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On the Ecology of the Vegetation of Breckland: III. General Effects of Rabbits on the Vegetation

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ON THE ECOLOGY OF THE VEGETATION OF BRECKLAND.

III. GENERAL EFFECTS OF RABBITS ON THE VEGETATION¹.

By E. PICKWORTH FARROW

(With Plates I—VI and one Figure in the Text)

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It was shown in Part II that rabbits produce so great an effect upon the vegetation of Cavenham Heath and other heaths of Breckland as to cause the main *Calluna* heath associations to degenerate to grass-heath and to determine the relative distributions of these two main associations². It therefore seemed advisable to devote considerable attention to any other effects which rabbits might have upon the vegetation. It is known that rabbits exert a very great effect upon vegetation elsewhere in the country, and as a single instance the influence of rabbits on the vegetation of Blakeney Point in Norfolk may be cited³.

¹ Part of a Thesis accepted for the degree of Doctor of Science in the University of London.

² **Farrow, E. P.** "Factors Relating to the Relative Distributions of *Calluna* heath and grass-heath in Breckland." This JOURNAL, **4**, No. 2, pp. 57—64.

³ **Oliver, F. W.** "Some Remarks on Blakeney Point, Norfolk." This JOURNAL, **1**, No. 1, pp. 14 and 15.

RABBIT-PROOF FENCES.

In order to see what other effects rabbits might have upon the vegetation, the rabbit-proof fence which runs across the southern end of Cavenham Heath was first examined. This southern fence runs from the point marked 14 to the point marked 15 on the map already given¹. It was erected 14 years ago. There is a sharp change in the character of the vegetation between the two sides of this fence (see Pl. I, Photos. 1 and 2). The difference chiefly manifests itself in the much greater height and luxuriance of the vegetation and in the far greater number of inflorescences on the protected side of the fence. On the unprotected side there are practically no inflorescences and much bare sand is exposed (see Photo. 1).

The area on the protected side of the fence is also far richer floristically than the larger unprotected area of Cavenham Heath, containing many plants which are not found at all on the main portion of the heath, which is subject to rabbit-attack. The following are some of the chief plants which occur on the protected side of the rabbit-proof fence whilst they are either rare or absent on the unprotected side: *Convolvulus arvensis*, *Silene inflata*, *Lychnis alba*, *Ornithogalum umbellatum*, *Lotus corniculatus*, *Geranium molle*, *Crepis capillaris*, and *Achillea millefolium*. Their absence on the unprotected side is probably chiefly due to the far greater amount of rabbit-attack in that position.

A comparison of Photos. 1 and 2 shows that there is a greater difference in the vegetation on the two sides of the fence in Photo. 2 than in Photo. 1. On the protected side of the fence in the region shown in Photo. 2, *Carex arenaria*, *Urtica dioica* and *Agrostis vulgaris* are growing fairly luxuriantly—much more so than the vegetation on the protected side in Photo. 1. This is probably chiefly because the region shown in Photo. 2 is at a lower level and in consequence not so dry as that shown in Photo. 1; so that water supply is probably not so severe a limiting factor to the growth of the vegetation. Although the protected vegetation can thus grow taller in this region yet the vegetation on the rabbit-attacked side of the fence is eaten nearly as close as that shown in Photo. 1, the heavy rabbit-attack keeping it down nearly to the same low level in both cases. Nevertheless the rabbit-attacked vegetation in Photo. 2 forms a somewhat closer turf than that in Photo. 1 and not so much bare sand is exposed.

In the region shown in Photo. 2 it should be noted that *Carex arenaria* is largely dominant on the protected side of the fence, and is absent on the rabbit-attacked side. The heavy rabbit-pressure in this region is sufficient to prevent this plant from effectually invading the rabbit-attacked area by rhizome growth through the fence and thus eventually smothering the grass vegetation.

¹ This JOURNAL, 3, No. 4, p. 217.

Carex arenaria is also present on the protected side of the rabbit-proof fence on the western side of the heath and is absent on the rabbit-attacked side. The same state of things also occurs in various other localities in Breckland.

RABBIT-PROOF CAGE ON THE RELATIVELY PROTECTED SIDE OF THE RABBIT-PROOF FENCE.

A few rabbits occur on the relatively protected side of the rabbit-proof fence seen in Pl. I, Photos. 1 and 2. In order to determine the effect of this small number of rabbits on the vegetation, a rabbit-proof cage was erected on the protected side of the fence¹.

For some time there was only a small difference between the vegetation inside and outside the cage, but *Galium verum*, *Crepis capillaris* and *Sedum acre* grew and flowered appreciably better relatively to the grasses inside than outside the cage (see Pl. II, Photos. 3 and 4), showing that these plants suffered more than the grasses from the relatively few rabbits present on this side of the fence. After a period of three years the difference between the vegetation inside and outside the cage became much more marked, showing that the attack of even a few rabbits may have a considerable cumulative effect on the vegetation. *Rumex acetosella*, *Sedum acre*, *Galium verum*, *Crepis capillaris*, *Carex arenaria*, *Agrostis vulgaris*, *Festuca ovina* and *Holcus lanatus* eventually grew and flowered much better inside the cage than outside. Inflorescences of the four first named plants were either non-existent or very rare outside the cage although they occurred freely inside (see Pl. II, Photos. 3 and 4). It was very apparent that on the whole plants with tall vertical shoots and inflorescences eventually suffer more from increasing rabbit-attack than plants with shoots which can grow very close down to the surface of the soil. Probably vertically growing and tall shoots and inflorescences attract the attention of the rabbits, and are easier for them to cut off than more dwarf growing plants. Such plants in grassland are also usually fewer in individuals per unit area than the grasses and are thus more readily exterminated.

