CHAPTER 1

Grouse Worldwide

ORIGIN OF SPECIES

Grouse are large birds adapted to cold. Creatures of the northern hemisphere, they live in Arctic, boreal and temperate regions, and spend the winter in northern or mountainous habitats without migrating south as many other birds do.[1] Their toes are bordered by small scales or feathers, which, like snowshoes, allow them to walk on snow.[2] A high metabolic rate and the habit of roosting in snow-holes help them to keep warm.[3] They subsist on low-quality but abundant foods such as woody shoots, catkins, buds, twigs, bark and conifer needles.

Molecular evidence shows that the ancestor of all grouse diverged from turkeys[4] in the Miocene (Table 2) and had given rise to all modern genera (Table 3) by about a million years ago.[6] In biogeographical terms, this is a recent and rapid response to climate change. Grouse evolved and diversified during a period[7] of global cooling, when new habitats such as boreal forest and tundra replaced more tropical vegetation in northern regions. This opened a new niche for large birds that could survive on coarse foods through long, cold winters.

The circumpolar distribution of grouse raises the intriguing question of whether the first grouse evolved in the Old World (Palaearctic) or the New World (Nearctic).[8] The continents of Eurasia and North America are geographically close, separated today by just 80km of shallow sea. Periodically, as the earth's orbit takes it further from the sun and an ice age begins, water freezes into continent-sized glaciers, sea levels drop, the lost land of Beringia emerges from the waves, and Alaska and Siberia merge into one (*see* Fig. 1). This facilitates movement of species between the northwestern Nearctic and the northeastern Palaearctic.

TABLE 2. A brief history of grouse.[5]

6 MILLION YEARS AGO	3 MILLION YEARS AGO	ABOUT 3–2 MILLION YEARS AGO	2–1 MILLION YEARS AGO	TODAY
Ancestor of all grouse diverges from turkeys in Nearctic	Ancestral *Bonasa* and ancestor of all other grouse diverge in Nearctic	Ancestral *Bonasa* spreads into Palaearctic and diverges into Nearctic and Palaearctic lineages	*Bonasa* species evolve separately in Nearctic and Palaearctic	*Bonasa umbellus*[N] *Bonasa bonasia*[P] *Bonasa sewerzowi*[P]
		Ancestral ptarmigan (*Lagopus*) spreads north and into Palaearctic	The three ptarmigan (*Lagopus*) species diverge	*Lagopus leucurus*[N] *Lagopus lagopus*[NP] *Lagopus mutus*[NP]
		Ancestor of forest and prairie grouse spreads to Palaearctic, where forest grouse evolve and diverge into ancestral *Tetrao/Lyrurus*, which spreads west, and ancestral *Falcipennis*, which spreads east and diverges into Nearctic and Palaearctic lineages	Palaearctic forest grouse diverges into *Tetrao* and *Lyrurus*	*Falcipennis canadensis*[N] *Falcipennis falcipennis*[P] *Tetrao urogallus*[P] *Tetrao parvirostris*[P] *Lyrurus tetrix*[P] *Lyrurus mlokosiewiczi*[P]

TABLE 2. A brief history of grouse.[5] (*continued*)

6 MILLION YEARS AGO	3 MILLION YEARS AGO	ABOUT 3–2 MILLION YEARS AGO	2–1 MILLION YEARS AGO	TODAY
		Ancestor of forest and prairie grouse spreads south in Nearctic, where prairie grouse evolve	Prairie grouse (*Centrocercus*, *Dendragapus*, *Tympanuchus*) diversify in Nearctic	*Centrocercus urophasianus*[N] *Centrocercus minimus*[N] *Dendragapus obscurus*[N] *Dendragapus fuliginosus*[N] *Tympanuchus cupido*[N] *Tympanuchus pallidicinctus*[N] *Tympanuchus phasianellus*[N]

[N] Nearctic distribution.

[P] Palaearctic distribution.

