in pairs through the prebreeding period, but if a female is introduced to a lone male in breeding condition, strong chases of this type will immediately occur and care must be taken that the female is not killed by the male. Thus, it would

seem that initial male-to-female responses are not greatly different from male-to-male behavior, except that the female attempts to escape and performs submissive responses such as huddling that usually serve to break off attacks by the male. I have not seen strong wing-drooping during such displays in the Gambel's quail, but evidently it does occur. Gorsuch (1934) described such an encounter as follows:

One day, while observing a whistling cock that was known to have used the same bush from which to call for over three weeks, a clucking sound was heard from down the wash and shortly a hen appeared. Immediately the cock sighted her his notes became fewer and shorter, and when she was within thirty feet of his perch he became greatly excited, jumping about the bush as if much disturbed, and talking to her meanwhile in a variety of notes. When she approached to within fifteen feet he . . . leaped to the ground and slowly but eagerly advanced to her. After walking around the hen in short circles several times, expanding his chest and trailing his wings in display they engaged in low-voiced conversation and wandered slowly away; it was definitely known that no nest existed within 200 yards of this whistler's post.

When males are chasing males, fighting may occur; however, this behavior is not territorial defense but only a means of establishment of social dominance. Such attacks consist of rapid pecking movements and short vertical flights as each bird tries to get above the other bird and peck its skull. After a few such attacks, one bird usually makes a quick retreat; in a small cage, the retreating bird may be caught by the dominant bird, whereupon its back, nape, and skull may be seriously damaged by pecking.

As the coveys are breaking up and strong pair-bonds are forming, cow calling by unmated males begins. In New Mexico this may occur as early as mid-March, but it reaches a high level in April and May, declining in June, and terminating completely in late July or early August. Its duration thus does not conform to the period of pair formation, and a census of calling males should obviously not be regarded as a census of pairs in the area. Rather, its cycle generally follows the testis activity cycle, and it is thus a reflection of male sexual tendencies of unpaired birds. Probably no cow calling occurs in mated males, according to Raitt and Ohmart, and the study of Ellis and Stokes (1966) confirmed this opinion. These authors indicated that the call, which they referred to as the *kaa*-call, is usually uttered from an exposed perch and has a function analogous to the advertising song of passerine species. During the call, the male stands in an erect posture with his abdominal patch wholly visible and the crest held vertically erect.

Gambel's quail are strongly monogamous. The gonadal activity cycle of the female lags about two weeks behind that of the male, and in New Mexico egg-laying begins in late April. Gorsuch (1934) indicated that a depressed area about 1.5 inches deep and 5 to 7 inches in diameter is scratched out and variably lined. The first egg is shortly after deposited, and the remaining eggs are then deposited daily, with lags of one to three hours on each succeeding day. After 4 to 6 eggs, a day is skipped, and the cycle begins again. After about three such cycles of 4 to 6 eggs, the clutch is complete. Gorsuch found clutches of up to 19 eggs at 44 nest sites, but 29 of the nests had 10 to 16 eggs present; thus, 12 to 14 must be regarded as a typical clutch.

Gambel's quail, pair

The female alone incubates, with the male usually sitting at a perch 40 to 80 feet away. When the nest is approached by an intruder, the male typically performs a "broken wing" distraction display (Gorsuch, 1934). Incubation usually requires from 21 to 23 days, with pipping usually occurring on the twenty-third day. Gorsuch estimated that about 10 days might be needed for nest selection and construction, 38 to 42 days for egg-laying and incubation, and nearly three months for raising the brood to an independent state. Thus, two broods cannot be raised successively by a single pair even with the long nesting season typical of the southwestern desert.

During highly favorable nesting seasons, supplementary nestings may be achieved by two different methods. The males may take over the care of the brood, leaving the female free to begin a second clutch, or, more commonly, the chicks may be "weaned" when about a month old and left in the care of older birds of the area, thus allowing the pair to start a second clutch (Gullion, 1956a). In one desert area where such double-brooding occurred, the average number of chicks per adult pair was 15, whereas in the valley habitats where double-brooding did not occur the average number of chicks per adult pair was 10.

When the young are hatched, the family leaves the nest-site and does not return. Brooding by the female occurs in shady and well-sheltered areas, while the male typically "stands guard." As the brood moves, the male usually takes the lead, with the chicks following and the hen bringing up the rear. Males leading young chicks regularly perform distraction displays, while the hen and

young "freeze," or both adults may fly off as the young remain in place (Gorsuch, 1934). Like all young galliforms, the chicks feed almost exclusively on insect life during the earliest part of their life but soon begin to take leaves and other succulent vegetation and within a few months are consuming about 90 percent vegetable materials (Gorsuch, 1934).

Evolutionary Relationships

The close similarities in downy and adult plumage patterns, as well as strong behavioral similarities, clearly indicate that the Gambel's and California quail are close relatives. The ecological differences between the two species prevent extensive sympatry, but where limited contact does occur hybridization has been found (Miller and Stebbins, 1964; Gee, 2003, 2004, 2005; Gee, Calkins, and Petren, 2003). It would seem reasonable that the Sierra Nevada range might have provided an effective geographic barrier that allowed speciation to develop to the point that now exists and has still virtually prevented any extensive population overlap, partly because of the major climatic differences prevailing on the two slopes of this range. It also seems possible to assume that the common ancestral type may have had a range in the southern part of the continent similar to that now occupied by the Gambel's quail, and that as the ancestral California quail adapted to the moderate climate of interior California, it gradually extended its range northward into the coastal portions of the Pacific Northwest.

California Quail

Callipepla californica (Shaw) 1798

Other Vernacular Names

California partridge, Catalina quail, codorniz Californiana, crested quail, San Lucas quail, San Quintín quail, topknot quail, valley quail

Range

From northern Oregon and western Nevada south to the tip of Baja California. Introduced into Hawaii, Washington, Idaho, western Oregon, and Utah. Introduced and established in southeastern Vancouver Island and the Okanogan and Kettle valleys. Also introduced and surviving on the southern Caribou Plateau and northern Vancouver Island, British Columbia, but this population is probably not self-sustaining (Davidson et al., 2015). Other successful international introductions include Argentina, Australia, Chile, and New Zealand.

Subspecies

(ex AOU *Check-list*, 1957)

- C. c. californica*: Valley California quail. Resident from northern Oregon and western Nevada south to southern California and Los Coronados Islands of Baja California. Introduced in eastern Washington, central British Columbia, western Idaho, Oregon, Utah, and Colorado.
- C. c. catalinensis* (Grinnell): Catalina Island California quail. Resident on Santa Catalina Island and introduced on Santa Rosa and Santa Cruz islands, southern California.
- C. c. plumbea* (Grinnell): San Quintín California quail. Resident from San Diego County, California south through northwestern Baja California, Mexico.
- C. c. canfieldae* (van Rossem): Inyo California quail. Resident in Owens River Valley in east central California.
- C. c. orecta* (Oberholser): Great Basin California quail. Resident in the Warner Valley, southeastern Oregon.
- C. c. brunnescens* Ridgway: Coastal California quail. Resident in the humid coastal region of California from near the Oregon boundary south to southern Santa Cruz County.

Measurements

Folded wing: Adults, both sexes, 105–109 mm (males average 5 mm longer than females) (Johnsgard, 1973). Males (*C. c. californica*), 106–117 mm, ave. of 35, 110.6 mm; females 105–111.5 mm, ave. of 13, 107.8 mm (Ridgway & Friedmann, 1946).

Tail: Adults, both sexes, 79–119 mm. (males average 4 mm longer than females [Johnsgard, 1973]). Males (*C. c. californica*), 83.8–99.5 mm, ave. of 35, 69.2 mm; females 79–88.5 mm, ave. of 35, 83.8 mm (Ridgway & Friedmann, 1946).

Weight (mass): Males, ave. of 418, 191 g (6.2 oz.); females, ave. of 272, 162 g (6.0 oz.) (Johnsgard, 1975a).

Identification

Adult California quail range from 9.5 to 11 inches long. The sexes are different in appearance. This widespread quail of the western foothills resembles the Gambel's quail inasmuch as both sexes have forward-tilting, blackish crests that are enlarged terminally into a "comma" or "teardrop" shape. Both sexes also have clear bluish gray to gray chests that become buffy toward the abdomen and have darker "scaly" markings reminiscent of scaled quail. The flanks are brownish gray with lighter shaft-streaks, and the upperparts are generally gray to brownish gray, intricately marked with darker scaly markings. Males have black throats and a chestnut-tinged abdomen and are chocolate brown behind the plume, while the area in front of the eyes and above the bill is whitish.

Field Marks

The combination of a "comma" crest and scaly markings on the lower breast and abdomen is distinctive for both sexes. Males of this species may be distinguished from the very similar Gambel's quail by the combination of a whitish rather than blackish forehead, no black abdomen patch, and a dull brown rather than chestnut brown flank and crown coloration. A three-note *chi-ca-go* call serves as a location call for both sexes.

Age and Sex Criteria

Females have dark brown rather than black crests and lack black throats.

Immatures have buff-tipped upper greater primary coverts, which are carried for the first year (Sumner, 1935; Leopold, 1939), and the outer two primaries are relatively pointed and frayed.

Juveniles resemble females but have forehead feathers with indistinct pale grayish terminal spots, and shorter and lighter crests (Ridgway and Friedmann, 1946). See the Gambel's quail account.

Downy young are very difficult to distinguish from young Gambel's quail (see that species' account), but they can be recognized from downy scaled quail by their less grayish white and more yellowish body tones, and by the fact that the pale spinal stripe in the California quail is cinnamon-buff rather than a dirty brownish buff. This species is considerably lighter and more yellowish on the lower back and tail than are downy elegant quail (*C. douglasii*).

Distribution and Habitat

The California quail exhibits a rather complex distribution pattern that extends along the western coast of North America for about two thousand miles, from the southern tip of Baja California, Mexico, to the southern part of Vancouver Island, British Columbia. Along this entire range its coastal distribution is almost unbroken except for forested areas associated with the Coast

and Olympic ranges. The climatic and precipitation variations along this coastal strip are considerable, ranging from hot scrub desert along much of Baja California, through a mild Mediterranean climate associated with chaparral vegetation in southern California and a cool, wet coastal forest (where the bird occurs in edge and successional vegetation stages) from central California northward to Puget Sound. In the interior of these coastal states, as well as in Nevada, Idaho, and Utah, the species also occurs in valleys and rain-shadow areas dominated by grasslands or semidesert sagebrush shrub, although many of these interior populations have been introduced.

In Mexico, Leopold (1959) reported that the highest populations are found in chaparral vegetation along the northwestern Baja coast and foothills and in scrubby tropical forest and brush land at the tip of the San Lucas Cape, but they also occur in desert washes wherever a combination of brushy cover and water is available.

In California several races occur, but all are associated with brushy vegetation in combination with more open weedy or grassy habitats and available water supplies. Heavy forest and dense chaparral is avoided even by the coastal race, although dense-foliaged trees may be used for night roosting. The exact vegetational composition is probably not so important as life-form characteristics of the dominant vegetation, namely an interspersed of brush and more open vegetational types (Grinnell and Miller, 1944).

In Oregon the species was probably originally confined to the counties bordering California (*californica*) and Nevada (*orecta*), but trapping and transplanting activities have spread the bird's range to most of eastern Oregon and many western Oregon counties, with consequent mixing of subspecies stocks (Masson and Mace, 1962). The highest populations occur in the Columbia Basin and in central and southeastern Oregon in dry, semi-desert vegetation.

The Washington population of California quail is likewise largely or entirely introduced and of uncertain subspecific designation. Its preferred habitat is thickets, brushy tracts, logged areas, and burned over districts. Although it is sometimes seen in second-growth timber, it avoids heavy woods (Jewett et al., 1953). The species is more common and widespread in eastern Washington but is local in the west, where it is adapted to human-created habitats (Wahl, Tweit, and Mlodinow, 2005).

In Canada the California quail is mostly limited to one small introduced population on the southern part of Vancouver Island and another centered in the Okanogan and Similkameen valleys (Lewin, 1965). More is known of the Okanogan and Similkameen valley populations than the island population, and Lewin (1965) reported that an estimated population of about 250,000 quail then occupied about 390 square miles of these river valleys. They are associated with orchards and irrigated areas, and are generally found below 2,000 feet elevation. A few also occur in native vegetation consisting of scattered thickets of aspen (*Populus*), rose (*Rosa*), Saskatoon berry (*Amelanchier*), and chokecherry (*Prunus*), but they do not extend into the higher coniferous woods (Lewin, 1965).

In western Idaho the species extends south along the Washington and Oregon boundaries east of the Snake River valley, expanding southeastward through the Snake River Plain to the southeastern corner of the state and adjacent northern Utah. In Utah the species was first introduced over a century ago and

Map 5. Residential distribution of the California quail as of the 1970s. Recent denser populations (averaging 10–30 birds per Breeding Bird Survey route, 2011–15) are stippled.

is now found in scattered areas in northern and northeastern Utah, south to about Bicknell. It is primarily limited to semiarid foothills and valleys, especially along streams (Rawley and Bailey, 1964). Some eBird sightings have occurred in Dinosaur National Monument.

In Nevada the range of the possibly originally native California quail has been greatly affected by release programs. The birds are usually associated with rose and willow thickets along streams, where cover and water are both available. Most recent sightings are from northern Nevada (north of Interstate 80). In northwestern Nevada the heaviest populations occur in agricultural areas, but the birds are found wherever springs exist. In northeastern Nevada their distribution is limited and spotty (Gullion and Christensen, 1957).

In northeastern Arizona a small relict population might possibly remain from transplants done in the 1960s (Engel-Wilson and Kulesky, 2002). A few scattered eBird sightings have been reported from southern and southeastern Arizona. An introduced population once occurred in north-central Colorado but is now extirpated.

Population Density and Hunting

Population densities doubtless vary considerably in this species according to habitat quality. Emlen (1939) reported on a "low density" winter population that contained 113 birds on a study area that represented a density of one bird per seven acres. However, if only the occupied home ranges of the birds were considered, the four coveys' total occupied area was 93 acres, or 0.9 acre per bird. Raitt and Genelly (1964) reported on a population that also contained four winter coveys on approximately 100 acres. Over an eight-year period this area had fall populations ranging from 25 to 140 birds and averaging 101 birds, or up to one bird per acre. Since the average fall age ratio was 1.47 juveniles per adult, the average spring breeding population (ignoring spring-to-fall adult mortality) must have been at least 41 adults. Thus a spring breeding density of approximately one bird per two acres would seem probable. These figures are in general agreement with those of Glading (1941), who recorded late winter densities on a study area in central California that varied over a six-year period from 1.7 to 3.9 acres per bird.

Maximum population densities noted for the species are some that have been reported from a private hunting club property, where artificial feeding and predator control measures were used. There, fall populations of up to 4.8 birds per acre were attained (Glading, Selleck, and Ross, 1945).

A 2004 estimate of the species' total North American population was 990,000 (Rich et al., 2004), 87 percent of which was in the United States and Canada. Data from the North American Breeding Bird Survey for the period 1966–2015 indicate that this species underwent a range-wide increase of 0.74 percent annually for the period 1966–2015, and a decrease of 2.93 percent annually for the period 2005–2015 (Sauer et al., 2017).

In 1975 I (Johnsgard, 1975a) estimated that 2.2 million California quail were being shot annually in the United States, plus a few in Canada, based on data from individual states and provinces. In 2016 California quail were legally hunted in the following states: Arizona, California, Idaho, Nevada, New Mexico, Oregon, Utah, and Washington, as well as in Hawaii. Some recent estimated statewide U.S. hunter-kill estimates are: California (2014–15), 300,000; Washington (2000–2001), 172,000; Oregon (average, 1994–2015), 62,000; and Nevada (average, 2006–15), 25,000.

Habitat Requirements

Emlen and Glading (1945) made a fairly detailed analysis of habitat needs of the California quail. They classified quail habitat into four general types: desert, range land, dry farming land, and irrigated land, of which the range land is most extensive and most important to the species. Within these general categories, the basic habitat requirements of food, water, escape cover, roosting cover, nesting cover, and loafing cover are variably available. Irrigated lands provide water but may be limited in the various cover types, especially for roosting, nesting, and loafing. Dry-land farming areas are even less suitable because they may lack available water in addition to escape cover or other cover types. Deserts usually provide both food and cover sources, and if water is locally available, they may support moderately large quail populations. Range lands vary greatly in quality of habitat, but the best offer available water, seed-producing herbaceous plants, and moderately open brushy cover that serves for escape, nesting, roosting, and loafing.

Edminster (1954) analyzed the aspects of cover that are most desirable for quail usage. Nesting cover is usually herbaceous rather than brushy, in a moderately open situation. Roosting cover is provided by tall shrubs or trees, with evergreen species being preferred for winter cover. Escape cover consists of dense growths of shrubs, vines, or herbaceous growth into which the birds can readily run when frightened. Feeding cover is usually not limiting, since the birds consume a large variety of seeds, but leguminous plants are preferred both for seeds and their leafy growth, perhaps because of their nitrogen content. Loafing cover consists of shady places under shrubs or trees, where relief from the midday sun is available and dry dust as well as grit may be readily available.

The California quail depends more on available water or succulent plant material than does the Gambel's quail, but it is more drought tolerant than the bobwhite (McNabb, 1969). Probably as long as insects and succulent vegetation are available the bird can survive indefinitely without surface water; moderately saline water sources (but not sea water) can also be utilized (Bartholomew and MacMillen, 1961).

Food and Foraging Behavior

The animal portion of the diet of California quail is relatively small and even during summer probably contributes no more than 5 percent of the diet of adults (Martin, Zim, and Nelson, 1951; Edminster, 1954). Otherwise, nearly the entire remainder of the diet consists of herbaceous leafy materials and seeds, with grains and fruits playing a very subsidiary role in most areas.

Edminster (1954) summarized much of the early food studies of California quail and concluded that the most important food sources were legumes (25–35 percent of all foods taken) and annual weeds (20–60 percent), followed by grasses (10–25 percent) and the fruits and leaves of woody plants (3–5 percent). Of the important legumes, bur clover (*Medicago*), lupines (*Lupinus*), deervetches (*Lotus*), clover (*Trifolium*), acacias (*Acacia*), and vetches (*Vicia*) are major food sources, especially their seeds. The leaves and seeds of filaree (*Erodium*) and the seeds of turkey mullein (*Eremocarpus*) are important food sources among the weedy herbs (Edminster, 1954; Martin, Zim, and Nelson, 1951).

Two more recent California studies confirm these earlier conclusions as to the significance of legumes for this species. Shields and Duncan (1966) found that during the fall and winter, seeds composed more than 80 percent of the bird's diet, with four species of legumes (in the genera *Lotus*, *Lupinus*, and *Trifolium*) alone making up 60 percent of the sample volume. With the start of the winter precipitation, the intake of leaves increased from 6 percent of the diet in November to 41 percent in January, with the leaves of forbs, clover, and grasses all being utilized.

The importance of legumes was also pointed out in the study of Duncan (1968), who compared the foods taken during fall in burned and unburned range land. Relatively little difference in the two habitat types was found, with seeds from five species of *Lotus*, *Lupinus*, and *Trifolium* making up from 66 percent of the early fall diet in unburned areas to 80 percent of the diet in burned areas. Among nonlegumes, filaree and turkey mullein were important seed sources.

Food studies from areas outside the California quail's native range are more limited and suggestive of greater dependence on non-natural food sources. In Nevada a considerable utilization of grain crops, such as wheat, barley, and corn as well

Fig. 11. California quail, adult pair

as the legumes alfalfa and sweet clover, is indicated by Martin, Zim, and Nelson (1951). In eastern Washington, Crispens (1960b) found that wheat seeds were the most important source of food throughout the year. Seeds of various weedy species, such as pigweed (*Chenopodium*), teasel (*Dipsacus*), and locust (*Robinia*), were selectively utilized, and both sunflower (*Helianthus*) and Russian thistle (*Salsola*) were highly preferred food sources. Surprisingly, legumes were found in very limited quantities among these samples.

The general lesson to be obtained from these studies is that the need for brushy habitat by the California quail is largely a reflection of its protective cover requirements, while most of its food sources come from herbaceous forbs, particularly legumes.

Mobility and Movements

Emlen's study (1939) of California quail movements is still the most complete and is summarized here. During the winter, the birds occupied home ranges roughly comparable to the size of the covey, with four coveys of 21 to 46 birds using home ranges of 17 to 45 acres. These covey locations were associated with the distribution of brushy cover such as shrubs, perennial weeds, and vineyards. Each covey tended to feed together but sometimes broke up into smaller feeding units. Usually the birds of a covey roosted together, but sometimes they used two or three roosting sites. The coveys were separated by distances of from

350 yards to a half mile, and contacts between coveys were thus infrequent. However, during intercovey contacts, a "social barrier" between members of the two groups existed, which virtually prevented any covey shifting. Winter movements were very restricted, with rarely more than a fourth or at most a half of the covey's home range being used during any single day. Over a period of time, however, the birds fed in different parts of the covey's home range.

Beginning in late February, coveys began to dissipate as pairs and unmated males broke away from the group and apparently moved into more open farm land that was not suitable for winter use because of its limited cover. About half of the 67 marked birds separated from their coveys by the first of April, and the birds that left were predominantly males. At least one male moved 1.5 miles before the nesting season. Further, younger males were evidently more inclined to leave the covey than older ones, since 14 of the 21 males that disappeared were young.

Only one of the 21 young males remained to nest on its winter territory, while 7 of 18 older males did so. Likewise, the young females tended to leave the winter range, while the adult hens all remained in the covey. By the middle of April the covey was composed of a nearly balanced ratio of the sexes and apparently consisted largely of older and mated birds. The second phase of covey breakdown was caused when these birds dispersed for nesting. Only a few nonnesting or late nesting birds remained around the winter roosting sites.

California quail, male crouching

Movements during the summer were highly restricted and were largely limited to those of unmated males. These birds began to crow call in late April with the start of the nesting period and would attempt to approach females of mated pairs. Of eight such birds, four established "crowing territories" near the nest of an established pair, while the others assumed a more nomadic existence, sometimes covering a mile in a single day.

Later, Genelly (1955) discovered that most such territories are held by old males, while the first-year males are principally nomadic. On the other hand, mated pairs limited their daily moves during egg-laying to 12 to 25 acres while foraging, and returned at night to a roosting site, sometimes held in common with a neighboring pair. When incubation began, movements were even more limited, to about 3 to 10 acres around the nest.

Many nesting attempts were unsuccessful, and losses of a member of the pair caused some shuffling. If a mated male was lost, the female soon mated with one of the unpaired "crowers" near the nest or became foster parent of an available brood. When males lost their hens they started crowing within a day, either at the same place or at distances from 0.25 to 1.5 miles away from the original nesting location.

With the hatching of young, the re-formation of coveys began, with broods forming covey nuclei. By the middle of August, nine such covey nuclei had been established, and these

attracted individual nonbreeders or unsuccessful breeders, so that the covey sizes gradually grew. Brood mobility was very low during the first few weeks of life, probably being limited to a few acres, but they ranged up to 10 to 20 acres by the end of the first month. Some older broods moved considerable distances when their brooding cover was destroyed, with one brood of ten-week-old chicks moving a mile from its point of hatching.

However, most broods remained close enough to the nest site that they wintered on the covey home range nearest their place of hatching. Although little interbrood shifting occurred in very young broods, this increased after the young were three to four weeks old, and the adults would tolerate the presence of other chicks of the same age. Contacts became more frequent when the chicks were somewhat older, and soon mergers of broods occurred, with nine broods gradually being incorporated into six subcoveys.

