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THE RELATIONSHIP BETWEEN HERRING GULLS AND THE VEGETATION OF THEIR BREEDING COLONIES

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SUMMARY

(1) A survey of the vegetation of eleven sites affected by herring gulls along the Aberdeenshire coast and on the Isle of May (Firth of Forth), and of adjacent unaffected areas, revealed that the vegetation of gull-affected sites consisted of a seasonal, species-poor community, in which annual and ruderal species predominated. Of particular prevalence were *Atriplex hastata*, *Holcus lanatus*, *Poa annua*, *Rumex acetosa*, *R. crispus*, *Stellaria media* and *Tripleurospermum maritimum*. By contrast, the vegetation on adjacent areas unaffected by gulls was generally a perennial grass sward in which *Festuca rubra* was the dominant species.

(2) Observations from a hide at two study sites revealed that four principal gull activities affect the vegetation of breeding sites: treading, the digging of scrapes and collecting of nest-materials, boundary clashes associated with gull territorial behaviour, and defecation. Each of these activities had an uneven spatial distribution within the colony area. Although all four activities exerted important influences on the vegetation, disturbance and destruction of vegetation associated with boundary clashes appeared to be a particularly significant activity for the plants occurring in gull colonies.

(3) Experimental fieldwork involving the removal of vegetation (to simulate the ultimate effects of gull disturbance) also revealed the importance of disturbance. Annual plants (*Stellaria media*, *Atriplex patula* and *Senecio vulgaris*) became established on an area formerly occupied by *Holcus lanatus*.

(4) Mapping of the distribution of plant species within the two study sites over a 2-year period suggested that although gulls were responsible for the vegetation of the colonies as a whole, factors other than gull activities played a more significant role in determining the detailed distribution of plant species within the colonies. At the sites studied, differences in soil-nutrient concentrations and sea-spray deposition appeared to influence the distribution of particular species.

(5) A glasshouse experiment suggested that edaphic factors might operate to exclude ruderals (particularly *Urtica urens*) from the poorest soil. On the richer soils, on which all species grew well, biotic factors such as interspecific competition might determine the distribution of the different species.

INTRODUCTION

Botanists have long recognized the special character of the vegetation associated with sea-bird colonies; however, few attempts have been made to determine how the birds are

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responsible. There has been a marked tendency after a visit to a bird colony and a brief description of its vegetation to sum up factors controlling such vegetation with an elaborate label: for example, zooplethismic (animal-increased—Poore & Robertson (1949)), ornithogenous (bird-created—Breslina & Karpovich (1969)), coprophilous (dung-loving—e.g. Chapman (1964)), ornithocoprophilous (bird-dung-loving—Gronlie (1948)) and nitrophilous (nitrogen-loving—e.g. Summerhayes & Elton (1928)). As some of these labels suggest, nutrient-enrichment from faeces has frequently been assumed to be the principal (or even the sole) effect of sea-birds on vegetation, and any studies which have gone beyond the mere description of vegetation (Russell 1940; Gronlie 1948; Gillham 1956; Géhu & Géhu-Franck 1961) have tended to emphasize soil-nutrient levels. No botanical studies have involved direct observations of bird activities under undisturbed conditions, to determine in what other ways birds might affect vegetation in their colonies.

Herring gulls, *Larus argentatus* Pontopp. (and other large gulls), are likely to have an effect on the vegetation of their breeding sites greater than most other sea-birds—with the possible exception of burrowing birds such as puffins (*Fratercula* spp.) and shearwaters (*Puffinus* spp.). Whereas many sea-birds nest on sheer cliffs possessing little or no vegetation, herring gulls require a flat surface on which to build their loosely-structured nests—areas more likely to have a vegetation cover. Though pairs have been known to nest singly, most herring gulls breed in colonies, which are generally near the coast and usually directly beside the sea. Within the colony each pair establishes a nest on a territorial area from which other birds are excluded. Sites selected as colonies include flat or gently-sloping areas which are inaccessible to predators, such as areas at the base of cliffs, offshore stacks and rocks sufficiently out of reach of tidal and wave action, and cliff-tops of pronounced slope. In areas with expanding gull populations, more accessible sites such as sloping banks and the tops of cliffs are also colonized, and on coastlines lacking any cliffs herring gulls frequently breed on sand-dunes. Along the Aberdeenshire coast, where this study was carried out, the vast majority of gulls nest on cliff-sites.

Herring gulls are one of the most abundant sea-birds along much of the coast of Britain (Cramp, Bourne & Saunders 1974) ('coastal bird' is a more apt term), and in Britain and elsewhere there has been a significant increase in numbers during this century, with an increase in the size and distribution of breeding colonies (e.g. Kadlec & Drury 1968; Harris 1970; Parsons 1971). On some areas, such as the Isle of May in the Firth of Forth, Scotland, this increase has been considered so detrimental to both the flora and fauna that control measures have been directed against herring gulls (Sobey 1976).

In spite of the drastic gull-control measures resorted to at some sites, the effects of herring gulls on the vegetation of their breeding colonies have never been studied in detail. The purpose of this study was to determine relationships between herring gulls and the vegetation of their breeding colonies; more specifically, to describe in detail the vegetation of herring gull colonies; to determine the activities of the birds affecting the vegetation of colonies; and, by relating the two, to attempt to account for factors controlling the vegetation.

Nomenclature of vascular plants follows Clapham, Tutin & Warburg (1962).

A SURVEY OF THE VEGETATION OF HERRING GULL COLONIES IN NORTH-EAST SCOTLAND

The vegetation of eleven gull-affected sites, ten of which were on the Aberdeenshire coast between the Ythan estuary and Peterhead, was assessed between 1970 and 1972 (Fig. 1).

The eleventh site was on the Isle of May in the Firth of Forth. All the sites were on coastal cliffs, stacks or banks. At most of the sites vegetation unaffected by gulls on adjacent areas was also described, to enable a comparative assessment of the two types of vegetation.

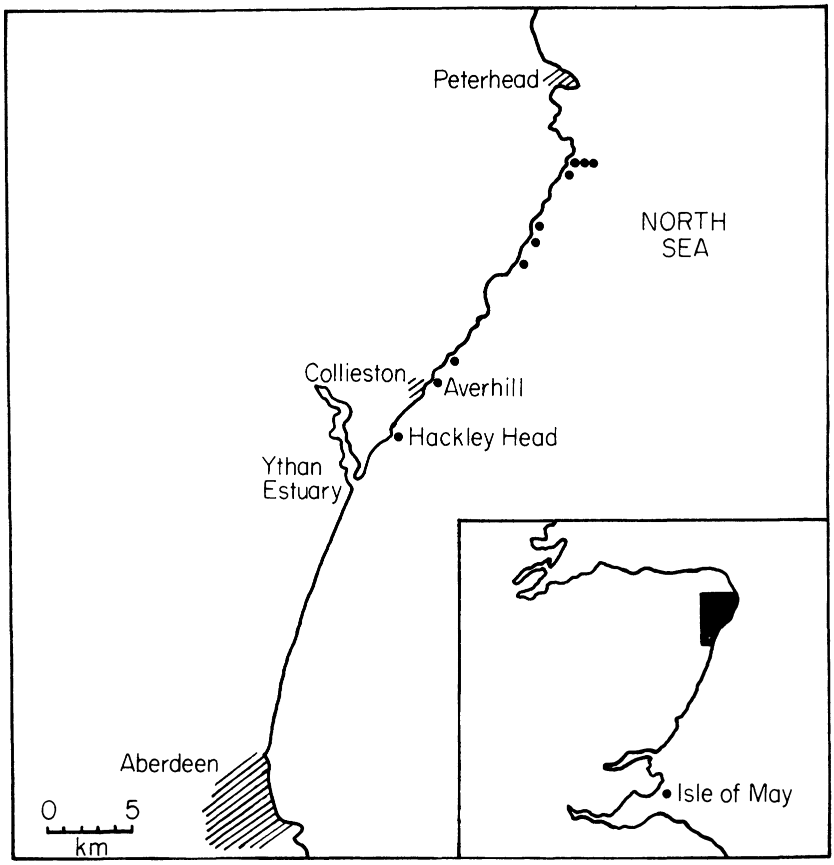

FIG. 1. The north-east Scottish coast, showing the location of the eleven gull-affected sites assessed in the survey (•).

Detailed descriptions of the individual sites are given by Sobey (1975), and only simplified floristic lists are presented here (Table 1). For each species the life-form and the habitat preference as designated by Clapham, Tutin & Warburg (1962) are listed, and the British distribution as shown in the *Atlas of the British Flora* (Perring & Walters 1962). Examination of Table 1 indicates marked differences between gull-affected and unaffected sites in a number of floristic features, and the more important of these differences are summarized in Table 2.

Results

Of the forty-one plant species occurring on the eleven sites affected by gulls, twenty-eight were classified as either 'abundant and widespread' or 'locally important' (Table 1). Within any one area, far fewer than twenty-eight species were found, and in fact large

TABLE 1. The plant species of eleven coastal sites in north-east Scotland affected by gulls and of eleven adjacent sites unaffected by gulls (casual species omitted); The following symbols are used:— Life-form: Th = therophyte, H = hemicryptophyte, Ch = chamaephyte, G = geophyte; British distribution: U = ubiquitous (universally distributed throughout Great Britain), M = maritime (species with distribution almost completely confined to coastal 10-km squares); habitat preference: R = ruderal (species designated by Clapham, Tutin & Warburg (1962) as occurring in waste places, disturbed ground, arable land or roadsides); G = grassland (species designated by Clapham, Tutin & Warburg (1962) as occurring in grassy places, grassland, meadows or fields); M = maritime habitats