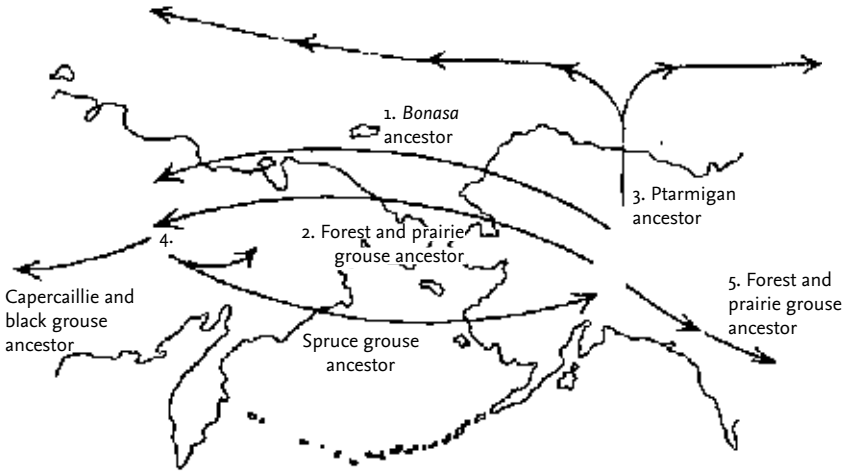

FIG 1. Map of Beringia, indicating today's sea-levels and showing the putative dispersal of ancestral grouse lineages. Arrows show how grouse, having evolved from turkeys in the northwest Nearctic (east), might have colonised the Palaearctic (west): (1) ancestor of all grouse spreads to Palaearctic, giving rise to today's woodland grouse (*Bonasa*); (2) ancestor of forest (*Falcipennis*, *Tetrao* and *Lyrurus*) and prairie (*Tympanuchus*, *Centrocercus* and *Dendragapus*) grouse evolves in Nearctic and colonises Palaearctic; (3) meanwhile, ancestral ptarmigan evolves in Nearctic, heads north and moves around the pole; (4) in the Palaearctic, ancestor of forest grouse begets two lineages – one stays in the Palaearctic, becoming capercaillie (*Tetrao*) and black grouse (*Lyrurus*), the other spreads across Beringia and gives rise to spruce grouse (*Falcipennis*); (5) ancestor of forest and prairie grouse begets prairie grouse. (Drawn by Dave Pullan)

Current opinion favours a northwestern Nearctic origin for grouse, which today are represented by 18–21 species, the number depending upon the authority.[9] In Britain we have four: red grouse (*Lagopus lagopus scoticus*), rock ptarmigan (*Lagopus mutus*), black grouse (*Lyrurus tetrix*) and capercaillie (*Tetrao urogallus*). A likely picture is that the ancestor of all grouse colonised the Palaearctic from the Nearctic via Beringia, giving rise to 'woodland' grouse of the genus *Bonasa*, today represented by ruffed grouse in North America, hazel grouse across Eurasia, and Chinese grouse isolated in the mountains of central China. Other modern grouse fall into three groups of related species: the 'ptarmigan' (*Lagopus*), the 'forest grouse' (*Falcipennis*, *Tetrao* and *Lyrurus*) and the 'prairie grouse' (*Tympanuchus*, *Centrocercus* and *Dendragapus*), the latter represented only in the Nearctic (Table 2).[10]

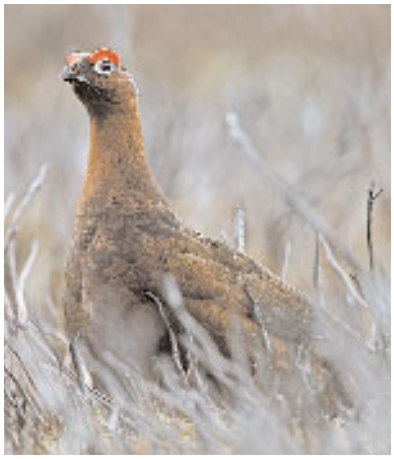

FIG 2. Cock red grouse in spring, standing alert with combs erect among dead grey sticks of burnt heather. (Chris Knights)