Sometimes ephemerals grow and flower when exposed to fairly heavy rabbit-attack and at first sight these might appear to be exceptions to the generalisation that vertically growing shoots and inflorescences suffer especially heavily from rabbit-attack; but the explanation in these cases probably is that though the ephemerals are as a whole heavily attacked by rabbits, their

¹ By means of rabbit-proof cages the rabbit factor can be entirely removed from the environment and its separate effect studied, if allowance is made for time. It is rarely that we can thus completely isolate an ecological factor in order to study its special effects. Wire netting of one inch mesh should be used, since it is possible that very small rabbits can squeeze through $1\frac{1}{4}$ inch meshes. Wire netting of heavy gauge should be used for the sake of durability.

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short annual period of vegetation exposes them to attack for a considerably less period than is the case with most other plants and that thus some of them manage to survive the rabbit-attack and are able to flower.

RABBIT-PROOF CAGE ON THE RABBIT-ATTACKED GRASS-HEATH ASSOCIATION.

Another rabbit-proof cage (see Pl. III, Photos. 5 and 6) was fitted up on the unprotected side of the rabbit-proof fence in the middle of the degenerate grass-heath association on Cavenham Heath, about half way between the point marked 13 on the map and the present degenerating edge of the *Calluna* heath. The rabbit-attack in the region where this second cage was erected is extremely heavy. The portion of the degenerate grass-heath which was enclosed inside this second rabbit-proof cage quickly began to go back to *Calluna* heath as can be well seen in Pl. III, Photos. 5 and 6. It has already been shown¹ that the *Calluna* roots remain alive in the soil for some time after all the upper portions of the *Calluna* plants have been killed by rabbit-attack and decayed by the damp luxuriant growth of *Cladonia*; and that the still living *Calluna* roots endeavour to send up fresh stems which are however normally quickly eaten off by the rabbits until the roots eventually die. Inside this cage, however, the young *Calluna* shoots produced by the still living roots are protected from rabbit-attack, and they have already grown to a height of 20 cms. and borne many flowers. (See Pl. III, Photo. 6. Note the great contrast between the vigorous and flowering young *Calluna* shoots inside the cage and the closely nibbled down shoots of *Calluna* outside on the right of the photograph.)

Thus it will be seen that the area of degenerate grass-heath enclosed inside this cage is quickly reverting to *Calluna* heath now that the heavy rabbit "pressure" on the enclosed area is removed.

Agrostis vulgaris and *Rumex acetosella* are also growing much better inside this cage than outside and are flowering fairly profusely, whilst outside no inflorescences of these plants can be found, all of them being eaten down by the rabbits. Possibly however one of the most interesting things about this cage is that each summer since it was erected it has contained a number of *Campanula rotundifolia* flowers (see Pl. III, Photos. 5 and 6) although no other harebell flowers occur on the grass-heath outside this cage for a great distance all around, in spite of the fact that the plant itself is present. This is a striking additional instance of the especially injurious effects of rabbits upon inflorescences. These instances make it appear highly probable that the presence of rabbits severely checks the reproduction of many plants by seeds.

¹ "Factors Relating to the Relative Distributions of *Calluna* heath and grass-heath in Breckland." This JOURNAL, 4, No. 2, p. 61.

This particular detrimental influence may well appreciably affect the flora of many regions in England and other countries where rabbits are numerous and ubiquitous.

EFFECTS OF RABBITS ON THE *CAREX ARENARIA* ASSOCIATIONS.

In addition to attacking the *Calluna* heaths and grass-heath areas rabbits frequently attack the dense *Carex arenaria* associations which are so common in parts of Breckland. Rabbits also attack *Carex arenaria* at Blakeney¹.

When the *Carex arenaria* associations in Breckland are competing with grass-heath (degenerated *Calluna* heath) the *Carex* associations are usually badly attacked by rabbits on their external edges, but when the *Carex* associations are competing with *Calluna* the external edges of the *Carex* associations are not usually much attacked by the rabbits. The probable chief cause of this difference in the rabbit-attack on the external edges, as opposed to internal edges, of the *Carex* associations under these two different conditions are dealt with in detail later on (see pp. 10—16).

Areas bare of *Carex* and often occupied by the typical degenerate grass-heath association and sometimes with decaying fragments of *Calluna* frequently occur around collections of rabbit burrows in the large dense *Carex arenaria* associations (see Photo. 6 in Part I)². The *Carex* shoots around these bare areas are always badly eaten by the rabbits.

Many of these large areas of *Carex arenaria* in Breckland were probably fairly recently typical *Calluna* heaths which have completely degenerated owing to rabbit-attack, and have now become replaced by pure *Carex arenaria* associations, except just around the rabbit burrows where the rabbits, after having caused the *Calluna* heath to degenerate, now keep back from their burrows the otherwise spreading *Carex* (cf. the absence of *Carex* on the rabbit-attacked side of the fence seen in Pl. I, Photo. 2). It was the frequent presence of the typical degenerate heath flora along with decaying remains of *Calluna* around rabbit burrows where the dense *Carex arenaria* is now kept back by the rabbits, that first suggested the probability that many of the *Carex* areas were fairly recently typical *Calluna* heaths.

It has already been stated that *Carex arenaria* very likely became established in this now inland district in ancient post-glacial times when the original bay of the Wash extended near to the western border of the district. The *Carex* has thus probably been in the district from ancient times, and could not have continually spread at its present rate or it would be all over the district by now. The probable explanation of the recent rapid spread of *Carex arenaria* in Breckland is that it is due to the presence of rabbits in the district. Rabbits have only been introduced into England since the

¹ Rowan, W. "Note on the Food Plants of Rabbits on Blakeney Point, Norfolk." This JOURNAL, 1, No. 4, p. 274.

² This JOURNAL, 3, No. 4, Plate XVIII.

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Neolithic epoch, and in many instances they have only been preserved from their natural enemies during the last few decades or more recently still. Though they attack *Carex arenaria* they apparently only eat it as a matter of necessity, while they eat *Calluna vulgaris* much more readily. Thus it comes about that, in a zone where *Carex* and *Calluna* are competing, rabbits confer a great relative advantage upon the *Carex* and enable it to spread, owing to the fact that, although they eat it severely, they eat its competitor to a greater extent. This differential action of rabbits upon competing plants has already been mentioned in connection with the degeneration of *Calluna* heath to rabbit-attacked grass-heath¹. It is a striking fact that rabbits should be able to confer such very great relative advantages upon certain species within a given sphere of competition even although they may eat these species very severely.

