a prominent land-mark just west of the present Meteorological Station. Norfolk Island pines are common in many coastal districts of New Zealand, of course, but mature cones are rarely produced. On Raoul, several trees had formed numerous cones which seemed to be fully grown. Raoul Island and Norfolk Island are on the same latitude, but this probably does not explain why the species usually fails to form viable seed in New Zealand.

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WINTER ECOLOGY OF THE PARTRIDGE (*PERDIX PERDIX*) IN THE CANADIAN PRAIRIE

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Of the higher vertebrates living in northern regions of the Northern Hemisphere, birds have a pronounced advantage over mammals in their facility for escaping winter through flight to warm southern climates. Very few birds stay behind when southern migration transfers the vast bird populations to suitable wintering grounds.

In North America more birds are found in winter in the boreal forest (the northern coniferous forest or taiga) than in the prairies to the south. The forest provides more food and shelter and various groups are present such as grouse (Tetraonidae), woodpeckers (Picidae), titmice (Paridae) and others.

FIGURE 1. *Prairie farmland in the Aspen Parkland zone in northern Alberta and Saskatchewan, just south of the boreal forest and the northernmost extensions of the partridge range in North America. Early April 1962.*

The boreal forest gives way southwards to the prairie through an ecotone, the Aspen Parklands, dominated by aspen poplar *(Populus tremuloides)*. Settlement northward from the prairies has appreciably opened up the aspen parklands (Fig. 1), and it is in this zone and in farmland districts cleared in the boreal forest immediately to the north of it that the partridge is found at the northernmost extension of its North American range.

From liberations near Calgary, south-western Alberta, in 1908, partridges spread rapidly north-east and south and now occupy practically all of the Canadian prairie as well as the aspen parklands. Along roads, clearings and settlements penetrating into the boreal forest, small partridge populations are also present.

THE PRAIRIE WINTER

The Canadian prairie, forming the vast habitat of the partridge, measures some 900

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by 400 miles at its northernmost extension. It is almost triangular, to the west bordering the foothills of the Rocky Mountains, to the north a falling line from north of Edmonton in Alberta to Winnipeg, Manitoba; the border to the United States forms the southern geographical limit, but partridges are common in the adjoining states of Montana, North Dakota and Minnesota.

The winter in the Canadian prairie is characterised by temperatures continuously below freezing for 4-6 months and as low as 50°F. below zero, with little snow and little wind. In this area partridges survive winters of an intensity not experienced in their native Europeon range.