FIG 3. Hen red grouse in late summer. She has paler, more barred plumage and smaller, pinker combs than the cock. (David A. Gowans)

FIG 4. Pair of red grouse, with the cock on the left showing bigger combs and darker plumage than the slightly smaller hen on the right. (Desmond Dugan)

FIG 5. Pair of ptarmigan in the Cairngorms during spring, part way between winter and summer plumage. The strutting cock displays his red comb and black feather necklace to the crouching hen, who retains more winter plumage than the cock. They are near the edge of small snow patches, which provide camouflage for the part-white birds. (Derek McGinn)

FIG 6. Capercaillie displaying to his retinue of hens. The orange breast distinguishes hen capercaillie from greyhens. Cock and hens both display white shoulder spots; these are shown by all four species of British grouse during courtship and aggressive display, but their precise function remains unclear. (Desmond Dugan)

FIG 7. Blackcock displaying to greyhen at a lek. (Chris Knights)

TABLE 3. Grouse species today.

RELATED GROUP	SCIENTIFIC NAME	COMMON NAME
Woodland grouse	*Bonasa umbellus* [N]	Ruffed grouse
	Bonasa bonasia [P]	Hazel grouse
	Bonasa sewerzowi [P]	Chinese grouse
Ptarmigan	*Lagopus leucurus* [N]	White-tailed ptarmigan
	Lagopus lagopus [NP]	Willow ptarmigan or red grouse
	Lagopus mutus [NP]	Rock ptarmigan or ptarmigan
Forest grouse	*Falcipennis canadensis* [N]	Spruce grouse
	Falcipennis falcipennis [P]	Siberian grouse
	Tetrao urogallus [P]	Capercaillie
	Tetrao parvirostris [P]	Black-billed capercaillie
	Lyrurus tetrix [P]	Black grouse
	Lyrurus mlokosiewiczi [P]	Caucasian black grouse
Prairie grouse	*Centrocercus urophasianus* [N]	Sage grouse
	Centrocercus minimus [N]	Gunnison sage grouse
	Dendragapus obscurus [N]	Dusky grouse (blue grouse)
	Dendragapus fuliginosus [N]	Sooty grouse (blue grouse)
	Tympanuchus cupido [N]	Greater prairie-chicken
	Tympanuchus pallidicinctus [N]	Lesser prairie-chicken
	Tympanuchus phasianellus [N]	Sharp-tailed grouse

[N] Nearctic distribution.

[P] Palaearctic distribution.

The current distribution of species has been explained by suggesting that the Palaearctic was colonised from the Nearctic on at least three occasions, initially by the ancestor of all grouse, and then separately by two of its Nearctic descendants, first the ancestral species that gave rise to ancestral forest and prairie grouse, and second the ancestral ptarmigan.[11] The ancestral forest grouse evolved further in the Palaearctic and begat ancestral *Falcipennis* and ancestral *Tetrao/Lyrurus*. Ancestral *Falcipennis* spread eastwards through Beringia, and then diverged into the Siberian grouse and the North American spruce grouse, a process possibly initiated when central Beringia was submerged between ice ages and sea separated Siberia from North America. Ancestral *Tetrao/Lyrurus* spread westwards, evolving into two species of capercaillie and two of black grouse. Meanwhile, the prairie grouse developed separately in North America, occupying habitats similar to those used by pheasants and partridges in the Old World.

Although grouse evolved during a period of overall global cooling, the climate oscillated between warmer and colder periods. As habitats became more widespread, species presumably expanded their ranges. When habitats contracted, small populations became isolated. Hence species probably evolved in two main ways. First, during colder periods, glaciers would have separated a widespread ancestral species into eastern and western populations. These would then have evolved into sister species that subsequently expanded their ranges during warmer periods and began to compete with each other. Capercaillie and black grouse are a likely example.