The subcoveys retained their identities until late November, when they condensed into four coveys that exhibited ranges nearly identical to those held the previous winter. Eight of 12 marked birds returned to the winter range held the previous year, while four occupied new winter ranges, but in all probability less than half of the total number of adults returned to their previous winter ranges.

California quail, male

Genelly (1955) supported Emlen's view that the dominant, nesting, territory-holding males are usually older birds, while those that are nomadic and unmated are primarily young birds. It would seem probable, therefore, that population dispersion and range extension would be primarily the result of movements by young birds, especially males. Lewin (1965) mentioned a report of a male being seen during midsummer some 22 miles north of regularly inhabited range. Also, when birds are released into new areas considerable movement sometimes occurs; Richardson (1941) noted several such movements in excess of 20 miles and one extreme case of a 95-mile movement.

On the basis of movements of recaptured birds at various trap sites, Raitt and Genelly (1964) obtained an index of relative mobility, which suggested that summer and winter movements are least, whereas spring and fall movements are more extensive, particularly during April and May. These observations tend to support Emlen's views that a good deal of individual movement occurs in spring, especially among males. Although fall mobility is also moderate, there is little interchange of covey members at this time, thus a "spring shuffle" rather than a "fall shuffle" may tend to bring about population mixing.

Vocal Signals

A complete analysis of the vocal repertoire of the California quail was provided by Williams (1969), whose terminology is in general followed here. See Figure 5 for sample sonograms.

Social integration calls include the contact call or *ut, ut* notes and the separation ("assembly") *cu-ca-cow* call. The *ut, ut* notes serve to keep individuals of a group in contact and are uttered frequently as the birds move about while foraging. When birds are separated visually, they may utter the call in a louder version, but it soon leads to the *cu-ca-cow* call. This loud, somewhat melodious call (sometimes written as *chi-ca-go*) is produced almost identically by both sexes, although there is a certain degree of individual variation in the call. Thus, males can definitely recognize the call of their own mates and will preferentially respond to them.

Besides serving as a general separation call, the *cu-ca-cow* plays an important role in reproduction by serving to keep the pair together. In spring the call increases in frequency even in birds that are not separated, when unpaired birds of both sexes begin to use it. However, paired females do not use it unless separated from their mates, and unpaired males soon change

from this call to the cow crowing call described earlier. This call is much like the last syllable of the separation call but is uttered from a conspicuous, usually elevated, position. The call is repeated fairly often, averaging from about three to eight per minute. Williams established that the rate of cow calling was under testosterone control and was associated with relative aggressiveness. Thus the functional and hormonal origin of the call and the associated establishment of crowing territories is analogous to the territorial behavior of unmated male songbirds.

The *squill* call (called the "sneeze" by Williams) was so named by Sumner (1935), who described it as a high-pitched staccato whistle, used in a situation of defiance to other males. The call is limited virtually entirely to males and occurs only during the breeding season. Somewhat in contrast to the related *meah* call of the Gambel's quail, its utterance does not indicate a mutual "stand-off," but rather it is associated with extreme threat and attempted social dominance. The neck-stretching caused by the head-throw raises the pitch of the vocalization to a near whistle, no doubt because of the increased tension on the tympanic membranes.

A second aggressive call of the male is the *wip, wip* call, which often precedes attacks on other males and may alternate with the *squill* call. It may also be uttered toward strange females, but I have never observed a male perform a squill call toward a female. Likewise, the *wip, wip* call has not been reported for females, which utter only *ut, ut* or *cu-ca-cow* calls in this situation.

When feeding, California quail utter soft and repeated *tu, tu* notes, which stimulate pecking by other birds. During the sexual tidbitting display of males to females this same call is uttered.

The calls associated with predator avoidance are several, of which the alarm *pit, pit* notes are perhaps most common. With almost any disturbance, these metallic-sounding calls are uttered, especially before the birds begin to flee. When actually fleeing on foot, they are more likely to utter a series of *chwhip, chwhip* sounds that are perhaps a variant of the earlier call. The avian predator alarm call is a low, throaty *kurr, kurr, kurr*, which may stimulate freezing or fleeing behavior by other birds. Following such disturbance, a soft *put, put* series of notes may be produced, which may prolong the freezing behavior. When held in the hand, adults of both sexes often utter a loud, down-slurred *pseu, pseu* note, much like the distress calls of other New World quails.

Williams reported that prior to or during copulation females sometimes uttered soft peeping calls, and males usually produced *ut, ut* notes that changed to *wip, wip* sounds during treading. When building her nest, the female uttered a low, repetitive *pa, pa, pa* series of notes, while the male uttered rather different sounds as he handled nesting material.

No special calls other than contact *ut, ut* calls were associated with incubation, and during brooding of young chicks the parents both uttered low *mo, mo, mo* notes when the chicks became scattered. Chicks that are lost utter a loud distress whistle, to which the adults respond with the *cu-ca-cow* call, especially from the male. Adults also uttered the food call when attracting young to a source of food.

In total, Williams found 14 adult call-types in the California quail. Of these, 11 were typical of both sexes, and 3 characteristic of the male only. Two of the 14 were associated with social contact, 6 were believed to have reproductive significance (including 2 agonistic calls), 5 were alarm responses, and 1 was associated with parental behavior. Most of the California quail's calls have their counterparts in the bobwhite. However, Williams related the absence of a call functioning to space winter coveys (as the *koi-lee*

is reported to do for the bobwhite) to the fact that winter coveys of the California quail are generally larger than in bobwhites and sometimes tend to come together into very large wintering flocks.

Social and Reproductive Behavior

The covey is the social unit of the California quail from late fall until early spring. Emlen (1939) and, later, Howard and Emlen (1942) pointed out quite clearly that in the California quail the covey is a relatively closed social unit, with little opportunity for intercovey mixing. This mixing is reduced or prevented during late winter and spring by attacks on outsiders by resident birds of the same sex; such established covey members always socially dominate aliens that are introduced into a covey. However, Howard and Emlen emphasized that this aggressive behavior is not territorial defense by covey members but rather a form of social dominance associated with confidence related to the residents' knowledge of the local range. Territorial behavior in the sense of a defended area does not occur in coveys or mated pairs of this species (or probably any New World quail); only some unmated "crower" males exhibit anything like proprietary behavior toward a specific piece of habitat.

The process of covey breakup and pairing has been well studied in this species, first by Emlen and later by Genelly (1955) and Raitt (1960). Perhaps because older males begin their reproductive development somewhat sooner than younger males, pairing that occurs prior to covey breakup involves primarily older males, which mate with both adult and first-year females. Such pairing probably begins in late February or early March, and during early stages of pair formation some shifting about of partners may occur. Most pairing occurs before the testes are much enlarged (Anthony, 1970), thus pair formation does not necessarily involve copulation or other strong sexual behavior patterns on the part of the pair, although copulation attempts may occur.

Genelly (1955) felt that an initial mating stage of "acquaintanceship" might be required, during which individual recognition develops. No striking displays need occur in association with pair formation (Raitt, 1960) and only rarely is the "rush" display of males seen. Genelly (1955) mentioned seeing it only when females were placed in traps, and I have seen it only when a female was introduced without prior contact into the cage of an unmated male.

This display consists of several low notes followed by an extension of the neck and a lowering of the head, a fluffing of body feathers, a raising and spreading of the tail, and a slight extension and marked drooping of the wings, so that the primary tips touch the ground. In this posture the male approaches the female in a series of short rushes, from which the hen typically flees. The highly aggressive origin of the display may be seen from the similarity of it to threat postures assumed toward other males, and the actual pecking attack that the male may perform on the female if she is unable to flee. In short, the display appears to be a strong assertion of dominance, and probably only the submission behavior of the female and her lack of male plumage features normally inhibits overt attack.

As the males and females of incipient pairs begin to remain with one another an increasing amount of time, male-to-male aggression also increases. This probably largely involves a chasing of other males from the vicinity of the mate, and an eventual exclusion of such unmated males from the covey. Since the sex ratio of spring coveys always has an excess of males, a forcible exclusion of surplus males is the only way the covey can remain

California quail, male dozing

intact and persist as an integrated social unit. Raitt (1960) noted three major forms of hostile behavior: side-by-side nudging, chasing, and overt fighting. Nudging is the least aggressive of the three and sometimes occurs among members of a pair or between adults and young, with the dominant bird pushing the other to one side as they both jostle for a common food source.

Chasing consists of a posture much like that mentioned as

typical of the "rush" display but in a somewhat less extreme form. The bird being chased usually flees on foot but if caught may be severely pecked on the back and nape. Most often such chases involve two males, but sometimes females chase females, and less frequently males will chase females. One case of a mated female chasing away an unpaired male has also been noted (Genelly, 1955).

Overt fighting is virtually limited to males and is essentially like that of other quail, with the two birds facing one another, making pecking attacks and short vertical leaps during which they attempt to peck the top of the opponent's head. Between attacks, a series of *squill* calls and associated rapid head-throws that maximally expose the black throat are frequent and no doubt serve as major visual and acoustical threat signals.

Genelly (1955) noted a continued increase in fighting incidence from January until May, with this rise largely reflecting fighting concerned with the defense of the mate. Defense of territory occurred only from March through June and consisted of fights among unmated males that had established crowing territories and subsequently repulsed other such males. Starting in July, fighting associated with the defense of the brood occurred, but by October all of the fighting, which gradually diminished in number until January, was concerned with peck order establishment in the fall and winter coveys. Genelly could find no evidence that California quails actively defend a nesting site, thus the term "nesting territory" is not appropriately applied to the species.

As the mated pairs gradually break away from the covey and locate nesting sites, unpaired males attempt to establish crowing territories in the vicinity of such mated pairs. Genelly first heard cow calls uttered by these males in March, and the calling persisted until mid-June. This period corresponds roughly to the period of testis growth that he plotted. The greatest concentration of crowing males was located where nesting pairs were also located. Genelly found only one instance of a mated male uttering a cow call and heard a captive female produce it on at least two occasions, so the clear function of the call is that of advertising the location of a sexually active, unmated male. Since laying females that lose their mates through death rapidly attain new mates, the biological advantage of crowing is readily important. However, the localization of crowing males in the vicinity of nesting females may tend to increase the predation rate on such nesting birds.

The gonadal cycle of the female lags by about two weeks that of males during spring (Genelly, 1955; Anthony, 1970), with adult females either developing slightly in advance of young ones (Genelly) or at approximately the same time (Anthony). Egg laying during Genelly's study in California started the second week of April, with a peak activity the third week in May, while in eastern Washington the peak of laying activity was about a month later, according to Anthony.

The rate of egg laying is about five per week, at least in captive birds (Genelly, 1955), and the eggs are apparently usually dropped about midmorning. The average clutch size has been reported as 10.97 eggs by Glading (1938b), 13.7 eggs by Lewin (1963), 13.7 (in New Zealand) by Williams (1967), and 14.2 eggs by Grinnell, Bryant, and Storer (1918). An average figure of 13 to 14 eggs in a complete clutch would seem to be a reasonable judgment, which might thus require a total of about 20 days to lay; this plus an additional 22-day incubation period would total 42 days from the laying of the first egg to the day of hatching (Lewin, 1963). My incubation records indicate that 22 to 23 days may be required for incubation under artificial conditions.

Although reneating is a regular aspect of California quail behavior, the question of the frequency of second broods is not yet fully resolved. Definite instances of second broods have been

recorded; McLean (1930) found one such case in a wild bird. Francis (1965) also reported two cases of confined quail in which the male took over the care of the young after about two weeks, when the female remated and began a new clutch, which was subsequently hatched and raised. McMillan (1964) noted that early nests and broods of quail were being cared for by males, while females were presumably freed to raise additional broods.

Finally, Anthony (1970) noted that during June and July a larger number of broods were tended by lone males than during August and September, suggesting either that there was high early female mortality or that females left the early broods in the care of males and went on to produce second clutches, the latter of which he believed to be the case. Incubation by males is probably not a regular feature of California quail behavior as long as the female is present; they do not exhibit highly vascularized brood patches such as occur in females (Genelly, 1955). The visual stimulus of an abandoned clutch of eggs may bring about hormonal changes in males that initiate brooding behavior and defeathering adequate to form a simple brood patch (Jones, 1969).

Broodless males, such as those who have lost their mates, have great interest in young chicks and, if admitted by the parents, make excellent foster parents (Emlen, 1939). However, although crowing males exhibit extreme interest in young broods, they are not allowed to tend them as long as they persist in their crowing behavior, according to Emlen. Parents and chicks gradually merge with unsuccessful adults and eventually with unmated males and with other well-grown broods, forming moderately large aggregations of birds.

Although the percentage of unsuccessful nesting attempts is high in California quail, the combination of persistent reneating, large clutch sizes, and occasional double-brooding usually assures a high ratio of young birds in fall coveys. Nesting losses have been estimated by Sumner (1935) to be about 60 percent, and other studies such as those of Glading (1938b) have revealed losses as high as about 80 percent.

In New Zealand, Williams (1967) reported a fairly high nesting success of 62.6 percent, if only nests with completed clutches were considered rather than all indications of nesting attempts being considered. His figures also indicate a fairly high incidence of egg fertility (93.8 percent) and hatchability of fertile eggs (89.8 percent). Anthony's studies indicate a surprisingly high survival rate of chicks, with an estimated 25.8 percent mortality during the first 15 weeks of study. Edminster's review of other studies (1954) suggests that a chick loss of about 45 to 50 percent may be normal.

Over an eight-year period, the yearly fall age ratio of a quail population studied by Raitt and Genelly (1964) varied from 0.56 to 2.22 immatures per adult, or a yearly average of from about 1 to 5 young reared per adult female, allowing for a somewhat unbalanced sex ratio in adults. Perhaps an overall average fall age ratio would be about 1.46 young per adult (Emlen, 1940), or about 3 young raised per female.

Evolutionary Relationships

The probable evolutionary history of the California quail is discussed in the account of the Gambel's quail.

Northern Bobwhite

Colinus virginianus (Linnaeus) 1758

Other Vernacular Names

American colin, bobwhite, codorniz común, cuiche común, masked bobwhite, partridge, quail

Range

Resident over virtually all of the eastern United States north to southern Maine, New York, southern Ontario, central Wisconsin, and central Minnesota, west to southeastern Wyoming (a population in the North Platte Valley, expanded from Nebraska), eastern Colorado, eastern New Mexico, and eastern Mexico, and south to Chiapas and adjacent Guatemala but excluding the lowlands of Yucatan. Also probably survives locally as introduced populations in the Columbia and Snake river basins of Washington, Oregon, and Idaho. Introductions into British Columbia have not been long-term successes (Davidson et al., 2012), and reintroductions in southern Arizona of the endangered race *ridgwayi* have been failures.

Subspecies

(mostly after AOU *Check-list*, 1957, and Aldrich, 1946. See also Eo, Wares, and Carroll [2010].)

- C. v. virginianus*: Eastern bobwhite. Resident of the southern Atlantic seaboard north to Virginia southwest to north central Georgia, southeastern Alabama, and northern Florida.
- C. v. marilandicus* (Linnaeus): New England bobwhite. Resident of New England north to southwestern Maine, southwest to east central New York, Pennsylvania, and central Virginia and south to southern Maryland and Delaware (part of *C. v. virginianus* in AOU *Check-list*).
- C. v. mexicanus* (Linnaeus): Interior bobwhite. Resident of much of eastern United States east of the Great Plains excepting the Atlantic Coast (part of *C. v. virginianus* in AOU *Check-list*).
- C. v. floridanus* (Coues): Florida bobwhite. Resident over most of peninsular Florida.
- C. v. texanus* (Lawrence): Texas bobwhite. Resident of most of southwestern Texas and northern Mexico, including parts of Coahuila, Nuevo Leon, and Tamaulipas.
- C. v. taylori* Lincoln: Plains bobwhite. Resident of the Great Plains from South Dakota southward to northern Texas and eastward to western Missouri and northwestern Arkansas. Introduced populations may still survive in Washington, Oregon, and in Idaho along the Columbia and Snake river basins.
- C. v. ridgwayi* Brewster: Masked bobwhite. Resident (possibly now extirpated) in central interior Sonora, and formerly north to southern Arizona. Restoration efforts in Arizona have failed.

Measurements

Folded wing (US races): Adults, both sexes, 98–119 mm (sexual differences negligible). *Wing (C. v. virginiana)*, both sexes,

ave. of 50, 108.9 mm (Brennen, 1989). Males (*C. v. virginiana*), 106–119 mm, ave. of 129, 111.5 mm; females 103.5–118 mm, ave. of 68, 116 mm (Ridgway & Friedmann, 1946).

Tail (US races): Adults, both sexes, 49–70 mm (males average 3 mm longer than females). Males (*C. v. virginiana*), 53.6–59.7 mm, ave. of 129, 2.1 mm; females 51.5–63 mm, ave. of 68, 57.7 mm (Ridgway & Friedmann, 1946).

Weight (mass) (US races): Mean weights (mixed sexes), 16 states, ranging from 233.2 g (Massachusetts) to 161.6 g (Florida) (Brennen, 1989). Males, ave. of 899, 173 g (6.1 oz.); females, ave. of 692, 170 g (6.0 oz.) (Johnsgard, 1975a). Both sexes, mixed races, ave. of 847, 178 g (Dunning, 1993).

Identification

The length of the northern bobwhite ranges from 9.5 to 10.6 inches. The adult sexes differ in appearance. Males vary greatly in coloration across the species' range. Males of most races have a white eye-stripe that extends from the bill through the eye back to the base of the neck, with brown to brownish black coloration above. The ear region is blackish to hazel brown in males, and this feathering extends backward below the white eye-stripe and expands under the throat to form a blackish chest collar under the white chin and throat of most races. In some southern populations (e.g., *ridgwayi*) the chin and throat are also black, and the lower chest may be either blackish or brownish. In northern populations the breast and abdomen are irregularly barred with black and white in males, but in southern Mexico all underparts are generally darker and lack white markings.

Females of all races have buffy chins, upper throats, and eye-stripes, and buffy tones likewise replace the white underpart coloration of males. Females also lack black collars and in general are more heavily marked with brown and buff barring or mottling both above and below.

Field Marks

Except in some parts of Mexico, the presence of a white throat and a white eye-stripe that contrasts with an otherwise brownish to blackish head will serve to identify male bobwhites. Likewise, no distinct crest is present in this species. Northern bobwhites most closely resemble the black-throated bobwhites (*Colinus nigrogularis*) of the Yucatan peninsula but are geographically isolated from them. The gray partridge might be confused with bobwhites, but the partridge has no white or pale buff on the head and also has a uniformly grayish chest. The male's whistled *bobwhite* location call of males in spring is distinctive, and similar whistled notes serve as separation calls in reassembling scattered coveys.

Age and Sex Criteria

Females have buffy chins and upper throats, as compared with the white (black in *ridgwayi* and some other Mexican races) chins

and upper throats of males. The whiter chins of males appear to some extent even in the juvenal plumage. The beak coloration (pale yellow present at the base of the lower mandible in females; beak uniformly black in males) is successful in determining sex of birds as early as six to eight weeks old (Loveless, 1958). The sex of birds at least eight weeks old can be determined on the basis of the central portion of the upper middle wing coverts (Thomas, 1969). Males have fine, black, sharply pointed and well differentiated markings here, whereas females have wider, dull gray bands that do not contrast sharply with the rest of the feathers.

Immatures can often be identified by the fact that their outer two primaries are more pointed than the others (Stoddard, 1931), and the upper greater coverts of the first seven primaries have buffy tips (Leopold, 1939). A few birds may still be of questionable age by these two criteria, in which case first-year birds may be identified by using the seventh upper primary covert, which is usually brownish with buffy tipping and is somewhat ragged. In adults this feather is darker, sleeker, and has more whitish downy tipping at the feather base (Haugen, 1957).

Juveniles have whitish mottling on the tail feathers and the primaries also have mottled buffy edgings. Pale shaft-streaks are also evident on the upperparts, producing a distinctive light overall coloration.

Downy young northern bobwhites can be distinguished from the *Callipepla* group by their lack of a crest and distinctive spinal stripe, and from *Oreortyx* young by their more buffy faces and underparts as well as their lack of clear black coloration dorsally. The mid-dorsal stripe of bobwhites is russet to chestnut and only slightly darker laterally than in the middle, and the pale stripe immediately below is tinged with brown. A narrow, discontinuous dark stripe extends from the back of the eye to beyond the ear region, where it merges with the darker scapular region.

Distribution and Habitat

The total distributional range of *Colinus virginianus* is a remarkably broad one, extending from the southern part of Maine on the east coast in a nearly unbroken series of populations to the Texas-Mexico border, and southward along the eastern foothills of the Sierra Madre Oriental almost to the Rio Usumacinta, and to the Chiapas-Guatemala border in the highlands and Pacific slope. The northern limits of the species' range are extreme southern Maine (Aldrich, 1946; Palmer, 1949), Massachusetts (Ripley, 1957), southern New York (Brown, 1956), and southern Ontario where as of 2017 it was classified as endangered. Attempted introductions into Alberta and Manitoba were failures. In the Great Lakes region bobwhites also occur on the southern half of Michigan's Lower Peninsula (Brewer, McPeck, and Adams, 1991), southern Wisconsin (Gromme, 1963), and southern Minnesota, where it is largely limited to the extreme southeastern part of the state along the Mississippi Valley (Longley, 1951).

The western limits of the species' native range are in wooded or brushy river valleys from South Dakota southward along the western limits of mixed-grasses prairies to western Oklahoma (Baumgartner and Baumgartner, 1992) and Texas (Lockwood and Freeman, 2014). In Nebraska the bird extends west along wooded river valleys (North and South Platte, Republican) to the Wyoming and Colorado borders (Mollhoff, 2016). In eastern Wyoming it is probably native only to the North Platte Valley (Faulkner, 2012) and does not reach the Bighorn Mountains region (Canterbury, Johnsgard, and Dunning, 2013). In eastern

Colorado the bobwhite is a local resident all the way west to the edge of the foothills (Bailey and Niedrach, 1967; Kingery, 1998; Andrews and Righter, 1992), and in extreme eastern New Mexico the species is largely restricted to the plum thickets or similar low shrubby growth (Ligon, 1961).

In the Oklahoma panhandle the bobwhite is limited largely to river bottom habitats (Baumgartner and Baumgartner, 1992), where tree thickets grow adjacent to pasture lands and relatively dense ground-level cover exists, but it is virtually lacking from the short-grass and sand sage (*Artemisia filifolia*) habitats utilized by the scaled quail (Schemnitz, 1964). In western and southern Texas the more arid-adapted Texas bobwhite replaces the plains bobwhite, and the birds exist in fair populations wherever excessive grazing does not occur (Texas Game, Fish and Oyster Commission, 1945). The western limits of current breeding coincide with the Pecos River (Lookwood and Freeman, 2014).

Except for the now extirpated Arizona masked bobwhite population, all the more western populations of bobwhites are the result of introductions. In 1970, an attempt to reintroduce the masked bobwhite into southern Arizona was begun by releasing 356 hand-reared offspring of wild birds that had been captured in Sonora during 1968. That effort was a failure, but well-established populations of bobwhites do occur in Washington, Oregon, and Idaho. In Washington the bobwhite is widely established in the Columbia River Basin, and it might still occur on a few islands (such as Whidbey) of Puget and Washington Sounds, where it was introduced in 1871 (Jewett et al., 1953). Introductions into Nevada have been failures (Alcorn, 1988).

Birds on the adjoining mainland may barely reach the British Columbia border in the vicinity of Huntingdon. An isolated British Columbia breeding populations on the southern Cariboo Plateau and northern Vancouver Island may be introduced and may not be self-sustaining (Davidson et al. 2015).