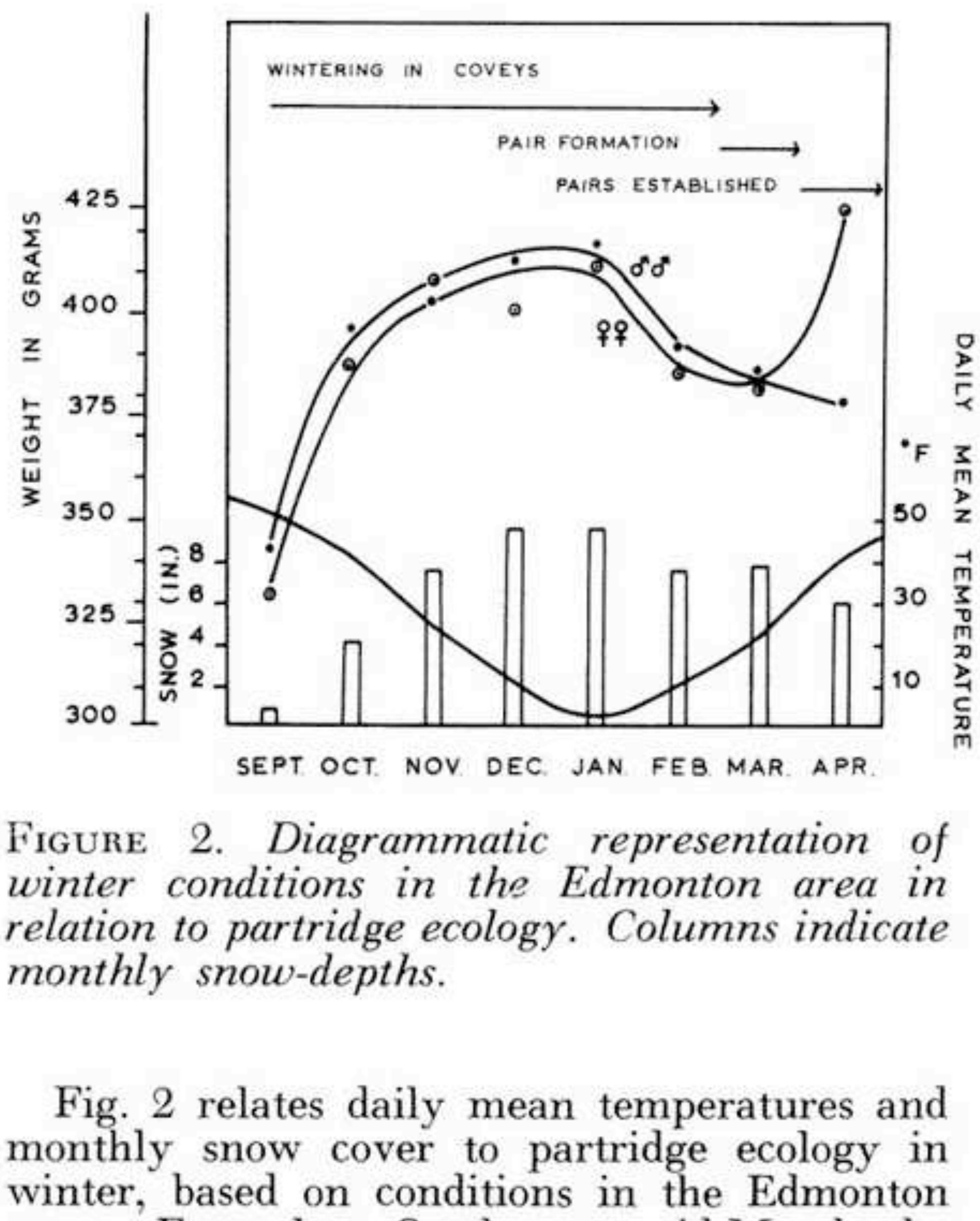

FIGURE 2. *Diagrammatic representation of winter conditions in the Edmonton area in relation to partridge ecology. Columns indicate monthly snow-depths.*

Fig. 2 relates daily mean temperatures and monthly snow cover to partridge ecology in winter, based on conditions in the Edmonton area. From late October to mid-March the temperature is constantly below freezing; a mean minimum temperature of just above zero °F. is reached in January. December-January are also the two months with deepest snow, up to 10 in. Due to easy wind-movement of the fluffy dry snow and evaporation caused by almost continuous sunshine, the snow cover is not uniform; there is for instance less snow on south-facing slopes and open fields.

WINTER BIRDS IN THE PRAIRIES

In the open farm landscape of the prairies the species and numbers of wintering birds are low. Only two passerines, the snow bunting *(Plectrophenax nivalis)* and the redpoll *(Carduelis flammea)* are regularly seen, feeding on seeds of forbs and grasses protruding above the snow; both species are winter visitors from further north and occur in wandering flocks. Magpies *(Pica pica)* are resident and common throughout the area; partridges killed and wounded by cars on the road are eaten by magpies. Two owls are present, the resident great horned owl *(Bubo virginianus)* of the parkland poplar stands, and the snowy owl *(Nyctea scandiaca)*, occuring irregularly as a winter visitor from the north. Usually near hedges, scrub or poplar stands a few pheasants *(Phasianus colchicus)* and sharp-tailed grouse *(Pedioecetes phasianellus)* are seen. Pheasants are more common further south and are here at their very northern limit and do not penetrate into openings in the boreal forest as does the partridge; while sharp-tailed grouse become more plentiful to the north. A few ruffed grouse *(Bonasa umbellus)* are also seen along hedges and near forested areas. Partridges do not compete for food with snow buntings and redpolls, as comparison of food habits showed; partridges are primarily eaters of waste grain during winter (cf. Westerskov in press). Habitat requirements of partridges overlap somewhat with those of pheasants and sharp-tailed grouse, as do food requirements, but they may not compete directly or indirectly; partridges prefer the open field habitat while the other two species resort to scrub and thickets although frequently feeding in the open. Both species of owls occasionally kill partridges.

WINTER ADAPTABILITY OF THE PARTRIDGE

While the partridge belongs to a southern faunal element in Eurasia, the advance of agriculture towards the north has caused an enormous expansion of its range far into the boreal forest biome (Westerskov in press); both in Scandinavia and in Russia. This northward extension demonstrates an ecologic amplitude and plasticity not expected considering the large, long established populations in northwestern Europe with generally mild winters.