Gull-affected sites	Life-form	British distribution	Habitat preference	Unaffected sites	Life-form	British distribution	Habitat preference
Abundant and widespread species				Abundant and widespread species			
*Atriplex hastata**	Th	M*	M	*Agrostis tenuis*	H	U	G
Cochlearia officinalis	H	M	M	*Festuca rubra*	H	U	G/M
Heracleum sphondylium	H	U	G/R	*Holcus lanatus*	H	U	R/G
Holcus lanatus	H	U	R/G	*Poa pratensis*	H	U	G
Poa annua	Th/H	U	R	*Rumex acetosa*	H	U	G
Rumex acetosa	H	U	G				
Rumex crispus	H	U	R				
Stellaria media	Th	U	R				
Tripleurospermum maritimum ssp. *maritimum*	H	M	M				
Locally important species				Locally important species			
Agropyron repens	H	U	R	*Armeria maritima*	H/Ch	M	M
Agrostis stolonifera	H	U	G/R	*Angelica sylvestris*	H	U	G
Armeria maritima	H–Ch	M	M	*Cochlearia officinalis*	H	M	M
Atriplex patula	Th	U	R/M	*Heracleum sphondylium*	H	U	G/R
Cirsium arvense	G	U	R	*Koeleria cristata*	H	M**	
Cochlearia danica	Th	M	M	*Leontodon autumnalis*	H	U	G
Festuca rubra	H	U	G/M	*Ligusticum scoticum*	H	M	M
Matricaria matricarioides	Th	U	R	*Lotus corniculatus*	H	U	G
Poa pratensis	H	U	G	*Plantago lanceolata*	H	U	G
Polygonum aviculare	Th	U	R/M	*Plantago maritima*	H	M	M
Puccinellia capillaris†	H	M	M	*Potentilla erecta*	H	U	G
Rumex acetosella	H/G	U	G	*Ranunculus acris*	H	U	G
Senecio vulgaris	Th	U	R	*Silene maritima*	H	M	M
Senecio jacobaea	H	U	R/G	*Trifolium repens*	H/Ch	U	G
Silene maritima	H	M	M				
Spergula arvensis	Th	U	R				
Spergularia marina	Th	M	M				
Urtica dioica	H	U	R/G				
Urtica urens‡	Th	U‡	R				

* *Atriplex hastata*—the maritime form of the *Atriplex hastata* aggregate (which according to the *Flora Europaea* (Tutin *et al*. 1964) includes *A. glabriuscula* and *A. babingtonii*).

† *Puccinellia capillaris*—distribution and habitat preference are taken from Hubbard (1968).

‡ *Urtica urens*—though locally absent, it is widespread in lowland Britain.

** *Koeleria cristata*—a maritime distribution in Scotland; habitat-listing is 'sandy places'.

areas—often nearest the sea—supported only a few or even a single species. In adjacent areas unaffected by gulls, fifty species were recorded, of which nineteen were 'abundant and widespread' or 'locally important' (Table 1).

TABLE 2. A comparative assessment of gull-affected and unaffected sites in terms of the life-form, British distribution and habitat preferences of the 'abundant and widespread' and 'locally important' species listed in Table 1; numbers of species in each category are given

	Gull-affected sites	Unaffected sites
Life-form		
Therophyte	11*	0
Hemicryptophyte	16	19
Geophyte	1	0
British distribution		
Maritime	8	6
Ubiquitous	20	13
Habitat preferences		
Ruderal	9	0
Ruderal or grassland	5	2
Ruderal or maritime	2	0
Grassland	3	11†
Grassland and/or maritime	1	1
Maritime	8	5

* One of these species, *Poa annua*, is sometimes a short-lived perennial.

† *Koeleria cristata*, listed by Clapham, Tutin & Warburg (1962) as occurring in sandy places, is classified here as a grassland species.

Eleven of the twenty-eight species of importance on gull-affected areas were therophytes (i.e. annuals) (Table 2), a life-form completely absent in the non-affected areas. These eleven annuals were of considerably greater importance in terms of ground-area coverage than the sixteen hemicryptophytes and the one geophyte. By contrast, on the non-gull areas the vegetation consisted entirely of perennial hemicryptophytes, with grass species predominating.

Associated with this dominance by annuals in gull-affected sites were marked seasonal changes in the vegetation—the lush growth of summer at some sites contrasted markedly with the bareness of the same areas in winter, when soil erosion appeared to be a significant factor, particularly on slopes. There were also seasonal differences of a less obvious nature, with different annual and perennial species reaching their growing peaks at different times of the year (Fig. 2). Some of the fast-growing annuals—*Stellaria media*, *Senecio vulgaris* and *Urtica urens*—produced several 'generations' at some sites during a growing season, with one generation usually of considerably greater importance than the others. By contrast, in the non-gull areas there was continuous vegetation cover on the sites throughout the year, and little notable seasonal variation.

Many of the species—of both the gull-affected and the non-affected areas—have a ubiquitous distribution in Great Britain (Table 2).

In terms of habitat preference, sixteen important species in gull-affected areas have ruderal affinities (Table 2). By contrast only two species of importance in non-affected areas (*Holcus lanatus* and *Heracleum sphondylium*) are prevalent in ruderal habitats; the majority are grassland species. The predominance in gull-affected areas of ruderals—species particularly associated with human disturbance—is an indication that similar factors may operate in gull colonies.

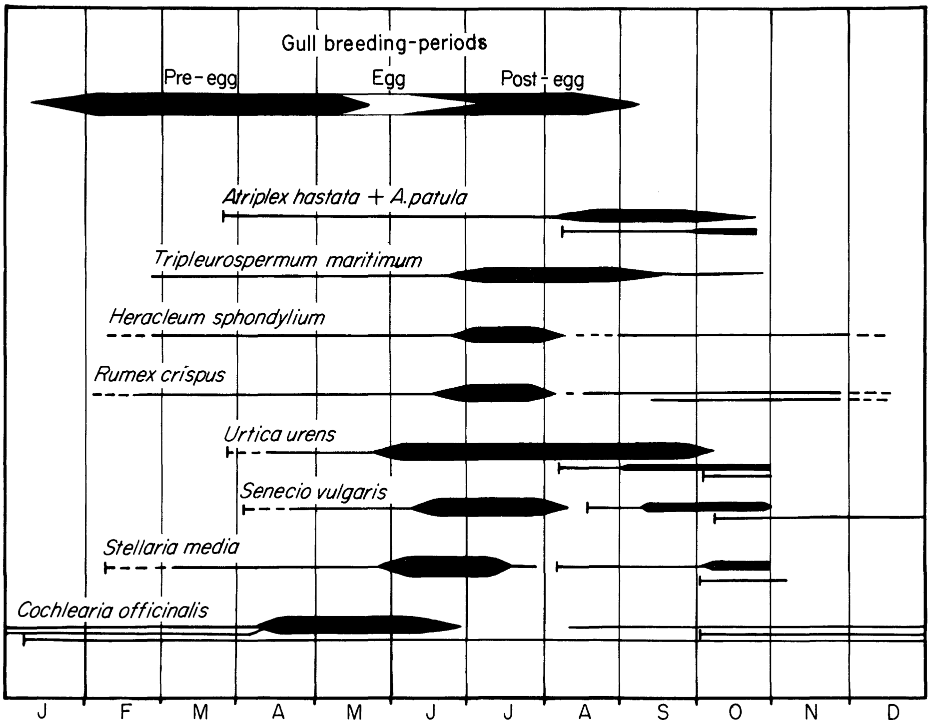

FIG. 2. The growing and flowering periods of the principal plant species at herring gull colonies in north-east Scotland—data collected at two study areas (Averhill and Hackley Head). The horizontal lines indicate vegetative growth, thickened bars the period of flowering; where a species has several generations their relative importance is approximately indicated by the thickness of the bars. Broken lines indicate uncertainty; vertical lines, the start of germination—where absent, new growth can be considered to be vegetative from established plant-parts. The gull breeding-periods on the sites are included for comparison.

Discussion

The vegetation of maritime cliff-tops and banks in north-east Scotland generally consists of a perennial grass sward dominated by *Festuca rubra*, a sward in which other grasses—*Poa pratensis*, *Agrostis tenuis* and *Holcus lanatus*—are usually of some importance, and in which a number of maritime and ubiquitous herbs occur. Such a fescue-dominated sward has been recorded on maritime cliff-tops and banks in several parts of the British Isles (McLean 1935; Poore & Robertson 1949; Gillham 1953; Malloch 1971), and both McLean (1935) and Gillham (1955) suggest that such vegetation may be the climatic climax in the absence of grazing under conditions of heavy exposure to spray-bearing winds. Where gulls are having an influence the perennial sward is absent, and in its place is a seasonal and often species-poor community in which annual and ruderal species predominate.

The survey has thus established that there is a distinct difference between gull-affected vegetation and that of adjacent sites with no gulls. Many questions, however, remain unanswered. Among the more obvious are:—What activities of gulls affect the site and its vegetation? How do particular plant species respond to these activities? Why are some plants capable of thriving in the presence of gulls while others cannot? Why are there distinct spatial and temporal variations in the vegetation within gull-affected areas? Detailed studies attempting to answer these questions are reported in the rest of this paper.

THE STUDY SITES

Two sites were selected for detailed studies: Hackley Head (National Grid reference NK 029268), a point of land on the Sands of Forvie National Nature Reserve near Collieston, Aberdeenshire, and Averhill (NK 048289), a large semi-isolated stack 0·6 km north of Collieston. Both sites were covered by unusually extensive areas of obviously gull-affected vegetation, and possessed the necessary criterion of being visible from nearby elevated positions at which hides could be placed.

Herring gulls were breeding on all the slopes around Hackley Head; 200 nests were counted in 1972. A few pairs nested on the cliff-top (eleven in 1972), which was also used to a minor extent during the breeding season as a 'club-site'—a communal, non-territorial, gathering area. In addition, immature great black-backed gulls (*Larus marinus* L.) roosted in spring on part of the cliff-top, and during winter herring gulls roosted on the lower part of the sea-facing cliffs as well as on rocks below.

The Averhill study area was part of a large herring gull breeding colony which included an area of bare rock below. A total of 132 nests was counted over the whole area in 1972. In addition, the rocky areas below were used as a winter roost by gulls.

Descriptive and experimental studies were initiated at both sites in February 1971. The primary objective of these studies was to determine the specific activities of herring gulls affecting vegetation and the spatial distribution of such activities within and around the study areas; and to describe in detail the spatial distribution and seasonal variation in the plant species composing the vegetation of the sites.

ACTIVITIES OF HERRING GULLS AFFECTING VEGETATION

Observations on gull activities

The cliff top at Hackley Head (an area of *c.* 1000 m^2) and two vegetated areas at Averhill (totalling 880 m^2) were marked with bamboo canes into grids of 4-m squares, and hides were positioned to give a satisfactory view of the gridded areas. Observations at the two sites were carried out on twenty-one occasions between 23 March and 21 August during 1971 and 1972. At regular intervals during a whole daylight period the gridded area was scanned from the hide with binoculars, and the position of each gull was recorded on a plan of the site, this taking *c.* 5 min. During the remainder of a 30-min period the occurrence of any activity affecting the vegetation was recorded.