EFFECTS OF RABBITS UPON THE *PTERIS AQUILINA* ASSOCIATIONS.

The rabbits often also attack some of the fronds of the dense *Pteris* associations which are common in Breckland. They do not appear to like the bracken fronds, which are apparently only attacked when the rabbits are very short of food, or when the alternative food supply consists of some very unattractive plant such as *Erica tetralix*. Only the fronds on the extreme edges of the bracken associations are attacked. The rabbits usually only nibble the softer parenchymatous parts of the frond stalk so that the upper part of the frond topples over, and this usually remains connected with the lower portion of the stalk until the exposed sclerenchyma decays sufficiently for the wind to blow the collapsed upper portion away. Apparently the rabbits only taste the frond stalks, since they usually do not eat them at all extensively even when hard pressed for food. It is very apparent that owing to some cause or other—possibly bitterness or toughness—bracken is not a suitable food for rabbits.

Sometimes, however, when a great depth and area of degenerate grass-heath, associated with many rabbit burrows and innumerable rabbits anxious for extra food, borders upon a bracken association, the total temptation of the rabbits to test the bracken stalks for food is sufficiently great to cause considerable depths of bracken on the edge of the association to degenerate. This has occurred on Cavenham Heath near the spot marked 2 on the map, where the rabbit-attack is extremely heavy.

Usually however the rabbits do not attack the bracken at all extensively, and as the edge of a bracken association advances by rhizome growth, the rabbits which have their burrows on the ground which has recently become occupied by the spreading bracken and which formerly lived on the more

¹ **Farrow, E. P.** "Factors Relating to the Relative Distributions of *Calluna* heath and Grass heath in Breckland." This JOURNAL, 4, No. 2, p. 64.

attractive vegetation previously occupying the ground are driven to go for their food to the more attractive vegetation on the zone immediately outside the advancing edge of the bracken. The result of this is that if, for instance, the bracken is advancing over *Calluna*, there is usually a bare zone, or a zone of *Calluna* degenerating rapidly owing to attack by rabbits coming from the ground recently occupied by the *Pteris*, just in front of the advancing edge of the *Pteris* association. Thus, especially in the cases of large *Pteris* associations which have already covered a large rabbit-occupied area, the advancing edge of the *Pteris* does not have to compete with the *Calluna* which formerly occupied the ground, and for this reason the bracken can advance much more rapidly than if it had had to compete with the original heather. The driven out rabbits eat the heather and thus tend to prepare the way for the advancing bracken. Thus the rabbits through attacking its competitors and scarcely attacking the *Pteris* at all confer a great advantage upon the bracken, which is thereby enabled to spread very rapidly—far more rapidly than it could otherwise do.

When bracken is competing with *Carex*, the presence of rabbits also confers a relative advantage upon the bracken by inflicting a differential rate of injury upon its competitor (as already described) owing to the fact that the rabbits attack the *Carex* more than the bracken; but in this case the advantage conferred on the bracken by rabbits is not nearly so great as where bracken is competing with *Calluna*, since the attack on the *Carex* relatively to bracken is not nearly so great as the attack on the heather relatively to bracken. It is hoped to measure accurately (by means of quadrats and orientated photographs) the relative rates of advance of bracken over *Calluna* and over *Carex* in the presence of rabbits and in the absence of rabbits respectively.

EFFECTS OF RABBITS UPON *JUNCUS* SPP., *SALIX REPENS* AND *ERICA TETRALIX*.

The rabbits also attack various species of *Juncus* on Cavenham Heath (chiefly *Juncus conglomeratus*, *J. obtusiflorus* and *J. supinus*). In some places *Juncus* is attacked very heavily. Often when the *Juncus* borders upon open water the rabbits can only reach the plants on the drier edge of the *Juncus* zone and the plants within reach of the rabbits are usually badly eaten down, all their inflorescences being eaten off, so that they are entirely prevented from flowering, while the plants growing where the water is deeper and thus out of reach of the rabbits produce inflorescences freely.

Sometimes the rabbits also attack young stems of *Salix repens*. They usually only do this however where their alternative food supply is very unattractive.

Erica tetralix is another plant which is not usually much attacked by rabbits at Cavenham. Apparently the rabbits do not like it—possibly this

may be largely due to the hairy nature of the plant. *Erica tetralix* is, however, eaten less reluctantly than bracken. The *Erica*, like *Carex*, *Pteris* and *Salix repens*, is eaten chiefly in places where there is no alternative source of food supply, or where the alternative sources of food supply are about as unattractive as these plants are themselves.

Erica, *Carex*, *Pteris* and *Salix*, all rabbit-attacked under these latter conditions, can be well seen in Photo. 2, Part I¹. In this instance, the rabbit-attacked *Erica* plants are surrounded, on one side by unattractive *Pteris* and on the other side by unattractive *Salix repens*. Under these special conditions, where the rabbits only have a choice of evils for their food supply, all these very unattractive plants are appreciably rabbit-attacked as can be seen in the photograph, and the *Erica tetralix* bushes have even taken on the particular rounded shape without projecting shoots characteristic of rabbit-attacked bushes. Since the rabbits do not eat *Erica tetralix* nearly so readily as they attack *Calluna vulgaris*, they confer a great advantage upon the *Erica* and enormously increase its possible distribution in a zone where it is competing with *Calluna vulgaris*, in spite of the fact that they eat it.

This increase in the distribution of *Erica* relatively to *Calluna* and the resulting raising of the *Erica* zone in a *Calluna* heath owing to the differential action of rabbits upon these two competitors has probably a bearing upon the occasional occurrence of *Erica tetralix* in certain very slight depressions on Cavenham Heath only slightly less dry than the surrounding *Calluna* heath itself, as well as in the much damper hollows. For if the distribution of the *Erica* relatively to the *Calluna* has been greatly favoured by the differential action of the rabbits and the *Erica* zone has thus been raised, the successful competition of the *Erica* with the *Calluna* in those places which are only slightly less dry than main *Calluna* heaths themselves may possibly be partly explained.