Winter temperatures at Edmonton, Alberta (from November-March) are much lower than within the partridge's native European optimum for the species (McCabe & Hawkins 1946:8). Limiting factors in the east appear to be deep winter snow as well as high summer temperatures, in particular high ground temperatures to the south (Westerskov 1964), and excessive summer rain (Dale 1942).

What, then, is the explanation of the outstanding success of the introduction of the partridge in the Canadian prairie? How does this comparatively small bird survive extreme cold in the long winter, in constant snow for months on end?

MORPHOLOGICAL ADAPTATIONS

The partridge, weighing in winter about 400g., is intermediate in size between the small species of quail (as *Colinus* in North America and *Coturnix* in Eurasia), mainly found to the south of its range, and the larger grouse species (as *Pedioecetes* and *Bonasa* in North America and *Lyrurus* and *Tetrastes* in Eurasia), mainly found to the north of its range and associated with the boreal forest. The larger the animal, the smaller its surface area and heat loss in relation to volume. Arctic and sub-arctic species and subspecies are therefore larger than their relatives in warmer climates. The medium-sized partridge can survive extreme cold provided it is properly fed. Its body size may be the safe minimum for efficient heat control and at the same time the maximum possible considering food availability.

To reduce its surface area in cold weather, the partridge pulls its neck in so that its head protrudes only slightly beyond the plumage.

FIGURE 3. *A covey of seven partridges moved across the snow-covered field. Notice how three birds (bottom left) did not sink into the hard wind-blown snow surface, while elsewhere all birds sank in.*

Foot and leg adaptations

When walking on hard wind-blown snow (Fig. 3), partridges do not sink through as do heavier bodied animals. In loose snow, partridges must furrow their way through, but the light snow-fall characteristic of the prairies is a major factor enabling free movement and easy access to food.

While the partridge is not so well adapted to walking on snow as are arctic and sub-arctic species such as snowshoe hare *(Lepus americanus)* and ptarmigan, the comparatively long tarsi (longer than in all three species of ptarmigan and spruce grouse, *Canachites canadensis*) enable it to move unhindered in snow-depths of $2\frac{1}{2}$ in. or slightly more without the abdomen touching the snow.

The tetraonids have feet well adapted to snow conditions: ptarmigan have feathered toes and the wood grouse have horny papillae (comb-like fringes) on the toes in winter. In both cases the supporting surface of the foot is increased, see Table 1. Ptarmigan have a weight loading of 20 g./cm² and while the partridge cannot measure up to some of the snow-adapted tetraonids such as ruffed grouse and sharp-tailed grouse, it is much more capable of moving on snow and has a better weight load: foot surface ratio (48 g./cm²) than either the pheasant or the sage grouse. Best adapted is the snowshoe hare which carries only 10-11 g. per cm².

TABLE 1. *Surface area of foot in relation to body weight of various birds and the snowshoe hare in the northern Great Plains.*

Species, sex, weight, date and place	Surface area of foot, sq. cm.	Loading g./sq. cm.
Snowshoe hare, ♀, 1820g. 7.11.61, Grand Prairie, Alta.	Front 19.2 Hind 64.5	10.9
Willow ptarmigan, ♂, 510g. 6.4.62, Ile-a-la-Crosse, Sask.	13.0	19.6
Sharp-tailed grouse, ♂, 861g. 7.11.61, Grand Prairie, Alta.	13.6	31.7
Ruffed grouse, ♀, 582g. 7.11.61, Grand Prairie, Alta.	8.3	35.1
Partridge, ♂, 390g. 7.11.61, Grand Prairie, Alta.	4.1	47.6
Pheasant, ♂, 1335g. 7.12.61, Tofield, Alta.	10.8	61.8
Sage grouse, ♂, 2870g. 2.5.62, Petroleum Co., Mont.	15.0	95.7

The partridge has a strong foot with comparatively long and broad toes, a typical ground-bird foot adapted to running and scratching. The foot has a further adaptation to cold ground, particularly developed in cold regions: the foot pads are covered with uneven cornified horn papillae in which there are no living cells (Fig. 4). Horn being a poor conductor, the thick cornified layer acts as insulation against frost, which is of much importance to species experiencing the prairie winters. Microscopic comparisons of foot pads of partridge and ptarmigan showed them to be of the same order of thickness although the grooves in the ptarmigan pads were slightly deeper. Madsen and Wingstrand (1959) showed that the horn papillae are especially long and thus efficient in birds which frequently rest on cold ice or rock, such as snowy owls and black shags *(Phalacrocorax carbo)* in Greenland. This adaptation appears to be particularly advantageous to species frequently resting on hard cold surfaces rather than snow, except hard snow.