Four distinct gull activities (or groups of activities) were found to have an effect on the vegetation of breeding sites: (1) treading and sitting; (2) nest-building (the digging of scrapes and the collecting of nest-materials); (3) boundary clashes (i.e. aggressive interactions between neighbours at territory boundaries); and (4) defecation and other additions of material to the sites by gulls. Herring gulls spent a large part of the year at the breeding sites—from January to early September (Fig. 2)—and a high proportion of the resident population (usually over two-thirds) frequented the colony at any one time.

Treading and sitting

The standing, sitting or walking of gulls on vegetation may have resulted occasionally in mechanical damage to plants, but a more obvious effect was a general suppression of vegetation in areas frequented by standing or sitting birds. In bare areas the sporadic presence of a bird may have acted to prevent the establishment of plants.

The hide observations revealed a marked pattern in treading pressure over the study areas (Fig. 3). Although birds moved fairly widely over their territories, there was a tendency for the non-incubating bird to frequent a particular area—often near the nest. A comparison of the spatial distribution of treading in the two successive years indicated that patterns in successive years were similar over much of the area, particularly where nest-sites were on the same spots. Where changes in nest-location occurred, however, the spatial patterns in treading also differed (at Averhill in 1972 twenty-five of the fifty-five nest-sites were at new locations).

Nest-building activities

The nest of the herring gull is a loose, bowl-shaped assortment of plant materials covering an area of *c.* 0·1 m^2. Effects of nest-building on vegetation differed on various parts of the site. On the actual area covered by a nest, the digging of the 'scrape' (a shallow depression in the soil), followed by the accumulation of nest-materials, and later the presence of incubating birds, eggs, and eventually chicks, prevented growth of any plants during the breeding season; on areas of bare rock, however, as Gillham (1970) suggests, nest material may serve as a substrate for future plant colonization. Over the rest of the territory and often beyond, the effects of nest-building on vegetation resulted from the collecting of nest-material. Records of types of material observed being collected at Averhill in 1972 (Table 3) indicate that dead material was collected more frequently than living. Detailed assessments of nest composition given by Sobey (1975) indicate that 90% (dry weight) of the nest material was dead when collected, and that the 10% green material consisted mainly of plants growing within the colony.

The observations on collecting (Fig. 3) indicated that most pairs confined their within-colony collecting to the area near their nest. Some birds brought in nest material from outside the colony, but this was observed on only 6% of the 353 collecting-trips recorded.

Boundary clashes

At territorial boundaries, aggressive interactions between two neighbouring birds frequently involved a rapid and vigorous pulling at plants, soil or anything else within reach. Such aggressive interactions have been termed 'grass-pulling' or 'pecking-into-the-

TABLE 3. The types of material collected by gulls during collecting-trips, or pecked at or pulled by gulls during boundary clashes on the south part of Averhill in 1972; the values are the number of collecting-trips or clashes (percentage values in parentheses) relating to each category of material

	No. of collecting-trips	No. of clashes
Dead plant material	104 (61·5)	48 (24·1)
Living plant material	67 (39·6)	123 (61·8)
Soil	2 (1·2)	54 (27·1)
Unidentified	12	17
Number of collecting-trips or clashes observed	169	199

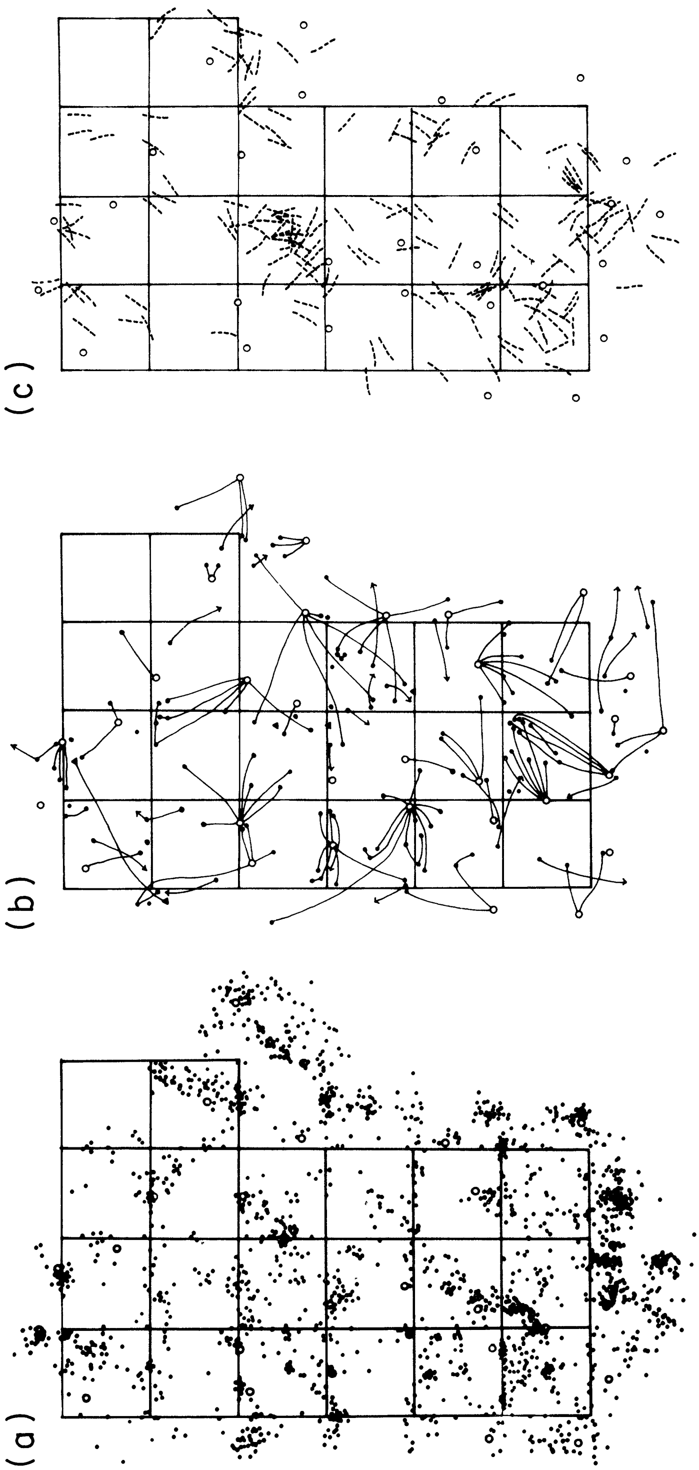

FIG. 3. Spatial distribution of bird activities on the south part of Averhill, 23 March–11 July 1972. Each grid square is 4 × 4 m. Nest locations are indicated by open circles. (a) Points at which adult gulls were observed standing or seated during the regular scans of the study area (excluding birds seated on nests), based on ninety scans during 9 observation days. (b) Points at which nest material was observed collected. The lines, showing the direction in which the material was carried, usually indicate the nest for which it was collected; points joined by the same line involved a single collecting-trip; points where birds from outside the area collected nest-material, and then flew off with it are indicated by triangles. (c) Location of boundary clashes. Each clash is denoted by a short broken line; the clashing birds, on opposite sides of the line, can usually be assumed to belong to the nearest nest behind the line.

ground' by ethologists (Tinbergen 1953, 1960), but they have never been mentioned by botanists looking at the vegetation of gull colonies. Close observation of clashing birds indicated that plants were particularly susceptible to attack (Table 3), with little discrimination occurring between living and dead material. When plants or debris were absent the soil was pecked.

It was also evident (Fig. 3) that a large proportion of the ground-area in the colony was subjected to boundary clashes, and that clash areas were broad zones rather than precise boundaries between nests. Changes in spatial distribution of boundary clashing occurred in successive years, with some of these changes attributable to changes in nest-location. Thus areas which escape clashes in one season may not do so in succeeding years. The observations over 2 years also indicated that boundary clashes were common throughout the period of study (23 March to 21 August), and are probably a feature of gull behaviour during the whole time that the birds are on the breeding sites.

Defecation

Five principal types of foreign material are deposited by herring gulls on their breeding sites: faeces, regurgitated crop pellets, drip from the nasal salt glands, gull corpses and feathers. By far the most significant of these, in terms of their effect on vegetation, are faeces. If faeces fall on to plant surfaces, they will obviously interfere with processes such as photosynthesis and transpiration. However, more important for plants is the effect of defecation on soil-nutrient concentrations—botanists have long considered this to be the principal factor responsible for the special character of bird-colony vegetation.

A special study of gull-defecating behaviour (Sobey 1977) revealed that adult gulls voided their larger faecal deposits almost exclusively on defecation areas or 'latrines' which were at some distance from the nests. Assessments in late May 1971 (Fig. 4) of the location of defecation areas also revealed that much of the colony area had few faecal deposits. In the following year the spatial patterns were generally similar; where changes did occur, it was apparent that some of these, though not all, were associated with changes in nest-site location.

The nutrient content of faeces

Faeces containing mussel shells (*Mytilus edulis* L.) were particularly prevalent on the study areas during much of the breeding season; a number of these were collected from the ground, and, after air-drying, analysed for total and available nitrogen, calcium, magnesium and sodium, and for total phosphorus and potassium. Faeces of a more liquid nature were collected from chicks by holding the birds over polythene bags; these samples were freeze-dried and analysed for total quantities of the above nutrients. Total nutrient estimations were carried out on a modified Kjeldahl digestion of the faeces, as outlined by Sobey (1975); 'available' nutrients were extracted in 1M KCl. The methods of analysis of individual elements were similar to those outlined below for soil properties, and are given in full by Sobey (1975).

The six chick faeces, most of which contained a high proportion of whitish urinary wastes, exhibited a wide range in nutrient content (Table 4): calcium varied by over fifty-fold, phosphorus ten-fold and nitrogen six-fold. By contrast, the faeces of the adult birds—all containing mussel shells—varied only slightly; they contained smaller concentrations of nitrogen, phosphorus, potassium and magnesium than the chick faeces, but were much richer in total calcium (mussel shells are largely calcium carbonate). Only a small part of the total nitrogen and calcium was in available form, but rather more of the sodium and magnesium.

