VEGETATION ANALYSIS OF THE TERRITORIAL BOUNDARY BETWEEN RED GROUSE *(LAGOPUS LAGOPUS SCOTICUS)* AND PTARMIGAN *(LAGOPUS MUTUS)*

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SUMMARY: The location of the boundary between the territories of red grouse *(Lagopus lagopus scoticus)* and ptarmigan *(Lagopus mutus)* is related to the vegetation of the hills where both these species occur. If the vegetation is dominated by tall, vigorous *Calluna vulgaris,* grouse occur. At greater altitudes where *Calluna* is shorter and less vigorous, significant levels of *Empetrum hermaphroditum* and *Vaccinium myrtillus* are also present and such vegetation is occupied by ptarmigan. An hypothesis is suggested in which the actual boundary between the two bird species is related to a critical height of *Calluna*. The different behaviour of the birds in relation to predators may influence the location of the boundary. Grouse shelter in tall *Calluna* while ptarmigan seek rock heaps.

INTRODUCTION

On heather-dominated hills in Scotland, the red grouse *(Lagopus lagopus scoticus)* occurs. On the upper parts of high mountains where there are significant areas above 800 m, ptarmigan *(Lagopus mutus)* replace the grouse. Above 800 m a vegetation dominated by *Calluna vulgaris* is replaced by an arctic-alpine mixed-heath community of *Calluna, Empetrum* and *Vaccinium* spp. with *Salix repens* in some areas. Grouse are thus associated with the *Calluna-dominated* vegetation and ptarmigan with the mixed heath. Grouse are known to feed very largely on *Calluna* while ptarmigan eat a wider range of food plants (see Moss, 1972 for grouse; Watson, 1964 for ptarmigan).

Both species are territorial in the breeding Season (see Watson, 1965 for the yearly cycle of ptarmigan; Jenkins, Watson and Miller, 1963 for grouse). They also mutually exclude one another so that at some point on the hillside a boundary occurs between the territory of a ptarmigan and that of a grouse.

The object of this study was to describe the adjacent habitats of the two species to see if reasons for the location of the territorial boundary could be found.

THE STUDY AREA

The study was carried out during May and June 1977, in two adjacent areas. The first was on Meall Odhar, 920 m (Nat. Grid ref. No. 155774) and the western slope of Glas Maol; the second on the Cairnwell, 932 m (Nat. Grid ref. No. 135774). These stand on either side of a high pass, 670 m, on the A93 road through Braemar and Spittal of Glen Shee (Fig. 1).

METHODS

There were two parts to this study. The first was to establish as precisely as possible the boundary between ptarmigan and grouse territories on the hillside. The second was to analyse the vegetation across this boundary.

1. *Determination of the boundary between ptarmigan and grouse*

Territory-holding cocks of both species can easily be identified by their flight behaviour and their various calls (see Watson and Jenkins, 1964 for grouse; Watson, 1972 for ptarmigan). In particular, the flushing calls and aerial displays with calls in flight are largely restricted to territorial cocks. When the snows are melting in the spring, the males

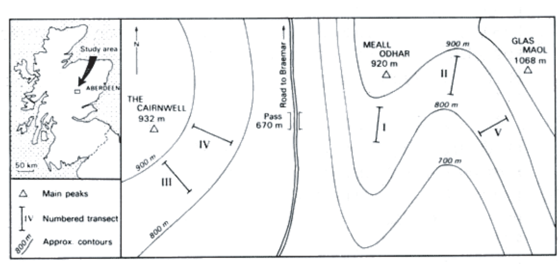

FIGURE 1. *Sketch map of Glen Shee study area (not to scale).*

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are fiercely territorial and vigorously defend the boundaries of their territories.

The ptarmigan and grouse in the study area were located by searching with binoculars and telescope and/or by moving slowly about flushing the birds. The positions of territory-holders seen were recorded on maps and/or marked on the hill with short canes. The locations of all observed interspecific disputes were similarly marked.

The males of both species often stand on prominent rocks and boulder heaps, sometimes giving territorial calls. Observed occurrences were recorded. In addition all likely boulder sites in the study area were visited and searched for droppings and feathers. From these it was possible to identify the species of the normal occupant.

In the first week, when snow covered much of the area, it was possible to track the movements of ptarmigan on the ground from one prominent point to the next. This information was useful in establishing the boundaries of the territories.

On the Cairnwell, there was a prominent ledge marked by rock outcrops. Below this was a steep face with *Calluna-dominated* vegetation and boulder scree alternating. The ptarmigan made much use of these outcrops as sites for "ground song and attack intention" (Watson, 1972). This suggested that the rock outcrops formed a natural boundary between ptarmigan and grouse territories.