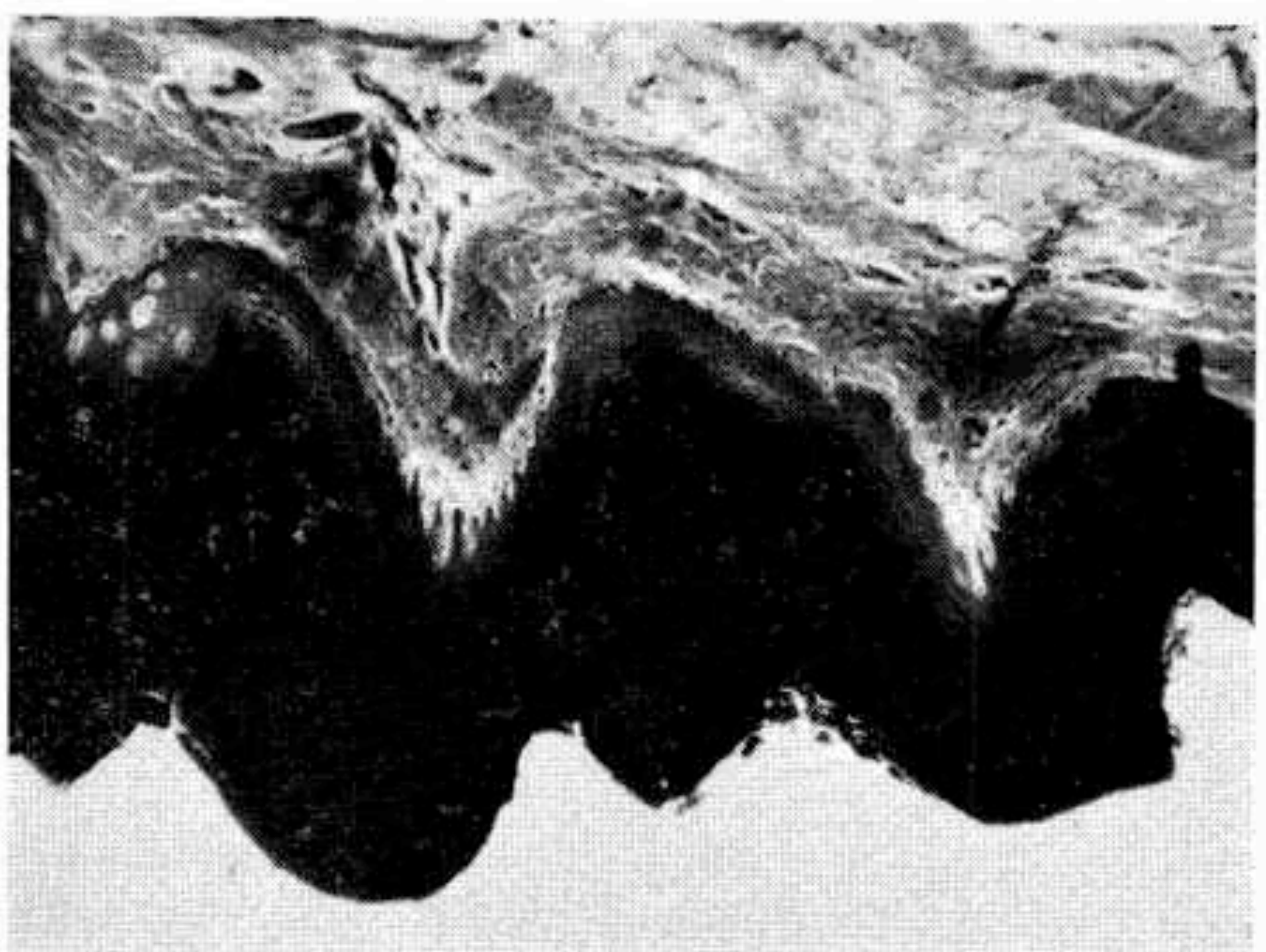

FIGURE 4. *Microphotograph of papillae of foot pad of partridge, Alberta, January 1962. Celloidin sections, 48*x. *Note the thick (dark) cornified layer* (stratum corneum) *in which there are no living cells.*

Adequacy of plumage

The partridge has not the feathered tarsi of the tetraonids, but in cold weather partridges fluff their feathers, partly or fully covering their legs as well as creating a thick, warm layer of insulating air. Moreover the plumage of the partridge is 16% heavier in winter than in summer (Table 2). The main difference is in the amount of body down and feathers with an 18% increase in winter over summer plumage. The winter plumage of the partridge comprises approximately 6% of its body weight and compares favourably with the tetraonids, e.g. 6% in sage grouse and 7% in ruffed grouse.