The interior Pacific Northwest range is far more restricted now than formerly, but in Washington the population is concentrated in the southern Puget Sound lowlands but has declined drastically and is now mostly dependent upon releases (Smith, 1996; Wahl, Tweit, and Mlodinow, 2005). In Idaho the bobwhite was first introduced in the Boise Valley in 1875 and might still occur locally in the lower Boise, Payette, and Weiser river valleys. In Oregon, where the bobwhite was first released in 1879, the species is probably still present in the Willamette Valley, as well as near the Columbia River in Morrow and Umatilla Counties, and in the Snake River drainage of Malheur County (Masson and Mace, 1962; Gilligan et al., 1994).

The Mexican distribution of the bobwhite was plotted by Leopold (1959), whose map was the general basis of my own 1973 map. By the 1970s Mexican distribution was believed to be restricted to three small areas of Sonora. The total masked bobwhite quail population there might have numbered 400 to 1,000 birds.

In 2002 Engel-Wilson and Kuvlesky reported that the largest number of remaining wild birds was on private ranch land at Rancho El Carrizo in northwestern Sonora, and some others were on Rancho Grande, about six miles south of Rancho El Carrizo. In Arizona the total known masked bobwhite population was then confined to captive-raised and released birds on the Buenos Aires National Wildlife Refuge, located south of Tucson along the international border.

In a 2014 review by the US Fish and Wildlife Service on the recovery status of this race, it was noted that there has been an overall downward trend in populations, both in the United States

Map 6. Residential distribution of the northern bobwhite as of the 1970s. Recent (2011–15) denser populations (averaging 10–30 birds per Breeding Bird Survey route) are stippled. Male head sketches illustrate racial variants, including *C. v. ridgwayi* and two similar races from southern Mexico (see Johnsgard, 1988).

and Mexico. Furthermore, “with the only known wild Mexican population approaching zero, and the sole United States population of reintroduced birds also approaching zero, the recovery criteria have not been met.”

Population Density and Hunting

It has been generally agreed that Leopold (1933) was correct in assigning a maximum (fall) quail density of one bird per acre, which he believed represented a saturation point of the species, rather than a carrying capacity of the land. He believed that the

area of the species’ probable optimum range, which then centered on the states of Missouri, Illinois, Indiana, and parts of Iowa, was most likely to support populations that would reach but not exceed the saturation point, and he further noted that populations in the more southern states of Mississippi and Georgia were also known to attain this population density.

However, on the northern and western parts of the bobwhite’s range the populations tended to fluctuate and along the western border of the species’ range its density at times exceeded the saturation point in the judgment of Leopold. He noted one Texas estimate of more than two bobwhites per acre at several sites in

Fig. 12. Northern bobwhite, adult pair

Kenedy County during 1930. In Texas the highest average breeding densities are attained in sandy mesquite semi-prairies, pine-oak woodlands with interspersed small farms, and transitional coastal prairie uplands, particularly the semi-prairies, where early fall densities during the mid-twentieth-century were generally one per 4 to 5 acres but sometimes attained a density of one bird per acre (Texas Game, Fish and Oyster Commission, 1945).

Edminster (1954) suggested that over the best quail range, fall densities may reach from 2 to 10 acres per quail and from 10 to 50 or more acres per bird in marginal range. Spring population densities are approximately half the fall figures, or up to a pair per four acres.

In a Kansas study area of about 640 acres, Robinson (1957) estimated that during 1952 a breeding population of 102 birds (including 36 mated pairs) was present, while in 1953 the breeding population was 91 birds, with 32 mated pairs. Thus, nesting densities of one nest per 20 acres might be expected from such late spring densities. He estimated the maximum carrying capacities of the land for bobwhites to be 53 to 54 coveys per section during late autumn, since at least 12 acres of habitat are needed to support a single covey. Because his fall coveys consistently averaged 11 to 13 birds, this would agree with other estimates of about one bird per acre as a maximum fall density. It should be noted, however, that he regarded this maximum density to be determined by the carrying capacity of the land, rather than to represent a saturation point associated with the species. Kellogg, Doster, and Williamson (1970) reported a density in excess of one bird per acre.

Data from the North American Breeding Bird Survey for the period 1966–2015 indicate that this species underwent a range-wide decrease of 3.48 percent annually over the period 1966–2015, and a decrease of 2.79 percent annually for the period 2005–15 (Sauer et al., 2017).

Also using North American Breeding Bird Survey data, Church, Sauer, and Droege (1993) reported a similar annual continent-wide decline in bobwhite populations of 2.4 percent annually over the period 1966–1991, and a 3.6 percent annual decline rate for 1982–1991. States with the highest percentage rates of annual population decline from 1966 to 1991 were Pennsylvania, 11.0%; Massachusetts, 10.9%; Michigan, 10.7%; Ohio, 7.1%; New York, 6.4%; Wisconsin, 5.5%; West Virginia, 5.2%; Louisiana, 5.2%; and New Jersey, 5.2%. Regionally, the highest decline rates occurred in the Northern Piedmont (11.1%), Ohio Hills (11.0%), Southern New England (10.7%), and the Great Lakes Plain (9.9%). Droege and Sauer (1990) also thoroughly documented the 1966–88 downward population trend of the bobwhite, using the same data base.

A 2004 estimate of the species' total North American northern bobwhite population was 9.2 million (Rich et al., 2004), 82 percent of which were estimated to be in the United States and Canada, and the rest were in Mexico. Considering that during the late 1960s the estimated annual kill in Texas alone was about 8 million bobwhites, the change of population size in the United States over the past half-century becomes distressingly clear.

In 1975 I judged that 35 million bobwhites were then being killed annually for sport in 37 states, plus small numbers in two Canadian provinces, based on available survey estimates from all

Fig. 13. Northern bobwhite, adult male in flight

49 mainland states and ten provinces (Johnsgard, 1975a). States with extremely high bobwhite kills during the late 1960s included Texas, 8 million; Oklahoma, 3 million; Missouri, 2.8 million; Florida, 2.5 million; Georgia, 2.5 million; North Carolina, 2.5 million; South Carolina, 2.5 million; Illinois, 2.02 million; Alabama, 2.1 million; Tennessee, 1.7 million; Virginia, 1.38 million; Mississippi, 1.25 million; Kentucky, 1.0 million; Iowa, 750,000; Louisiana, 700,000; Indiana, 550,000; and Arkansas, 400,000.

In 2016 bobwhites could be legally hunted in the following 34 states: AK, AL, CO, CT, DE, FL, GA, IA, ID, IL, IN, KS, KY, LA, MA, MD, ME, MI, MO, MS, NC, NE, NH, NJ, NM, NY, OH, OK, PA, RI, SD, TN, TX, VA, WA, WV, and WY. Some comparison kill estimates for several of these states as having very high estimated kills of a million or more annually are of interest. In Texas annual bobwhite kills have declined at a rate of 5.6 percent annually since 1980, a total reduction of 55 percent, and over the same period the scaled quail decline rate was 2.9 percent annually, a

58 percent reduction. In Oklahoma the kill declined 89 percent, from about 2.8 million in 1980 to 750,000 in 2008, a 73 percent reduction. Georgia kill totals were reduced from about 4 million birds in 1982 to about 900,000 in 1998, a 78 percent reduction. In Illinois the total decline was from 2.5 million in 1955 to 30,000 in 2015, a 75 percent reduction. In Alabama the estimated reduction totaled 95 percent between 1970 and 2014. In Virginia a reduction of 99 percent occurred from 1.38 million wild quail shot in the late 1960s to 19,000 in 2011 (which were supplemented by an additional kill of 85,000 pen-raised quail).

Habitat Requirements

Edminster (1954) classified the cover types used by bobwhites into four general groups: grasslands, croplands, brushy habitats, and woodlands. He regarded grasslands to be of value primarily during the spring and summer, when they provide nesting

cover, some feeding cover, and limited roosting cover. Crop-lands receive major use during summer and fall, when they provide feeding, loafing, dusting, and limited roosting sites. Brushy areas and woodlands are used throughout the year for escape and roosting cover but are vital during fall and winter for feeding. Edminster believed that 30 to 40 percent of the land area in grassland, 40 to 60 percent in crop fields, 5 to 20 percent in brushy cover, and 5 to 40 percent in woodland cover would represent ideal habitat, producing a maximum of habitat interspersion and edge margins between habitat types.

Casey (1965) reviewed previous analyses of bobwhite habitat requirements and concluded that three major vegetative types must be present, including grassy nesting cover, cultivated crops or a similar source of food, and brushy cover. He believed that woodlands are not necessary if a brushy cover equivalent to a woodland understory is present. He further believed that a vital habitat factor is the presence of a brushy or woody covey "headquarters," using the earlier concept proposed by Robinson (1957). Such a headquarters must have protective vegetation to provide loafing cover during midday and be separated by about 140 yards from any other covey headquarters. Robinson has found that among ten such headquarters that were in continuous woody vegetation the mean distance between adjacent headquarters was 138 yards. He suggested that such headquarters should consist of areas at least 15 yards square (0.05 acre), although some reports indicate that dense woody clumps as small as six feet in diameter might serve too.

Roosting cover requirements for bobwhites vary somewhat between summer and winter (Rosene, 1969), with the typical roosting behavior serving in winter to maintain body heat through the use of a disk-like formation of birds oriented with their tails together and bodies touching on both sides. Quail use the same circular formation in summer, too, but then the importance of the formation for heat retention is reduced. The ideal size of such a roosting disk is 10 to 15 birds, and thus the behavior largely regulates the size of winter coveys, a situation in marked contrast to the southwestern desert quail species. Although coveys larger than 15 birds will probably form two such roosting disks, coveys that become smaller will join with nearby groups to maintain this minimum roosting group size.

Rosene noted that in the southeast, good winter roost sites are usually on gentle slopes with good drainage, with herbaceous vegetation about two feet high, with bare ground below and exposed sky above. Similarly, in southern Illinois, the sites selected for roosting were usually on medium to low elevations with good drainage, often with south or southwesterly (rarely east or north) exposures that remained warm late in the afternoon, and on bare ground or ground covered only with duff (Klimstra and Ziccardi, 1963). Associated vegetation was typically herbaceous, averaging 59 centimeters (23 inches) high, with relatively little light obstruction. Wheat stubble cover resulting from combining with associated weedy herbs provided ideal roosting cover, and limited burning or grazing may also improve grassland cover for roosting purposes.

Nesting cover requirements are essentially open herbaceous cover with nearly bare ground. The vegetation is usually less than 20 inches high, and the stems are sufficiently far apart for the birds to walk through easily. Dead herbaceous material is needed to make the nest lining; thus areas that were not burned the prior spring are preferred over burned areas. Nests

are usually within 50 feet of cover edges or other bare ground situations (Rosene, 1969).

To a much greater extent than is the case with the desert-living quails, water in the form of dew or surface water is needed by bobwhites. In the more arid parts of the species' range, the bobwhite becomes increasingly dependent on irrigated areas, river valleys, or other relatively moist habitats. Finally, like all quail, suitable dusting sites are needed in the form of dry and rather powdery soil. Roadsides, field edges, or burned areas all provide such dusting sites, which the birds may visit daily if weather permits.

Food and Foraging Behavior

Literally dozens of papers have been written on the food consumption of bobwhites, and it would be impossible to summarize all of them in the available space. Rosene (1969) provided a thorough summary, and the following discussion is based largely on his review.

The animal portion of the bobwhite's diet varies from about 30 percent in summer to only about 5 percent in winter, with the availability of insects largely determining the incidence of foods from this source. However, in southern Florida, where insects are available the year around, the cycle of insect use is similar, indicating a preferential use of insects according to protein needs, which are highest during the period of reproduction.

Based on a study of 1,400 quail crops obtained in Alabama, Rosene concluded that eight of the 13 most important plant food items were seeds of legume species, and seeds of all types made up 93 percent of the fall diet. Over 3,000 samples obtained from four different soil-type areas of Alabama indicated some regional differences in food consumption. On the sandy coastal plains soils, acorns almost equaled legumes in importance during November, but through the winter the use of legume seeds increased to as much as 62 percent by February. In the dark clay "black belt," acorns were not important, and legume seeds contributed over half of the November through February foods. In the red soils of the Piedmont and the red limestone valley soils of northern Alabama legume seeds also provided more than half of the food by volume.

To the west and north, the importance of cultivated grains and weedy herbaceous plants becomes more evident. In Texas, important winter foods in the six different regions varies somewhat, but in four of these regions doveweeds (*Croton* spp.) are most important, and they are among the top five food sources in the other two regions. Danglepod (*Sesbania*) and panic grass (*Panicum*) were the primary food sources in these two regions but had reduced importance elsewhere (Texas Game, Fish and Oyster Commission, 1945).

Winter foods of major importance in Oklahoma include weedy herbs such as ragweed (*Ambrosia*), sunflower (*Helianthus*), and trailing wild bean (*Strophostyles*), as well as acorns and cultivated plants such as sorghums and lespedezas, judging from various studies summarized by Rosene. Robinson's study of Kansas bobwhites (1957) indicated that during a nine-month period sorghum, wild beans, and foxtail millet (*Setaria*), were most important and all of these foods were eaten during most of the nine months.

In Missouri, fall and winter foods vary in different regions, but on a statewide basis the five most important seed-producing plants are probably Korean lespedeza, corn, ragweed, sorghum, and oats (Korschgen, 1948).

Fig. 14. Northern bobwhite, adult male frontal throat

In the northern parts of the bobwhite's range, especially the "corn belt," the availability of corn or other grain is clearly of some importance for winter survival. In Nebraska corn is perhaps the most important winter food (Damon, 1949), and in Indiana the four most important fall foods were corn, sassafras, Korean lespedeza, and ragweed (Reeves, cited by Rosene, 1969). Winter foods in southern Illinois include, in diminishing importance by volume, corn, soybeans, Korean and common lespedeza, acorns, and wheat (Larimer, 1960).

Bobwhites typically have two foraging sessions a day: one in early morning and one in late afternoon that lasts until dark. Little if any feeding is done when the vegetation is wet following rain or heavy dew, and the birds move only as far from their roosting cover as is needed to obtain adequate food. Birds of a covey feed together without aggression, and males may attract their mates to a choice morsel of food by using the tidbitting display. Grit may be picked up at the time of foraging or searched out separately along roadways or cuts.

Mobility and Movements

Bobwhites are among the most sedentary of quails, and virtually no major seasonal movements are normally performed. Some

early records of "migrations" were no doubt the result of dispersals following unusually high fall populations (Rosene, 1969). Perhaps the nearest approach to a true migration may be seen in the Smoky Mountains, where, at elevations from 3,500 to 6,500 feet, bobwhites occur on grass "balds" during the summer but are rare or absent there from September through April, when they move to lower ground (Stupka, 1963).

During the winter covey period, each covey occupies a range which is large enough to fulfill its roosting, foraging, and escape-cover requirements but which rarely exceeds 50 acres. Rosene (1969) estimated the covey ranges of more than one thousand coveys in Alabama and South Carolina and found averages in four areas that ranged from 8.2 to 17.9 acres. Farther west and north the winter covey ranges may tend to be somewhat larger; Schemnitz (1961) summarized studies from Missouri and Texas that indicated an average winter covey range of 24 acres, and one from Oklahoma reported an average covey range of almost 50 acres. Robinson (1957) believed that a minimum of 12 acres was required to support a covey of bobwhites during the critical winter season in Kansas.

With the coming of spring, coveys gradually move from their winter range into the nesting range. In some areas, particularly in the south, these movements may not be very great. In one

Northern bobwhite, alert male

Kentucky study (Wunz, cited in Rosene, 1969), six of nine coveys moved less than one-quarter mile between late winter and early spring, and none moved more than three-quarters of a mile. Of 34 birds, 24 moved less than one-quarter mile. Similarly, in Florida all but one of 20 birds moved less than one-quarter mile between April 1 and mid-June (Loveless, 1958), and in Missouri most quail move less than one-half mile during the spring period (Murphy and Baskett, 1952).

In one Wisconsin study (Kabat and Thompson, 1963), movements of marked quail observed between April 8 and May 26 averaged 0.6 miles from the winter range, while between May 27 and June 23 the average distance for marked birds was 1.3 miles from the winter range. This would indicate that a considerable number of birds, perhaps unmated males, continue to move about for some time after the breakup of coveys. Robinson (1957) noted that movements of males during the breeding season were almost twice as far as during the nonbreeding season, with females' movements averaging only slightly less than those of males, and the difference between yearling and adult birds insignificant.

Summer movements by mated pairs and pairs with broods are relatively negligible. Studies of summer mobility in Missouri (Murphy and Baskett, 1952) and in Florida (Loveless, 1958) indicate that nearly 90 percent of the birds moved less than half a mile. In both instances, records of longer movements were believed to have been the result of movements of unmated males. Simms, Smith, and Atkinson (1993) estimated mean home ranges of 10.9 hectares (27 acres) for masked bobwhites on the Buenos Aires National Wildlife Refuge (range 0.2–2.7 hectares), with core areas averaging 1.1 hectares (range 0.2–2.7 hectares).

By fall, with the growth of the young completed, and the integration of the broods into coveys, considerable social reorganization occurs. Unmated males and unsuccessful pairs probably attach themselves to pairs with well-grown young, and members of individual broods may break up and become affiliated with different fall coveys. This period of instability has been called the "fall shuffle."

Agee (1957) investigated this phenomenon in Missouri and, surprisingly, found that fall movements (0.14 mile) averaged less than summer movements (0.39 mile) and were only somewhat

Northern bobwhite, male

greater than average winter movements (0.08 mile). He found that whistling males tended to join coveys near their summer ranges, with 11 of 19 males apparently joined to the first family group they encountered. Of seven family groups, five had eventual winter ranges that overlapped their summer brood ranges, and a maximum movement of 200 yards was noted. Four fall coveys were developed from two families each, plus unmated males and apparently unsuccessful pairs, while one covey comprised the young from only one family. No quail in or with a brood moved more than 710 yards during the fall or winter, and most moved less than 400 yards.

In contrast to these findings, the studies of Duck (1943) indicate that in some areas fall movements may be considerable. In 12 or 13 counties of northwestern Oklahoma, there is a distinct shift from summer ranges in sagebrush uplands and mixed grasslands to winter ranges in canyon bottoms and dune lands. Eleven quail that were banded during August and September and were recovered in December had moved an average distance of 9.7 miles, and one was found 26 miles from the banding point, which is the maximum known case of a seasonal movement of bobwhites that I have encountered.

Yearly movements between successive winters provide a general index to bobwhite mobility traits; Kabat and Thompson

(1963) noted that the average distance moved by both sexes between successive winters in Wisconsin was only 0.78 mile, with males moving significantly farther than females. In no case was a movement of more than 4 miles recorded among more than 100 birds for which such records were obtained.

In summary, it would seem that in general bobwhites are not highly mobile, even during the fall period. Indeed, such mobility and potential range extension as does occur may be related more directly to late spring and summer movements by young birds, particularly males.

Vocal Signals

The paper by Stokes (1967) provides a complete summary of the vocalizations of the bobwhite, which are perhaps the most diverse and complex of those of any US species of quail. See Figure 5 for sample sonograms.

The bobwhite call, already mentioned, is limited almost exclusively to males during the breeding season, particularly unmated ones. Group movement calls used by both sexes are a series of increasingly louder *hoy*, *hoy-poo*, and *koi-lee* or *hoyee* notes that have been called the separation call (Stokes, 1967), scatter call, and covey call (Stoddard, 1931). Stokes has established that it

not only functions to reunite separated pairs but also probably serves to space coveys, to attract unmated males to unmated females, and to repel intruders. Softer contact notes, *took* and *pitoo*, are used when the birds are feeding together. However, the typical food-finding call is a soft *tu-tu-tu-tu* series of notes uttered with the bill pointed toward the source of food. This is used both by the male during the tidbitting display and by parents directing young to food.

When frightened by ground predators, a soft, musical *tirree* is initially uttered, but this usually quickly changes to an *ick-ick-ick* or *toil-ick-ick* as the birds become more alarmed. These latter notes are similar and no doubt correspond to the repeated *pit* or *chip* notes of *Callipepla* species. As the source of danger disappears, a soft *tee-wa* note may be uttered. The avian alarm note is a throaty *errrk*, and a loud, down-slurred distress *c-i-e-w* is produced when the birds are held in the hand. A somewhat similar but softer *psieu* note is uttered by adults during distraction display, which may be followed by repeated, staccato tip notes. Females may utter a "take-cover" call when a brood is disturbed, causing them to hide and freeze.

Agonistic calls of the bobwhite are greater in number than those of *Callipepla*; Stokes has recognized four different calls functioning in this situation. These are the "caterwaul," *squee*, *hoy*, and *hoy-poo*. Of these, only the caterwaul and *squee* are limited to the agonistic situation, while the *hoy* and *hoy-poo* have group- and pair-contact functions as well. Both caterwauling and the *squee* may be performed by both sexes but are more frequent in males. The *squee* note, a long series of whining or muttering-like sounds, is indicative of a thwarted attack or a balance between attack and escape tendencies.

The caterwaul, however, is a loud, raucous call sounding like *h-a-o p-O-O w-e-i-h'* that is clearly indicative of a dominant status and a strong attack tendency and is often associated with frontal display. Rarely do males utter this call toward strange females, but it is typically elicited when a strange pair is visible, and less often when a single rival male is seen. Its nearest functional equivalent in *Callipepla* is the head-throw of the scaled quail or the *squill* of the California quail, although the associated postures and sounds are quite different from either of these.

Stokes has mentioned several additional calls typical of parent-young interactions, including a "broody call" of the parents, two different alarm notes, as well as the "take cover," distraction, or "decoy ruse" call, and the food-finding calls already mentioned. Chicks have at least two calls, a "contentment" note and a distress or separation call.

Social and Reproductive Behavior

During the winter the social unit is the covey, which, as mentioned earlier, tends to average from about 10 to 15 birds, largely because of the need for efficient temperature maintenance during roosting. Kabat and Thompson (1963) noted that coveys drop in average size from about 17 birds in November to 7.5 birds by late March, representing a 56 percent winter loss. Other studies indicate covey sizes of from about 12 to 15 birds as typical, suggesting that covey size is a reflection of behavior rather than a possible index of population density. There appears to be no definite indication of specific age or sex structure in these winter coveys; males or females may predominate, and the size of the covey bears no apparent relationship to its age composition.

With spring, however, social structuring of the covey begins to develop. Rosene (1969) considered the breeding period to begin with the first *bob-white'* whistling, which may be as early as January in the South and early March in the northern states. However, if the bobwhite is like the western quails, much pair formation will have occurred before whistling is well underway. Further, it is most unlikely that pair formation under natural conditions is normally characterized by the male's performance of the elaborate display described by Stoddard (1931).

His description is worth quoting, since it is the typical posture elicited when a male in breeding condition is initially exposed to either a strange female or male:

The display is a frontal one. The head is lowered and frequently turned sideways to show the snowy-white head markings to the best advantage, the wings are extended until the primary tips touch the ground, while the elbows are elevated over the back and thrown forward, forming a vertical feathered wall. The bird, otherwise puffed out to the utmost in addition to the spread, forward-thrust wings and lowered, side-turned head, now walks or advances in short rushes toward the hen, and follows her at good speed in full display in case she turns and runs.

I have never seen the head-turning as described by Stoddard, but otherwise his description agrees with my own observations. The similar if not identical responses of males to other males clearly indicates the aggressive nature of this display, and its probable function in initial establishment of social dominance. Males in the same cage will not hold this posture long but rather engage in actual fighting if they are roughly equal in social rank. When prevented from fighting by cage walls, they will often perform the display whenever they are allowed to see one another.