When all the information from these observations had been collated a boundary was marked across the slope which it was hoped represented the true inter-specific territorial boundary. The first vegetation plot (20 m X 20 m) was then set up across this line and extending 10 m each way into what were thought to be ptarmigan and grouse territories. This plot was called the boundary plot (plot D, Fig. 2). Thus, even if the true boundary was mis-identified by up to 10 m, it would still fall within plot D.

2. *Analysing the vegetation*

The vegetation was analysed by a series of transects running up and down the slope and across the boundary between the two species of bird (Fig. 1). The transects were also chosen to include different environmental conditions (such as an exposed ridge, a sunny face, a shady face) and also to avoid large screes without vegetation.

Each transect consisted of seven contiguous 20 m X 20 m plots, A (uppermost) to G (lowest). The centre one, D, was the boundary plot referred to above.

In each plot, 25 square quadrats of sides 0.5 m were located using random co-ordinates. Cover abundance was recorded on the Domin scale (Bannister, 1966):

+ = 1 individual	6 = 26- 33 %
1 = 1-2 individuals	7 = 34- 50 %
2 = less than 1 %	8 = 51- 75 %
3 = 1- 4 %	9 = 70- 90 %
4 = 5-10 %	10 = 91-100 %
5 = 11-25 %	

The records of plant occurrence in each quadrat gave a measure of frequency. The quadrat frame was divided up with strings to help the estimation. The following were recorded:

1. The average angle of slope of each plot, measured with an Abney level.
2. The proportion of the plot covered by rock outcrops, boulders or scree heaps. This was estimated visually and checked by noting the number of random co-ordinates which fell on the total rock areas. Quadrats that were totally rock were not included in the 25 used for the vegetation analysis.
3. A cover value for each species of vascular plant in the quadrat.
4. Total cover of lichens and bryophytes. These were not identified to species as they do not contribute significantly to the diet of either bird species.
5. The mean height of *Calluna* to the nearest cm.
6. A cover value for rocks, assigned as for the vegetation.

Detailed analysis of the data was restricted to *Calluna vulgaris*. *Empetrum hermaphroditum, Vaccinium myrtilius* and *V. vitis-idaea*. The first three species make up the bulk of the ptarmigan diet, particularly in winter at the time the territories are set up (Watson, 1964). *Vaccinium vitis-idaea* was inc;udej because it was prominent although it contributes only little (< 2 %) to the diet. For grouse, *Calluna* alone makes up the bulk of the diet (Moss, 1972).

For each quadrat for these four species, the cover data were transformed to a linear scale using the Bannister transformation (Bannister, 1966):

Domin	+	1	2	3	4	5	6	7	8	9	10
Bannister	1	5	10	22	60	70	91	108	137	172	195

These cover data were then summed for each plot and a mean and 95% confidence limits were calculated for each species. The frequency of the species was noted. The mean:!: 95 % limits for the height of *Calluna* was calculated for each plot. Correlation coefficients were calculated for all combinations of mean cover values of the four species and the mean height of *Calluna* (Table 1).

TABLE 1. *Correlation coefficients of association between species*

	Calluna cover					*Empetrum* cover				
	I	II	III	IV	V	I	II	III	IV	V
Calluna height	+0.86*	+0.93*	-0.14	+0.44	-0.76*	-0.89*	-0.27	–0.76*	-0.89*	-0.78*
Calluna cover	-					0.78*	-0.37	+0.73	0.60	-1.00*
Empetrum cover										
V. myrtillus cover										

* p=0.05 when r=0. 71, and p=0.01 when r=0.83 for transects I, II, IV, V (with 6 d.f.)
p=0.05 when r=0.76 for transect III (with 5 d.f.)

Much of the interaction between grouse and ptarmigan occurs before the snow clears. Nesting begins soon after the clearance and before the vegetation shows much spring growth. Thus, in the early quadrats the deciduous *Vaccinium myrtillus* was largely leafless at the time of the study and allowance was made for this when estimating the cover.

RESULTS

1: *Calluna vulgaris* (Fig. 2 (a))

(a) *Height*

The most consistent change through the transects was the change in height of *Calluna*. At the top of the transects it was a dwarf, prostrate form usually heavily frost-burnt. Passing down the transect the height increased until there was a uniform, tall, closed canopy. In transect III, the height appears to be increasing slightly in the upper plots. This was probably because *Calluna* was protected in the top plots by barriers of rock boulders on either side.

(b) *Frequency and Cover* (Fig. 2 (b))

The frequency and cover of *Calluna* was usually close to 100% below the boundary (plot D) and declined above it. This generalisation is modified by areas of late-lying snow or damp seeps which depressed the *Calluna* on, for example, transects II and V. The very steep slope in the lower plots of transects III and IV prevented a uniform canopy of *Calluna* developing. Sheep tracks also reduced the cover in these plots.