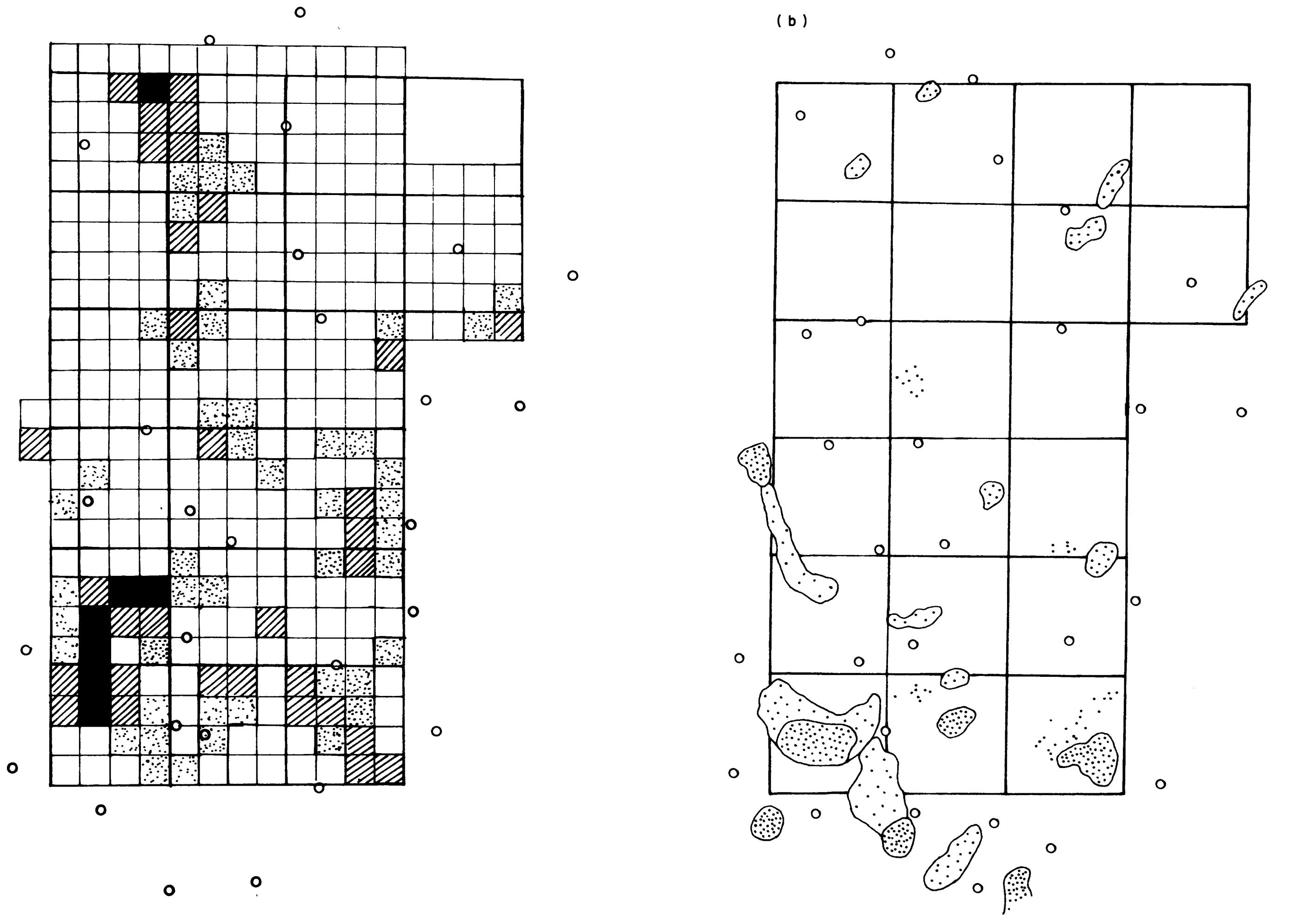

FIG. 4. The distribution of gull faeces on the south part of Averhill. (a) Faecal deposit count, 25–28 May 1971; ■ = $\geqslant$ 20 faecal deposits m^{-2}, ▨ = 11–19 faecal deposits m^{-2}, ▩ = 6–10 faecal deposits m^{-2}, □ = 0–5 faecal deposits m^{-2}. (b) Latrine locations on 17 May 1972; enclosed areas represent scattered accumulations of faeces (areas with large amounts are distinguished by denser stippling), while separate dots indicate a light covering of faeces. Each grid square is 4 × 4 m; nest locations are indicated by open circles.

TABLE 4. Chemical analyses (air-dry basis) of faeces collected at Averhill in 1971; samples 1–6 were from adult birds and 7–12 from chicks

Sample number	1	2	3	4	5	6	7	8	9	10	11	12
Total N (%)	1·38	1·50	0·87	1·19	0·63	0·78	12·5	21·7	6·2	8·3	5·0	3·6
NH_4^+ (m-equiv. per 100 g)	3·6	3·8	2·2	5·6	1·9	2·5	—	—	—	—	—	5·0
NO_3^- (m-equiv. per 100 g)	trace	0·32	0·09	0·27	0·31	0·28	—	—	—	—	—	N.D.*
Available N (% of total)	3·7	3·8	3·7	6·8	4·6	4·9	—	—	—	—	—	2·5
Total P (mg per 100 g)	147	161	126	172	70	85	5230	1520	3900	3430	490	2100
Ca (m-equiv. per 100 g)												
Total	650	693	851	805	817	689	280	20·4	489	121	5·3	79·5
Available	0·37	0·42	0·24	0·20	0·27	0·27	—	—	—	—	—	0·53
Mg (m-equiv. per 100 g)												
Total	7·8	8·7	6·1	10·7	6·5	10·7	39·0	11·2	34·4	50·7	23·5	26·0
Available	—	2·7	—	2·3	2·2	2·2	—	—	—	—	—	2·6
Total K (m-equiv. per 100 g)	4·5	4·4	1·7	2·4	1·8	1·9	41·8	70·8	23·1	45·9	17·8	18·5
Na (m-equiv. per 100 g)												
Total	17·2	18·3	18·5	16·7	17·9	16·1	22·3	17·6	11·7	15·4	16·3	12·9
Available	4·9	4·4	3·8	5·4	5·1	5·3	—	—	—	—	—	12·6

* not detectable.

The effect of defecation on soil-nutrient levels

To determine the effect of defecation on soil-nutrient levels, soil samples were collected from thirty separate points at Averhill on 19 August 1971 near the end of the breeding season. The points selected represented a range in bird effects—some were heavily coated with faeces while others were unfouled. Seventeen soil properties were analysed for each sample (Table 5). In order to determine the extent to which the effects of defecation on nutrient levels carry over from one season to the next, the same thirty soil sites were re-sampled on 15 February 1972, just prior to the spring re-occupation of the breeding territories. Twelve soil properties were re-analysed (Table 5).

Methods of analysis

A modified Kjeldhal digestion (in sulphuric and perchloric acids) was used to extract total nitrogen and phosphorus, 1M acetic acid to extract available cations and phosphorus, 1M ammonium acetate to extract exchangeable hydrogen, and distilled water to extract nitrate and chloride. Sodium and potassium were analysed by flame photometry, calcium and magnesium by atomic-absorption spectrophotometry, ammonium, nitrate, and chloride by specific ion electrodes, and phosphorus (total and available) by the vanado-molybdophosphoric method (Jackson 1958). Total nitrogen was extracted from the Kjeldhal digest by steam distillation under alkaline conditions, and the nitrogen concentration of the distillate determined by titration with 0·01M HCl. Total exchangeable bases were estimated from the pH change of the acetic acid extract, and exchangeable hydrogen from the pH change of the ammonium acetate extract (Jackson 1958). Conductivity and pH of the distilled water extract were measured electrometrically. Organic matter content was determined as loss-on-ignition at 400 °C for 8 h. Further details are given in Sobey (1975).

Results

The thirty sites were ordinated by a principal components analysis of the soil variables. The factors most likely to be affected by bird-defecation (the available and soil-solution components) all had high positive loadings on the first component (Sobey 1975), and this component was accordingly interpreted as representing a gradient of bird-fertilization. The fifteen sites nearest the positive end of the component were arbitrarily grouped as 'latrines', and the remaining fifteen were considered as 'unfouled'. Comparison of the soil properties of the two sets of sites is given in Table 5. In August the concentrations of all the available nutrients (except magnesium) were significantly higher in the latrines than in the unfouled areas; exchangeable hydrogen was significantly lower in the latrines. The greatest difference was in available ammonium, the mean value of which was eight times higher in latrines than in non-latrines. By contrast, there were no significant differences between latrines and unaffected areas in organic matter, total nitrogen, total phosphorus, available magnesium, soil moisture and soil depth. It would thus appear that the available concentrations of phosphorus and nitrogen are largely independent of the total concentration, which appeared to be closely related to soil organic-matter content.

Though the concentrations of all the available nutrients were still somewhat higher in February in the latrines than in the unfouled sites, only potassium and nitrate were significantly so ($P < 0{\cdot}05$). The absence of a statistically significant difference between latrines and non-latrines for most nutrients results from a general decline between August

TABLE 5. Soil properties of 'latrines' and 'unfouled areas' at Averhill, August 1971 and February 1972; means and 95% confidence limits (n = 15) are given (N.D., not determined); concentrations of cations and anions are in m-equiv. per 100 g air-dry soil unless otherwise stated; levels of significance for t-tests comparing latrines and unfouled areas, and August and February values, are shown (***, $P < 0·001$; **, $P < 0·01$; *, $P < 0·05$; NS, not significant)