EFFECTS OF RABBITS UPON *SOLANUM NIGRUM*, *CONIUM MACULATUM*, *URTICA DIOICA* AND *U. URENS*.

Solanum nigrum, *Conium maculatum*, *Urtica dioica* and *U. urens* are the only herbaceous plants which have been found on Cavenham Heath which are not attacked by rabbits more or less severely in one place or another. It has already been indicated that the heavy rabbit-attack by destroying their competitors and practically not eating these poisonous and stinging plants at all must confer a very great advantage indeed upon them. It is very striking to see for instance a herbaceous *Solanum nigrum* plant green and growing vigorously although it is surrounded on all sides by brown, dead and decaying rabbit-attacked *Calluna* and loose *Cladonia*.

¹ "General Description of Breckland." This JOURNAL, 3, No. 4, Pl. XVIII.

EFFECTS OF RABBITS ON SEEDLING TREES RESULTING IN CONFINING
TREE GROWTH TO THE VALLEYS.

It has already been stated that various artificial plantations of birch and introduced pines have been made upon the upper portions of many of the Breckland heaths—upon Cavenham Heath for instance—although previously there were no tree plantations in the district. Seeds from some of these plantations have apparently been able to colonise some of the minor valleys. In many of these cases (see Photo. 1, Part I)¹ there were very few trees in the valleys 50 years ago, but these have apparently produced much seed and they are colonising the surrounding region with many young trees.

In practically all cases the bases of the stems of these young trees are very badly attacked by rabbits (see Pl. IV, Photos. 7 and 8) and in most instances the young trees die from this rabbit-attack. Though practically all the young trees in the valleys are badly attacked by rabbits, and though most of them succumb to the attack, yet some of them do manage to struggle on and survive it, and when they reach a certain height—apparently about 3 feet in the case of *Pinus sylvestris* on Cavenham Heath—their stems become relatively immune to the more serious effects of the rabbit-attack and the trees can then grow with comparative ease.

By far the greater proportion of those young trees which do manage to survive the rabbit-attack to which all of them are subjected, are those situated near the bottoms of the valleys; and as one passes up the sides of the valleys, a greater and greater proportion of the young trees succumb to rabbit-attack, until near the upper edges of the valleys all the young trees eventually succumb before they can reach a size when they would become immune. The rabbit-pressure, as indicated by the number of rabbit dung pellets per unit area, is approximately constant all over the sides of the valleys, and the survival of the young trees on the lower portions of the valley sides is not due to a diminished intensity of rabbit-attack in these zones.

It appears probable that the true explanation is that near the bottoms of the valleys, where there is a much greater available water supply, the young trees can just produce fresh tissue faster than the rabbits eat it and can often just repair the damage caused by the rabbit-attack and survive it. Thus they just manage to grow and struggle on until they reach a size when they become relatively immune and can grow comparatively easily. On the sides of the valleys where the water supply is much less, the growth of the young trees is retarded and they cannot produce fresh tissue as quickly as the rabbits eat it. Thus they are killed by the rabbit-attack before they can reach a sufficient size to become immune.

A portion of the upper area of Cavenham Heath (marked 16 on the map) near the Icklingham road has been fenced off from rabbit-attack and little

¹ "General Description of Breckland." This JOURNAL, 3, No. 4, Pl. XVIII.

pine trees are growing inside this rabbit-proof enclosure on the dry upper portion of the heath. In this locality the young pine trees can only grow slowly even when protected from rabbits, yet nevertheless they can grow if protected even on this dry upper portion of the heath, while outside the rabbit-proof enclosure on the dry upper areas, pine seedlings are always killed by the rabbits before they can attain any size.

It is thus seen that the rabbits prevent the dry upper areas of Breckland from being colonised by young pines and from being ultimately converted into fairly useful pinewoods. Such pinewoods would probably be of far more value to this island country than are the rabbits. If it had not been for the largely incidental suppression of the natural enemies of the rabbits consequent upon pheasant preserving, a considerably larger area of Breckland would probably now have been converted into subspontaneous pinewoods.

The limitation of tree growth to the damper valley bottoms and sides consequent upon biotic attack on the seedlings, whereas if it were not for this the tree growth would spread all over the drier upper areas, is an extremely interesting biological phenomenon which probably has a great bearing upon the zonation and distribution of natural vegetation in many parts of the world—for instance in parts of Australia. In this connection it is interesting to note that tree growth on the prehistoric steppes of Continental Europe was apparently largely confined to the valley sides¹. Many herbivorous animals were present on these prehistoric steppes, and it seems very possible that the limitation of the tree growth to the valley sides was largely due to the action of biotic attack upon the seedlings, as happens in Breckland at the present day. It is clear that the factor of biotic attack, in addition to the water factor, must be taken into account in considering such cases.

ZONATION OF VEGETATION AROUND RABBIT BURROWS IN BRECKLAND.

It has already been mentioned that areas bare of *Carex* often occur around collections of rabbit burrows in the dense and extensive *Carex arenaria* associations in Breckland (see page 5 and also Pl. XIX, Photo. 6 in Part I). Some instances were observed, however, on Tuddenham Heath, in which *Carex arenaria* is associated with collections of rabbit burrows in *Calluna* heath whilst it is absent elsewhere (see Pl. V, Photo. 9). These cases are very interesting because this distribution of *Carex* in relation to the collections of rabbit burrows is quite opposite to the apparently more usual cases in which the *Carex* is absent around the collections of burrows whilst it is present elsewhere. In order to obtain information with a view to determining the causes of this reversed distribution of the *Carex* in the two classes of cases the transition zone between the *Carex* association, where it is present immediately around

¹ Geikie, J. "The Tundras and Steppes of Prehistoric Europe." *Scottish Geographical Magazine*, 1898.