2. *Empetrum hermaphroditum* (Fig. 2 (c))

Empetrum showed the reverse trend to *Calluna*. In both frequency and cover it declined from the top to the bottom of the transects. The decline showed a significant (p = 0.05) negative correlation with *Calluna* height, in all transects except II (see Table 1). Snow lay late on this transect inducing growth of *V. myrtillus* rather than *Empetrum*. The decline in *Empetrum* in the upper plots of transect V is related to a greater cover and frequency of *Calluna* away from late-lying snow in the boundary plot. This transect is lower in altitude than the others.

3. *Vaccinium myrtillus* (Fig. 2 (d))

For this species frequency showed little change down the transects but cover values declined from top to bottom in transects I, II and V. This decline was significantly correlated with both *Calluna* height and cover (Table 1). In the two steep transects III anj IV where the *Calluna* canopy is not uniform there was no decline in *Vaccinium*. Overall, the decline of *Vaccinium* is less marked than for *Empetrum* but it should be noted that the amount of *Vaccinium* is always greater, and sometimes appreciably so, than that of *Empetrum*. It is also possible that the cover values of the deciduous *Vaccinium* were underestimated early in the season.

4. *Vaccinium vitis-idaea* (Fig. 2 (e)

This species occurs constantly but with very low cover throughout the transects. No significant overall trends with the height of the plots in the transects can be seen although the very high values in transect V are in plots Band C which were those most affected by late-lying snow. In this transect, *Vaccinium vitis-idaea* is significantly negatively correlated (p = 0.01) with *Calluna* cover and positively with both *Empetrum* and *Vaccinium myrtillus* (Table 1).

As was mentioned earlier, *Vaccinium vitis-idaea* contributes very little to the diet of either species of bird.

DISCUSSION

The most significant difference in plant species across the boundary between the territories of

V. myrtillus cover					*V. vitis-idaea* cover				
I	II	III	IV	V	I	II	III	IV	V
-0.87*	-0.94*	+0.04	+0.49	-0.85*	+0.18	-0.64	+0.20	+0.80*	-0.65
-0.88*	-0.95*	-0.24	-0.16	-0.98*	-0.22	-0.71*	+0.33	+0.50	-0.96*
+0.64	+0.33	-0.23	-0.11	+0.99*	-0.08	+0.27	+0.07	-0.76*	+0.95*
					+0.12	+0.81*	+0.61	+0.06	+0.93*

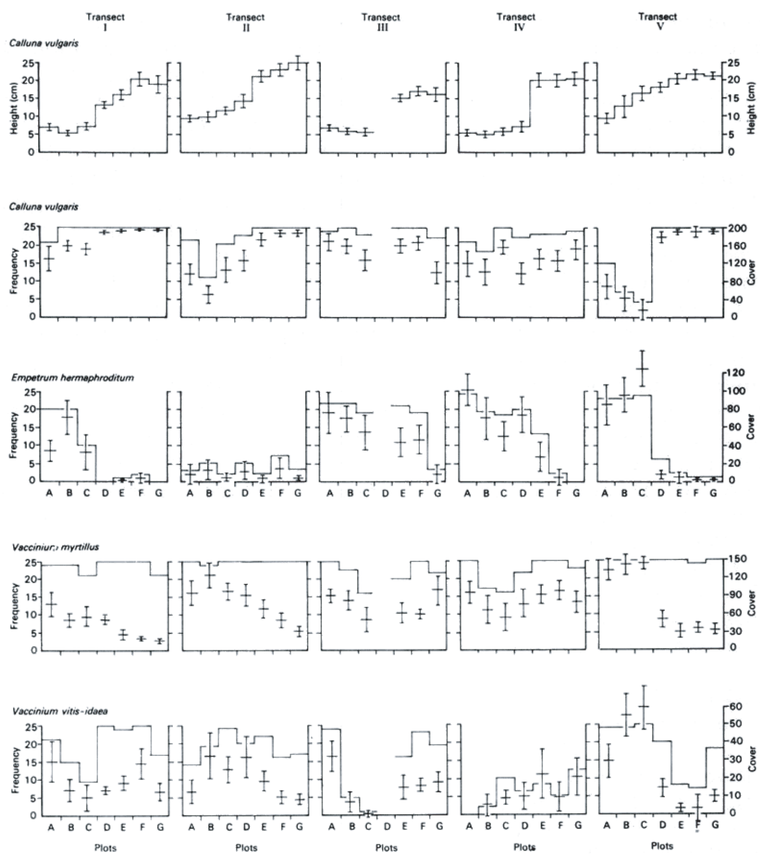

FIGURE 2. *Height of* Calluna *and frequency and cover of* Calluna, Empetrum *and* Vaccinium *spp. along each transect. Row 1: mean height (cm) ± 95% confidence limits. Rows 2-5: frequency in 25 quadrats shown as solid line. scale at left; cover (maximum 195) shown as bar ± 95% confidence limits. scale at right. For each transect, plot A is the uppermost and G the lowest.*

ptarmigan and grouse seems to be the distinctive preponderance of *Empetrum* in the ptarmigan area. There is also a less consistent increase in *Vaccinium myrtillus.*