TABLE 2. *Weight of plumage of partridge and two species of grouse.*

	Weights of plumage, g.			
	Partridge		Ruffed grouse	Sage grouse
	Winter	Summer	Winter	Spring
Body feathers and down	14.07	11.97	25.82	57.04
Wing coverts	4.13	3.60	4.49	18.62
Primaries and secondaries	3.63	3.57	4.46	16.98
Rectrices	0.83	0.48	1.51	4.19
Total weight of plumage	22.66	19.62	36.28	96.83
Body weight	385	375	510	1732
Plumage weight as percentage of body weight	5.9	5.2	7.1	5.6

NOTE. All birds examined were females: partridges, December 1961 and June 1962, Alberta; ruffed grouse, November 1961, Alberta; sage grouse, early May 1962, Montana.

The partridge displays one weakness in plumage not shared with the tetraonids: partridges are thinly feathered under the wings and this may be the cause of their reluctance to flush on exceptionally cold mornings. Exposure in flight of this thinly feathered under-wing means a rapid chilling, aggravated by the rapid intake and circulation of cold air through the air-sacs. This suggestion needs further study, but is supported by the observations of Leopold (1937) that weather-killed bobwhite quail *(Colinus virginianus)* had a coating of ice under the wing.

Winter fat deposits

During the autumn partridges in the prairies increase rapidly in weight (Fig. 2), mainly as a result of the addition of thick layers of subcutaneous and visceral fat.

This depot fat is present primarily in the form of subcutaneous dermal fat in regions of the feather tracts, along the sides of the breast, around neck, base of tail and vent, and on tibia and thigh; a second store is as visceral fat, surrounding the intestines. The subcutaneous fat-layer insulates against heat loss and is a store of reserve energy. The visceral fat in the body cavity is mainly a source of emergency energy.

Both male and female partridges weigh about 70 g. more in January than in September (when there is very little body fat); this additional weight is mostly fat deposits. Body fat yields approximately 8 kcal./g. of fat oxidized; as long as the partridge is well fed or has to rely on depot fat to maintain body temperature for only short periods, it is in no danger. When, however, reserve fat has been used up, the bird has to resort to conversion of its body protein into heat at a yield of only 0.8 kcal./g. of body protein (Kabat *et al.* 1956: 31).

In extreme cold weather in the prairies, partridges consume some 50-75 g. of waste grain and weed seeds daily, a very large intake necessary to maintain adequate body temperature. As one gram of grain furnishes 278 kcal., a daily intake during cold spells of 65 g. of grain yields approximately 180 kcal. A maximum fat accumulation of some 70 g. would yield approximately 560 kcal., if readily convertible, but more work is needed on this point. Consequently, if extreme weather conditions (continuous snow-storm at zero temperatures) forced partridges to survive on stored depot fat, they should be able to survive only some 3 days of starvation. Gerstell (1942: 45) showed that a pair of caged partridges, kept at 0°F. and an air movement of 5.8 miles per hour, survived for 4 days 19 hours (female) and 5 days 20 hours (male). Their weight loss amounted to approximately 40%, showing that not only depot fat but also body protein had been utilized in producing body heat before death.

The body fat in wintering partridges thus not only provides insulation against the cold, it is also a ready source of metabolizable energy which in extreme emergencies can sustain the bird for 3-4 days without food, longer in less extreme temperatures.

BEHAVIOURAL ADAPTATIONS

In their winter habitat partridges reduce their activities to the barest minimum needed to secure sufficient food and grit, safe roosting, and avoidance of predators. They have the one main problem: to obtain sufficient food during the short winter's day of about 8 hours to maintain their high body temperature through 16 hours of darkness.