	19 August 1971			15 February 1972			Comparing sites in August and February (P)	
	Latrines	Unfouled areas	Comparing latrines & unfouled areas (P)	Latrines	Unfouled areas	Comparing latrines & unfouled areas (P)	Latrines	Unfouled areas
Na (available)	9·13 ± 0·80	7·80 ± 0·87	*	19·8 ± 2·7	16·8 ± 2·7	NS	***	***
K (available)	2·07 ± 0·33	1·28 ± 0·15	***	1·51 ± 0·12	1·38 ± 0·08	*	***	NS
Ca (available)	29·8 ± 15·7	9·57 ± 2·6	*	14·2 ± 9·3	6·88 ± 1·31	NS	**	*
Mg (available)	7·75 ± 1·56	6·88 ± 0·88	NS	7·87 ± 0·78	6·95 ± 0·80	NS	NS	NS
NH_4^+ (available)	3·32 ± 1·72	0·410 ± 0·147	**	0·464 ± 0·284	0·201 ± 0·040	NS	**	**
Total exchangeable bases	42·3 ± 15·1	21·5 ± 2·7	**	28·9 ± 8·1	22·2 ± 2·7	NS	*	NS
Exchangeable hydrogen	12·6 ± 3·0	19·3 ± 2·6	***	N.D.				
P (available) (mg per 100 g)	30·6 ± 8·6	18·1 ± 2·6	**	22·4 ± 4·6	18·8 ± 2·1	NS	**	NS
NO_3^-	2·58 ± 0·93	0·50 ± 0·23	***	0·76 ± 0·18	0·52 ± 0·08	*	***	NS
Cl^-	N.D.			11·6 ± 3·8	8·58 ± 1·89	NS		
Organic matter (%)	36·2 ± 4·6	38·1 ± 4·3	NS	N.D.				
Total N (%)	1·23 ± 0·16	1·29 ± 0·13	NS	N.D.				
Total P (mg per 100 g)	223 ± 31	221 ± 20	NS	N.D.				
Soil moisture (%)	56·8 ± 12·2	41·5 ± 8·5	NS	93·2 ± 11·2	77·9 ± 10·7	*	***	***
pH	5·86 ± 0·27	5·61 ± 0·23	NS	5·06 ± 0·32	5·43 ± 0·18	*	***	NS
Conductivity ($mS\ cm^{-1}$)	1·67 ± 0·35	0·75 ± 0·14	***	2·87 ± 0·41	2·20 ± 0·81	NS	**	***
Soil depth (cm)	21·7 ± 5·2	21·7 ± 2·8	NS	N.D.				

and February in the concentration of available nutrients in latrines to levels approaching those of unaffected areas. Most of these declines in the latrines were statistically significant. By contrast, in unaffected areas most of the nutrients were at about the same level in February as in August, only calcium and ammonium showing statistically significant declines in the 6-month interval. Another seasonal difference—this time common to all sites—was the marked rise in available sodium concentrations in winter as a result of a heavier incidence of sea-spray.

The plant colonization of areas artificially bared to simulate the effect of gull disturbance

In order to determine whether disturbance on its own, in the absence of defecation, would lead to the establishment of bird-associated plant species in areas where they did not naturally occur, an attempt was made to simulate artificially the ultimate effect of the physical activities of gulls: the complete removal of vegetation cover.

In May 1972 an area of 2 × 16 m, extending from the gull-affected vegetation on the cliff-top of Hackley Head across a transition area to a section of unaffected fescue sward was cleared of its vegetation. 'Paraquat' was applied on 16 May, and after 13 days, when much of the vegetation was dead, the sward and any surviving perennials were removed with a spade to leave an almost completely bare soil surface. The development of vegetation on the bare strip was noted throughout the following two growing seasons.

Seedlings of *Stellaria media*, *Senecio vulgaris* and *Atriplex patula* germinated immediately over much of the area, and *Holcus lanatus*, *Rumex crispus* and *Heracleum sphondylium* grew vegetatively from rootstocks which had survived the clearance. By August, less than 3 months after clearance, much of the area, particularly the upper part, was covered by plants, notably *Atriplex patula* and *Senecio vulgaris*; however, the lower section from which the sward had been removed remained bare.

In the following growing season, the area which had been cleared was still distinguishable from the surrounding vegetation, and on 18 July 1973 a Domin cover-abundance assessment of part of the cleared area and of an uncleared 'control' strip directly adjacent revealed that *Stellaria media*, *Atriplex patula* and *Senecio vulgaris* were the dominant species along much of the strip, including an area which prior to clearance was dominated by *Holcus lanatus* (Fig. 5). Disturbance alone (or at least the presentation of a bare surface) without nutrient addition had thus resulted in the germination and growth of bird-associated annuals on areas where previously they had been of less significance. The former sward area was still largely bare, and remained uncolonized to the end of the study. This may have been due to two factors: it is very likely that this area was initially lacking in a seed supply; also, its nutrient status was probably very low, not only because of the lower soil fertility under the sward, but also because much of the topsoil and organic matter had been removed when the sward was cleared.

Discussion

There is a marked spatial pattern in the distribution within the breeding colony of the four gull activities affecting vegetation. As a result, the nature and intensity of the bird-effect can vary considerably over short distances, and during any one season plants less than a metre apart can be subjected to very different types of gull-activity. Because of a certain amount of change from year to year in the spatial pattern of each activity, however, the same effects are not necessarily felt on the same spots in successive years. Thus, over a period of several years it is likely that many areas will experience all four activities to varying degrees.

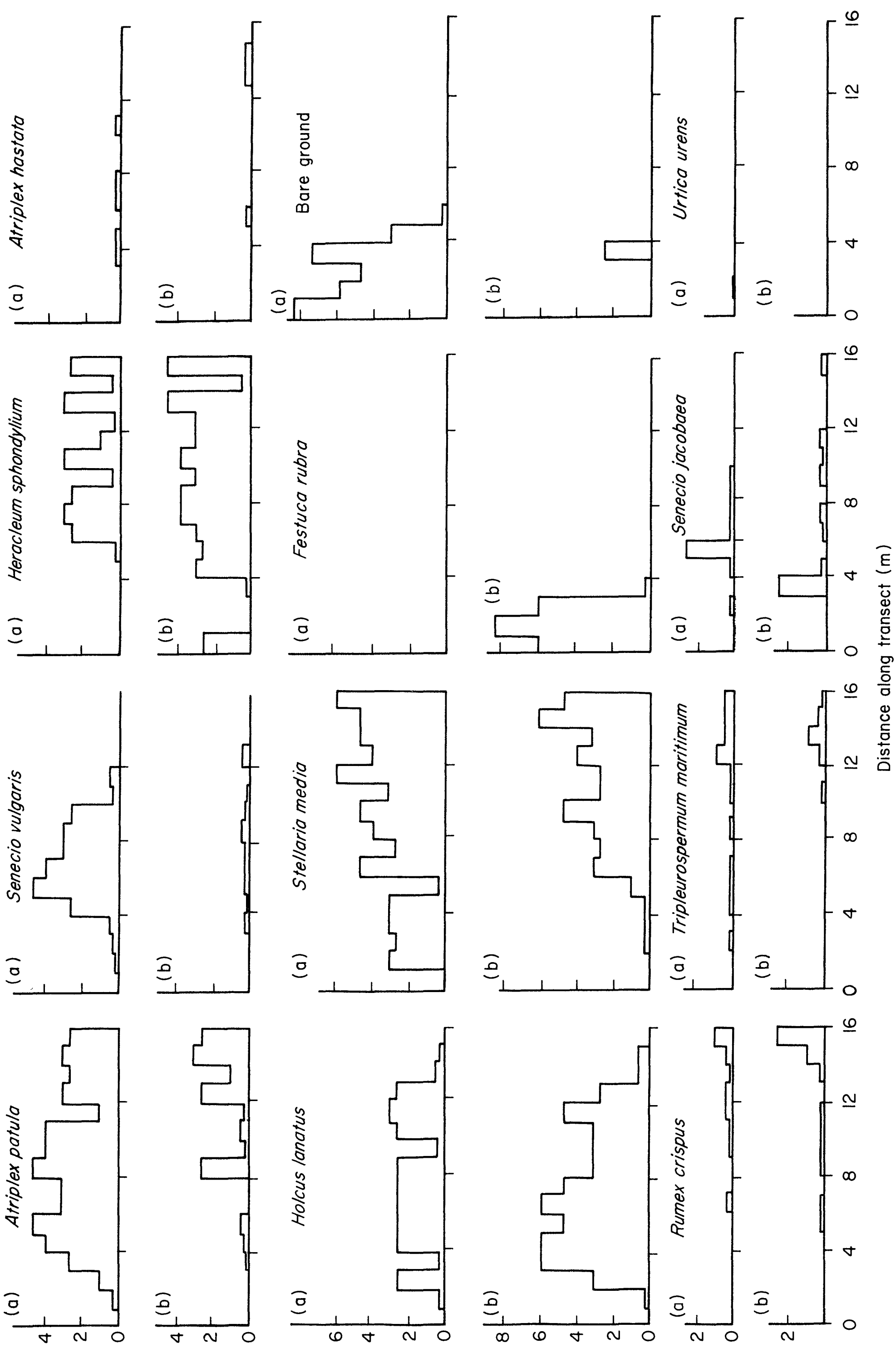

FIG. 5. The cover-abundance of plant species on 18 July 1973 along (a) a 1-m-wide strip on the top of Hackley Head cleared of its vegetation in May 1972, and (b) of an adjacent untouched control strip. Transformed values (Bannister 1966) of Domin numbers are plotted.

When translated to plant terms, the four activities have three distinguishable effects on vegetation: the treading of the birds causes physical suppression; the pecking and pulling of collecting and boundary clashes causes destruction and disturbance; and defecation results in nutrient-enrichment, though to concentrations which may be detrimental. All plant species occurring within the colony will come into contact at some time or other with each of these effects. What then is the relative effect of these various activities on the vegetation occurring within and around a gull colony?

Since most of the nest materials are already dead when collected, much of the collecting that does occur has little effect on the current season's vegetation; and because collecting is dispersed throughout the colony, few areas within the colony are subjected to heavy collecting pressure. The observations thus suggest that the effect of collecting on the vegetation *within* a colony is not particularly severe. Observations at Hackley Head, however (reported by Sobey (1975)), suggest that perennial vegetation on the colony-fringes when subjected to heavy collecting pressure is more drastically affected: at Hackley Head a large amount of nest-material was collected from an area dominated by *Holcus lanatus* and from an adjacent fescue sward, and gaps in the sward suggested that it was unable to withstand this concentrated pressure.

The effect of boundary clashing on the vegetation is considerably more drastic than that of collecting. Unlike collecting, boundary clashing is concentrated on specific areas within the colony, and living plant material is indiscriminately attacked where present. The number of 'pecks' involved in most clashes is also considerably greater than in any collecting-trip. Calculations derived from the observations give an *average* value of twenty-seven clashes per m^2 for the whole Averhill area during the 4-month period from April to July; boundary zones will in fact have values much higher than this. The importance of disturbance *per se* is also supported by the field experiment, which indicates that clearance of the vegetation alone, without the addition of nutrients, is sufficient to lead to the establishment of colony annuals on areas where they did not formerly occur. It seems very probable that a primary attribute of any plant species occurring in herring gull colonies is an ability to cope with such disturbance, and though it is perhaps unwise to single out any one activity as being of greater importance than the others, the observations suggest that the disturbance associated with boundary clashing is of particular importance to the vegetation.