These changes in turn appear to be related to the growth form of *Calluna.* The results indicate that when *Calluna* forms a uniform cover and reaches a height of roughly 13 cm it inhibits lower growing plants, especially *Empetrum.* In transect IV, *Empetrum* remains high in frequency and cover values in plot D where *Calluna* is short. In transect V, the reciprocal relationship of *Calluna* with *Empetrum* and *Vaccinium* is particularly marked. The relatively high levels of *Empetrum* in transect III, plots E and F are probably due to the rather open canopy of *Calluna* which results from the steepness of these plots. Where the slope is less and the *Calluna* canopy more complete, *Empetrum* is again suppressed.

This relationship between *Calluna* and *Empetrum* has been noted before (Watt and Jones, 1948). They describe a codominance of the two species as an Ecotone between *Calluna*-dominated vegetation below and an *Empetrum IV* accinium-dominated one above.

These results suggest the hypothesis that the separation of ptarmigan and grouse is principally related to the height of the *Calluna* canopy (Fig. 3). In sheltered lowland sites *Calluna* can grow into a bushy shrub over one metre tall (Gimingham, 1960). With increasing altitude in the mountains its height decreases until at its upper limit it has a dwarf prostrate habit often less than 8 cm (Gimingham, ibid). However, the height of *Calluna* is also influenced by exposure. At the same altitude more exposed sites such as ridges and northerly faces have shorter *Calluna* (Watt and Jones, 1948; Poore and McVean, 1957). Exposure is particularly important in the relationship between *Calluna* and *Empetrum* (Watt and Jones, 1948). In the study area, the top of transect V, an exposed site, is below the bottom of transect II, a sheltered site.

Other observations outside of the transects support this hypothesis. The very exposed ridge between the Cairnwell and Carn nan Sac (914 m) to the west is at least 120 m lower than the boundary plots on the Cairnwell sites. The ridge is covered with short *Calluna. Empetrum* and *Vaccinium* and is occupied exclusively by ptarmigan. This ridge is contiguous with two higher areas which support ptarmigan, the Cairn well (932 m) and Carn a'Gheoidh (974 m).

The suppressive effect of *Calluna* can also be seen outside the study area. *Empetrum* and *Vaccinium* can grow quite satisfactorily at lower altitudes. They are, for instance, found abundantly on steep areas and snow hollows where the snow lies late in the season. In both these habitats *Cal una* is absent.

Tile association of grouse with *Calluna* and ptarmigan with mixed heath (particularly *Empetrum)* correlates with their diet. According to Moss (1972), *Calluna* makes up 95 % of the grouse diet in winter and 90% in the summer. On the other hand, a mixture of *Calluna. Empetrum* and *Vaccinium myrtillus* makes up 97% of the ptarmigan diet in winter and 66 % in the summer (Watson, 1964). The summer figure is lower because the fruits and seeds of a variety of species become available in late summer.

The exact location of the boundary may be influenced by other factors than food supply. Most grouse nest in *Calluna* vegetation. In a study of an area about 600 m a.s.l., the *Calluna* at nest sites had a mean height of 17 cm (Jenkins, Watson and Miller, 1963). Grouse with nests or young will crouch when predators such as golden eagles *(Aquila chrysaetos),* a major natural predator of grouse and ptarmigan, fly over (Watson and Jenkins, 1964). The colour of grouse makes them difficult to see in *Calluna* vegetation.

Ptarmigan nests are usually in the open and partly sheltered by a large boulder. When pursued by golden eagle, ptarmigan fly among boulders and scree heaps, swerving to avoid capture by the less agile eagle (Watson, 1972).

Finally, it must be acknowledged that the significance of the results of the vegetation analysis depends on the accuracy with which the boundaries between the territories have been determined. For such purpose, grouse and ptarmigan

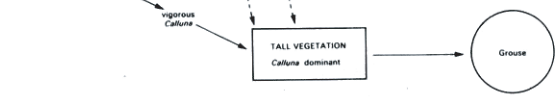

FIGURE 3. *Illustration of the hypothesis that the boundary between the territories of grouse and ptarmigan is principally related to the height of* Calluna.

are ideal species. As Watson (1965) has pointed out, both can be observed from less than 100 m without disturbance. The sexes are easily distinguished and territorial males show very distinctive behaviour. Early in the season they are particularly alert and ready to ward off possible intruders by territorial calls, by display flights and by physical attack where necessary. With the range of clues available, the accurate determination of the boundary is entirely possible. The locations of the transects were chosen where the inter-specific boundaries had been most clearly observed.

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