One of their responses to this demand is extreme economy in energetic output. Field observations showed that on cold days partridges do not fly at all unless forced to, and their only movement, on foot, is from roost to feeding area; but since partridges in this situation usually roost in snow-covered stubble, they roost right on their feeding ground. In this event the only movement during the day is scratching and searching for food on the spot. Their rapid digestion requires constant renewal of grit which they must usually get from roadsides or railway lines. Aside from such movements to collect food and grit, partridge behaviour during winter is characterised by inactivity.

To collect enough food, partridges have to feed almost constantly through the day with only a vestige of slackening in effort during the middle of the day. When not feeding in cold weather, they sit still, maybe preening themselves for a while, then sleeping while one or two birds of the covey act as sentinels. The resting birds are immobile, on lowered tarsi covered with abdominal down and feathers to reduce heat loss from the bare legs, feathers ruffled to trap a thick layer of insulating air, neck drawn in and head bent back, and bill stuck in among the ruffled shoulder feathers. This last action not only reduces the body surface area from which heat is lost; but, more important, the partridge breathes prewarmed air from between its down and thus further reduces heat loss.

Snow roosting

Throughout southern parts of their range, in both Eurasia and North America, partridges winter in areas without snow. In the Canadian prairie, especially in its north-western extension, they have adapted themselves to life in the usually light cover of dry fluffy snow. In Europe and eastern North America, partridges "jug" or huddle (cf. Fig. 5) in a typical roosting pattern; the covey of some 5-10 birds (a family group with possible additions) sits in a tightly packed circle to reduce heat loss and facing outwards so that they can suddenly flush in all directions.

Surprisingly, this well-developed and efficient roosting mechanism is not generally adopted in the northern Great Plains. Examination of a number of roosts and observations of coveys settling down for the night showed without exception that these partridges have adopted the grouse/ptarmigan snow-hole roosting habit. In open fields with a light snow-cover (3-5 in.)

the covey roosts within a square yard or two, with the birds bedded down in the snow either singly or two or occasionally three together; each bird hollows out a depression in the snow so they are sitting on the ground. When roosting, their heads are held low and invariably under the snow-surface; in these small roosting hollows, hidden and sheltered, the partridges sleep comfortably and safely. Because of the low temperatures, the snow is dry and fluffy.

FIGURE 5. *Covey of partridges huddled in tight "rosette" or "jug" on hard blown snow, Ontario, January, 1962.*

Where the snow is deeper, 12 in. or more, partridges adopt the habit of grouse of plunging into the snow, as I observed several times. The covey comes flying and plunges straight into the snow, disappearing from sight. Moving about on or near the ground with a deep but porous dry snow layer above them, they often move forward several yards before settling down. The birds stay in contact with one another through low calling while still moving ahead under the snow. Examination of such snow-roosts showed tunnels and small hollows in which the birds rest, a foot or more under the surface. On two occasions I flushed coveys bursting through the snow and breaking the surface individually and within a couple of square yards.

This habit of digging into the snow to roost is facilitated by the dry snow, characteristic of the northern prairie. It is only towards spring, with thaws during the day and frost during the night, that hard snow-surfaces are experienced, and both roosting and feeding are impeded. Partridges then seek more open ground and in any case do not then experience low temperatures to necessitate their roosting in snow-holes.

Flocking behaviour

The partridge is among the most gregarious of birds and its family ties are strong. From hatching, the brood remains with its parents through summer, autumn and winter till the coveys break up and pairs form in early spring (Fig. 6). There is some interchange of individuals between coveys — but almost exclusively in autumn—as can be seen from occasional changes in numbers of birds in various coveys and from the presence of young birds of different ages in coveys. Pairs that have not reared a brood may join together or join coveys. Winter coveys are of some 6-9 birds, falling slowly through the winter till they break up from mid-March onwards.