Stokes (1967) has studied this "frontal" display and concluded that its function is aggressive rather than sexual, serving to establish social dominance. Only when a female fails to respond in kind does a male accept her as a female. Strictly sexual displays of the male bobwhite include lateral display, bowing, and tidbitting. During lateral display the male walks slowly about the female, with tail fanned and its upper surface tilted toward her. The flank feathers are held loosely and drooped toward the ground and the head is somewhat lowered, but the wings are not distinctly drooped.

Lateral display is silent and usually brief. Bowing is closely associated with lateral display and consists of incomplete pecking movements, while the body is held horizontally and the bird walks around the female. During the breeding season the food call of the male is used in conjunction with pecking movements, which collectively serve as a tidbitting display and attract females, especially the male's mate. Tidbitting probably serves as a major means of pair bond maintenance, since it extends well beyond the period of actual pair formation.

Female displays include wing-quivering movements and an inconspicuous lateral presentation display. Copulation is not preceded by any specific precopulatory behavior but is often preceded by female presentation behavior and is initiated by crouching on the part of the female. The female calls during copulation, but no obvious postcopulatory display is present (Stokes, 1967).

Nest-building, performed by both sexes, is initiated by the digging of a scrape a few inches deep and 4–5 inches in diameter

Northern bobwhite, pair

(Rosene, 1969). This scrape is then filled with dead leafy materials, so that the bottom of the nest is nearly level with the adjacent soil. Grasses or other herbaceous plants are arched over the top of the completed nest, effectively concealing it. The first egg is usually deposited one or two days later, and the egg-laying rate is approximately one per day with about 18 to 20 days needed to complete a clutch of about 14 eggs.

The average clutch size has been variously reported as 14.4 (Stoddard, 1931), 12.5 (Schemnitz, 1964), and 13.2 (Klimstra and Scott, 1957). There may be yearly variations, and in addition late clutches tend to have fewer eggs than do early-season clutches (Stoddard, 1931). Hatching typically occurs on the twenty-third day after incubation is initiated.

Robinson's study (1957) indicated that in Kansas during 1952 some nesting attempts were begun in early April or mid-April, while male calling did not become common until late May and early June, so that there was a lag of about a month between the peaks of nesting activity and calling. Peak calling occurred

in mid-June, which was near the period (late June) Robinson estimated to be the time of maximum hatching. Fatora, Provost, and Jenkins (1967) also noted that male calling reaches a peak about a week before hatching. Robinson thought that "in addition to unmated males, mated males whistle in the breeding season, especially at the time of emergence of the young."

However, Stoddard (1931) concluded that the whistle is "largely" that of unmated males, while Rosene (1969) thought that mated males "may or may not" whistle while the female is on the nest. Perhaps the best answer to this question comes from Robeson (1963), who compared the whistling behavior of a definitely unmated male and an apparently mated male. He found that the unmated male usually uttered six or more calls per minute and called from eight to ten minutes, with the last note of the *ah-bob-white* call being loud and piercing. The bird almost always responded to a whistled covey call and was highly mobile, moving up to one-quarter mile in three hours. By contrast, the apparently mated bird called four or fewer times a

minute, for durations of two minutes or less, and the last note of the call was soft and subdued. It was not observed to respond to the covey call and was wholly sedentary.

From these and other reports, it would seem that nearly all the calling by male bobwhites is attributable to unmated birds that are announcing the locations of their whistling territories. These birds tend to establish such territories as close as possible to those of mated pairs, thus accounting for the positive relationship between the locations of calling males and nesting sites (Klimstra, 1950a). Such males with established whistling territories forcibly expel other males from the immediate area and these nonterritorial birds, presumably most often yearlings, are no doubt responsible for the considerable summer movements recorded among males.

In all likelihood, males that fertilized their mates early in the breeding season will have been past the peak of their fertility by the latter part of the female's incubation period. Should her nest be destroyed at that time, the availability of "surplus" whistling males still in maximum breeding condition makes a rapid remating and initiation of a fertile second clutch highly likely. Such a possibility would seem to provide the adaptive function of unmated males' whistling and more than counterbalance the potentially dangerous effect that their conspicuous presence near active nests might provide.

The rapid decline in whistling at or shortly before the time of hatching probably is an indication that these birds are passing out of their reproductive condition. The gonadal cycle may be somewhat independent of the molt cycle as to hormonal control (Watson, 1962c), but it is probable that mated males would be first to go out of reproductive condition. At least in the case of males that have been participating in incubation (which may involve about 25 percent of the nests judging from Stoddard's data), prolactin levels are undoubtedly high (Jones, 1969a). The birds' abilities for further gamete production are as a result probably quite limited, since high prolactin levels have been found to interfere with sperm production in such birds as phalaropes and white-crowned sparrows.

It is typical for females to reneat at least once if their first attempt is unsuccessful, and perhaps as many as two or even three reneating attempts may be made. However, not only are reneats somewhat smaller in average clutch size but also the likelihood of successful hatching declines during summer (Rosene, 1969). There is so far no indication that bobwhites ever normally have second broods under natural conditions, but in a captive situation three different pairs were observed to produce a second brood by the male undertaking brooding responsibilities when the young were about two weeks old, and the female then starting a second clutch (Stanford, 1953).

Roseberry and Klimstra (1984) found that males incubated about 26 percent of Illinois clutches. Curtis et al. (1993) reported five cases of double-clutching in 36 radio-tagged females, and found that 27 percent of 30 clutches in North Carolina, plus 20 percent of 56 clutches in Florida, were incubated by tagged males. It is possible that such behavior is most common in wild populations where there are unusually long potential breeding seasons, such as in Mexico. However, in the Arizona masked bobwhite population the breeding season is surprisingly short (about 90 days), as it is timed to coincide with early summer (monsoonal) rains that typically begin in June and no doubt stimulate both plant and insect life. There, breeding is

most successful when summer rainfall exceeds 7.9 inches (US Fish and Wildlife Service, 2014).

Although nesting losses may on the average be as high as 60 to 70 percent, persistent reneating attempts by females is likely to result in at least half of the adult females in a population bringing off a brood. Hatchability of eggs is usually high, and in Wisconsin and Iowa the initial brood size may be 13 to 16 chicks (Klimstra, 1950b; Kabat and Thompson, 1963). Most chick mortality probably occurs during the first two weeks, and by late October and November the average brood size may be reduced to about 8.5. By that time the broods have been joined by unmated males and unsuccessful pairs, and the resulting fall coveys will have grown to about 12 to 17 birds.

Fall age ratios in hunter-kill samples may range from as high as 85 percent juveniles (6.6 young per adult) to as low as 72 percent juveniles (2.4 young per adult), judging from a survey by Kabat and Thompson (1963). In general, about 80 percent of the fall population can be expected to consist of juvenile birds, which thus also roughly corresponds to the average annual mortality rate of the species. The resultant life expectancy for a bobwhite is less than a year; therefore, relatively few birds are likely to survive to breed more than once.

Evolutionary Relationships

There can be little doubt that the nearest living relatives of *Colinus* are the species of *Callipepla*. Holman (1961) indicated that on the basis of skeletal structure these species might be considered congeneric, and I (1970) judged that the same conclusion might be made on the basis of hybridization evidence. Were it not for the taxonomic problems at the species level existing within the bobwhites, this would probably be the best treatment, but considering that three fairly distinct populations of bobwhites exist and at least for the present are regarded as full species, the application of the generic name *Colinus* to this population complex seems the most practical method of emphasizing their close relationships to one another without too seriously obscuring the relationships of the bobwhite group to the more typically crested quails of the American Southwest.

Among the *Colinus* × *Callipepla* hybrids produced in my lab (involving Gambel's, California, and scaled quails), only those with one California quail parent have exhibited any fertility beyond the F generation in that second generation (F2) hybrids have hatched and survived to maturity. It seems reasonable to believe that the ancestral *Colinus* type diverged from an ancestral *Callipepla* well before any splitting of the latter's gene pools into populations representative of any of the living species. The southernmost point of current common contact between the genera is southern Mexico, and this area would seem to be a possible region of origin for the genus *Colinus*.

Possibly the Isthmus of Tehuantepec served as an initial extrinsic isolating factor, splitting the early *Colinus* population into northern (pre-*virginianus*) and southern (pre-*cristatus*, pre-*nigrogularis*) segments. Or, perhaps the mountainous highlands of northwestern Guatemala provided such a barrier, but at least at present the latter group of mountains seems to be the primary barrier between the *insignis* population of *virginianus* and the *incanus* population of *cristatus*. Curiously, no such major barrier separates the coastal populations of *virginianus salvini* and *cristatus hypoleucus*, which are presently separated by only about

300 kilometers (180 miles) of Guatemala coastal plain between Chiapas and El Salvador.

Assuming that *Colinus* originated in the area of what is now interior Chiapas, the pre-*virginianus* stock probably followed river systems northward to the coastal plain of the Caribbean, where it then moved northward along the Gulf Coast, ultimately reaching what is now the eastern half of the United States, where its northward expansion was ultimately limited by cold winters and its western limits set by the arid climates and resulting absence of woody vegetation. The birds also dispersed from the Chiapas highlands to the Pacific coast of Mexico, and north-westward along that coastline in savanna or similar habitats until blocked from further expansion by the arid coastal desert of Sonora, with the interior Sonoran masked bobwhite population representing the point of maximal northwestern expansion.

This population was evidently subsequently isolated from the other black-throated and coastal-dwelling populations by extinction of populations between Sinaloa and Guerrero. The Valley of Mexico and adjoining temperate uplands were likewise colonized, probably through movement upward along river systems draining into the adjacent Gulf coastal plains. These birds exhibit the white-throated and fairly light-bodied characteristics of the Atlantic coastal populations, rather than the black-headed and generally dark-bodied condition typical of Pacific coastal birds and those of the Chiapas highlands.

South of the Guatemalan highlands, the ancestral *Colinus* stock probably followed coastal plains and arid highlands southward and eastward, perhaps initially giving rise to a Caribbean coastal population that subsequently developed into *nigrogularis*, as well as a series of more southerly populations that ultimately crossed the Panama Isthmus and spread out over a considerable portion of northern South America. For reasons not presently clear, these populations acquired (or more probably retained) a more distinctly crested condition in males than did those occurring farther north, but this is of minor taxonomic importance. Local adaptations also modified the degree of body darkness, especially the amounts of brown and yellow feather pigments. Maximal loss of pigmentation occurred in the arid Guatemala highlands and adjacent El Salvador, while many of the more southerly populations evolved a fairly dark coloration.

The current geographic distributions of the three recognized bobwhite species (*virginianus*, *nigrogularis*, and *cristatus*)

in southeastern Mexico and Guatemala present an interesting problem of evolution and geographic isolating factors. As mentioned, the black-throated bobwhite is effectively isolated from *virginianus* by an extensive area of wet, tropical lowlands that has doubtless been in existence for a very long period. It is difficult to imagine that the Yucatan population of bobwhite originated by a separation from a common ancestral population in the lowland Campeche Gulf area, and I thus regard the fairly close geographic proximities of these two populations as fortuitous.

Considering the current range of the black-throated bobwhite as a whole, it must generally be accepted that it centers on the Caribbean, extending all the way southward to approximately 15°N latitude. There it is separated from the interior bobwhite populations of Guatemala and Honduras by climatic and topographic barriers. There are few topographic barriers between the current ranges of *cristatus* and *nigrogularis*, and their ecological distributions in eastern Guatemala, Honduras, and Belize are arid tropical scrub valleys and lowland savannas, especially those dominated by pine.

The apparently completely allopatric distributions exhibited by the three major bobwhite types pose a problem in species-level taxonomy. Perhaps they should be regarded as allospecies (Amadon, 1966), to emphasize the obviously very close relationships existing among them. I agree with Monroe (1968) that *leucopogon* cannot be considered a valid species, and with Mayr and Short (1970), who regard the entire *Colinus* group as comprising a superspecies complex. Holman (1961) remarked that the recent species of *Colinus* exhibit fewer interspecific skeletal differences than do those of *Odontophorus* or *Callipepla* ("*Lophortyx*") with *nigrogularis* and "*leucopogon*" each having only four unique characters (out of 109 total characters examined), whereas *virginianus* had two unique characters. Mayr and Short (1970) concluded that *nigrogularis* should probably be considered conspecific with *virginianus*, and the greater similarities in vocalizations that occur between these two forms than exist between *nigrogularis* and *cristatus* would favor that viewpoint (Cink, 1971). Using genetic (RNA) data, Williford (2014) concluded that *C. virginianus* and *C. nigrogularis* are more closely related to one another than either to *C. cristatus*, the two lineages splitting about 2.5 million years ago.

Montezuma Quail

Cyrtonyx montezumae (Vigors) 1830

Other Vernacular Names

Black quail, codorniz encinera, codorniz pinta, crazy quail, fool quail, harlequin quail, Massena quail, Mearn's quail, painted quail, squat quail

Range

Southwestern United States (southeastern Arizona, southeastern New Mexico, and western Texas) south to Oaxaca, Mexico. The doubtfully specifically distinct ocellated quail (*C. ocellatus*) ranges from southern Oaxaca to Nicaragua.

Subspecies

C. m. mearnsi Nelson: Mearn's Montezuma quail. Local, mostly rare resident in trans-Pecos region and Edwards County, western Texas, southeastern New Mexico, and southeastern Arizona south from Baboquiveri Mountains east to New Mexico border, and from the Mogollon Rim south to central Mexico, including northern Coahuila. Now greatly reduced in range and numbers across its entire range.

Measurements

Folded wing: Males, 113.5–129 mm, ave. of 31, 123.6 mm; females, 110.5–126 mm, ave. of 26, 119.0 mm (Ridgway and Friedmann, 1946). Males, ave. of 54, 123.3 mm; females, ave. of 30, 119.3 mm (Stromberg, 2000).

Tail: 51–61.5 mm, ave. of 31, 55.7 mm; females, 47.5–58 mm, ave. of 26, 52.9 mm (Ridgway and Friedmann, 1946). Males, ave. of 51, 57.96 mm, females, ave. of 22, 58.53 mm (Stromberg, 2000).

Weight (mass): Males, ave. of 45, 195 g (6.9 oz.); females, ave. of 22, 176 g (6.2 oz.) (Johnsgard, 1975a). Males, ave. of 46, 193.7 g, females, ave. of 23, 179.4 g (Stromberg, 2000).

Identification

Adult Montezuma quail are 8 to 9.5 inches long. The sexes are very different in appearance. *Males* have a unique facial pattern of black or bluish black and white and a soft, tan crest that extends backward and downward over the nape. The upperparts of males are grayish to olive brown, extensively spotted and marked with black, white, and buffy markings. The sides and flanks are dark grayish, with numerous rounded spots of white, cinnamon, or rufous brown, depending on the population. The breast is unmarked brown, grading gradually to black on the abdomen and under-tail coverts.

Females are generally cinnamon-colored, with blackish markings extensive on the back. Females have a small, buffy crest that is less conspicuous than the male's and a mottled brown and buffy face with a whitish chin and throat. The upper surfaces

of the back and wings are extensively mottled, and the underparts are mostly buffy with black flecks or streaks in the abdominal region.

Field Marks

Males are unmistakable if their distinctively patterned face can be seen or if their extensively spotted flank pattern is visible. Females are more uniformly cinnamon-colored below than are other species of quails. Unlike the scaled quail of the same region (which occurs in more open habitats), frightened Montezuma quail rarely run and instead tend to crouch and hide. Their distinctive call consists of a series of uniformly paced whistling notes, slowly descending in scale. They are rarely found far from pine-oak woodlands throughout their entire range.

Age and Sex Criteria

Females lack the black and white ornamental patterning of the face and throat of adult males, having instead a white or buffy chin and throat.

Immatures may be recognized by the upper greater primary coverts (Petrides, 1942; Leopold and McCabe, 1957), which are edged with buffy or barred near the base with buff, whereas in adults they are spotted with whitish (males) or barred with wide white markings. Also in immatures the outer two coverts are pointed, rather than rounded. The condition of the outer primaries does not appear to be very useful in determining age.

Juveniles initially resemble adult females, and young females continue to do so but may be recognized by the transverse barring on the head rather than longitudinal striping as in adults. Juvenile Montezuma quail males soon acquire dark underparts and flanks, but whereas adult males have a double row of white spots on a dark background in young males these feathers are pale, with a double row of dark. The head remains juvenile-like for some time (Swarth, 1909).

Downy young of the Montezuma quail may be recognized by the patch of ochreous buff on the rear of the wings, and the relatively unpatterned back, which varies from argus brown in the mid-dorsal area to a cinnamon buff, which forms two incomplete stripes just below the darker mid-dorsal area. The crown is a light chestnut and the rest of the head is pale cinnamon buff, with a narrow dark line extending from the back of the eye to the posterior tip of the crown.

Distribution and Habitat

The US distribution of the Montezuma quail is limited to small parts of Texas, New Mexico, and Arizona. The birds formerly occurred in nearly all the Texas counties west of the Pecos River from El Paso to Brewster Counties and in the Edwards Plateau formerly west to Crockett and Val Verde Counties, east to Burnet and Bexar Counties, and south to Kinney and Uvalde Counties.

As a result of overgrazing by the mid-1940s the bird was present in good numbers only in the Davis Mountains and parts of the Big Bend region (Texas Game, Fish and Oyster Commission, 1945). Now it is limited in Texas to the Chianti and Glass Mountains (Brewster County), Sierra Diablo, Sierra Vieja, and Edwards County, having disappeared from the rest of the Edwards Plateau (Harveson et al., 2007). It is also nearly extirpated from the Chiso Mountains, although it was recently documented in Big Bend National Park (Holderman, Sorola, and Inglis, 2007).

The species was once fairly common in southwestern New Mexico, especially near the headwaters of the Gila, San Francisco, and Mimbres Rivers (Bailey, 1928). Now its range is greatly restricted to where rank grasses still grow, particularly near the summits of mountains in the Capitan, Sacramento, San Mateo, Black, and Mogollon ranges, and in extreme southwestern New Mexico near the Arizona and Mexico borders (Ligon, 1961).

Arizona's population of Montezuma quail was historically found from the Mogollon rim area south to the Mexico border, occurring most commonly in the oak-grassland (encinal) zone and, to a limited extent, also in pine forests (Bishop, 1964). Most of the later sight records Bishop listed were for Cochise, Santa Cruz, and eastern Pima counties. They are still present in the southeastern parts of the state, from the Baboquiveri Mountains east to the New Mexico border, and from the Mexico border north to the Mogollon Rim, especially in encinal oak woodlands (Engel-Wilson and Kuvlesky, 2002).

The Mexican range of the Montezuma quail was mapped by Leopold (1959 and later by Howell and Webb (1995); the two maps closely conform with mine, but all might be overly optimistic, based on recent habitat changes. Leopold concluded that it occurred in essentially all the pine-oak upland vegetation from Sonora, Chihuahua, and Coahuila south to near the Isthmus of Tehuantepec in Oaxaca. Binford (1968) reported that in Oaxaca the bird occurred at elevations of from 3,500 to 10,000 feet.

South of the Isthmus in comparable vegetation the ocellated quail occurs in Chiapas. Binford indicated that the extreme northwestern locality records for the ocellated quail are near Tapanatepec and north of Santa Effigia. The two populations are isolated by the tropical lowlands of the Isthmus of Tehuantepec and represent allopatric replacement forms occupying the same habitats and foraging niches. The somewhat intermediate male plumage traits of the Salle's race of Montezuma quail, occurring mostly in Guerrero and Oaxaca, further brings into question the validity of considering the ocellated quail as a distinct species. Thus, it shows the reduction of melanism on the underparts that is so strongly evident in the ocellated quail, as well as the replacement of white spots on the flanks with brown markings.

Population Density and Hunting

Leopold and McCabe (1957) provided two estimates of population density. One was an estimate of 26 birds per section (27 acres per bird), based on a count of at least 45 birds on 1,120 acres made by Wallmo (1951) in Arizona. In northern Chihuahua, Leopold and McCabe estimated that at least 28 to 30 adults per section occurred in fairly well-populated range, or 21 to 24 acres per bird.

Bishop (1964) reported that one study area in Arizona consisting of about 120,000 square yards (24.8 acres) had 5 pairs at

Map 7. Residential distribution of the Montezuma quail. The historic Mexican distribution (after Leopold, 1959) is shaded. The recent (2000–15) US distribution is stippled.

nesting time, or 5 acres per pair. Another study area of about 33 acres had 9 pairs in mid-July, or 3.7 acres per pair. Thus, in favored habitats substantial breeding densities might occur. In Arizona Montezuma quail do best in summers of above-average precipitation.

Bishop estimated fall population densities in two areas. One area of 130 acres had a minimum of 45 birds, while another of 160 acres had 62 birds; thus fall densities may sometimes reach about 3 acres per bird. Bishop estimated that over a large area the oak-juniper habitat might have averaged about 40 birds per square mile in early December of 1963. In Arizona Montezuma quail do best in summers of above-average precipitation.

Recent population density estimates have been much lower than these earlier estimates. Populations in the Trans-Pecos region of Texas were judged by Sorola (1986) to be 0.003 and 0.004 bird per acre (1 bird per 250–333 acres), while Albers and Gehlbach estimated a density of 0.04 bird per acre (1 bird per 25 acres) in the Edwards Plateau. Robles et al. (2002) provided estimates for Mexico that averaged 1 bird per 14 acres. In good habitats, densities may range as high as 1 bird per 1.4 acres (Stromberg, 2000).

Fig. 15. Montezuma quail, adult male

Montezuma quail have been reported on various Mexican breeding bird censuses of the Audubon Society, but on none of these has the population been particularly high. Thus, on both a cactus-acacia grassland and a pinyon pine-oak woodland area of Durango, the estimated breeding population was one male per 30 acres (*Audubon Field Notes* 18:560–561, 1964), while on a pine-oak-mesquite grassland ecotone area of 15 acres, the population was also estimated at 0.5 males (*Audubon Field Notes* 11:449–450, 1957). Such low breeding densities probably reflect habitat disturbance, particularly grazing effects.

Data from the North American Breeding Bird Survey are not reported for this species. A 2004 estimate of the species' total North American population was 1.5 million (Rich et al., 2004), 10 percent of which were in the United States and Canada.

In 1975 I (Johnsgard, 1975a) estimated that 6,000 Montezuma quail were then being shot annually in the United States, based on data from the three states where hunting was permitted. In Arizona an estimated 4,095 birds were shot during the five years 1965–69, averaging 819 per year. In 2016 Montezuma quail were legally hunted only in Arizona (with a limit of 8 birds

per day, including any other quails) and New Mexico (with a daily limit of 15 per day, including any other quails).

During the 2014 season an estimated total of 342 Montezuma quail were shot in New Mexico, where hunting extends through the winter from November 15 to February 15. In Arizona hunting also extends from November to February, but no information on recent Arizona hunter-kills was available to me. Brown (1979) estimated that populations in Gardner Canyon of Arizona's Santa Rita Mountains were reduced 51 to 75 percent each year, with 84 to 96 percent of the reductions caused by hunters. Stromberg (2000) commented that hunting seasons and limits are typically set by governors and political appointees, who ignore the advice of professional biologists.

Habitat Requirements

Leopold and McCabe (1957) concluded that the Montezuma quail is an "indicator species" of the pine-oak vegetative zone in Mexico but emphasize that it is neither the pines nor the oaks by themselves that compose ideal quail habitat. Rather,

Fig. 16. Montezuma quail, adult male fleeing from ferruginous pygmy-owl

the understory characteristics represent the critical factor, particularly the presence of bulb-bearing forbs and sedges. These plants can tolerate some periodic burning or limited logging but are severely affected by grazing. Grazing also probably reduces cover for escape and nesting, but it is the presence of plants upon which the Montezuma quail depends for both food and moisture that is essential.