Like the other activities, the effect of defecation, primarily felt through soil-nutrient concentrations, varied widely over short distances within the colony. It was also evident that these effects were seasonal—there were significant declines in the available bird-added nutrients in latrines during the absence of the gulls in winter—probably due to volatilization (of ammonium) and to leaching associated with the heavier winter rains and the deposition of sea-spray. The emphasis of previous workers on defecation as the principal (or only) factor controlling the vegetation of sea-bird colonies has thus proved to be inapplicable to the herring gull colonies studied.

FACTORS AFFECTING THE DISTRIBUTION OF PLANT SPECIES IN HERRING GULL COLONIES

Plant species occurring in gull colonies exhibit marked patterns in their distribution. A principal aim of this study was to determine the factors responsible for these patterns, in particular whether the marked small-scale patterns in bird activity in any way determined the patterns in the distribution of plant species. The influence of other factors, in particular innate soil properties, was also examined, with experiments in the glasshouse on the role of soil factors in determining the distribution of plant species.

The effect of bird activities on plant distribution

The percentage cover of shoots of all plant species within selected parts of the study areas at Hackley Head and Averhill was carefully mapped several times during 1971 and 1972 (Sobey 1975). Representative data are shown in Figs 6 and 7.

Averhill

The distribution of plant species within the breeding colony bears little obvious relation to the pattern in bird activities. The two predominant species, *Atriplex hastata* and *Cochlearia officinalis*, tended to blanket areas on which there was a mosaic of bird-activity (Fig. 6). The only relationship noted between bird activities and vegetation distribution was on a small scale, and was not perfect: some of the defecation areas on the north part of Averhill supported second generations of *Stellaria media*, *Senecio vulgaris* and *Urtica urens* in late summer after the birds had abandoned the colony; however, late summer generations of these species also occurred on areas not used for defecation.

Several factors are likely to contribute to this lack of a direct correlation between the two distributions:—

(1) Bird activities during a breeding season can have only a limited effect on that season's distribution of perennials, which are well-established before the birds arrive on the site. The distribution of annuals, though more likely to be influenced by current bird activities, is also very dependent on events of the previous season.

(2) Because most of the plant species, and particularly the annuals, are capable of rapid growth, small-scale spatial patterns in vegetation can change markedly over short periods. Plants within a colony can thus recover quickly from gull effects such as suppression and disturbance when this pressure is relaxed, and an area bared by boundary clashing can sometimes be almost indistinguishable from surrounding areas a month after the clashing has ceased.

(3) Since the various bird activities occurring within the colony are not completely segregated in spatial terms, during the lengthy breeding season any spot is likely to experience several activities to varying degrees. This, in combination with the changes in the spatial pattern of bird activities in successive years, is likely to prevent discrete plant distributions associated with a particular gull activity from developing.

(4) Finally, and most importantly, there is strong evidence from the Averhill distributions that factors other than birds are of importance in determining the distribution of plant species. *Atriplex hastata* was generally the dominant species on lower-lying areas close to the sea, suggesting that the influence of sea-spray may control its distribution. Assessments of sea-spray deposition, using collecting tubes devised by Malloch (1972), revealed a far heavier deposition of salt on the lower *Atriplex* areas: the deposition of sodium during the winter period 7 November 1972 to 30 January 1973 was 25·9 kg ha^{-1} per day, while on the upper area lacking *Atriplex hastata* it was only 3·4 kg ha^{-1} per day. It was also evident that the distribution of one species could influence the distribution of other species directly: in 1971, as indicated in Fig. 6, the August distribution of *Atriplex hastata* on the south part of Averhill was complementary to the February distribution of *Cochlearia officinalis*, suggesting that the presence of *Cochlearia officinalis* in early spring prevented *Atriplex hastata* from establishing on areas where it might otherwise have

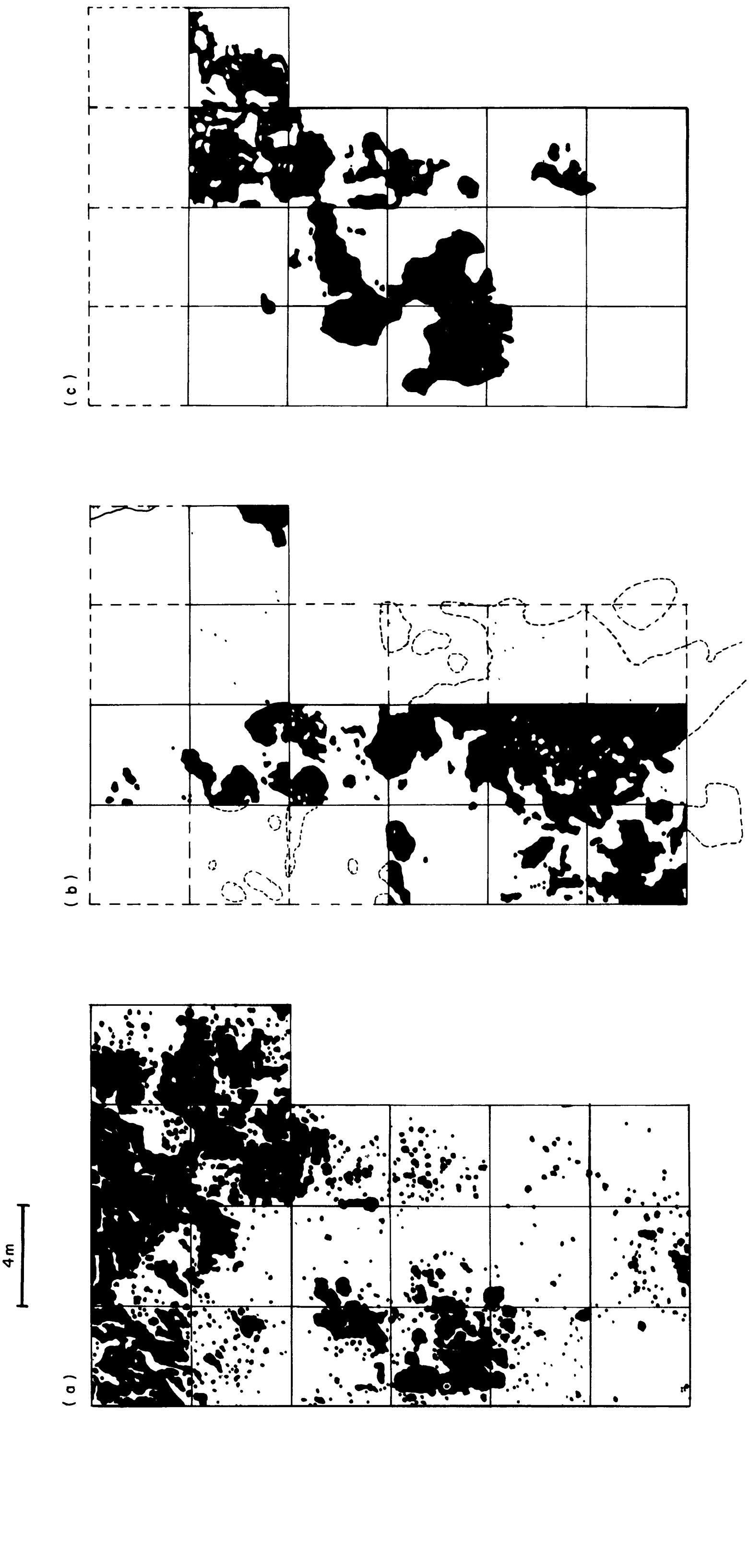

FIG. 6. The distribution on the south part of Averhill in 1971 of (a) *Cochlearia officinalis* (February 1971), (b) *Atriplex hastata* (August 1971), and (c) the 'second generations' of *Stellaria media*, *Urtica urens* and *Senecio vulgaris* (October 1971). The 4 × 4 m squares enclosed by broken lines were mapped only approximately.

occurred. More strikingly, the second generation of *Stellaria media* and other annuals showed an almost exact spatial correlation with the February distribution of *Cochlearia officinalis*—the *Cochlearia officinalis* having died down in July, thus leaving the area available for colonization.

In 1972 the plant distributions also suggested that factors other than gull activities might exert an important influence on the distribution of plant species at Averhill. The bareness of a large area on the north part of Averhill, even at the height of summer, appeared to be due to heavy winds and stormy weather in the previous January, when *Atriplex hastata* litter, together with much of the loose surface soil, was blown from part of the north site. On this small area at Averhill the effects of gull activities in determining the distribution of plant species were thus subordinate to the effects of weather. Furthermore, *Stellaria media*, of considerable importance in 1971, was very scarce throughout 1972. A vulnerability to erratic environmental factors and a lack of stability appear to be a general feature of the vegetation of gull colonies, dominated as it is by annuals.

Hackley Head

The distribution of plant species at Hackley Head is broadly correlated with a general gradient in gull activity: detailed observations reported by Sobey (1975), and summarized in Fig. 7, revealed that gulls were only rarely observed on a fescue sward, which gave way sharply to a *Holcus*-dominated area about 40 m from the headland. In passing from this sward across the *Holcus* zone to an area of *Stellaria media*, *Atriplex patula* and *Rumex crispus*, the level of bird presence increased. The *Holcus* zone was also particularly subjected to the collecting of nest-material by birds nesting on the slopes. *Atriplex hastata* and *Urtica urens* were of greatest importance on the slopes, while *Tripleurospermum maritimum*, *Heracleum sphondylium*, *Senecio vulgaris* and *Stellaria media* were more significant on the top—an area of intermediate bird activity. *Festuca rubra* and most of the other species comprising the sward were apparently incompatible with gull activities. Only two sward species, *Holcus lanatus* and *Rumex acetosa*, attained any importance in the gull-affected area; and because they were more luxuriant on the periphery of the gull area than in the sward, it appears they may be favoured by limited gull activity. Since all the other species on the slopes and top of Hackley Head did not occur on adjacent areas outside the colony, they appear to be definitely associated with gull activity. It is notable that towards the slopes, the area of heaviest gull activity, there is a decline in the role of perennials, the slopes themselves being almost completely dominated by annuals.

However, examination of Fig. 7 suggests that variation in gull activities over the site cannot account for many of the plant distributions observed. On areas subjected to the same general intense breeding activities, particularly on the slopes, different species (e.g. *Atriplex hastata*, *Urtica urens*) occurred as discretely-bounded, almost pure stands, and at the same time, as at Averhill, these pure stands blanketed indiscriminately areas on which marked small-scale patterns in the four gull activities occurred.