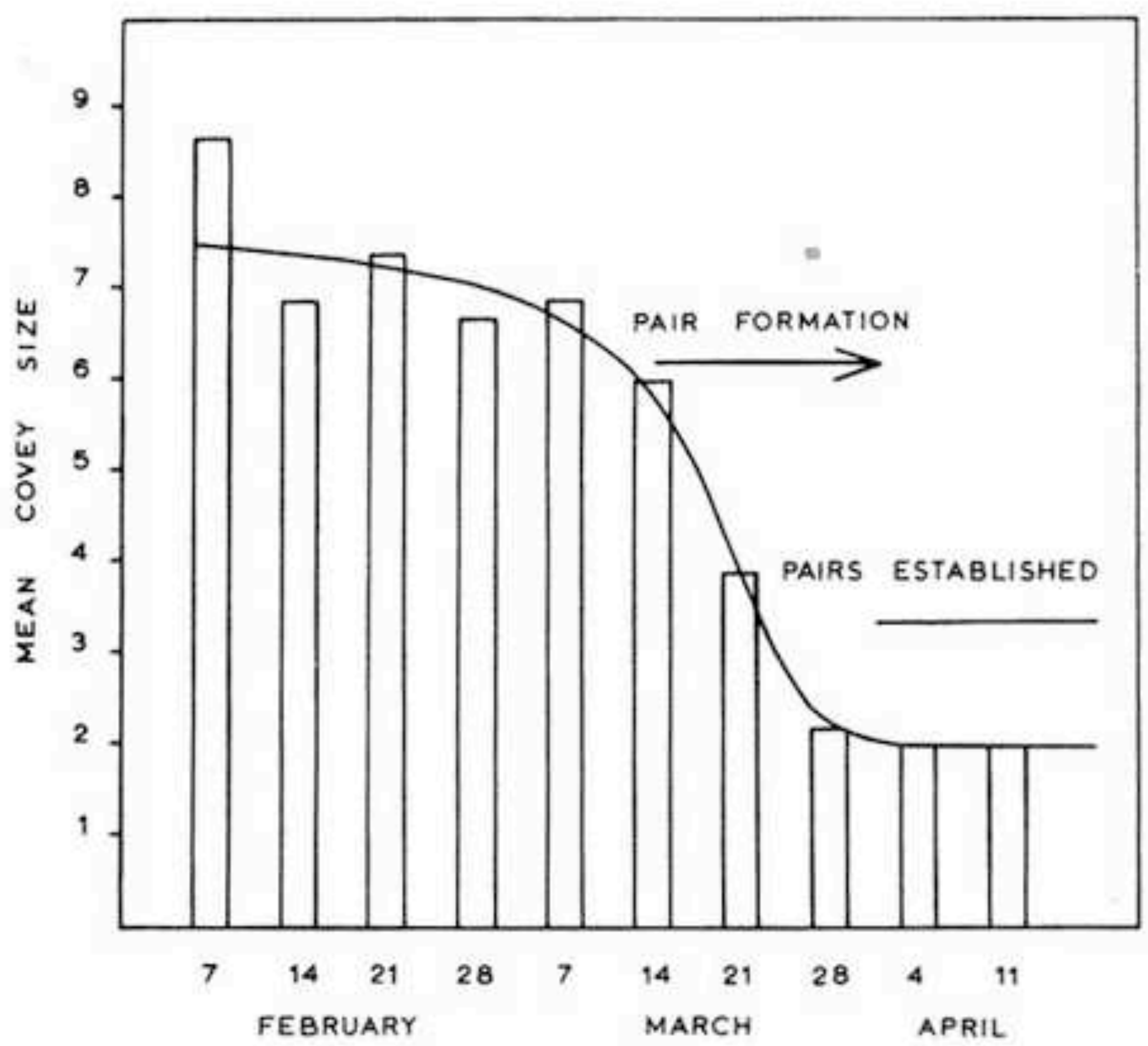

FIGURE 6. *Observations of a total of 403 partridges in 43 coveys and 82 pairs during late winter to early spring, showing time for pair formation.*

Winter flocking behaviour in partridges may be partly an expression of a highly developed specific sociability; but the tenacity with which coveys are maintained and re-grouped, indicates that flocking is an effective adaptation to survival in an open flat habitat, for better protection against predators, for better food location and partly as an aid in heat conservation (through huddling or roosting together or in groups of two or three, closely associated).

CHANGE IN FOOD HABITS

The one outstanding difference between the ecology of partridges in Europe and North America—and probably the main factor accounting for the successful acclimatization and in particular winter survival in the Canadian prairie—is their change in winter food habits.

Food habit studies from Hungary (Vertse *et al.* 1955), Czechoslovakia (Janda 1956), Germany (Brüll & Lindemann 1954), Britain (Middleton & Chitty 1937), Denmark (Hammer *et al.* (1958) and Finland (Suomus 1958) clearly show that throughout its European range the partridge during the winter feeds mainly on green leaf material and to a smaller extent on weed seeds and waste grain. Even in its northernmost range, in Finland, the observations of Suomus (1958) as well as my own (unpubl.) of shorter duration showed that green sprouts, particularly of rye, under the snow were the preferred food. The Czechoslovakian study showed that green foliage made up 70% by volume of total winter food, and in Britain 68% (Middleton & Chitty 1937).