Bishop (1964) agreed that Montezuma quail could probably get enough moisture from succulent foods to survive without other free water and noted that in many areas of southern Arizona such water is lacking except during the summer rainy season. He did, however, observe at least one bird drinking from a puddle after a thundershower and noted that the possible dependent relationship of reproduction to available water in the free state, as well as in succulent foods, is still not known.

Bristow and Ockenfels (2002) estimated seasonal habitat selection tendencies by measuring vegetation variations at flush sites in Arizona. They concluded that during the brood season the birds select area with higher grass and forb diversity, and

with more trees present, than at randomly chosen plots. Other studies have indicated that the birds avoid overgrazed areas, and that they are dependent on bunchgrass vegetation for hiding and thermal cover, which in turn is dependent on summer precipitation (Brown, 1978, 1982).

Food and Foraging Behavior

Martin, Zim, and Nelson (1951) noted that in a sample of birds collected primarily in winter from Texas, Arizona, and New Mexico, chufa or nut grass (*Cyperus*) sedge tubers were most important, followed by oaks (acorns), bulbs of wood sorrel (*Oxalis*), and brodiaea (*Brodiaea*) and sunflower (*Helianthus*) seeds. About 70 percent of the winter food samples were of plant origin, with various insects and other arthropods composing the animal food.

Leopold and McCabe (1957) provided a complete summary of food items found in Montezuma quail, based on their own observations and previous studies. They estimated that about 40 percent of the summer foods eaten were of vegetable origin.

Montezuma quail, male

Although acorns were listed in seven different studies, the major food item would appear to be bulbs, from various lily species (*Echeandia*, *Brodiaea*) and especially from the sedge *Cyperus esculentus*. Other succulent foods that are dug up are the bulbs of wood sorrel and the tubers of buttercups (*Ranunculus*). Seeds of legumes, grasses, pinyon pine (*Pinus edulus*), and forbs are used, as well as the fruits of juniper (*Juniperus*), ground cherry (*Physalis*), sumac (*Rhus*), caltrop (*Kallstroemia*), and various ericad shrubs (*Arbutus*, *Kalmia*). During the summer rainy season a variety of insect life is also eaten, especially beetles and the larval stages of moths and butterflies.

A monthly analysis of Montezuma quail food consumption in Arizona has been made by Brown (1969a), who noted that by weight plant material composed from 90 to more than 99 percent of the monthly samples, with animal materials being of significance only from June through September, when beetles in particular were consumed. The two primary vegetable food sources were wood sorrel bulbs, which were consumed in large amounts from June through January, and nut grass (*Cyperus esculentus*) bulbs, which were equally important from January through April. In April and May, seeds (*Paspalum*, *Lotus*) and buds (*Gilia*) were taken in limited amounts, and during July and August the tubers

of morning glories (*Ipomoea*), seeds of *Glactia*, and fruits of manzanitas (*Arctostaphylos*) also appeared in the diet.

Bishop and Hungerford (1965) provided a similar seasonal food analysis, based on the study of 221 crop contents. Throughout the year the major foods were acorns, bulbs of wood sorrel, seeds, sedge tubers, and insects. During the winter months of January through March, wood sorrel bulbs were the primary food, with other plant materials such as acorns, seeds, and tubers of secondary importance. In April, May, and June an increasing amount of nut grass or sedge tubers were taken, as well as green acorns, and the importance of wood sorrel began to decline. From July through September insects and green acorns made up the bulk of the foods, with *Oxalis* and *Cyperus* of minimal significance. However, from October through December these two food sources, as well as acorns, again became the predominant sources of food intake.

In summary, it would appear that for all except the summer months, the availability of *Oxalis* and *Cyperus* underground parts is crucial to the survival of the Montezuma quail, with acorns and other seeds or fruits of secondary importance.

The typical foraging behavior of these quail is well documented. Leopold and McCabe (1957) noted that the birds typically

Montezuma quail, male

dig a hole about two inches long, an inch across, and two to three inches deep while extracting bulbs. They do not eat the dried hulls but leave them near these diggings. When eating acorns, the birds also open the pericarp and remove the meaty center.

Bishop (1964) also noted that when *Oxalis* bulbs are dug up, the birds make cone-shaped holes, with one side of the cone dug away and the bulb hulls left in the hole. When searching for foods nearer the surface the birds made fan-shaped depressions about one-eighth inch deep in duff and litter under bushes and trees, which sometimes covered several square yards in area. He noted that the birds often scratched with one foot and then the other, with frequent pauses to examine the scratched area for foods. Often the members of a covey fed so closely together that they touched one another, apparently without hostility, with up to eight feeding in a circle only 14 inches in diameter. He observed that birds apparently fed throughout the day, and only those that were collected after 3:00 p.m. had full crops.

Mobility and Movements

Nearly all observations of Montezuma quail indicate that they are not highly mobile. In spite of their strong legs they do

not run when disturbed but rather tend to squat and “freeze.” When flushed, they usually fly only 50 to 100 yards (Leopold, 1959). Bishop (1964) noted that birds were usually less than 20 feet away when they flushed, and they flew no more than 100 yards, after which they would run rather than fly again. At least on the winter range, coveys apparently return day after day to the same foraging place, and the covey home range may be no more than 200 yards in radius (Leopold and McCabe, 1957). It is not uncommon to find a covey using the same 15 yards of a canyon area on consecutive days or at greater intervals (Miller, 1943).

In New Mexico as well as elsewhere, a definite altitudinal movement between summer and winter has been noted (Ligon, 1961; Leopold and McCabe, 1957); however, these appear to be relatively short movements, probably not exceeding a few miles. Bishop's (1964) study did not indicate such a seasonal migration; areas that contained birds prior to the nesting season had all supported coveys during the previous hunting season. As the nesting season approached the birds moved less, and he found no evidence that either member of a pair moved more than 150 yards from a nest site. Shortly after hatching, the brood range was even less than this; as the chicks grew it gradually

increased but even then did not exceed an area of more than 200 yards in radius.

Vocal Signals

The vocalizations of the Montezuma quail are neither so loud nor so varied as those of forest-dwelling relatives such as *Odonophorus* and *Dactylortyx*, but this is not surprising in view of the relatively more open habitat that the Montezuma quail uses and its probable greater reliance on visual signals. Certainly, more plumage dimorphism exists in this species than in any other of the species of the other genera in this subgroup.

Leopold and McCabe described the separation or assembly call of the Montezuma quail as a low quavering whistle with the separate notes slowly descending in pitch. Fuertes (1903) described it as owl-like, and Bishop (1964) reported that it is higher in pitch but lower in volume than the calls associated with the breeding season. Adults of both sexes and chicks utter this call, although Bishop (1964) indicated that, in contrast to Leopold and McCabe, he had never heard males produce the call.

Recordings of the separation call made by L. Irby Davis in Jalisco and filed in the Laboratory of Ornithology's Library of Natural Sounds indicate that this call consists of six to nine uniformly spaced notes, with each lasting about 0.3 second, and the entire series lasting about 2.5 seconds, during which time the fundamental frequency gradually drops from about 4,000 Hz to 3,500 Hz. Eight such call sequences occurred during a 67-second recording period, or a rate of about one every eight seconds (see Fig. 5 for sonogram; it was also illustrated by Stromberg [2000], who called it the descending call).

According to Bishop, a similar call is produced by females, a series of nine high-pitched, low-volume notes of descending pitch, audible up to 150 yards away and resembling the call of the canyon wren (*Catherpes mexicanus*). When wild males were separated from their mates, females would utter the descending call on early evenings or mornings until a pair bond was formed with a new male (Stromberg, 2000). Levy, Levy, and Bishop (1966) found that males began to respond to playbacks of the descending call in June, and their period of strongest response was about the beginning of August, or during the period of maximum nesting activity. In contrast to Gambel's quail, male Montezuma quail would respond throughout the day to such playbacks. Further, although the Gambel's quail that were attracted were clearly unmated males, these authors apparently believed that mated male Montezuma quail could also be attracted by such calls. Brown (1976) used playbacks of this call to census males during the nesting season between July and October.

Another major call is produced by males during the breeding season and is probably an indication of the location of unmated males. Leopold and McCabe (1957) said that it is a high-pitched *buzz* sound that ascends in pitch rapidly to an inaudible level. In contrast, Bishop described it as a descending whistle combined with a buzzing sound, which can be heard up to 200 yards away under favorable conditions. Stromberg (2000) illustrated a sonogram of the call.

In addition to these two call-types, a few other vocalizations have been noted. A few workers have mentioned conversational or contact notes that occurred when birds were in a covey or foraging, and sometimes a squealing call when they were flushed (Leopold and McCabe, 1957). Bishop (1964) mentioned that he

frequently heard a moaning-crying sound produced by adults when their young were in danger, and he heard the same distress call when he picked up crippled or captive birds. Stromberg stated that a quiet moaning cry is uttered as a possible contact call that is used when the covey is moving quietly through dense cover.

I have had little experience with the Montezuma quail and thus cannot evaluate their vocal similarities to other species. However, while in Chiapas I inquired of several people as to the calls of the ocellated quail. In the vicinity of San Cristóbal and southward toward the Guatemala border, where at least until recently the species was fairly common in pine and pine-oak forests, the local vernacular name for the bird is "colonchango," which I was told referred to the call of the male. A woman who had frequently kept the species in captivity told me that the male has a beautiful whistled song, which sounded to her like *pico-de-oro*. A man who had obtained a male as a young bird some six months earlier told me that it had just begun to sing about two weeks previously, and had two different calls. One was the *col-on-chang-o* song, which no doubt corresponds to the *pico-de-oro* vocalization, and the other was a vibrating and whistled *preet*. This latter call is perhaps equivalent to the buzzing call of the Montezuma quail, or possibly to the separation call. While handling the bird I was unable to stimulate it to utter any distress calls. Because of its song, the ocellated quail is far more highly valued as a cage bird in that part of Chiapas than is the local bobwhite, which is much more readily available and thus more frequently seen as a cage bird.

Social and Reproductive Behavior

While in coveys during the nonbreeding season, Montezuma quail form small flocks that probably represent family groups. Leopold and McCabe noted that the average covey size of 62 coveys was only 7.6 birds, and rarely have groups of more than 25 ever been reported. These coveys spend the day following a usual activity pattern of morning and evening foraging, with the intervening hours spent resting, dusting, and preening, with some digging for food. During rainy weather they may remain huddled together, and at night they roost on the ground, often facing outward in a semicircle around a rock or a grass clump (Bishop, 1964).

Pairing evidently occurs well before the nesting season actually is underway. Records summarized by Leopold and McCabe (1957) and observations by Bishop (1964) indicate that most pairing in Arizona may occur during March through May, beginning as early as February. In spite of this early pairing, gonadal development does not usually begin until June, with the earliest Arizona records for broods occurring about mid-June, and eggs being found as late as September 20 (Wallmo, 1954).

Bishop (1964) concluded during his study that few females began laying before June 28, and most laying probably occurred during July, or about four months after pairing was initiated. It is believed that nesting in this species is adaptively timed so that broods appear soon after the summer rains have provided new green plant growth and an abundance of insects, although the physiological mechanism of such timing is still obscure (Leopold and McCabe, 1957).

Although lone, presumably unpaired, males began to appear as early as mid-May, Bishop did not hear any male calling until

Montezuma quail, female and male

mid-June. Most male calling occurred from late July to mid-August, or during the peak period of incubation. Bishop believed that the majority of calling males were mated ones, but Leopold and McCabe said calling during the breeding season is largely and perhaps entirely by lone males. Bishop indicated that he often heard males calling from 50 to 100 yards away from nest sites, but attraction to nesting sites is typical of unpaired male quail and need not indicate that the calling bird is the mate of the nesting female. A peak of male calling during incubation on the part of unmated males is also characteristic of several of the United States species (see California quail account), and the incidence of male calling is probably correlated with the gonad cycle.

The participation of the male in nest-building, incubation, and nest defense is still slightly uncertain. One study of captive birds indicated that the male might help to construct the nest, which would be in agreement with observations on *Odontophorus*, which also builds a domed nest. Prior to building the nest a scrape is made, which may be one to three inches deep (Bishop, 1964). The cavity may be five to six inches wide and is lined with vegetative material such as grass or oak leaves and often some down (Wallmo, 1954). The sides of the cavity usually consist of grass stems that may appear to be woven together, and which are roofed over the top of the scrape to form a chamber four to five inches high. The side entrance to the nest is often well hidden by

a mat of grass stems that hang down over the entrance. Bishop reported that this mat acts like a hinged door, so that it falls back into place whenever the female enters or leaves the nest.

The average clutch size was reported by Leopold and McCabe to be 11.1, with an observed range of 6 to 14 eggs (Leopold and McCabe, 1957). The egg-laying rate of wild females is as yet uncertain, but three captive females in the collection of F. S. Strange laid 87 eggs during a 61-day period, averaging about 3 days per egg. During 1967 and 1968, egg-laying by his birds consisted of the following monthly totals: 7 in May, 45 in June, 42 in July, 20 in August, and 6 in September. As noted earlier, the late nesting strategy of Montezuma quail is thought to be an adaptation that takes advantage of summer rains, making fresh plant growth and increased insect populations available to the chicks.

Bishop never observed males on or very near the nest, but Willard (in Bent, 1932) reported seeing males sitting on eggs in about half of the nests he examined. Stromberg (2000) likewise referred to males tending nests. Males have also been reported sitting next to incubating hens, and without question remain with the female to help guard and rear the young.

The incubation period is probably 24 to 26 days, which is in general agreement with *Odontophorus* but longer than the incubation periods of other quails in the United States (Leopold and McCabe, 1957).

Both parents actively participate in brood care; Leopold and McCabe (1957) reported two instances of injury-feigning on the part of the male. The decumbent crest of the male is spread laterally during such disturbances. In eight of ten observed cases, Bishop (1964) noted that pairs with broods under a month old acted in the same fashion, with the female being first to expose herself and attempt to lead intruders away from the brood by feigning a broken wing. If necessary, the male may also appear and behave similarly, after first sending the chicks into hiding by uttering a series of moaning cries. In two instances the male was evidently the first to expose itself and perform distraction displays. There have been some accounts of males tending nests (Falvey, 1936) and suggestions that second clutches might sometimes be produced (Stromberg, 2000).

When newly hatched, the birds are fed insects, seeds, and bulbs by the parents, but by the time they are two weeks old they begin to forage for themselves (Bishop, 1964). Probably little brood mixing occurs, since the average reported brood sizes of 6.8 to 8.4 young is not much below the average clutch size (Leopold and McCabe, 1957). However, some broods containing two age-classes have been seen (Wallmo, 1954). Young birds can fly short distances five to six weeks after hatching, when their body weight is about half that of adults, and they can fly as far as adults by eight weeks (Stromberg, 2000). These are unusually long fledging and physical development periods.

Probably little merging of family units occurs during the fall. Brown (1969b) noted that before the hunting season, 70 coveys containing 451 birds occurred on 2.95 square miles, indicating an average covey size of 6.4 birds. These 23.7 coveys per section were thought to be the result of a breeding population of about 24 breeding pairs per section. Hunting seasons in Arizona during the years 1965 through 1969 provide age and sex ratio population data not previously available for the species. Of 4,095 birds shot during those five years, 71.5 percent were young and 56.4 percent were males (Brown, 1970). This age structure would represent a juvenile-to-adult ratio of 2.5:1, or more than 5 young raised per adult female on the average, assuming that young birds are not more vulnerable to shooting than are adults. Comparisons of age ratios based on wing samples with those based on average covey sizes of well-grown broods are in close agreement, suggesting that coveys do consist of family units, and probably little differential age vulnerability to shooting exists, judging from data presented by Brown (1969a).

Evolutionary Relationships

Most of the anatomical specializations that are exhibited by the Montezuma quail are related to its digging behavior associated with foraging. Miller (1943) has mentioned its arched back, strong legs, long claws, and dorsally narrowed pelvis, which are all associated with the strong leg muscles related to its digging abilities. The posterior iliac crest of *Cyrtonyx* is the most highly developed of the entire group (a reflection of muscle attachments associated with digging adaptations) and even exceeds that of *Dactylortyx* (Holman, 1961).

Dactylortyx and *Rhynchortyx* are like most other New World quail genera in having a moderately broadened anterior face of the postacetabular ilium that narrows abruptly posteriorly, but in these the posterior process of the ilium forms a moderately long, narrow dorsal roof, rather than a short and broad roof (Holman, 1961). *Odontophorus* is variable with regard to this character, suggesting that an evolutionary trend may be traced from *Odontophorus* through *Dactylortyx* and *Rhynchortyx* to *Cyrtonyx*. The angle of the ischium relative to the iliac crest is also greater in *Cyrtonyx* than in the other genera (Holman, 1961), which is probably also related to muscular digging adaptations.

Holman (1961, 1964) suggested that *Cyrtonyx* is part of a monophyletic group of New World quails that also contains *Odontophorus*, *Dactylortyx*, and *Rhynchortyx*, whereas the other North American species are part of a group including *Dendrortyx*, *Philortyx*, *Oreortyx*, *Callipepla*, and *Colinus*.

Using genetic (RNA) data, Williford (2014) concluded that *Cyrtonyx* is part of a clade that also includes *Odontophorus* and *Dactylortyx*, whereas a *Dendrortyx* group includes that genus plus *Colinus*, *Callipepla*, *Oreortyx*, and *Philortyx*. A third group consists of the single genus *Rhynchortyx*.

From these considerations as well as distributional patterns, ecological and behavioral considerations, and plumage comparisons, I would judge that *Cyrtonyx* evolved from an *Odontophorus*-like ancestral type in a forested or woodland environment and gradually became increasingly efficient at surviving in more xeric habitats than were its ancestors. It is the only species of the *Odontophorus* subgroup that has become fully emancipated from a fairly dense forest habitat and thus has extended its range much farther to the north in arid climates than have any of the others.

Family Phasianidae: Pheasants, Partridges, and Relatives

Tribe Perdicini: Old World Partridges and Relatives

Chukar, adult

Chukar

Alectoris chukar (Gray) 1830

Other Vernacular Names

Chukor, Indian hill partridge, rock partridge ("rock partridge" is also often used to refer to *A. graeca*)

Range

Native to Eurasia, from France through Greece and Bulgaria (typical *graeca*) southeastward through Asia Minor and southern Asia (typical *chukar*). These two populations should probably be regarded as separate species (Watson, 1962a,b), and all of the introduced United States stock is apparently referable to *A. chukar*. The racial origin of the birds introduced into North America is varied and includes not only Indian stock (probably *A. c. chukar*, as recognized by Sushkin, 1927) but also some Turkish stock (*cypriotes* or *kurdistan*). These Turkish birds probably merged with Indian stock or have disappeared, except in New Mexico and California.

The present range of the North American population is from southern interior British Columbia southward through eastern parts of Washington, Oregon, and California, and east in the Great Basin uplands through Nevada, Idaho, and Utah. The greatest numbers are found in Washington, Oregon, Nevada, Idaho, Utah, and California, and moderate populations are present in Wyoming and southern British Columbia. Small to marginal populations occur in western Colorado; central, northwestern, and southeastern Montana; and northernmost Arizona (Christensen, 1999).

Measurements

Folded wing (various races): Adult males, 144–76 mm; adult females, 140–70 mm. Males average 7 mm longer than females of the same subspecies (Johnsgard, 1973). Males (Middle East), ave. 168 mm; females ave. 154 mm (Cramp and Simmons, 1980).

Tail: 78–105 mm (range of both sexes) (Johnsgard, 1975a). Males (Middle East), ave. 82.3 mm; females ave. 78.9 mm (Cramp and Simmons, 1980).

Weight (mass): Males, ave. of 44, 557 g (19.6 oz.); females, ave. of 50, 444 g (15.7 oz.) (Johnsgard, 1975a). Males (India), usual weights of 100, 623–652 g; females 425–482 g (Hume and Marshall, 1880). Wild birds (Nevada), males ave. 615 g; females 502 g (Christensen 1979).

Identification

Adult chukar are 13 to 15.5 inches long. The sexes are identical in appearance, with white or buffy white cheeks and throat separated from the breast by a black collar or necklace that passes through the eyes. The crown and upperparts are grayish brown to olive, grading to gray on the chest. Otherwise, the underparts and flanks are buffy, with conspicuous black and chestnut

vertical barring on the flanks. The outer tail feathers are chestnut brown. The bill, feet, and legs are reddish, and males often have slight spurs on the legs.

According to Watson (1962a,b) chukars from Turkey and farther east are specifically different from those occurring from Greece and Bulgaria through western Europe. Birds from the Asia Minor and India populations have been successfully introduced in several states and, according to Watson (1962a,b), represent the species studied by Stokes (1961) and identified as *A. graeca*. There is no evidence that wild birds representing *graeca* now occur in North America. Watson states that in addition to a number of minor plumage differences, *A. graeca* differs greatly from *A. chukar* in voice, with males of *graeca* emitting a clear ringing series of whistling notes whereas *chukar* males produce only clucking or cackling sounds.

Field Marks

The striking black and white head pattern of this species can be seen for considerable distances in the arid country that this bird inhabits, as can its contrasting flank markings. In flight the reddish legs and chestnut outer tail feathers are usually visible. The distinctive "*chu-kar*" call often provides evidence for the presence of this species.

Two other closely related Old World species have been locally introduced in some western states and might be encountered as escapes from game farms or shooting preserves. These include the Barbary partridge (*Alectoris barbara*) and the red-legged partridge (*A. rufa*). All have *chu-kar* calls and red legs, but the Barbary partridge has a reddish brown collar rather than black, and a grayish throat and face that terminate in a chestnut crown. The red-legged partridge more closely resembles the chukar partridge, but its black neck collar gradually blends into the breast by breaking up into a number of dark streaks, whereas in the chukar partridge the collar is clearly delineated from the grayish breast. Barbary partridges were unsuccessfully introduced in California (Harper, 1963), and red-legged partridges were introduced without long-term success in various states including Washington, Utah, Texas, and Colorado.

Age and Sex Criteria

Females have no apparent plumage differences from males, and measurements must be used. After the third primary (counting from inside) is fully grown (by about the sixteenth week of age), the distance from the tip of the feather to the wrist joint is diagnostic for sex, with males measuring over 136 mm (averaging 139.3 mm) and females measuring under 136 mm (averaging 131.8 mm) (Weaver and Haskell, 1968).

Immatures may be recognized by the fact that the length of the upper primary covert for the ninth primary is less than 29 mm long in immatures and is 29 mm or longer in adults (Weaver and Haskell, 1968). Since some chukars molt their ninth primary

the first year, determining age by the use of the outer primaries is often difficult, but in general the presence of faded vanes and pointed tips on the outermost one or two outer primaries would indicate an immature bird. These feathers may also have a yellowish patch near the tip.

Juveniles may be identified (until about 16 weeks of age) by the presence of mottled secondaries, with those that are innermost usually persisting longest (Smith, 1961). Retention of the outermost secondaries of this plumage into the first-winter plumage was observed in one captive bird (Watson, 1963).

Downy young are rather reminiscent of scaled quail downies, but the head lacks a crest or a distinctly recognizable crown patch. Instead, the crown is only slightly darker brown than is the rather grayish face, which has an eye-stripe extending back past the ear region. The underparts are buffy white, and the back pattern is similar to that of the scaled quail.

Distribution and Habitat

Christensen (1970) first comprehensively mapped the distribution of this introduced species. His indicated range was considerably greater than that shown by Aldrich and Duvall (1955) or Edminster (1954) and was demonstrative of a then still-expanding range. It is probable that essentially all of the habitats suitable for this species have now been occupied. Evidently much of the arid Great Basin highlands between the Cascade and Sierra ranges and the Rocky Mountains provide the combinations of climate, topography, and vegetation that best suits the chukar, and little or no success has been achieved in introducing the species to the grassland plains east of the Rocky Mountains, in spite of repeated attempts.