the burrows, and the surrounding *Calluna* heath was first examined (see Pl. V, Photo. 10). In passing from the *Carex* zone to the Callunetum the *Carex arenaria* shoots and leaves gradually become shorter, weaker and fewer in number, and occur chiefly along the numerous rabbit tracks (see Pl. V, Photo. 10). On the other hand, the *Calluna* bushes gradually become more numerous and of greater height until the typical *Calluna* heath association itself is reached (see Pl. V, Photo. 10). The *Calluna* bushes of the transition zone tend to have the rounded form, with no projecting shoots, characteristic of rabbit-attacked bushes. The transition zone is, in fact, a narrow but otherwise typical zone of *Calluna* heath degenerating through rabbit-attack, with the addition that a generating zone of *Carex arenaria* is associated with it, and with the exception that, in these special cases, a luxuriant growth of *Cladonia* has not up to the present been found associated with the degenerating *Calluna*. Possibly this may be largely owing to the presence of the generating zones of *Carex arenaria*. A comparison of these degenerating *Calluna* zones with those outside large spreading *Carex* associations on the heaths where the *Calluna* is degenerating and the *Carex* is spreading confirmed the belief that these degenerating *Calluna* zones had similar origins, the degeneration of the *Calluna* and spread of the *Carex* being in both cases due to rabbit-attack on the *Calluna*.

The presence of *Carex arenaria* around some collections of rabbit burrows in the *Calluna* heath, although it was absent elsewhere, and its absence around other collections of rabbit burrows whilst it was present elsewhere, thus appeared to be due to the following series of events. Some rabbits originally made a collection of burrows in the *Calluna* heath and brought about the degeneration of the immediately surrounding *Calluna* (see Part II, Pl. VI, Photo. 1). After the surrounding *Calluna* had degenerated, *Carex arenaria* colonised this area relatively bare of *Calluna*, the rabbits eating the more attractive surrounding *Calluna* at the edge of and outside the *Carex* rather than the less attractive *Carex* which was colonising the degenerated area itself; until eventually, owing to the differential action of the rabbits on the *Calluna* and the *Carex*, a fairly large area occupied by *Carex arenaria* on degenerate *Calluna* heath around rabbit burrows in the *Calluna* heath was produced (see Pl. V, Photo. 9). After the *Carex* had colonised these areas the rabbits continued to go to the edge of the more attractive *Calluna* outside the *Carex* for their food rather than eat the relatively unattractive *Carex* which had colonised the area around their burrows. A degenerating *Calluna* zone outside the edge of a spreading *Carex arenaria* association was thus produced¹ (see Pl. V, Photo. 10) and eventually a fairly large area of *Carex* around the collection of rabbit burrows in the *Calluna* heath resulted (see Pl. V, Photo. 9).

¹ Cf. the production by rabbit-attack of a degenerating *Calluna* zone outside the edge of a spreading unattractive *Pteris* association (see p. 7).

It appeared probable also that, as the degeneration of the *Calluna* through rabbit-attack proceeded, and as the resulting *Carex* association increased in diameter, the rabbits from the central burrows eventually had to go so far to reach the more attractive *Calluna* outside the edge of the spreading *Carex* association that, rather than do this, they tended to eat the relatively unattractive *Carex* because it was much nearer to their burrows, thus eventually producing secondary areas around rabbit burrows bare of *Carex* inside the now larger *Carex* associations.

It appeared that if this theory of the origin of the reversed distributions of the *Carex* relatively to the collections of rabbit burrows is true, smaller areas bare of *Carex* would very likely occur around some of the individual burrows in the collection of rabbit burrows which was, as a whole, associated with *Carex arenaria* in the *Calluna* heath. A search for such smaller incipient bare areas around individual burrows in the smaller *Carex* associations was then made and their actual existence was discovered (see Pl. VI, Photo. 11) although they had not been seen before. The actual existence of these small incipient bare areas around individual burrows affords striking confirmation of the theory of the origin of the reversed and apparently anomalous distribution of *Carex arenaria* in relation to the collections of rabbit burrows.

It may be noted that the close association of the *Carex* (seen in Pl. V, Photo. 9) with the collection of rabbit burrows strongly confirms the theory already given (see page 5) that the recent rapid spread of *Carex arenaria* in Breckland and the resulting large *Carex arenaria* associations are associated with and due to the presence of rabbits in the district and their differential action upon the *Calluna* heath and the *Carex*; and do not depend, for instance, upon localised edaphic conditions.

Ordinarily the presence and competition of the *Calluna* prevents the *Carex* from gaining ground on the *Calluna* heaths, but when the *Calluna* heath has partly degenerated from rabbit-attack, *Carex arenaria* can colonise the degenerated area if its seeds are present, the rabbits eating the *Calluna* on the degenerating edge outside the *Carex* association rather than the relatively unattractive *Carex* in the centre. When the *Calluna* has degenerated to a considerable distance from the burrows, the rabbits, rather than go this distance to the *Calluna*, tend to eat the relatively unattractive *Carex* immediately around their burrows, thus producing secondary areas bare of *Carex* around the burrows although the *Carex* is associated with the burrows as a whole.

Thus the reversed and apparently anomalous distribution of the *Carex* in relation to the rabbit burrows is explained. It is the relative distance of the more attractive *Calluna* with resulting variation in the rabbit-pressure on the *Carex* which is the determining factor in the two classes of cases. Both conditions are really different stages fairly wide apart in the same biotic succession. These phenomena are illustrated in the accompanying diagram (Fig. 1). The apparently anomalous case of the

presence of *Carex* immediately around the collection of burrows and its absence elsewhere (see Pl. V, Photo. 9) is developmentally a more primitive condition than the more obvious and apparently more natural case of its absence around the burrows and its presence elsewhere; but when, as often happens, the more attractive *Calluna* has degenerated to a considerable

FIG. 1. The Biotic Zonation of Breckland—Zonation of Vegetation around Isolated Rabbit Burrow. For further description see text, pages 10—16.

distance before *Carex* has colonised a particular collection of burrows, the primitive condition of close association of the *Carex* with the collection of burrows may never occur, owing to the rabbit-pressure on the available food being sufficiently great to keep the spreading *Carex* back from the collection of burrows from the first.