Analysis of 304 partridge crops collected in the northern Great Plains from October to March (Westerskov in press) showed that waste grain made up 68.5% of total food volume, weed seeds 24.8% and green foliage 6.7%. Volume of green foliage eaten dropped from 17.5% in October to 1.3% in December.

Long (1947: 769) showed that the calorific value of grain is about 1261 kcal. per pound compared with 317 kcal. per pound of lucerne leaf (alfalfa). Using this calorific value for lucerne to represent green foliage generally, it appears that on a volume basis grain gives approximately four times more heat than green leaves. Even when feeding on grain, prairie partridges are feeding constantly throughout the day. It is inconceivable that partridges could collect this volume of green material in the time available, nor could they store and utilize in crop and gizzard a four times bigger volume of food per day.

The presence in the prairie farmland of an abundance of high calorific food in the form of waste grain and weed seeds enables the partridge to obtain daily sufficient energy for maintenance. Much grain is left on the ground in stubble-fields after harvest, and trucking of grain to granaries and its transport by rail lead to further wastage.

Finally, because of the practically continuous below-freezing temperatures for months on end, the grain and weed seeds do not rot or germinate, but stay dry and intact on the ground under the light snow. Moreover, the partridges have no difficulty digging through the dry fluffy snow to the ground. Only occasional thaws, especially towards spring, create short periods of difficulty.

Physiologically the partridge is well adapted to sustain appreciable cold. Ecologically it has proved capable of adapting to much colder and longer winters in Canada, where introduced, than in Europe whence it was imported. In the northern Great Plains the partridge has adopted a set of behaviour patterns which permit maximum intake of high calorific food with minimum expenditure of energy.

SUMMARY

Partridges *(Perdix perdix)* were introduced into the Canadian prairie in 1908 and have acclimatized successfully in spite of rigorous winters.

They are morphologically well adapted to exist in cold winters with limited snow: long enough legs and favourable weight load, heavier winter plumage, layers of fat acting as insulation as well as emergency energy. Partridges respond to winter with extreme economy in energy: they never fly unless forced to, and when not feeding sit still with ruffled feathers, tarsi covered, beak among shoulder feathers to breathe pre-warmed air. They roost in a huddle ("jug") on hard snow or in holes in loose snow. Throughout winter they live in coveys, with security against predators.

The major factor in successful winter survival of partridges in the prairies is their change in food habits. In Europe they feed mainly on green leaf material during winter, while in the prairies partridges feed almost exclusively on waste grain and weed seeds. During zero weather a partridge consumes daily some 50-75 g. of grain and weed seeds to maintain body temperature, and only this high calorific food can sustain them; green foliage would require four times the bulk to yield the same number of calories, and could not be obtained or stored and utilized in crop and gizzard in the time available. Both waste grain and weed seeds keep intact, not rotting or germinating in the dry snow in temperatures almost constantly below freezing. So there is an abundant food supply, readily available.

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MORTALITY RATES IN TWO POPULATIONS OF CALIFORNIA QUAIL IN CENTRAL OTAGO, NEW ZEALAND

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Two populations of California quail (*Lophortyx californicus* (Shaw))—one subject to fairly heavy shooting pressure, the other protected—were studied over a number of years to determine the effect of hunting on mortality rates. Both populations were situated in similar habitats in Central Otago. The shot population was at Poison Creek near Queensberry, the protected population at Cairnmuir near Cromwell, about 20 miles away.

Access to both was under some control: shooting at Poison Creek was by permission only and on condition that a full record was kept of the day's bag and all bands returned to the landowner. There is no reason to believe that unauthorized hunting was appreciable or that bands were not returned. Access to the birds at Cairnmuir was under close surveillance and although 29 out of 990 banded in approximately 11 years were recovered by shooting, clearly most, if not all, of these had emigrated from the area occupied by the covey beforehand.

Mortality rates at Poison Creek were calculated in three ways: (i) from bands recovered from shot birds, using these to construct a composite dynamic life table as explained by Hickey (1952); (ii) from capture-recapture data, using a stochastic model devised by Jolly (i.e. 1965); and (iii) from capture-recapture data, using known survivors to construct a composite dynamic life table (Raitt & Genelly 1964).