There is thus a strong indication that factors other than gulls influence, or even control, the within-colony distribution of plant species at Hackley. *Atriplex hastata*, as at Averhill, was generally the dominant species on areas closer to the sea, suggesting that sea-spray deposition may be the factor determining its distribution; and there appeared to be some association between species-distribution and soil properties not directly attributable to the birds. The pure stand of *Urtica urens* on the slope coincided with a humus-rich and apparently highly fertile soil, the fertility of which appeared to be due to erosion effects and subsequent accumulation rather than directly to gull activities. An assessment of

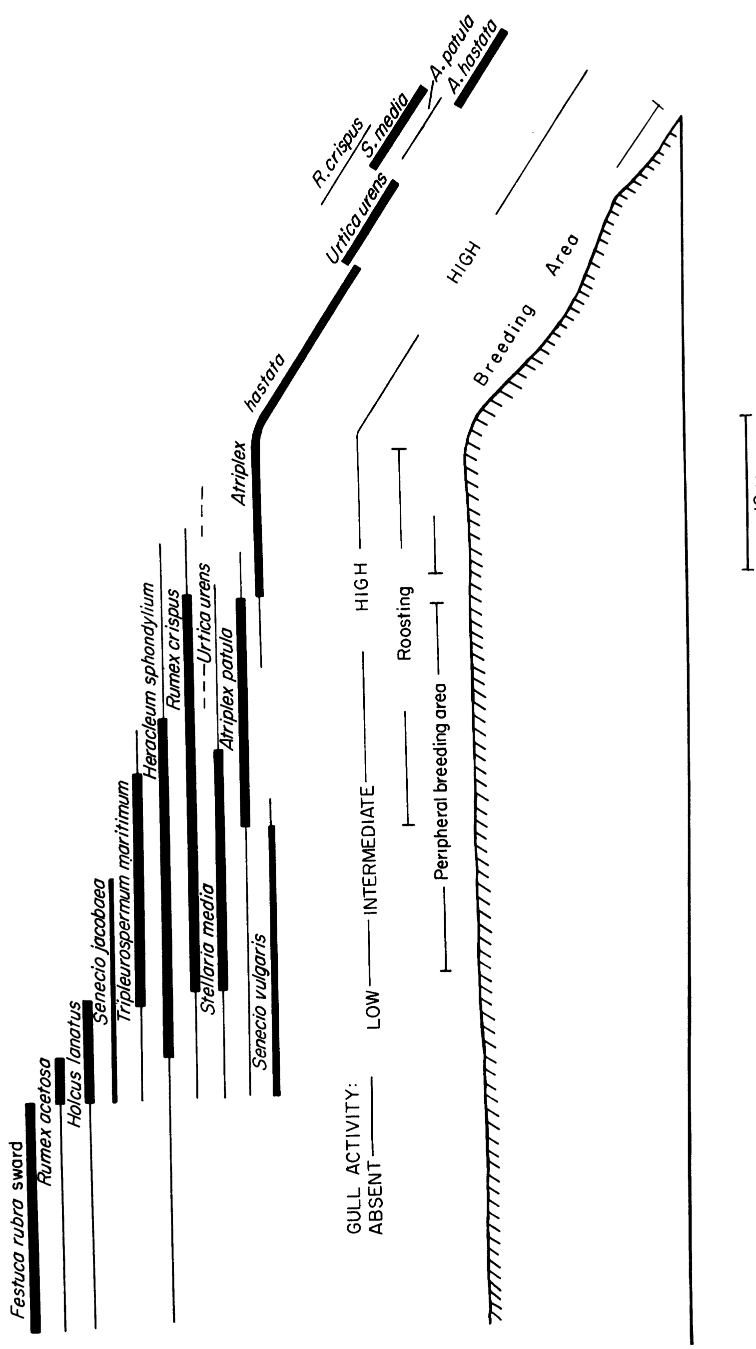

FIG. 7. The general distribution of the principal plant species and of gull activities at Hackley Head. For each plant species the thick bar indicates the zone where it was most abundant.

soil properties was thus considered to be essential in an understanding of some of the distributions observed.

Soil properties at Hackley Head

The soils of Hackley Head are derived from two different parent materials: one, a reddish till, serves as a parent material only where exposed on the slopes; over much of the top of Hackley Head and on parts of the lower sea-facing slopes, however, the soil parent material is a sand continuous with that of the Sands of Forvie.

The soils on the top and slopes of Hackley Head were sampled along selected transects on several occasions. Detailed results of the analyses are given by Sobey (1975). Representative data, mainly for the February and March samples, at the beginning of the gull breeding season, are shown in Fig. 8. Samples collected in May and October exhibited a similar pattern to those of February and March, with a local seasonal enrichment of some factors due to gull defecation.

Figure 8 shows that on the top of Hackley Head there was an increase in the concentration of most of the soil nutrients towards the cliff-edge. This was particularly evident for total and available phosphorus, available potassium and available calcium, and there was a suggestion of a similar trend for organic matter and total nitrogen. On the slope nutrient concentrations were on the whole higher than on the top, but there was some spatial variation: higher values of organic matter, total and available phosphorus, and total nitrogen and ammonium were recorded at the top of the headland and on the

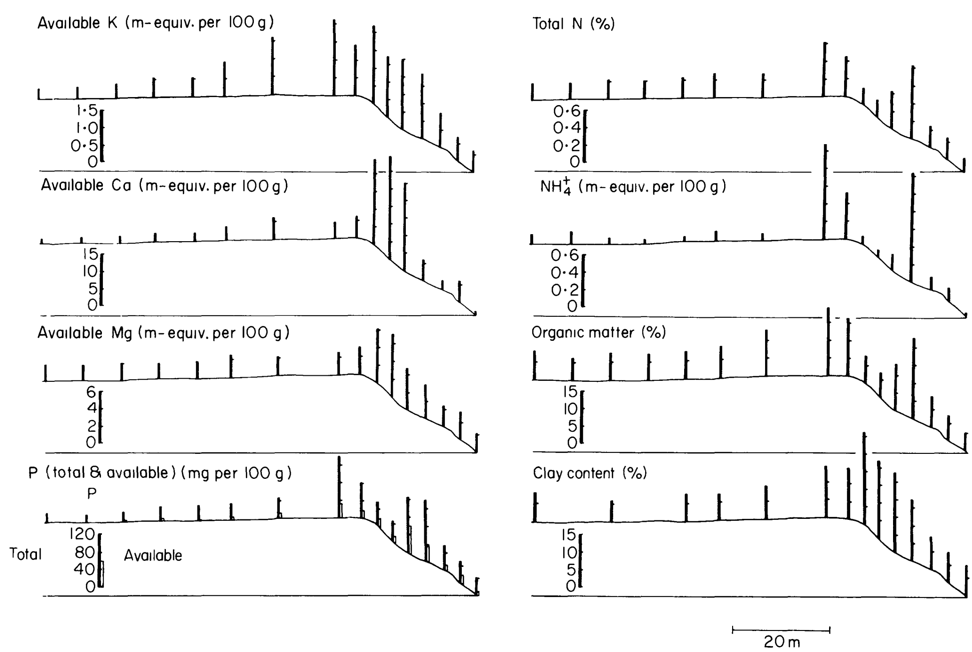

FIG. 8. Soil factors at Hackley Head along a transect running from the fescue sward towards the cliff-edge and down the slope (see Fig. 7 for vegetation distribution and gull activities along the same transect). Potassium, calcium, magnesium, ammonium and available phosphorus values are for 1 March 1971 (cliff-top samples) and 15 February 1972 (slope samples); Organic matter and clay-content values are for 1 March 1971 (cliff-top samples) and 5 October 1971 (slope samples); total nitrogen and phosphorus values are for 5 May 1971 (cliff-top samples) and 5 October 1971 (slope samples).

mid-slope area. The higher values of these factors on the top of the headland appeared to be due to the direct effect of defecation by gulls, which roosted on the area in late winter; the high values of the mid-slope soils (an area not particularly used for roosting) appeared to be associated with long-term erosion from the steeper slopes above, resulting in accumulation of surface materials, including plant debris, organic matter and faeces.

High concentrations of calcium and magnesium and a high clay content were recorded on the upper slope, where soils are derived from glacial drift of Old Red Sandstone origin. Similar soils of the nearby Collieston Association also have high calcium and magnesium concentrations (Glentworth & Muir 1963).

The performance of several plant species under glasshouse conditions on soils of differing fertility from several parts of Hackley Head

The soil analyses from Hackley Head indicated that the distribution of a number of plant species might have some association with concentrations of soil nutrients: *Festuca rubra* occurred at the lowest concentrations, *Holcus lanatus* at higher ones, *Stellaria media*, *Atriplex patula* and *A. hastata* at still higher levels, and *Urtica urens* at the highest concentrations (the mid-slope area). Accordingly, a preliminary glasshouse experiment was carried out, in which the growth of different plant species on different soils taken from several parts of Hackley Head was compared.

Methods

Surface soil (to a depth of *c.* 10 cm) was collected on 13 April 1972 from the following locations at Hackley Head:

(1) an area on the top of the headland outside the gull colony, supporting a *Festuca rubra* sward;

(2) an area on the cliff-top with abundant *Stellaria media* and *Atriplex patula*, as well as *Rumex crispus*, *Tripleurospermum maritimum* and *Heracleum sphondylium*;

(3) the upper part of the slope, supporting an almost pure stand of *Atriplex hastata* (the clay-rich soil derived from glacial material of Old Red Sandstone origin);

(4) the mid-slope area supporting *Urtica urens* (the organic-rich soil);

(5) an area on the slope just below the *Urtica urens* zone, supporting *Atriplex hastata* as well as some *Stellaria media* and *Atriplex patula*.

The concentrations of the available nutrients, as well as other soil properties, were determined for each of the soils (Table 6). On 17 April 1972, six plant species (*Festuca rubra*, *Holcus lanatus*, *Stellaria media*, *Urtica urens*, *Atriplex hastata* and *Atriplex patula*) were sown separately in each of the soils (in 36 × 21 × 5 cm plastic trays with holes to allow for drainage). After germination the plants were thinned, to leave twenty plants in each tray. Because the *Atriplex* species germinated poorly in the trays, seedlings from Hackley Head had to be transplanted to bring numbers up to twenty. The plants were grown for 2 months under glasshouse conditions, and on 12 June 1972 the shoots were cropped, oven-dried and weighed.