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When the rabbit-pressure is very great, as on Cavenham Heath, and the *Calluna* heath is degenerating rapidly, the rabbit-pressure is often also sufficient to keep down the *Carex* shoots and practically obliterate the normally intermediate *Carex arenaria* zone which would otherwise become apparent, so that the developmentally intermediate *Carex arenaria* zone is practically absent and the *Calluna* heath appears to degenerate directly to grass-heath. The same effect is observed under conditions of less heavy rabbit-attack when *Carex arenaria* seeds and rhizomes are absent, i.e. in those regions which the spreading *Carex arenaria* has not yet reached.

THE BIOTIC ZONATION OF BRECKLAND.

Examination of the accompanying photographs (Photos. 9, 10 and 11) and the explanation which is given above will make it clear that the effect of the rabbits is to produce a particular zonation in the vegetation immediately around their burrows as is illustrated in the accompanying diagram (Fig. 1, p. 13). The centrifugal order of the various vegetation zones in this zoned vegetation around rabbit burrows in Breckland is as follows: 1. (bare sand and lichens), 2. grass-heath zone, 3. *Carex arenaria* zone, 4. typical heath zone (*Calluna* etc.), 5. tree zone (pine woodland, etc.).

This typical zonation of vegetation around rabbit burrows on otherwise uniform and level sandy tracts in Breckland is a very beautiful and striking example of a dynamic vegetation succession or developmental series of conditions produced by the differential effects of the diminishing intensity of biotic attack upon various types of vegetation as the distance from the rabbit burrows increases.

If the intensity of the radiating rabbit-attack from the burrows gradually increases the various zones in the zoned vegetation around them would gradually expand outwards (as is indicated by the arrow heads in Fig. 1) until eventually practically the whole of the area associated with the burrows would become occupied by dwarf grass-heath vegetation.

If, on the other hand, the radiating intensity of the rabbit-attack from the burrows gradually diminished the various zones in the zoned vegetation around them would gradually contract and close up to the centres until eventually practically the whole of the associated sandy area would become occupied by pine woodland.

It is thus seen that variation in the intensity of the rabbit-attack alone is sufficient to change the dominant type of vegetation in Breckland from pine woodland to dwarf grass-heath vegetation through the phases of *Calluna* heath and *Carex arenaria*, and that for each given intensity of rabbit-attack there is a certain associated vegetation. In other words, if the rabbit-attack were non-existent or very slight, pinewood would be the dominant type of vegetation on a particular area. If the intensity of the rabbit-attack were

slightly greater and remained at a certain constant level *Carex arenaria* would tend to be the dominant type of vegetation on the area, and if the intensity of the rabbit-attack were much greater still, grass-heath would tend to be the dominant type of vegetation on the area.

It should be noted however that the presence of *Pteris aquilina* in any locality interferes with the typical biotic zonation of Breckland, for although *Pteris* cannot dominate grass-heath under conditions of extremely heavy rabbit-attack yet it can dominate *Carex* and *Calluna* under all intensities of rabbit-attack.

The following theory to account for this production of zoned vegetation around rabbit burrows in Breckland may possibly be interesting. Suppose the amount of rabbit-attack emanating from the burrows to be gradually reduced to zero, then the *Carex arenaria* of the *Carex* zone which can grow taller than the grasses would gradually invade and smother the more dwarf grasses of the grass-heath zone, and the central grass-heath zone would eventually disappear. The *Calluna* of the *Calluna* zone which can grow taller than the *Carex* would gradually invade and smother the more dwarf central *Carex* zone and the central *Carex* zone would eventually be obliterated. In the same way the pine trees of the outer pinewood zone would gradually colonise the central *Calluna* zone and would eventually smother the more dwarf *Calluna*¹. Probably the enormous advantages that plants which can grow tall possess in being able to dominate and often eventually to exterminate more dwarf competitors largely no doubt owing to interception of the light are not sufficiently emphasised in the existing literature relating to vegetation. Although tall growing plants possess enormous potential advantages over more dwarf competitors yet it will be noticed that all the different kinds of plants concerned in this zonation accord with the generalisation already given on page 3, that taller growing plants eventually suffer more from increasing biotic attack than do more dwarf growing competitors. Increasing biotic attack has the effect of an increasing downward pressure on associated vegetation. It will be noticed that there is an upward gradation in height of the different types of vegetation as the distance from the rabbit burrow increases. Suppose now the biotic attack from the burrows to rise gradually from zero to a maximum. The pinewood round the burrows would eventually disappear owing to death of the old trees and continual destruction of the individual seedlings. The resulting open and well-lighted space could eventually become colonised by the more dwarf *Calluna* which does not suffer so much from the biotic attack as do the seedling trees. When the rabbit-attack immediately around the burrows became greater the *Calluna* heath itself in this position would degenerate and would be replaced by the more dwarf *Carex arenaria*. As the biotic attack from the burrows gradually

¹ Cf. the occurrence of *Calluna* in well-lighted spots in woods. **Tansley, A. G.** *Types of British Vegetation*, 1913, p. 99.

increased the above zones would gradually expand outwards, and the central portion of the *Carex arenaria* association immediately around the burrows would eventually degenerate to still more dwarf grass-heath. Thus the characteristic biotic succession and zonation of the vegetation around rabbit burrows in Breckland would be produced. It will be seen that, if the above theory is true, this interesting zonation largely arises owing to the opposition between the more injurious effects of biotic attack upon taller growing plants and the advantages which taller growing plants would normally possess over more dwarf growing competitors, and that the conditions of the zonation at any time largely represent the effects of a balance between these two opposing influences. Probably there are many other zonations and successions in natural vegetation which depend for their existence upon the opposition and balance between the more injurious effects of biotic attack upon taller plants and the otherwise natural advantages of tall growth. *Indeed the zonation and present dominance and distribution of the different types of natural and semi-natural vegetation in the various parts of the uncultivated portions of the British Isles and of other countries which have been subjected to a large amount of biotic attack by grazing animals may largely depend upon variations in the intensity of the biotic attack in different regions producing variations in the balance between the progressively more injurious effects of increasing biotic attack upon the taller kinds of plants and the great natural advantages which the taller growing plants otherwise possess over their more dwarf competitors.*

SUMMARY AND GENERAL REMARKS.