The history of chukar introductions in the United States has been summarized by a variety of authors, including Cottam, Nelson, and Saylor (1940). Bohl (1957) and Christensen (1954, 1970, 1996). All told, at least 42 states and six provinces have attempted introductions; at least 14 states and one province have had sufficient success to declare legal hunting seasons on the bird.

Through virtually all of the chukar's adopted North American range, the typical vegetation is an *Artemisia*-grassland community, although in the southern part of its range in California and Mexico the chukar also occurs in a saltbrush-grassland community type (Christensen, 1970). It ranges in altitude from below sea level in California's Death Valley to as high as 12,000 feet in the White Mountains. Harper, Harry, and Bailey (1958) noted that in California the bird's distribution generally follows the 5–20-inch annual rainfall isohyets. Christensen (1970) noted that in Nevada habitats, the annual precipitation varies from about 3.5 to 12 inches.

Throughout most of the species' North American range, the summers are hot but short and winters are long and moderately cold. At higher elevations snow may cause the birds to move downward into snow-free areas, but many areas in good chukar range have recorded extreme winter temperatures that are well below zero (Christensen, 1970).

Population Density and Hunting

Remarkably little information is available on population densities of the chukar, and because of their considerable mobility

Map 8. Introduced North American distribution of the chukar, as of the mid-1970s. Recent (2011–15) denser populations (averaging 10–30 birds per Breeding Bird Survey route) are inked; less dense populations (averaging 3–10 birds per survey) are stippled.

and tendency to “clump” at natural or artificial watering areas it is difficult to judge populations occurring over broad areas. Moreland (1950) reported that on one study area of 61 square miles, a fall population prior to the hunting season was determined to consist of 1,705 birds, which would represent 22.9 acres per bird. He also noted that on one area of 360 acres, 37 chukars were flushed, in addition to a variety of other upland game. This suggests that in favorable habitats substantial densities might occur, possibly in excess of 10 acres per bird.

Harper, Harry, and Bailey (1958) estimated that on a study area of 60,000 acres, a fall population estimate of 6,060 birds was indicated, or approximately 10 acres per bird. Molini (1976), using helicopter surveys, estimated a mean density of 22 birds per square kilometer on one Nevada study area, but a range from 19 to 31 birds in high-quality habitat to 9 birds in low-quality habitat. He judged that Nevada might have a base population of about 750,000 birds, but with annual extremes of 200,000 to 2 million birds, depending on reproductive success.

Natural or artificial watering sites for chukars may attract as many as 100 birds (Alcorn and Richardson, 1951; Harper, Harry, and Bailey, 1958). Assuming that the birds rarely travel more than a mile to water (Harper, Harry, and Bailey), such a water source might be expected to have an effective “range” of about 2,000 acres. Thus, visits by 100 birds might suggest a population density of about 20 acres per bird.

The first state to open a hunting season on chukars was Nevada, which had begun its introductions in 1935 and initiated

Fig. 17. Chukar, adult walking

a season in 1947. From that time through 1967 about 968,000 chukars were killed in Nevada. In 1949 Washington declared its first season, 18 years after introducing the species. Its total kill of an estimated 1,337,000 birds through 1967 represented the largest sport kill of any state. Idaho was the third mainland state (Hawaii had its first season in 1952) to open a hunting season on chukars, starting in 1953, following introductions that had started in 1933. From 1953 to 1967, an estimated 994,000 birds were shot there. Hunters shot more than 218,000 chukar there in 1980 (Alcorn, 1988).

California followed with an open season in 1954, after an intensive introduction program that was started in 1932 and continued through the 1950s in nearly all of the state's counties (Harper, Harry, and Bailey, 1958). An estimated 438,000 birds had been shot there through 1967. Wyoming's first open season was held in 1955, following introductions that began in 1939. Estimated hunter kills through 1967 were 160,000 birds. Oregon and Utah both opened chukar seasons in 1956, after initially

introducing birds in 1951 and 1936, respectively. The total estimated kills through 1967 were 346,000 for Utah and 1,235,000 for Oregon. The latter figure was second only to that of Washington and was based on seven fewer seasons. In Washington the birds are widespread in the eastern half of the state and are most common in the middle Yakima, Columbia, and eastern Snake River valleys. They are the third-most hunted gallinaceous game bird in the state, with a kill of 27,000 birds in 2000–2001 (Wahl, Tweit, and Mlodinow, 2005).

Colorado and British Columbia had their initial hunting seasons in 1958; in the case of British Columbia, only eight years after the initial introduction. An estimated total of 107,000 birds were shot during the ten seasons through 1967. Compared with 22,000 shot in 1960, only 565 were killed in 1985. The British Columbia population is currently mostly limited to the Okanogan and Thompson-Nicola valleys; the small Vancouver Island population has essentially disappeared (Campbell et al., 1990b; Davison et al., 2012).

Montana's success with introduced chukars warranted its first open season in 1959, and approximately 20,000 birds were harvested through 1967. A very limited degree of introduction success occurred in Arizona, which first opened a season on chukars in 1962 and reported an estimated total of 250 birds harvested through 1967. It is now apparently absent from that state. South Dakota's introduction efforts were even less successful. They resulted in a very few birds being shot after it finally opened a season in 1966 (Christensen, 1970), and the species has since disappeared from the state. There are no recent records of birds surviving in Nebraska, Minnesota, or Wisconsin, in spite of extensive early introduction programs (Christensen, 1999).

In 1975 I (Johnsgard, 1975a) estimated that 650,000 chukars were shot in the United States in 1970, based on data from nine states where hunting was then legal. Chukars were then also legal game in British Columbia, where about 8,000 birds were taken.

In 2016 chukars were legally hunted in 13 mainland US states: AZ, CA, CN, CO, ID, NH, NJ, NV, OR, SD, UT, WA, and WY, as well as in Hawaii. Some recent estimated statewide US hunter-kill estimates are: Oregon (2014–15), 81,000 (vs. 123,000 in 1968); Nevada (10-year average to 2015), 77,600 (vs. 49,000 in 1967); California (2014–15, including some gray partridges), 56,000 (vs. ave. of 73,500 in late 1960s); Washington (2014–15), 12,600 (vs. ave. of 113,000 in late 1960s); and Wyoming (2011–15 average), 6,400 (vs. ave. of 15,000 in 1960s). Although data from some western states were unavailable, it would appear that US hunter kills have declined since the 1960s except in Nevada, where they have increased. During the 49-year period 1947–95, hunters killed more than 20 million chukars in Oregon, Idaho, Nevada, Washington, California, and Utah (Christensen, 1996).

Data from the North American Breeding Bird Survey for the period 1966–2015 indicate that this species underwent a range-wide increase of 1.47 percent annually during the period 1966–2005, followed by a sharp decrease of 5.51 percent annually for the period 2005–2015 (Sauer et al., 2017), suggesting a 50 to 60 percent overall decline during that latter period. Droegge and Sauer (1990) documented the mostly upward trends in these surveys evident from 1966 to 1988.

Habitat Requirements

The habitat requirements of the chukar include topographic as well as vegetative characteristics. Foremost among the topographic features that are needed by chukars is the presence of rocky slopes, which the birds use for escape (by running upslope), and roosting cover. The slopes should exceed a 7 percent grade and have an elevation range of more than 200 feet. Observations in Washington (Moreland, 1950; Galbreath and Moreland, 1953) indicated that optimum range includes from a quarter to half of the area in talus slopes, rock outcrops, cliffs, and bluffs; about half the surface covered by sagebrush and downy brome ("cheatgrass") (*Bromus tectorum*); and a small amount of brushy creek-bottom habitat present, as well as wheatgrass (*Agropyron*) and bluegrass (*Poa*).

In the northern portions of the chukar's range, the amount of snow cover may be a major factor in survival. The birds are known to be able to survive winter temperatures as low as -30°F (Moreland, 1950), but several major winter losses have been reported when snow cover more than a few inches in depth has persisted for several weeks (Christensen, 1970).

Nesting cover is little different from that used for foraging purposes, and usually consists of sagebrush or a mixture of sagebrush and grassland on mountains several hundred feet above creek bottoms, often on south-facing slopes (Galbreath and Moreland, 1953). The availability of water during the summer months is a significant habitat factor. Harper, Harry, and Bailey (1958) noted that of 317 adult and young chukars seen on two California study areas between April and June, 288 birds (91 percent) were seen within a half-mile of water. Further, reproductive success in California appeared to be correlated with normal or above normal late winter and early spring precipitation and associated with improved vegetative growth for food and nesting cover.

Sites for dusting and obtaining grit are no problem in the arid habitats utilized by chukars, and roosting sites are usually abundant. Preferred roosting locations include talus slopes or similar rocky areas, sometimes underneath shrubs or low trees (Bohl, 1957; Christensen, 1970, 1999). During winter in Washington, the birds may roost in protected niches and caves on rocky cliff faces (Galbreath and Moreland, 1953). Circular roosting, similar to that of gray partridges and bobwhites, has been noted in various areas.

Food and Foraging Behavior

Fairly extensive studies on the foods of the chukar are available from several states, including Nevada (summarized by Christensen, 1970, 1999), Washington (Galbreath and Moreland, 1953), and California (Harper, Harry, and Bailey, 1958). More limited data are available from New Mexico (Bohl, 1957) and Colorado (Sandfort, 1954). However, virtually all of these analyses point to a predominating importance of grasses, especially downy brome (cheatgrass) (*Bromus tectorum*) leaves and seeds, and the seeds of weedy forbs such as Russian thistle (*Salsola*), filaree (*Erodium*), and fiddleneck (*Amsinckia*). In contrast to the western quails, chukars apparently consume surprisingly few legume seeds, although locust (*Robinia*) seeds are sometimes utilized, and the leaves of alfalfa (*Medicago*), clover (*Trifolium*), and sweet clover (*Melilotus*) are highly preferred foods when they are available.

On a year-round basis, the seeds of downy brome and grass leaves are probably the most important foods, judging from studies in Washington (Galbreath and Moreland, 1953). These are supplemented during the spring by the leaves of various herbs such as dandelion (*Taraxacum*), fringecup (*Lithophragma*), and shepherd's purse (*Capsella*). The crowns and seeds of wheatgrass (*Agropyron*) and the fruits of serviceberry (*Amelanchier*) and hawthorn (*Crataegus*) are consumed during summer, wheat (*Triticum*) kernels are utilized during the fall, and various forb and shrub seeds or fruits are eaten during the winter.

Young birds eat the usual array of insect or other animal materials, but adult consumption of animal foods is rarely more than 15 percent by volume. These consist primarily of grasshoppers, crickets, and ants.

Foraging activity is usually high during midmorning and may extend through the afternoon, with the birds moving widely while searching for food (Christensen, 1970). During hot days, they may feed early in the morning and again in late afternoon, spending the hottest period in shady canyons near a supply of water. Toward evening they again gradually move back into the canyon slopes to spend the night, foraging on the way.

Although the birds are said to be adept at scratching the ground free of litter to expose seeds, they have only a limited capacity to dig through snow. Snow depths as great as eight inches may force the birds out of mountainous areas and into the lower foothills, but even there the birds can scratch through snow that is only an inch or two deep (Christensen, 1970).

Mobility and Movements

Considerable dispersal ability is present in the chukar, and following releases into a new habitat a large number of cases have indicated that the birds may travel extensively before becoming localized. Bohl (1957) listed dispersion records from three release points in New Mexico, which included maximum mobility records of 38 miles in about seven months, 22 miles in a year, and 38 to 40 miles in a year. Brood movements of 10, 11, and 18 air-distance miles were also reported from one release site. In California, one banded bird was known to have moved 20 miles in three months, and another banded bird was found 33 miles from the point of banding after 27 months (Harper, Harry, and Bailey, 1958). In Nevada one adult bird was killed 21 miles from where it had been caught and banded only ten days previously. All of these examples indicate the chukar's remarkable ability to move across unfamiliar terrain with surprising speed. In Nevada, chukars may be found 80 to 140 miles away from the initial or closest release site within 19 years (Christensen, 1999).

Seasonal movements are known to occur in chukars as well; these often involve altitudinal migrations to lower valley areas during the wintertime, followed by a return to higher elevations in spring (Galbreath and Moreland, 1953; Christensen, 1970). Following the growth of succulent plants after fall rains, the birds may also move into waterless areas that were previously unoccupied during the summer (Christensen, 1970). Individual daily ranges have not been well studied, but various lines of evidence suggest that the birds may often move about in an area as wide as a mile in the course of a day, and Bump (1951) reported that the birds might travel as far as two or three miles to reach waterholes.

Vocal Signals

The studies of Stokes (1961, 1963) on the chukar, and Goodwin (1953) on a related species of *Alectoris* provide the basis for the terminology of vocalizations in this genus. Some of these calls were mentioned in the preceding section and need not be reviewed here. Alarm signals noted by Stokes (1961) include a ground alarm note, *whitoo*, which is also used when birds are flushed or held in the hand. A short, guttural *kerrr* note serves as an aerial predator note, which may be repeated as a continuing alarm or "on-guard" call while the bird soars overhead. An "all's-well" note, a soft, plaintive *coo-oor*, may be uttered when the source of danger is gone, as well as by loafing or foraging birds. Foraging birds also utter a food call, a slow *took* note or a rapidly repeated *tu-tu-tu-tu* series of notes, depending on their degree of excitement.

Several calls may serve dual sexual and agonistic functions and are characteristic of the breeding season but not entirely limited to it. The best known of these is the rally call. This consists of a series of repeated *chuck* notes, which at progressively more intense stages sound like *per-chuck!* and *chuckam*. A single

series of these calls may last up to 20 seconds, and as many as three series may be uttered in a minute. This call serves several different functions. It functions in both sexes as a scatter call to reassemble broken coveys throughout the nonbreeding period. Second, it may serve in unmated males as an advertising call that may attract available females. Third, during the breeding season it has aggressive characteristics and may serve to repel other males. To what extent this latter function might serve to space breeding pairs is still uncertain, but if it is a significant spacing mechanism for paired birds this would set the chukar's rally call apart functionally from the advertising calls of male New World quail, which are characteristic primarily of unpaired males and are only infrequently utilized after pair formation has occurred.

Besides the rally call, males in breeding condition may utter a harsh, repeated *chak* note reminiscent of an old steam engine, thus the name "steam-engine call." This call is evidently indicative of a conflict between attack and escape, especially when in the presence of a more dominant bird. Dominant males often alternate between the rally call and an excited squeaking series of notes, called by Stokes the *squee* call, apparently reflecting a stronger attack than escape tendency. A bird being attacked may also utter a raspy squealing note lasting a second or more, indicative of extreme submission.

Finally, a variety of sexually significant notes are present, which are limited to the breeding season and characteristic of behavior associated with copulation and nesting. These include a copulation-intention note, the tidbitting and *pitoo* calls, and the nest-ceremony calls already mentioned earlier.

Social and Reproductive Behavior

From the appearance of broods in late summer until the beginning of pair formation in spring, the social unit of the chukar is the covey. Covey sizes range widely, often from 5 to 40 or more birds, perhaps averaging about 20. It is possible that, as in the bobwhite, the circular roosting behavior during winter places an upper and lower limit on optimum covey size in this species, but apparently few winter counts of covey sizes have been made.

In late winter the coveys gradually begin to disband as pair formation progresses; Mackie and Buechner (1963) found that in Washington this period of breakup occurred from February through March, with older birds pairing sooner than young birds. Although chukar are basically monogamous, the researchers also found that the pairing of one male with two females might occur in about 10 percent of the total pairings.

Although some earlier authors suggested that after pair formation has occurred the male establishes and defends a breeding territory, later studies (Mackie and Buechner, 1963; Blank and Ash, 1956) indicated that no true territorial behavior is present, although males will repel other males from the vicinity of their mates. Stokes (1961, 1967) believed that the *chu-kar* or rally call when uttered by paired birds tends to repel other males; thus it may have some spacing effect. Indeed, Stokes indicated that his limited observations of wild birds suggested that the birds do defend well-defined territories.

As in the New World quail and the gray partridge, pair formation is a subtle process. It may occur only gradually, after some initial shuffling of mates (Stokes, 1961). Several displays and calls are associated with courtship, and most of these postures are noted here (see Figs. 3 and 18).

Fig. 18. Chukar social behavior, including (A) pre-flight posture, (B) male advertising ("steam-engine") call, (C) adult separation ("rally") call, (D) cautious approach, (E) fleeing, (F) submissive crouching, (G) aggressive head-tilting, (H) male head-tilting with far-side wing-lowering, (I) male waltzing (far-side view), (J) male tidbitting, (K) copulation, and (L) female brooding. (After Stokes, 1961)

Chukar, adult

Because the females have plumage identical to that of the males, it is not surprising that initial responses of males to females are aggressive ones. Stokes (1961) has described these postures, and the following description is based on his work. Reproductively active males usually initially perform three postures when first exposed to females. Head-tilting (Fig. 18) is the most common aggressive display, during which the bird tilts his head away from the opponent, simultaneously turning sideways so as to expose his barred flanks to the greatest degree. The neck and chin feathers may be raised, and the bird often stands in an erect, stiff posture ("lateral stance").

A more intense form of aggressive display is "circling," in which the dominant bird moves about another while tilting his head, again exhibiting his flank feathers. The most extreme form of circling is "waltzing," in which the head is held low and the body nearly horizontal as the outer wing is lowered to the point that the primaries touch the ground, and the inner wing is nearly concealed by the flank feathers (Fig. 3). Between bouts of waltzing the bird may stand erect and utter a long call, sounding like *errrrrrrr* or *errrk*. The female usually responds to these displays simply by continuing her normal activities, such as foraging, preening, or dusting.

As the male loses his aggressive tendencies, perhaps by recognition of the nonaggressive female-like responses of the other bird, he may move off some distance and begin pecking

at various edible or nonedible objects. This tidbitting display (Fig. 18) is performed in association with a special call, which sounds like a rapid *tu-tu-tu-tu* that becomes progressively more rapid and higher in pitch. A second call, sounding like *pitoo*, may also be uttered while tidbitting. If the female is sexually active, she may then run to the male and begin pecking in the same area. The male then moves off in a stiff-legged "high-stepping" posture, gradually working toward the rear of the female and again performing tidbitting.

This behavior may lead to copulation, which begins with the female facing away from the male and crouching. The male stands erect briefly, often from three to ten feet away, then utters a precopulatory "rattle" note, *uh-uh-uh-uh*, and approaches in the high-stepping posture. As he mounts the female, he stops calling and grasps her nape, and copulation then occurs (Fig. 18). No calls are uttered during copulation, and afterward the male may move away in a high-stepping posture while the female vigorously shakes her feathers.

A second important element of sexual behavior between a pair is the "nest ceremony." In this display the male enters a clump of vegetation, crouches, raises and spreads his tail, and turns while performing nest-scraping motions. He also utters a special call, a soft, continuous *churrr*, and may vibrate his wings and tail. Females may perform the same ceremony, particularly when the mate is nearby, and Stokes suggests that the display performs an

Chukar, adult walking

important role in keeping the male closely associated with the female during the nesting period or for attaching the male to a clutch of eggs that he might take over for incubation.

Eggs are deposited in the nest by the female at the rate of about 1 to 1.9 days per egg (average 1.3 days), with the longer intervals typical earlier in the season and shorter extremes late in the season. Clutches range from about 10 to more than 20 eggs, with the average of four nests being 15.5 eggs (Mackie and Buechner, 1963). An incubation period of 24 days is typical (Christensen, 1999).

Some authorities (e.g., Galbreath and Moreland, 1953; Alcorn and Richardson, 1951; Mackie and Buechner, 1953) believed that the pair-bond may normally last until early in the incubation period, after which the males may desert and gather together in groups. However, other observations (Goodwin, 1953; Stokes, 1961) suggest that the male may not only help raise the brood but may sometimes take over the first clutch, freeing the female to lay a second one. Mackie and Buechner (1963) noted that males were present in about 10 percent of 103 brood observations, but among many cases of two birds tending broods, both appeared to be females. Christensen (1970) could find no definite case of a male chukar incubating under noncaptive conditions, although brood patches have been reported in wild males (Christensen, 1999).

There is little question that renesting by unsuccessful females does occur, but the incidence of such renesting has not yet been established. Mackie and Buechner doubted that renesting is likely after the final stages of incubation or after hatching, but they did find a nesting period extending for about five months from early March until mid-August. Some cases of males tending broods have been reported in Greece and Turkey (Watson, 1962a).

Following hatching the young leave the nest with the female parent and within a few weeks are likely to become mixed with

members of other broods. Christensen (1970) reported seeing 30 to 50 chicks with up to three adults, and sometimes seeing coveys of more than 100 chicks associated with up to ten adults. Perhaps the association of broods at watering places facilitates such inter-brood transfers in this species, and thus brood-size data are of somewhat limited value. In Nevada between 1960 and 1969, yearly statewide averages of brood sizes ranged from 8.5 to 12.5 chicks, but it would seem that fall age-ratio data might provide a better index of reproductive success.

Christensen noted that during 1968 and 1969 adult-to-young ratios of 1:4.14 (79.5 percent immatures) and 1:5.05 (83.4 percent immatures), respectively, existed. This ratio is close to those typical of bobwhites and suggestive of a high annual mortality rate. However, statewide age ratios based on summer field surveys in Nevada between 1951 and 1969 varied enormously, from 1:0.4 to 1:8.8, and would indicate remarkable yearly variations in productivity. Very low adult-to-young ratios were associated with drought years, such as 1953 and 1959, while high adult-to-young ratios were associated with years of favorable precipitation. The highest ratios occurred in those years when precipitation resulted in ideal plant growth (green grass in fall and winter, and an adequate seed crop in spring) without adversely affecting the nesting season (Christensen, 1970, 1996).

Evolutionary Relationships

There is little purpose in discussing the evolutionary relationships of these introduced species because their nearest living relatives are far beyond the geographic limits established for this book. Readers are referred to Watson's (1962a,b) and Randi's (1992, 1996) discussions of Old World speciation in the *Alectoris* partridges.

Himalayan Snowcock

Tetraogallus himalayensis G. R. Gray 1843

Other Vernacular Names

Himalayan snow partridge

Range

Resident in the Himalayas, from northeastern Afghanistan eastward along the high Himalayas through northeastern Pakistan, Ladakh, and Nepal to western China (Xinjiang, Qinghai, and Gansu provinces). Introduced locally into the United States (Ruby Mountains and contiguous East Humboldt Range, Nevada).

US Subspecies

T. h. himalayensis Gray: Eastern Himalayan snowcock. Resident from Afghanistan east through Pakistan to western China (Xinjiang Province), Uygur Autonomous Region, in western Kashi and the Tianshan Mountains. Of the five described subspecies, only the nominate race was introduced into the United States.

Measurements

(See also Johnsgard, 1988.)

Folded wing: Adult males, 329–340 mm; adult females, 275–325 mm (Dement'ev et al., 1952).

Tail: Both sexes: 173–193 mm (Ali and Ripley, 1978).

Weight (mass): Males (Russia), 2.2–3.1 kg (Dement'ev et al., 1952); females (India), 1.36–1.8 kg (Ali and Ripley, 1978).

Identification

Adult Himalayan snowcock are 20 to 22 inches (508–559 mm) long. This is the only sage-grouse-sized (of at least three pounds) gallinaceous bird in North America that lacks leg (tarsal) feathers and that has extensive white feathering on the head and breast.

Field Marks

Any large grouse-like bird (about the size of a female greater sage-grouse) seen in the high Ruby Mountains of Nevada will be this species. It is found in steep, rocky habitats, usually in pairs or small groups, or in alpine meadows above about 7,000 feet (2,130 m) in winter and often above 11,000 feet (3,350 m) in summer. Loud whistled notes, sometimes lasting several seconds, and shorter whistles or other loud calls help localize the birds.