Second, during warmer periods, small populations of an ancestral species would have become isolated in the south as the species' range shifted northwards. The white-tailed ptarmigan in North America, the Caucasian black grouse and the Chinese grouse are obvious examples of new species that evolved after populations became isolated in mountain fastnesses. The white-tailed ptarmigan subsequently expanded its range in North America and now competes with rock ptarmigan and willow ptarmigan. By contrast, the Caucasian black grouse and the Chinese grouse remain isolated.

Today, isolated southern populations have similar potential for evolving into separate species through geographical isolation. Thus the red grouse is evidently diverging from its ancestor, the willow ptarmigan. The main ice-sheet of the last glaciation, when Britain was still connected to the rest of Europe, melted about 11,500 years ago and the North Sea then came into existence. It is presumably since then that the red grouse developed its distinct characteristics, adapting to heather moorland and losing the ptarmigan habit of turning white in winter. British rock ptarmigan and black grouse have presumably been separated from their parent stocks for just as long, but their habitats have not put such selective pressures upon them. British capercaillie, however, probably became extinct in the 18th century and we owe our present stock to reintroductions.[12] Fossil remains show that hazel grouse occurred in Britain at the end of the last glaciation.[13] We know of no evidence of hazel grouse in Britain after the North Sea arose, but it seems likely that they were here.

HABITAT

Many species of grouse are widely distributed, different populations often depending on different plant species. Such apparent complexity is much simplified when we classify habitats in terms of their structure and broad plant classes, rather than individual plant species. For example, capercaillie winter in evergreen forests,

which can comprise species of pine, spruce, fir or even holly.[14] In such terms, each grouse species has quite narrow requirements for particular habitats.

As a group, grouse use many habitats. The three *Bonasa* are birds of mixed deciduous-coniferous forests, using mainly deciduous trees for food and conifers for cover.[15] The hazel grouse inhabits regenerating forest and has quite specific requirements for forest structure, but this can be fulfilled by different tree species and management regimes.[16] The birds need dense deciduous or coniferous cover from ground level up to about 2m in height, closely interspersed with their deciduous food trees.[17] In addition, they seem particularly vulnerable to habitat fragmentation. Silvicultural practices have made potential hazel grouse habitat rare in Britain, but it might be possible to accommodate reintroduced birds in our extensive conifer plantations by providing, for example, pollarded deciduous copses along stream banks.

After the *Bonasa* bloodline had separated from the common ancestor of all other grouse (Table 2), the three other main groups of grouse – ptarmigan, forest grouse and prairie grouse – diverged from one another. In the north, the ancestral ptarmigan gave rise to the three modern ptarmigan species, birds of tundra and Arctic-Alpine habitats, including subalpine scrub. The willow ptarmigan also occupies the edges of bogs and clearings in boreal forest, and the use of heather moorland by red grouse can be seen as an extension of this habit. Where willow and rock ptarmigan occur together, the rock ptarmigan uses drier and more open habitats, often higher up, as in Scotland. Rock ptarmigan are so called because they use rocks or boulders for cover, sidling up to them at the approach of a bird of prey, and hence are usually found on rocky ground. Where all three ptarmigan species occur together, the white-tailed ptarmigan breeds at the highest elevations.

The forest grouse make more use of coniferous trees than *Bonasa*, for food as well as for cover. Spruce grouse and capercaillie feed on pine or spruce needles for much of the year, taking ground vegetation such as blaeberry (synonym bilberry) or other *Vaccinium* species in spring and summer. Both species usually prefer pine as winter food but also eat spruce or other conifers. The Siberian grouse, however, seems to prefer spruce as its winter diet. The range of the capercaillie corresponds largely to that of its main winter food, Scots pine. Similarly, the range of the black-billed capercaillie corresponds largely to that of its different winter staple, Dahurian larch. Black grouse are primarily birds of forest edges and early stages of forest succession, usually avoiding dense forest. They also occur in a wide range of structurally similar habitats such as moors, heaths and rough agricultural fields. Their main winter foods are dwarf shrubs such as heather and blaeberry, but when these are covered in snow they take to trees such

as birch and pine. Caucasian black grouse are birds of the tree-line, where montane forests merge into subalpine meadows.