It is thus seen that in addition to causing the main *Calluna* heaths to degenerate to grass-heaths, which rapidly revert to *Callunetum* on protection from rabbits, these animals also produce various other striking effects upon the vegetation. One of their most important effects is that they are especially injurious to taller growing plants and to inflorescences. *Campanula rotundifolia* and many other plants are entirely prevented from flowering.

The rabbit-attack tends to reduce greatly the number of species of plants present on any area and is especially destructive to various dicotyledonous species, thus tending to favour the growth of grasses relatively to dicotyledons.

The rabbit-attack also limits tree growth to the damper valleys where the young trees can grow comparatively vigorously while if it were not for the rabbit-attack tree growth could spread over and dominate the upper areas.

In addition to attacking the *Calluna* heaths, grass-heaths, and young trees the rabbits also attack the large *Carex arenaria* and *Pteris aquilina* associations which are common in Breckland, and the possible and actual distributions of all these plant associations are very greatly modified by the differential effect of the various intensities of rabbit-attack upon the various competing species. Indeed the chief characteristic of the vegetation of Cavenham Heath is the extreme mobility of the various plant associations

due to the differential action of varying intensities of rabbit-attack upon them in upsetting the balance and thus altering the ultimately dominant types of vegetation.

The vegetation of Blakeney Point is also considerably more mobile than might have been suspected¹. Probably the changes in the vegetation due to topographical changes are more rapid at Blakeney Point than on Cavenham Heath owing to the presence of mobile shingle banks and sand dunes in the former case; but on the other hand, the general changes in the vegetation are far more rapid on Cavenham Heath than on Blakeney Point owing to the greater operation of biotic factors on Cavenham Heath which completely outweighs the comparative absence of topographical changes.

The different intensities of the biotic attack at varying distances from the rabbit burrows produce a characteristic zonation of the vegetation around the burrows on the otherwise uniform sandy plains of Breckland. This zonation is a very striking and beautiful example of a dynamic biotic succession depending for its existence upon the different amount of biotic attack at various points. The existing dominances of the different kinds of vegetation on their various zones around the burrows, and also the existing dominances of the corresponding kinds of vegetation on the ground occupied by the corresponding large *Calluna* heaths, *Carex arenaria* and grass-heath associations of Breckland, ultimately depend for their existence and maintenance upon the existence and maintenance of different intensities of biotic attack upon the vegetation of the corresponding areas, and the respective dominances of these different kinds of vegetation do not depend upon specially localised differences in the soils.

The very complex distributions of these various plant associations on different areas in Breckland was for long unexplained, but we now know that they primarily represent individual developmental phases in a particular degenerative succession of taller vegetation due to the varying intensity of biotic attack at different points².

Ecological factors are sometimes grouped solely as climatic and edaphic, but the highly important biotic factors which are capable of exerting such great influences upon vegetation should probably always be included in the classification, and the extent to which they are or have been present in

¹ Oliver, F. W. "Blakeney Point in 1913." This JOURNAL, 1, 1913, p. 4.

² It is instructive to realise that much time might have been wasted in the first place in examining and analysing the soils under the different plant associations in Breckland on the supposition that the differences in the vegetation were due to differences in the soils. Various differences in the water contents, etc., of the different soils would undoubtedly have been detected, but these particular differences would have been largely consequent upon the occupation of the soils by different kinds of vegetation (owing to differing intensities of biotic attack) and not *vice versa*. These considerations emphasise the advisability when beginning an ecological study of a particular area of spending at first a considerable time in looking round and collecting general information before embarking on laborious work on the basis of merely preliminary hypotheses.

particular cases and their effects should probably always be considered when dealing with the existing zonation and distribution of natural and semi-natural vegetation in any district. Apparently the presence of rabbits alone is sufficient to change the dominant vegetation of Breckland where *Pteris* is absent from pinewood through *Calluna* heath and *Carex arenaria* associations to dwarf grass-heath.

Note on the Effects of Rabbits upon the Vegetation of West Newton Heath, near Sandringham, in North-west Norfolk.

Although rabbits often produce areas bare of *Carex* around collections of their burrows in the dense *Carex arenaria* associations of Breckland, the writer has not yet seen areas bare of the highly unattractive *Pteris* around individual collections of rabbit burrows in the *Pteris* associations of Breckland. Apparently the rabbits eventually prefer to migrate right outside of the spreading *Pteris* associations to a region with more attractive food, rather than to eat the unattractive *Pteris* when it has spread a long way all around their burrows. In Breckland, they are apparently always eventually able to find a more suitable region with more attractive food to migrate to and so are able to avoid ultimately having to eat the unattractive *Pteris*.

The writer has however seen areas bare of *Pteris* around rabbit burrows in a *Pteris* association on West Newton Heath near Sandringham in North-west Norfolk (see Pl. VI, Photo. 12). The rabbits are much less numerous per unit area on this heath than they are on most of the Breckland heaths, but in spite of this, if they are so hungry that they have to eat the very unattractive *Pteris* around their burrows in this locality, the actual rabbit pressure on the vegetation of West Newton Heath must be far greater than that on the Breckland heaths where the phenomenon does not occur. If, in spite of the relatively few rabbits, the actual rabbit-pressure on the vegetation of this North-west Norfolk heath is far greater than that on the Breckland heaths, the results of rabbit-attack observed in Breckland may have a wider application than might otherwise have appeared to be the case. Probably the heavier rabbit-pressure at the present day on the vegetation of West Newton Heath largely arises out of the fact that most of the vegetation now consists of unattractive *Pteris aquilina* and of unattractive *Erica tetralix* so that the rabbits have to eat these plants, and any more attractive plants which remained would probably be very quickly suppressed. The extensive distribution and the great purity of the unattractive *Erica* and *Pteris* associations on West Newton Heath at the present day are thus probably largely due to the cumulative effect of rabbit-pressure in bringing about the degeneration of any more attractive previous plant associations and in ultimately severely eating off more and more rapidly as they became rare any isolated relatively attractive plants amongst the mass of unattractive vegetation.