Age and Sex Criteria

Females can be distinguished from males by the fact that females lack tarsal spurs and their maximum adult wing length is 315 mm, whereas the minimum wing length of adult males from Russia is 320 mm (Dement'ev et al., 1952). The minimum

Map 9. Introduced distribution of the Himalayan snowcock in Nevada. Elko County is outlined; the occupied Ruby Mountains and adjoining East Humboldt Range are inked and also shown at enlarged scale below.

bill-to-tail length of males from India is 660 mm, whereas in females the maximum is 597 mm (Hume and Marshall, 1880).

Immatures differ from adults in that the three outer (juvenile) primaries are pointed and mottled with rufous buff toward their tips. Additionally the chestnut patches on both sides of the nape are more united, and the mantle is usually buff-colored (Johnsgard, 1988). Juveniles have duller and less clearly marked plumages than adults, with the white areas of adults replaced by gray (Dement'ev et al., 1952). At one year the adult plumage is present, but yearling birds do not breed.

Downy young have richly variegated stone-gray upperparts, and the juvenile feathers (which emerge at five days) have black tips and subterminal pale buff markings. The head is very pale cream buff with several black streaks extending back along the crown, eye region, and malar areas (Christensen, 1998).

Fig. 19. Himalayan snowcock, adult male

Distribution and Habitat

Like other snowcocks, this species is associated with alpine meadows, rock fields, sparsely vegetated ridges, and the edges of snowfields above tree line. Typical habitat in Nevada includes steep slopes, which allow swift escape flights from predators such as golden eagles. It also includes boulder-strewn snowfields with scattered stunted willow thickets surrounded by nearly barren talus slopes (Floyd et al., 2007).

Population Density and Hunting

No population density studies have been made in Nevada, but one Chinese estimate (Liu, 1994) was of 4.0 to 7.3 adults per square kilometer in spring. Christensen (1998) stated that considering a minimum of 262 square kilometers of occupied habitat in Nevada, the region's minimum adult spring population might be about 1,000 birds.

The Nevada Division of Wildlife imported North America's

Himalayan snowcock, adult male

Himalayan snowcock, male calling

first snowcock in 1961 from Pakistan. Later importations eventually resulted in the release of 19 birds into the Ruby Mountains. After extensive game farm propagation efforts, and multiple releases from 1970 to 1979, the species had been established as a wild sustaining population by the early 1980s (Christensen, 1998). Hunting was first allowed in 1980 and has continued on an annual but restricted basis through 2016. An estimated average of about 8 birds have been shot annually between 1980 and 2015 with extremes of from 2 to 23 birds.

Habitat Requirements

In the Ruby Mountains, the subalpine vegetation is dominated by whitebark pine (*Pinus albicaulis*) between 8,500 and 10,600 feet (2,592–3,233 m), with limber pine (*Pinus flexilis*) occurring at the northern extension of the species' range, and the shrub mountain mahogany (*Cercocarpus*) reaching as high as 8,500 feet (2,592 m). The subalpine zone of the Ruby Mountains between 8,700 and 9,500 feet (2,675–2,888 m) includes at least 50 forb species, among which are grasses, sedges, legumes, buttercups, and cinquefoils. These herbaceous plants are abundant in protected pockets and ledges and on talus slopes. Annual precipitation in the Ruby Mountains averages 45 inches (114 cm) at 10,000 feet (3,040 m), much of which falls as snow. Average temperatures at the base of the mountains are 27°F (−3°C) in January and 68°F (20°C) in July, with a minimum record of −33°F (−36°C) (Christensen, 1998).

Introduced birds in Nevada favor well-vegetated alpine turf and alpine tundra habitats, usually found in glacial cirques. Most birds there remain above 10,000 feet (3,000 m) during winter months (Stiver 1984). Baker (1930) reported that in Asia these birds occur from 12,000 to 17,000 feet (3,600–5,100 m) during summer, and sometimes in winter occur as low as 7,000 feet (2,100 m), preferring rocky, precipitous slopes having little vegetation. Mountain meadows are a favorite habitat, and in some areas the birds may feed on small grass-like herbs such as *Gager lutea*, according to Baker. Evidently grass is a major source of food, and they also eat seeds and moss rhizoids but probably very little animal materials.

Food and Foraging Behavior

In Nevada, cinquefoil (*Potentilla fruticosa*) was observed to be a favorite food, with sheep fescue (*Festuca ovina*) and alpine fescue (*F. brachyphylla*) used where cinquefoil was absent. Bulbs and roots are dug up using their stout beaks and powerful claws, sometimes from under snow up to 6 inches (15 cm) deep (Christensen, 1998).

In the closely related Tibetan snowcock, the known foods similarly include grasses and a variety of herbs, such as *Stellaria* (chickweed), *Saxifraga* (saxifrage), *Oxytropis* (locoweed), *Potentilla* (cinquefoil), and *Primula* (primrose) (Dement'ev et al., 1952).

Mobility and Movements

These birds are essentially sedentary but move vertically with the season, over a range of as few to a thousand meters. Flights tend to be fairly short, such as from 165 to 328 feet (50 to 100 m) from roosting areas to the bottom of a slope, or exceptionally to 656 feet (200 m). However there are also records of flights

of at least 0.5 mile (0.8 km) by frightened birds, and of at least 0.9 miles (1.5 km) in open areas of broad topography (Christensen, 1998).

Home ranges of breeding pairs in Nevada are still unstudied, but studies in China suggest that pair home ranges vary from 0.06–0.48 square mile (0.15–1.26 km²) (Ma, 1992; Liu, 1994).

Some long-distance movements of birds along mountain crests have been recorded in the Ruby Mountains, with birds having been seen at least 10 miles (16 km) from release sites (Christensen, 1998).

Vocal Signals

Snowcock males of all species produce very loud advertising calls during spring. Christensen (1998) described a variety of calls, mostly named after apparently comparable calls described for the chukar. Adult calls include a ground alarm, a hawk alarm, a food call, a rally call, and a sexual call. The sexual call is limited to males, and consist of a whistled *shi-er, shi-er, shi-er*, uttered while raising the tail and exposing his white under tail-coverts. This call serves both to advertise territories and to attract females.

In the closely related Caucasian snowcock, the male's advertising call lasts about six seconds and consists of repeated ooy syllables that terminate in a loud oooooeeeeeey-yeeeo that is audible for up to about a kilometer (Cramp and Simmons, 1980). In the Tibetan snowcock the vocalizations are apparently similar and include a clear whistle, a call similar to that of a curlew (*Numenius arquatus*), and a subdued chuckling that gradually becomes louder until it reaches a climax (Ali and Ripley 1968).

Other calls described by Christensen (1998) are uttered by both sexes. The rally call is similar in cadence and intensity to that of the chukar. It consists of a series of *kuks* that start slowly but increase in scale and vigor and end in a sharp whistle; it is followed by a reversed call that descends in scale. This call is uttered by both sexes and is the sound most commonly heard from captive birds.

Call frequency in wild birds increases during evening hours and typically ends with calling from roosting sites (Christensen, 1998).

Social and Reproductive Behavior

When courting, the male reportedly spreads his wings slightly, depresses his tail, and slightly ruffles his feathers. In this posture he runs back and forth in front of the hen or circles around her, presumably in what corresponds to the waltzing display (Baker 1930). Captive males in Nevada exhibit yellow orbital skin that takes on an orange tint when a bird is paired. Paired birds are inseparable while foraging (Christensen, 1998).

Nests in the wild have often been found at the extreme crest of a hill or just beyond on the leeward side, sheltered by scrubby grass or rocks but never in bushes or dense grassy vegetation. The clutch reportedly numbers four to five but sometimes up to seven and rarely more. Only the female incubates, but the male remains close to the nest and acts as a lookout (Baker 1930).

In captive Nevada birds, breeding behavior began during February and probably peaked in April, with egg-laying starting in mid to late March and usually peaking in early May. Game-farm females usually did not begin breeding until two years of

age and had an average annual egg production of 11.3. The clutch size in the wild varies from 8 to 12 eggs. Only the female incubates, which begins after the laying of the final egg. The mean incubation period is 27.5 days, including one day between pipping and emergence from the eggshell. Parental care is by the female only, with brooding females sometimes associating in loose groups (Christensen, 1998).

Based on a small sample of seven broods, the average size in Nevada was found to be 5.7 chicks (Stiver, 1984). Captive-raised birds are 75 percent grown at 16 weeks and average 1,262 g at 94 days. Sexual maturity is not reached until the second year of life. At least in captivity, breeding efforts were most productive among birds in the 3- to 5-year age class (Christensen, 1998).

During fieldwork for the *Nevada Breeding Bird Atlas* (Floyd et al., 2007), two possible but not confirmed breeding-block records were obtained, and the species was estimated to be fairly common in three breeding blocks. Most breeding-season sightings have been in the vicinity of Lamoille Canyon in Elko County. Other repeated sightings have been made at various locations in the central Ruby Mountains, such as Thomas Peak, Ricco Peak, Griswold Lake, and Island Lake.

In the geographically related and slightly sympatric Tibetan snowcock of Ladakh and northwestern Xinjiang (China), breeding

occurs mainly from the end of May until early July, although one late egg record is for August 25. The clutch size has been generally reported as from 4 to 7 eggs but usually only 4 to 5 (Baker, 1930). There is no information on the incubation period or development of the young, although fledged broods of 4 to 6 young have been seen in mid-July (Dement'ev et al., 1952). It is also unreported as to whether males regularly accompany broods or whether they instead gather into flocks following the nesting season.

Evolutionary Relationships

The five species of snowcocks include two that have white abdomens and three that have gray, the latter including the Himalayan snowcock. The other two that have gray abdomens are the Caucasian snowcock (*T. caucasicus*) and Caspian snowcock (*T. caspius*). Marion (1961) suggested that *caspius* and *himalayensis* might well be considered subspecies, with *caucasicus* apparently less closely related. General adult plumage pattern similarities would tend to support this relationship with *caspius*, although their relatively distantly separated geographic ranges might cast doubt on it.

Gray Partridge

Perdix perdix (Linnaeus) 1758

Other Vernacular Names

Bohemian partridge, English partridge, European partridge, Hungarian partridge, Hun

Range

Native to Europe and Asia but successfully introduced into North America and now disjunctively established in southern Canada and the northern United States. Some small, isolated, and declining populations exist in New York, Vermont, Ontario, Quebec, Prince Edward Island, and Nova Scotia. The major population now extends from Illinois west through the prairie regions of Iowa, southern Minnesota, the Dakotas, and through the Prairie Provinces of Canada from Manitoba west and north to central Saskatchewan and north-central Alberta. Smaller and somewhat disjunctive populations occur in the Pacific Northwest from southern British Columbia (Okanagan Valley), Washington, and eastern Oregon, extending east to northern Utah, southern and eastern Idaho, and northern Montana, and south through eastern Montana to central and eastern Wyoming. Populations in Ohio, Indiana, and Iowa have largely or entirely disappeared.

Subspecies

The North American population was possibly derived from stock representing several different geographic races, but at least some introductions, including those in Alberta, New York, and Wisconsin, were of the nominate race *P. p. perdix*, largely obtained from birds originating in Hungary, Bohemia, and western Czechoslovakia (now the Czech Republic) (Carroll, 1993).

Measurements

Folded wing: Adult males, 144–57 mm; adult females, 146–54 mm (males average 152 mm; females 150 mm) (Johnsgard, 1988). Males (Washington state), ave. of 10, 153.9 mm; females, ave. of 23, 156.0 mm (Carroll, 1993).

Tail: Adult males, 78–84 mm; adult females, 76–80 mm (males average 80 mm; females 78 mm) (Johnsgard, 1988).

Weight (mass): Males, ave. of 87, 396 g (14.0 oz.); females, ave. of 57, 162 g (13.7 oz.) (Johnsgard, 1975a). Males, ave. of 10 adults (Iowa), 401 g; females, ave. of 4 adults (Iowa), 376 g (Carroll, 1993).

Identification

Adult gray partridge are 12 to 13 inches long. The sexes are 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); vertical chestnut barring similarly

interrupts the gray flanks. 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; 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 of a grayish brown bird without bright markings. Chukar partridge also exhibit rusty outer tail feathers in flight, but they have conspicuous white throats. The bobwhite occurs in some of the same regions as the gray partridge, but it is smaller and shows a grayish tail when flushed. In spring a raspy *tur-ip* call may be heard (Godfrey, 1986), which has also been described as a “rusty-gate” or *keee-uck!* call (McCabe and Hawkins, 1946).

Age and Sex Criteria

Females lack the dark horseshoe pattern on the abdomen of males and 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 these 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 by 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, it 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 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

Map 10. Introduced North American distribution of the gray partridge as of the 1970s. Recent (2011–15) populations (averaging 1–3 birds per Breeding Bird Survey route) are inked.

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 be recognized. The earliest established populations were those of the Pacific Northwest, where birds were 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 40°N and 50°N latitude. Moderately sized populations also occur in eastern Washington in shrub-steer, dryland wheat, and other farming areas, sometimes up into the ponderosa pine zone (Wahl, Tweit, and Mlodinow, 2005).

They also extended north to south-central British Columbia, and south to the Willamette Valley of Oregon (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 bunchgrass 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 bunchgrass 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 (Gullion and Christensen, 1957). Their abundance there fluctuates widely (Alcorn, 1988). 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 50 miles from agricultural lands in the aspen zone. This Pacific Northwest population has undergone considerable retraction of its range; it is now (2017) 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 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

Fig. 20. Gray partridge, adult at rest

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.

Both Montana and North Dakota 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 gray partridges as early as 1907, the birds have never become widely established and at present (2017) are limited to the extreme northeastern corner of the state.

Over 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 third and smallest population segment includes the Great Lakes–Upper Midwest region, which in my 1973 survey included eastern Wisconsin, southern Michigan, eastern Indiana, western Ohio, southern Ontario, and northern New York. Yeatter (1935) extensively studied this population 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. No records of breeding birds in Michigan appeared in the 1991 Michigan breeding bird atlas (Brewer, McPeck, and Adams, 1991).

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 four miles per

Fig. 21. Gray partridge, adult landing

year, until they had moved 102 miles north in 29 years. Between 1944 and 1954 the birds further extended their northern range at a rate of about eight miles a year and also moved southwesterly at a rate of about one mile per year (Resadny, 1965). Apparently the Wisconsin population has become fairly stabilized in the southern and eastern regions, with limitations of soil and land use restricting further range extension.

The Illinois population is a southern extension of the large Wisconsin population and in the early 1970s was limited to the northeastern corner of the state, where moderate numbers were harvested each year. It too is apparently now gone. In Indiana the status of the gray partridge was still moderately favorable into the 1970s, when the birds were being hunted to some extent over the northeastern part of the state; some may still survive there.

In Ohio a fairly extensive release program was carried out between 1909 and 1940, and by the late 1920s the birds were well established on the lacustrine limestone and glacial limestone soils of western Ohio. The population probably peaked in the mid-1930s, and by 1965 it had apparently all but disappeared from the state. Judging from hunter-kill data of the 1960s it seems likely that the Great Lakes–Upper Midwest gray partridge populations were highest in Wisconsin, with progressively fewer birds in Iowa, Illinois, Indiana, and Ohio. No hunting seasons on the species were allowed during 2016 in the last three of these states.

Early attempted introductions in New York were failures, but nearly 30,000 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 by 1952

(Brown, 1954). The New York population is now limited largely to St. Lawrence Valley. The birds survived best in areas having soils of limestone origin.

Lastly, 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) indicated no eastern Canada population, whereas Aldrich and Duvall (1955) reported one extending all the way to the mouth of the St. Lawrence River. Godfrey's estimation (1986) of the eastern Canada distribution indicated that most of the area south of 49°N latitude was then occupied range, as was Prince Edward Island, eastern New Brunswick, and Nova Scotia (locally), but they are probably fairly small and no recent details were available to me. These populations apparently date from introductions made in the 1920s.

Based on eBird sightings, it is likely that the northern range limits shown for Alberta (to about Lesser Slave Lake) and Saskatchewan (to about the Saskatchewan River) by both Godfrey and Salt and Salt (1976) are still fairly accurate, in spite of the apparent substantial population declines of this species in the Prairie Provinces and upper Midwestern states. Perhaps global warming will allow for further northward expansions there and help compensate for major population losses in Ohio, Indiana, and elsewhere in the corn and hay-growing regions of the American Midwest.

Population Density and Hunting

Early density figures for United States populations of the gray partridge came from the Great Lakes states. 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 estimated 7.5 to 26 acres per bird, averaging 15 acres per bird over the entire study 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 historically for England, where estimates of a pair per 8 to 10 acres were not uncommon (McCabe and Hawkins, 1946). The nearest comparable figures I have found are old records 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 federal game refuge (Hammond, 1941). It would seem probable that densities in the prairie provinces of Canada may have exceeded these, at least during favorable years. In England, historic May densities varied from 1.9 to 10.7 acres per pair, with densities of less than five acres per pair considered high (Jenkins, 1961).

Somewhat more recent breeding density estimates include less than 1 pair per square kilometer in North Dakota during the 1980s, 1.77 to 32.1 pairs per square kilometer in Wisconsin in 1980, and 4.3 pairs per square kilometer in prime Saskatchewan habitat during the 1970s (Carroll, 1993). Some high fall population density estimates include 48 birds per square kilometer in South Dakota, 15 to 84 birds per square kilometer in Idaho, and 32 to 54 birds per square kilometer in Saskatchewan (Carroll, 1993).

Data from the North American Breeding Bird Survey for the period 1966–2015 indicate that this species underwent a range-wide decrease of 1.80 percent annually for that period, and a decrease of 1.98 percent annually for the period 2005–2015

(Sauer et al., 2017). Droege and Sauer (1990) also documented the 1966–88 downward population trends of the gray partridge evident from the North American Breeding Bird Survey data.

The 1908 Alberta releases of gray partridges were so successful that the first hunting season was held there in 1913. Saskatchewan was colonized by Alberta birds, and a season there was established in 1927, followed by one in Manitoba in 1931. The average yearly continental hunter kill of gray partridges was in excess of 400,000 birds during the 1970s.

In 1975 I (Johnsgard, 1975a) estimated that 650,000 gray partridges were then being shot annually in the United States and Canada, based on data from individual states and provinces. Gray partridges were legal game in eight Canadian provinces in 1970, with a total kill of at least 250,000 birds. The largest Canadian kills were in Alberta (105,000 in the early 1950s) and Saskatchewan (132,000 in the 1960s).

The estimated total yearly hunter kill in 14 states of the United States where the birds were legally hunted during the late 1960s was probably about 400,000, with most of this occurring in Montana (93,000), Oregon (75,000), North Dakota (69,000), and Idaho (65,000). In North Dakota the mean 1986–98 annual kill was 186,000, in Saskatchewan 91,600, and in Iowa 91,100 (Vander Zouwen, 1990).

In 2016 gray partridges were legally hunted in 12 states: IA, MN, MT, ND, NE, NH, NV, OR, SD, UT, WA, WI, and WY. Some recent statewide U.S. hunter-kill estimates are: Montana (long-term average), 46,000; South Dakota (2014–15), 11,000 (vs. 7,500 in 1969); Oregon (average, 1994–2015), 10,000; Washington (2014–15), 5,100 (vs. ave. of 25,100 in late 1960s); and Wyoming (2011–15 average), 4,400 (vs. ave. of 2,600 in late 1960s). Recent data for Canada were not available to me.

Habitat Requirements

In spite of numerous attempts to introduce the gray partridge in virtually all parts of temperate 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 supporting natural grasslands and seem to 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 up to about 5,000 feet in the bunchgrass 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).

In New York the greatest numbers occurred in areas of 30 to 45 percent croplands, with large areas of pasture and hay present. Major factors favoring the birds there included dry weather during the hatching and brooding seasons, large areas planted to grain crops, ample nesting and brooding cover, the presence of few pheasants, and fairly light hunting (Brown, 1954). In Wisconsin the birds are most abundant on red clay soils, particularly on flat lands that are about 65 percent cultivated. They survive best 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).

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 hay fields and grain fields 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 100 feet from the edge, as had been earlier noted by Yeatter.

Brooding cover is essentially like nesting cover: hayfields, grain fields, 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. 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).

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 to obtain food, at least to a depth of a foot (McCabe and Hawkins, 1946; Westerskov, 1965).

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 compose 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 (Westerskov, 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 (1,320 feet), rarely as much as half a mile (2,640 feet). In Michigan, Yeatter (1935) noted a similar winter mobility that averaged about a fifth of a mile (1,050 feet), and 20 percent of the coveys had a cruising radius of no more than one-eighth of a mile (660 feet). Over the course of a year, Yocom found that a single female had a cruising radius of seven-eighths of a mile (4,594 feet).

In spite of their sedentary nature, the gray partridges in Canada exhibited a remarkable rate of range expansion during the years immediately following their introduction. Leopold (1933) calculated that during the early years after their introduction in Alberta, a maximum average range extension of 28 miles a year occurred, which is little short of astonishing. Comparable estimates of range extension in Michigan and Wisconsin were only 2 to 4 miles a year during the period shortly after successful introduction.

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 adults and sounds like *giip, giip*. 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 rather than mated males and is associated with a threatening posture. He also noted that threatening males sometimes uttered a harsh *tit-tik-tik*. Carroll (1993) provided a sonogram of this call and considered it to be a territorial announcement, mainly used by unpaired males. It is mostly uttered from late winter to spring, and most often heard just before sunrise and after sunset.

According to Yocom (1943), birds in a covey often utter soft conversational or contact *chrrr* notes when settling down for the night. 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.

Kimmel (1985) described an additional call that has variously been called the "fright call," "alarm call," or (in my terminology) the distress call. It is the call uttered by a chick or adult when it is in the grasp of a predator.

Fig. 22. Gray partridge social behavior, including (A) male threat-upright, (B) sinuous neck display of female, (C) male courtship upright posture, (D) male courtship display with wing-lowering, (E) upright alert posture, and (F) precopulatory behavior. (After Jenkins, 1961a)

Gray partridge, adult

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, usually numbering about ten by the time the chicks are two months old (Yocom, 1943). Johnson (1964) 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 12 to 13 birds, there is a monthly decline that averages about a 9 to 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) reported

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 6 to 8 yards from one another, each alternately chasing and being chased. Once two birds were seen by an 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 the "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 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 in *Alectoris*), and that the nearest thing to territorial behavior is the stability exhibited in covey structure.

Gray partridge, adult

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 that Jenkins observed was between yearling hens, but older females would also sometimes participate. Because females didn't choose young males of their own covey for mates, the males 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 the females, which usually resulted in attacks by males within the covey, but it sometimes was able to lure a female away from the covey. Pair formation is 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 himself to a mated pair, remaining 15 to 20 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 male's dorsal surface toward the female, but evidently there is little or no wing lowering (see Fig. 22). 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 upward, and the two birds might rub their beaks together. Whether a tidbitting display occurs as a courtship display in the gray partridge is not known, but Jenkins noted that feeding behavior includes courtship feeding, suggesting that such a display is present.

According to Jenkins, and also 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 (Fig. 22), grasps her nape, and copulation occurs.

Yocom (1943) reported that the female performs nest building, with the male standing guard. A scrape is dug first, usually about 2.5 inches deep and 6 to 8 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 about 1.1 days per egg (McCabe and Hawkins, 1946).

The average clutch size of first nestings is probably 15 to 17 eggs, with somewhat lower figures being reported for England, which are among the highest average clutch sizes known for any bird. 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 20 eggs than in those that are much smaller. 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 at 24 to 25 days, and the female is believed to perform all of the incubation. However, in two instances a male has been observed sitting beside the female on the nest, and it is thought that this might occur only near or at the time of pipping (McCabe and Hawkins, 1946). Both sexes participate equally in brood care (Carroll, 1998).