The prairie grouse apparently diversified in the southern Nearctic. Four species (*Tympanuchus* and *Centrocercus*) live year-round in open habitats that are dominated by grasses and shrubs. The blue grouse *Dendragapus obscurus* occupies a wide range of breeding habitats, from sea-level to above 3,000m in altitude, and from open old-growth forest to shrubby grasslands. Even so, the key component seems to be a mixture of herbs, grasses and shrubs.[18] Although the blue grouse's breeding habitat is relatively open, most populations winter in denser coniferous forest.

STATUS

In Britain, capercaillie are on the verge of a second extinction and black grouse are in steep decline. In both cases this is thought to be due to habitat degradation compounded by climate change.[19] The range of ptarmigan has been much reduced by browsing domestic stock animals, which have degraded to inhospitable grassland many hills that were once clothed in the dwarf shrubs upon which birds of the grouse family rely. Red grouse depend largely upon heather moorland, which in Scotland declined in extent by almost a quarter between the 1940s and 1980s.

Fortunately, the plight of capercaillie and black grouse has been recognised and steps are being taken to improve their habitat. Within its present range, the ptarmigan population seems to be sustaining itself with no further decline. And, though diminished, heather moors and stocks of red grouse, maintained for sport shooting, are probably greater than they would be without management.

Worldwide, the 18 recognised species of grouse are represented by about 130 subspecies. The conversion of natural habitats to agricultural land has led to big contractions in their ranges, especially in temperate lands such as Britain. Species that have large ranges, including remote boreal or Arctic habitats, are under no immediate threat of extinction. Those in most danger depend largely upon habitats threatened by agriculture or have distributions that are restricted for biogeographical reasons. Thus, grouse of North American prairie (*Tympanuchus* spp.) and sagebrush country (*Centrocercus* spp.), having lost much ground to cropland and rangeland, probably depend upon management of the remnant habitat for their survival. Warnings include the fate of the heath hen *Tympanuchus cupido cupido*, a distinctive subspecies of the greater prairie-chicken that became extinct in 1932, and the current plight of Attwater's prairie-chicken *Tympanuchus cupido attwateri*, which may soon be gone. Three species with small distributions – the

Caucasian black grouse, the Chinese grouse and the Siberian grouse – are considered vulnerable. Perhaps the newly recognised Gunnison sage grouse is in most danger, for it has a restricted distribution on degraded rangeland.[20]

WORLDWIDE AND LOCAL PERSPECTIVES

The view that all life on earth is interconnected is becoming more concrete as scientists unravel the complex interplay between the physical and living processes that mould the biosphere. Like a page from prehistory, the biogeography of grouse continues to reflect the evolution of the planet. In subsequent chapters, we shall see how trends and fluctuations in grouse numbers throughout the twentieth century reflected climatic fluctuations and human activities. Climate and mankind are, of course, interrelated. The present plight of capercaillie and black grouse in Britain, for example, is attributable partly to changes in climate, which in turn is influenced by agriculture, deforestation and industry.

Fluctuations in grouse numbers, however, are not mere passive reflections of external forces. Healthy grouse populations rear more than enough young to sustain their numbers. This generates competition for living space between extended families, and that conflict generates unstable fluctuations in numbers, reminiscent of tribal struggles in humans.[21] Less fancifully, it explains the long mystery of population cycles that has fascinated ecologists since their science began.

Apologists for development often argue that the loss of endangered populations is just part of evolution, and that we should accept the inevitable with good grace. Our growing concern for other species, however, is also part of evolution. The gifts that they give us, including a rich enjoyment of natural diversity and insights into our own nature, should be there for our children too.

SUMMARY

Grouse diverged from turkeys in the New World during the Miocene. They occupied boreal forest and tundra, habitats created by global cooling. Modern genera and species evolved from populations that became geographically isolated as their habitats contracted during subsequent climatic oscillations. As habitats expanded again, some species came to overlap, while others remain isolated in restricted ranges. Isolated species, and those that depend largely upon habitats threatened by agriculture, are the most endangered.