Photo 1. RABBIT-PROOF FENCE ACROSS THE SOUTH SIDE OF CAVENHAM HEATH—WESTERN END. Note difference in the vegetation on the two sides. On the protected side there are many inflorescences, while on the unprotected side there are no inflorescences, the vegetation is nibbled closely down and much bare sand is exposed. (See page 2 of the text.)

Photo 2. SOUTHERN RABBIT-PROOF FENCE ON CAVENHAM HEATH—EASTERN END (looking in the opposite direction to Photo. 1). Note greater difference in the luxuriance of the vegetation on the two sides. Explanation of this greater difference is given in the text. Note presence of *Carex arenaria* on the protected side of the fence and its absence on the rabbit attacked side. (See page 2.)

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Photo 3. *SEDUM ACRE* FLOWERING INSIDE THE RABBIT-PROOF CAGE ON THE RELATIVELY PROTECTED SIDE OF THE FENCE. The *Sedum acre* flowers can be well seen in the photo. while outside the cage no flowers of this plant occur although the plant itself is freely present. There are also far more *Crepis*, *Carex*, *Agrostis*, *Festuca* and *Holcus* inflorescences inside than outside the cage and the vegetation is considerably more luxuriant as can be seen in the photo. (See page 3.)

Photo 4. *GALIUM VERUM* FLOWERING INSIDE RABBIT-PROOF CAGE. *Galium verum* flowers inside the cage can be well seen in the photo. while outside the cage flowers of this plant are very scarce and those which do exist are very poor. (See page 3.) Note also the luxuriance of the vegetative portions of the *Galium* inside the cage. Outside the cage the vegetative portions of this plant are eaten down very closely by the rabbits.

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Photo 5. RABBIT-PROOF CAGE ON MIDDLE OF THE DEGENERATE GRASS-HEATH ASSOCIATION. Note *Campanula rotundifolia* flowers inside the cage (show whitish) although there are none outside for a very great distance all around. (See page 4.) Note the very vigorous and flowering young *Calluna* stems inside the cage. The grass-heath association inside the cage, which was formerly *Calluna* heath, is very quickly going back to *Calluna* heath now that the rabbit-pressure is removed. (See page 4 of the text.)

Photo 6. *CAMPANULA ROTUNDIFOLIA* FLOWERS AND VIGOROUS FLOWERING YOUNG *CALLUNA* STEMS 20 CMS. HIGH INSIDE RABBIT-PROOF CAGE. The large white objects inside the cage are *Campanula* flowers and the small whitish specks are *Calluna* flowers. The large white objects outside the cage are bared flints, many of them being prehistoric flint implements. Outside the cage any *Campanula* inflorescences and *Calluna* stems are nibbled down very closely to the surface of the sandy soil and are quite unable to produce flowers as can be well seen in the photo. (See page 4.) Note the closely nibbled down and almost flat *Calluna* hummock on the right of the photo, in line with the front of the cage.

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Photo 8. YOUNG *BETULA ALBA* TREE ON VALLEY SIDE WITH STEM BADLY ATTACKED BY RABBITS. Note that the stem has become badly contorted as a result of the rabbit-attack probably owing to uneven release of internal stresses consequent upon uneven eating by the rabbits.

Photo 7. YOUNG *PINUS SYLVESTRIS* TREE IN VALLEY WITH STEM BADLY ATTACKED BY RABBITS. The rabbit-attacked stem can be well seen. It is doubtful if this particular tree will be able to survive the rabbit-attack but it may possibly do so. (See page 9.)

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Photo 9. AREA OCCUPIED BY A RELATIVELY SMALL DENSE *CAREX ARENARIA* ASSOCIATION AROUND A COLLECTION OF RABBIT BURROWS IN A *CALLUNA* HEATH—TUDDENHAM HEATH. The photo. shows a phenomenon which is of very great interest in view of the fact that the *presence* of the *Carex arenaria* around the collection of rabbit burrows and its absence elsewhere appears to be exactly the opposite to the frequent and apparently more natural instances in which the *Carex* is *absent* around the collections of rabbit burrows while it is present elsewhere. (See page 10.)

Photo 10. TRANSITION ZONE ON EDGE OF A *CAREX ARENARIA* ASSOCIATION AROUND A COLLECTION OF RABBIT BURROWS IN A *CALLUNA* HEATH. (Note also *Carex arenaria* around another collection of rabbit burrows in the middle distance.) Note that the *Carex arenaria* shoots and leaves gradually become fewer in number, less in height and weaker in this transition zone, occurring chiefly along the rabbit tracks, while the *Calluna* bushes gradually become greater in height as the typical *Calluna* heath is entered. This is a rather narrow zone of *Calluna* heath degenerating through rabbit-attack but a generating zone of *Carex arenaria* is associated with it. (See page 10.)

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Photo 11. SMALL INCIPIENT GRASS-HEATH AREA BARE OF *CAREX* AROUND INDIVIDUAL RABBIT BURROWS IN AN AREA OF *CAREX* WHICH IS, AS A WHOLE, ASSOCIATED WITH RABBIT BURROWS IN *CALLUNA* HEATH. The discovery of these small incipient bare areas around individual burrows affords striking confirmation of the theory relating to the apparently anomalous and reversed distribution of the *Carex* in relation to the collections of rabbit burrows. (See page 12.) Compare the zonation of the vegetation seen in the picture with that indicated in the diagram, Fig. 1, page 13 in the text.

Photo 12. AREA BARE OF *PTERIS* AROUND RABBIT BURROWS IN A *PTERIS* ASSOCIATION ON WEST NEWTON HEATH, NEAR SANDRINGHAM. An area associated with rabbit burrows and almost devoid of *Pteris* fronds can be well seen in the photo. This phenomenon is rare in East Anglia and the writer has not yet seen it in Breckland. (See page 18 of the text.)

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