The rate of nesting failure may be fairly high; three different US studies have indicated nesting failures averaging 68 percent, often with mowing of hayfields being a major source of nesting losses. However, partridges are known to attempt re-nesting regularly, with only a slight average reduction in clutch size.

Following hatching, the 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.

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. A greater degree of habitat interspersation is 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 hatching success and chick survival, with a ratio of 3.9:1 perhaps being an average age ratio, judging from data on more than 14,000 birds sampled in North Dakota from 1950 to 1963 (Johnson, 1964). This would represent about 8 young per pair surviving to the start of the hunting season, which agrees well with the average covey sizes of 10 to 12 birds typical for that time of year.

Evolutionary Relationships

Inasmuch as the other probable relatives of *Perdix* that are found in Asia 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 developed or lacking during the breeding season, and male hostile behavior is associated primarily with protection of the female from unmated males. 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.

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 species, the males, and especially young males, are forced to leave their coveys in spring and attempt to seek out mates from other coveys, and they may make themselves conspicuous by crowing behavior. This behavior probably brings about a certain degree of population mixing and may facilitate range extension.

Tribe Phasianini: Pheasants and Their Relatives

Ring-necked pheasant, adult male

Ring-necked (Common) Pheasant

Phasianus colchicus Linnaeus 1758

Other Vernacular Names

Bianchi's pheasant, Chinese pheasant, green pheasant, ring-necked pheasant, white-winged pheasant

Range

Native to eastern Asia but introduced extensively into North America and now widely established. Ranges in North America from south-central British Columbia southward in the Pacific coastal states to California's Imperial Valley and extreme northern Baja California. Also occurs locally in the intermontane region along river valleys or in irrigated areas of Idaho, southern Nevada, northern and eastern Utah, and eastern New Mexico.

Widespread in the grasslands east of the Rocky Mountains from southern Alberta eastward across southern Saskatchewan, southwestern Manitoba, southeastern Ontario, southernmost Quebec, northern New York, southern New Hampshire, southern and eastern Vermont, eastern Maine, New Brunswick, and Nova Scotia to Prince Edward Island, easternmost Newfoundland and possibly Cape Breton Island.

Also ranges in the eastern United States from Maine and Vermont south and west through Connecticut and Massachusetts to New Jersey, Pennsylvania, Ohio, Indiana, Illinois, Missouri, Kansas, western Oklahoma, northwestern Texas, and eastern New Mexico.

Pheasant ranges and populations in Canada are clearly declining. Breeding Bird Survey data from Alberta, once the heart of Canada's pheasant range, indicate the birds are now fairly common only south and east of Calgary. British Columbia also still supports good regional pheasant populations, but only in the Kettle and Columbia valleys and the Georgia Depression (Davison et al., 2012).

Subspecies

P. c. torquatus L. Ring-necked pheasant. Native to eastern China, south from Shandong to the borders of northern Tonkin. Introduced into North America and Hawaii, now widespread in both.

P. c. bianchii Buturlin. White-winged (Bianchi's) pheasant. Native to eastern Uzbekistan (Bukhara Province). Introduced into various arid parts of the American Southwest during the mid-twentieth century, including the Rio Grande Valley of New Mexico, where hybridization with *torquatus* occurred, variably obscuring the form's distinctive white lesser wing-coverts. Other subspecies of the white-winged pheasant group might also have been introduced into the United States, including birds from Afghanistan (probably *P. c. principalis* P. L. Sclater).

P. (c.) versicolor Vieillot 1825. Green (Japanese) pheasant. Native to Japan. Introduced into some East Coast locations in the United States (Maryland, Delaware), where hybridization with

local ring-necked pheasants has occurred. (Often considered to be a distinct species; here regarded as an allospecies.)

Measurements

Folded wing (*P. c. torquatus*): Adult males, 240–253 mm; adult females, 208 mm (Johnsgard, 1989). Adult males (various racial populations), 235–258 mm; adult females, 210–220 mm (Giudice and Ratti, 2001).

Tail: Adult males (*P. c. torquatus*), 425–560 mm; adult females, 266 mm. Adult males of *versicolor*, 270–425 mm; females, 207–275 mm (Johnsgard, 1989). Adult males (various racial populations), 425–536 mm; adult females, 290–320 mm (Giudice and Ratti, 2001).

Weight (mass) (introduced North American population): Males, ave. of 6,378, 1325 g (46.4 oz.); females, ave. of 759, 952 g (33.6 oz.) (Johnsgard, 1975a). Trautman (1982) tabulated a great deal of weight data on birds from South Dakota, and reported an annual average adult male weight of 44.5 oz. (1,263 g), and a similar yearly female average of 32.3 oz. (916.5 g), based on sample sizes of 13,124 and 2,071, respectively.

Identification

Adult ring-necked pheasants are 21 to 25 inches long (females) or 30 to 36 inches long (males). The adult male ring-necked pheasant is almost impossible to confuse with any other species; its long, pointed, and barred tail distinguishes it from all other North American species except the greater sage-grouse, and the latter has feathered rather than spurred legs and lacks the pheasant's iridescent coloration. Green pheasant males lack a white neck-ring, and adults are extensively iridescent green. Female green pheasants differ conspicuously from *P. colchicus* in that their mantle feathers are almost entirely black in the middle, with iridescent greenish tips.

Female ring-necked pheasants also have a relatively long and strongly barred tail, but their legs lack spurs, and they have a dull mottled brown plumage throughout. They are about the same size as female greater sage-grouse, but the latter have a dark abdomen patch and feathered legs, whereas female ring-necked pheasants are buff on the underparts and have bare legs. Sharp-tailed grouse might perhaps be confused with female pheasants, but the tails of the former are much shorter, and they also have feathered legs.

Field Marks

Pheasants are likely to be found in open grassland and cropland areas where some brushy cover also exists, and unless pressed are more likely to run than to fly. In any case, the male's long tail is distinctive. Males often utter a croaking call on takeoff, and the long, pointed tail of both sexes is distinctive. In the spring

Map 11. Introduced North American distribution of the ring-necked pheasant as of the 1970s. Denser populations at that time are indicated by darker shading. Recent populations (2011–15, averaging 30–100 birds per Breeding Bird Survey route) are inked.

the male's territorial call is a useful indication of its presence; it is a loud, double-noted *Ko-or OK* or *korrk-kok* or *kok-ok-ok*, with the last syllable staccato, which is followed by a much softer wing-whirring sound. Except during the nesting season, males are frequently seen in company with a harem of several females.

Lone females are harder to identify, as their tails are shorter than those of the males. Their general plumage pattern and color are similar to those of a sharp-tailed grouse, but they are more buffy and less white on their sides and underparts than are sharp-tailed grouse.

Fig. 23. Ring-necked pheasant, male walking

Age and Sex Criteria

Females can normally be readily recognized in the hand by their absence of tarsal spurs, iridescent coloration, or extensive bare red skin around the eye. Some old females or those with damaged ovaries may assume a rather male-like plumage, but they lack spurs. Females also have a relatively long and strongly barred tail but lack iridescence and are a dull mottled brown and buff throughout.

Immatures closely resemble adults by their first fall of life; young males attain their adult plumage by about 4.5 months of age. Unlike most North American gallinaceous birds, pheasants do not retain their two outer juvenal primaries through the winter. The presence of growing or recently replaced outer primaries thus indicates a young bird. Yearling males may also usually be distinguished from adults on the basis of their tarsal spurs, which are lighter in color, usually blunter and not decurved, and softer and less glossy than in adults.

Distribution and Habitat

Pheasant habitats vary greatly geographically, but in Europe the birds occur from lowlands and broad river valleys to foothills and dry uplands, in areas without deep winter snows or severe cold, becoming limited in mountains to narrow wooded valleys and gorges, and infrequently occurring above 700 meters (Cramp and Simmons, 1980). Similar habitats are used in Hawaii, where they are found from sea level to 11,000 feet, in areas where the rainfall varies from under 10 to more than 300 inches annually. They occur in all types of soil, topographic and climatic

conditions, and in cultivated areas as well as forested, grassland, desert, or other waste areas (Schwartz and Schwartz 1951).

In their native China, pheasant habitats include three general environments: the overgrown edges of rivers, hilly areas close to large cultivated fields having small bamboo groves and low pine thickets, and flat and level lands cultivated with rice, wheat, or rape (*Brassica*) (Cheng 1963). In Russia the primary biotype similarly consists of shrubbery and thickets of bulrushes in river valleys, cultivated terrain, and to some extent brush-covered river valleys of mountains, mostly to elevations of 1,500 to 2,600 meters, and rarely to 3,400 meters (Dement'ev et al., 1952). Desert-adapted subspecies sometimes occur in quite arid areas with alkaline soils, but the birds in these locales are largely limited to riverine habitats or other areas with available fresh water.

Population Density and Hunting

Great variations in population density have been reported in North America, even in such small areas as Pelee Island, Ontario, for example, where an introduced pheasant population rose from 36 birds in 1927 to about five birds per acre (on a land area of 10,000 acres) by 1934 (Stokes, 1954). A similar enormous but temporary buildup of population density (to 3.87 birds per acre) occurred on the 397-acre Protection Island off the coast of Washington within five years after pheasants were introduced there (Einarsen, 1945). Populations in Washington have declined significantly in recent years with increased human population and declining grain production; by the late 1990s the average hunter kill was about 100,000 per year (Walsh, Tweit, and Mlodinow, 2005).

Fig. 24. Ring-necked pheasant male social behavior, including (A) normal facial appearance, (B) facial skin engorgement, (C) crowing, (D) wing-flapping, and (E) lateral display to female. (Mostly after Glutz, 1973)

Edminster (1954) judged that in North America, first-class pheasant range should have then supported about one adult per 3 to 4 acres in spring, while poor range may have had one adult per 15 to 20 acres in spring. Estimated autumn (adult

plus young) densities in first-class range were one bird per acre and in poor range one bird per 5 to 10 acres. Studies in south-central Nebraska over a period of a decade resulted in estimates of adult (spring) densities of about 3 to 8 birds per

Fig. 25. Ring-necked pheasant, males fighting (above) and copulation (below). (After Glutz, 1973)

100 acres in three different study areas of good pheasant habitats (Baxter and Wolfe, 1973), and these densities would appear to have been fairly representative of many Midwestern areas at that time. Spring estimates of as high as about 80 females per square mile were reported in Iowa during the very high populations of the early 1940s, but more typical densities for the same area were in the range of no more than 40 females per square mile.

Data from the North American Breeding Bird Survey for the period 1966–2015 indicate that pheasants underwent a range-wide decrease of 0.64 percent annually for the 50-year period

1966–2015, and a decrease of 0.29 percent annually for the decade 2005–15 (Sauer et al., 2017). Droege and Sauer (1990) documented the downward population trends of the ring-necked pheasant in eastern North America by analyzing the North American Breeding Bird Survey data for the 1966–88 period.

In 1975 I (Johnsgard, 1975a) estimated that 12 million ring-necked pheasants were then being shot annually in the United States, based on data obtained from nearly all the contiguous states. Some recent approximate statewide US hunter-kill estimates include South Dakota (2014–15), 1,256,000; California (2014–15), 181,000; Nebraska (2015–16), 166,000; Montana

Fig. 26. Green pheasant male social behavior, including (A) normal facial appearance, (B) facial skin engorgement, (C) crowing, and (D) mutual threat. (In part after Glutz, 1973)

(long-term average), 130,000; Oregon (2014–15), 45,000; Washington (2014–15), 37,000; Colorado (2014–15), 34,000; Wyoming (2011–15 average), 33,000; Texas (2014–15), 11,000; and New Mexico (2014–15), under 100. Because of incomplete or no hunting data for several states, I was unable to estimate overall national kills, but it is unlikely they would have exceeded much more than 2 million.

In Canada, hunters can still legally hunt pheasants on public lands (and on private hunting preserves) in every province except Newfoundland and Labrador. However, Canadian hunter-kill data are very hard to locate. British Columbia and the Prairie Provinces of Alberta and Saskatchewan evidently still support substantial pheasant populations, but their densities appear to be shrinking, at least at their northern range limit. As recently as the 1980s, about 100,000 pheasants were being released

annually for sport hunting in Alberta, where there were about 19,000 hunters, but in recent years some 6,000 Alberta hunters have killed only about 14,000 birds annually.

Habitat Requirements

In North America, pheasants are largely associated with cultivated lands (grains, soybeans, alfalfa, etc.) that have nearby grassy and weedy cover, or shrubby areas such as hedges, ditches, marshy edges, woodland borders, brushy groves, and the like. The birds become increasingly limited to irrigated areas in the western and southwestern parts of their North American range. Ring-necked pheasants do not thrive in areas of heavy snowfall nor in areas of either extreme winter cold or intense summer heat. They have long been especially associated with

Ring-necked pheasant, male hiding in grass

the “corn belt” and associated calcium-rich soils of central North America (Edminster 1954).

The pheasant’s winter habitat, at least in the colder parts of its range, must offer adequate cover extending above snow line and a source of food. These conditions are met in marshes, plum thickets, shelterbelts, and heavy brush in ravines and along fencerows or railroad rights-of-way. Grain such as corn or milo can provide a supply of food, even if it must be scratched out from under a foot or two of snow.

The ideal spring habitat consists of a diversity of cover types that provide food, escape cover, and nesting sites. Fields of alfalfa, sweet clover, or small grains, and fencerows, are favored nesting sites. Roadside ditches, particularly those that have an abundance of early-maturing rather than warm-season grasses, are also valuable for nesting. Brooding habitats must have an abundance of insects, edible green vegetation, and adequate escape and roosting cover.

Food and Foraging Behavior

Very great local, regional, and seasonal differences exist in the foods of this species, which is relatively omnivorous and

opportunistic, tending to consume large and energy-rich foods that are easily available, such as cultivated grains, mast, fruits, and other vegetable matter (Johnsgard, 1986, 1999; Trautman, 1952; Korschgen, 1964; Olsen, 1977; Hill and Robertson, 1988).

The relative abundance of insects and other animal life in the diet also seems to be highly variable, except that in young birds (up to about four months old) it is invariably higher than in adults. Thus, Ferrell, Twining, and Herkenbaum (1949) reported that 20 birds up to 3 weeks old averaged 82.9 percent animal foods, 23 from 4 to 6 weeks old averaged 47.2 percent, 21 from 7 to 9 weeks old averaged 55.1 percent, 31 from 10 to 12 weeks old averaged 12.5 percent, and 34 from 13 to 16 weeks old averaged 1.8 percent.

Mobility and Movements

Significant movements in this species seem to be limited to populations in northern areas that are forced out of breeding areas during winter. In North America, various studies have similarly indicated a rather high level of sedentary behavior (e.g., Gates and Hale, 1974). Cramp and Simmons (1980) have summarized the data for Europe, where in Sweden, Norway, Denmark, and

Ring-necked pheasant, male portrait

Britain movements greater than a few kilometers during a bird's lifetime are unusual, and few if any birds move more than 10 kilometers (6 miles). However, exceptional cases of movements as far as 40 kilometers (25 miles) have been noted in Sweden, and in Finland one adult male was found to have moved 210 kilometers (130 miles) in 13 months.

Vocal Signals

Probably the most important and certainly the most conspicuous vocal signal of male pheasants is their crowing call. This call is loud, sudden, and harsh, typically consisting of two or three syllables, and reportedly sounding rather like *korrk-kok*, *KO-or OK*, *ko-koro* or other transcriptions. It may be audible up to a mile or so under favorable situations and is usually followed by much less audible wing-whirring. During this display, the tail is slightly cocked, or may be held down against the ground as an apparent brace, but the former is more common. These displays may occur every 10 to 15 minutes during the peak of the display season but are most common in early morning and late afternoon. During this and other displays, the facial wattles are engorged and the ear-tufts raised (Figs. 24 and 26).

As many as 12 other adult calls have been described in this species (Heinz and Gysel, 1970). None of these seems to be clearly associated with sexual display, with the exception of hissing, which occurs during intense lateral display and sometimes immediately after copulation.

Social and Reproductive Behavior

Sociality patterns probably vary greatly with population density and levels of disturbance, if not other factors, but at least in North America some patterns have emerged. The study of Collias and Taber (1951) may be representative. They found that during winter the birds formed temporary flocks, in which individuals moved about and fed together as a more or less coherent unit with a shifting membership. Males and females sometimes fed together but also often formed unisexual groupings. Roosting groups during winter varied from two to two dozen birds or more, with larger groups typical of very cold weather.

The locations of roosts varied somewhat, although there were favorite roosting sites. Gradually these groupings changed to harems of hens, with each harem dominated by a single male, as the breeding season progressed. Shifting of male groups from

Ring-necked pheasant, adult females

the period in which they occurred in pairs, trios, or larger groupings to the period of male dispersal and territorial establishment was associated with active increase in testis size, the start of male display toward females, and the onset of intimidation behavior (fighting or threat display) among the females.

Both males and females were found to exhibit dominance hierarchies, which seemed to be related to age and perhaps also to weight. All males were found to dominate all females, and males that began to crow and display early in the season generally dominated the males that began later.

A harem system of mating is well documented for this species, and male success in attracting varied numbers of females seems to be related to relative male-to-male and male-to-female dominance characteristics. Although supposedly "territorial," there is little evidence for well-defined male territories in this species. This may account for the great variations in the sizes of crowing territories as judged by various observers, with estimates ranging from as small as 3 to 4 acres to as large as 25 to 75 acres (Edminster 1954). Taber (1949) accepted the concept of male crowing territories but thought their boundaries were highly plastic and affected by population density as well as by such local environment features as relative cover and

topography. Kozłowa (1947) avoided calling these areas territories and instead referred to them as "cruising routes" because she never saw a male expel another from them. She believed that each route was not more than 400 to 500 meters (1,300–1,600 feet) in length and was regularly traced and retraced by males for both foraging and sexual purposes.

During the winter, mixed or single-sex groups of pheasants congregate in areas of food and cover, but by early spring the males begin to disperse and establish "crowing areas." These areas are not typical territories and have indefinite boundaries, but by his crowing and wing-whirring displays the male may attract a harem of several females. After fertilization the female leaves the male's company to establish a nest, which may or may not be within the area originally occupied and advertised by the male.

Postural advertisement displays of this species have been described and illustrated by Kozłowa (1947), Taber (1949), Cramp and Simmons (1980), and Glutz (1973). One of the most important is wing-whirring, which normally occurs in association with crowing. The male typically selects a prominent location, draws up his body, pauses, and, sometimes after an inaudible wing-flap, utters his crowing call and almost immediately performs a brief but vigorous wing-whirring.

Ring-necked pheasant, male

During the wing-whirring display, the tail might be slightly cocked, or held down against the ground as an apparent brace, more commonly the former. These displays may occur every 10 to 15 minutes during the peak of the display season but are most frequent in early morning and late afternoon. During this and other more obviously sexual displays the facial wattles are engorged and the ear tufts are raised by male ring-necked pheasants (Fig. 24). Similar display posturing and facial engorgement occurs in male green pheasants (Fig. 25).

When two displaying males encounter one another, they may face each other or walk in parallel, holding their tails high, the wattles swollen, and the plumage on the back of the neck erected, while uttering a hoarse *krrrah* note. They may also perform a lateral intimidation display, with wing-lowering on the nearer side as well as tail-tilting and partial tail-spreading, but with the head held high rather than low as in courting (Fig. 25). Or, the birds may face each other with heads held low, rumps raised, and tails straight out behind, sometimes pecking at grass, and uttering purring threat notes. This may grade into actual fighting with biting and kicking by both males (Fig. 25). The subordinate male or loser of an encounter retreats with his feathers sleeked against the body and the wattles retracted. Females may perform similar intimidation displays to one another (Glutz, 1973).

When displaying sexually to a female, the male assumes a lateral ("waltzing") display posture while strutting around the female in semicircles, holding his head somewhat retracted, the nearer wing drooped, the tail tilted toward the female, the body feathers fluffed, and the facial wattle engorged. A vocal hissing sound is often associated with this posturing, and the tail feathers may be vibrated, producing a fluttering sound. As done by many other galliforms, tidbitting (food-offering) is also performed, with an associated vocalization of low notes uttered at the rate of about three per second (Stokes and Williams, 1972) while the bird crouches and holds his folded tail high.

At least early in the mating season, copulation is usually preceded by lateral display or tidbitting, but later the male might simply chase the female and attempt to forcibly mount her. Following copulation the male may hiss and renew his lateral displaying, but no other specific postcopulatory male displays occur.

Nests are normally constructed on the ground, in thick grassy, weedy, or shrubby vegetation. Occasionally, however, elevated sites—such as on straw stacks or in old tree nests of other birds or squirrels—may be used. Relative nest concealment, as influenced by the surrounding height and density of the vegetation, seems to be especially important in site selection; there is less evidence that the overall size of the nesting habitat is important and little or no evidence that the nest location is significantly related to the distance to the nearest habitat edge.

Nests often appear to be clustered within the presumed limits of a male's crowing territory, and perhaps the males adjust their territorial boundaries to include their mates' nest sites (Baskett, 1947; Seubert, 1952). Dumke and Pils (1979) found that females tended to establish their nests less than a half mile away from

their wintering range and typically at the edges of their prenesting range and the territories of associated males.

Nests are a scooped-out depression in the soil to which a lining of feathers and plant materials is gradually added during egg laying. Eggs are laid at the approximate rate of 1.4 days per egg until the clutch of a dozen or more is complete. A Wisconsin sample (Gates and Hale, 1975) had 574 clutches that averaged 11.2 eggs with statistically significant yearly differences in average clutch size and with a seasonal decline in average size as well. Clutches begun after May 15 in Wisconsin—presumably mostly or all renesting efforts—averaged 10.0 eggs, whereas those begun earlier averaged 12.5 eggs. Compound clutches ("dump nests"), resulting from the efforts of more than one female, are not uncommon.

Up to three renesting efforts have been observed following clutch losses. Seubert (1952) observed that 57 percent of 132 females that had been disrupted from or deserted their first nest established second nests, and that 7.5 percent of those disrupted from their second nests attempted a third nesting. In a more recent study, Dumke and Pils (1979) found that 69 percent (32 of 47 birds) of the unsuccessful females they studied renested a first time, 41 percent (at least 11 of 27 birds) renested a second time, and 1 of 11 females renested a third time. All told, these birds averaged 1.8 nests each, and an estimated 75 percent of the females succeeded in producing broods. Four females were found to have renested following the loss of broods.

Incubation by the female alone begins with the laying of the last egg and requires approximately 23 days. The entire clutch hatches almost simultaneously; the female and her newly hatched young may leave the nest only a few hours after hatching. The female attends her brood throughout their juvenile period, usually for six to eight weeks but up to 80 days. Males are not involved in nest protection or with brood care.

By their eighth week of life, young males are beginning to show their sexually distinctive breast coloration, but molt in the young birds continues through the fifth month of life. Both adult females and males also molt during this period. By fall the adults and young begin to gather in fields of ripening grain, from which they gradually move into heavier cover as winter begins.

Females may lead juvenile females into wintering areas, and both sexes are gradually incorporated into winter flocks. Males become sexually mature at one year, but 15 to 29 percent of yearlings might fail to establish mating territories (Cramp and Simmons, 1980).

Evolutionary Relationships

Obviously the nearest relative of the common pheasant is the green pheasant, and the two should be considered no more than allospecies (Johnsgard, 1986), if not only subspecies, as they were so treated in the sixth edition of the *Check-List of North American Birds* (AOU, 1983). Where both of these forms occur together as a result of introductions, they tend to hybridize, and the green pheasant typically suffers (Schwartz and Schwartz, 1951).

III. References

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Northern Bobwhite

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