Results

The results are presented in Fig. 9:

(1) All species except *Urtica urens* on soil 1 (from under the fescue sward) survived and grew on the various soils under glasshouse conditions.

(2) The annual species (*Stellaria media*, *Urtica urens*, *Atriplex hastata* and *A. patula*) responded to the soils in a similar way: they produced the greatest dry weight on soil 4, followed generally by soils 3 and 5, and usually considerably less on soil 2. They did very poorly on soil 1, and in fact thirteen plants of *Urtica urens* did not survive.

Table 6. Chemical analyses of the five soils from Hackley Head used in the glasshouse experiment; concentrations are in m-equiv. per 100 g unless otherwise stated

Soil no.*	Na	Available cations K	Ca	Mg	NH_4	Total exchangeable bases	NO_3	Cl	Available P (mg $100\,g^{-1}$)	Soil moisture (%)	Conductivity (mS cm^{-1})	pH
1	1·2	0·32	1·3	1·4	0·04	4·6	0·14	0·41	0·58	14	0·18	5·9
2	3·9	0·81	3·4	2·6	0·20	8·3	0·87	2·2	6·23	26	0·91	4·2
3	6·8	1·76	80	10·6	0·05	>60	0·81	2·3	15·3	19	0·81	7·0
4	10·4	1·33	5·4	4·4	0·59	13·8	3·2	7·1	17·0	56	2·73	3·6
5	8·8	0·96	3·5	3·5	0·87	10·1	1·5	7·0	17·0	33	2·08	3·8

* See text.

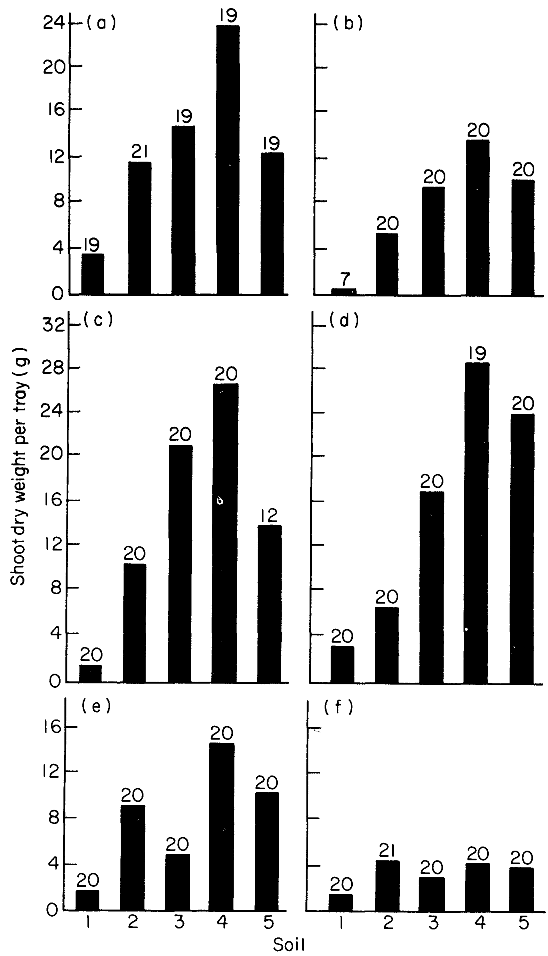

Fig. 9. Total shoot dry weight per tray of the plant species grown in the glasshouse on five different soils from Hackley Head. The number of plants present in each tray at the time of harvest is indicated at the top of each bar. (a) *Stellaria media*, (b) *Urtica urens*, (c) *Atriplex hastata*, (d) *Atriplex patula*, (e) *Holcus lanatus*, (f) *Festuca rubra*.

(3) The response of *Holcus lanatus* was generally similar to that of the other ruderals, except that, like *Festuca rubra*, it did comparatively poorly on soil 3. This finer-textured soil was at times noticeably waterlogged in the glasshouse, and might have been particularly inimical to the growth of the grasses.

(4) *Festuca rubra* differed markedly from all other species in its response to the soils. It grew equally well on soils 2, 4 and 5, and its dry weight on the poorest soil (on which it occurs naturally) was relatively greater than that of the other species (36% of its weight on the best soil), which suggests that its nutrient requirements for optimum growth are lower than those of the other species.

Discussion

The fact that the various species responded favourably in the glasshouse to soils on which they do not occur in the field implies that edaphic factors *per se* are not entirely responsible for the field distributions observed. This is clearly illustrated by the fact that all the species grew best on soil 4, which in the field supports only *Urtica urens*. The absence of the other five species from this soil in the field cannot thus be attributed directly to unfavourable edaphic factors. However, the very poor performance of the ruderals (*Stellaria media*, *Urtica urens* and the *Atriplex* species) on soil 1 suggests that low soil fertility (particularly for *Urtica urens*) could act directly to exclude these species from this soil.

Such an experiment necessarily ignores the role of biotic factors, in particular interspecific competition, which could be of direct importance in restricting the various species to soils of different properties; for example, it may be that a greater competitive ability of *Urtica urens* under high nutrient concentrations acts to exclude the other species from the soils on the slopes of Hackley Head; when nutrients fall below a certain level, the competitive advantage could lie with other species better adapted to lower nutrient levels.

GENERAL DISCUSSION

Since particular plant species are associated with the presence of gulls, and normal coastal vegetation is absent or much reduced in gull colonies, it can be concluded that gulls are responsible for the vegetation associated with their breeding sites. The observations of bird activities suggested that disturbance associated with boundary clashes is a particularly significant activity. Though such disturbance is likely to be directly deleterious to any plant—be it annual or perennial—it will lead to a situation especially suitable for annuals: the exposure of a bare soil surface. Annuals, being fast-growing, prolific seed-producers, are not only capable of tolerating disturbance but also require repeated disturbance, with the exposure of bare surfaces, for their perpetuation on a site. It is pertinent that the perennials which do occur in colonies (e.g. *Rumex crispus*, *Rumex acetosa*, *Tripleurospermum maritimum*, *Heracleum sphondylium*) have deep, stout tap roots difficult for gulls to uproot. Further support for the importance of disturbance is provided by the experimental work at Hackley Head, which indicated that disturbance on its own (i.e. the clearance of an area), without added fertilization, resulted in the establishment of colony annuals on areas where they did not naturally occur.

The importance of the other gull activities must not however be dismissed. Defecation is of obvious importance in the local enhancement of soil-nutrient concentrations. At least one species (*Urtica urens*) appears to require high soil fertility for successful establishment. Defecation is thus likely to be of direct importance in determining the distribution of some species, and will affect the performance of most plants which come in contact with the resulting higher nutrient concentrations. Observations at Hackley Head by Sobey (1975) also suggest that, where sufficiently intense, defecation can on its own bring about the destruction of the fescue sward found along cliffs.

Generally, however, it appears that if a species is to establish successfully in a gull colony, a necessary attribute is an ability to withstand the disturbing and destructive activities of gulls. When gulls move on to a new site, most of the species present in the pre-gull vegetation succumb to one or other of the gull activities, or to all in combination. Some, however, such as *Holcus lanatus* and *Rumex acetosa* (as noted at Hackley Head and also on the Isle of May—Sobey (1976)), are capable of surviving limited activity, and may even expand in range and performance. Generally, however, the establishment of a gull colony results in the development of a new plant community specifically adapted to the changed conditions. Annuals (both ruderal and maritime) are especially able to take advantage of such continual disturbance. The particular annuals which arrive on a site will depend to some degree on their methods of dispersal as well as on chance, but having once arrived and the paramount requirement (repeated disturbance, with the exposure of bare soil) being provided, each annual species appears to distribute itself as a result of the interaction between its specific ecological requirements and tolerances and the nature of the habitat. Interspecific competitive ability of species under the various conditions occurring in a colony is likely to be a factor of considerable importance in determining their spatial distributions. The noticeable segregation of the annuals into almost pure stands suggests that such competitive interactions generally result in an 'all or nothing' situation.

It is during such competition that site-factors other than gull disturbance appear to play a significant role in determining the distribution of the species within the colony—factors such as soil fertility (which may be inherent, or bird-affected through defecation) and sea-spray deposition. The distribution of *Urtica urens* is probably determined by soil fertility levels (possibly nitrogen and phosphorus), as shown for *U. dioica* (Pigott & Taylor 1964). Where fertility falls below a threshold, and in the presence of other species better able to compete under lower nutrient levels (e.g. *Stellaria media* or *Atriplex hastata*), *Urtica urens* cannot establish. Circumstantial evidence suggests that a factor determining the success of *Atriplex hastata* is the effect of sea-spray deposition: *A. hastata* is generally found in colonies on areas closer to the sea, where other species apparently cannot exist. In areas where the influence of sea-spray is less (e.g. the top of Hackley Head), species such as *Atriplex patula* and *Stellaria media* occur.

It should be stressed that the vegetation, dominated as it is by annuals, is vulnerable to erratic changes in environmental factors such as those produced by storms; there is thus a certain instability in colony vegetation, evident as small-scale but notable shifts in species-distribution from year to year. It is possible, however, that the vegetation as a whole, once established, may achieve a steady-state 'bioclimax'. Two factors may prevent this from occurring: the continual addition of faeces to a site may increase the concentration of less mobile nutrients such as phosphorus or calcium; or, in certain situations, erosion resulting from gull activities may lead to the eventual degradation of the system to bare rock, as has happened on parts of the Isle of May (Sobey 1976).

The approach adopted in the present study, with equal emphasis on the birds and on the vegetation, has clearly proved worthwhile. The significance of gull activities, which would have been ignored had only the vegetation been examined, has been realized. It has thus been demonstrated that some of the labels applied by botanists to such vegetation (e.g. nitrophilous or coprophilous), though possibly applicable to certain species, are inappropriate for the vegetation as a whole. That specific labels are inappropriate is because the influence of gulls on the vegetation of their breeding sites is not simply one of nutrient-enrichment nor of disturbance—rather it is a complex of interacting effects, superimposed upon which are a host of other environmental factors with which plants have to cope if they are to establish on a site.

The theory developed here should be applicable generally to other herring gull breeding sites, and to other gull species with habitat preferences and behaviour similar to herring gulls. As noted in the Introduction, gull numbers have been increasing in many areas, and changes in vegetation brought about by gulls have been cited as justification for reducing numbers at some sites. The reduced aesthetic appeal of colony vegetation compared with that normally occurring, and the ecological degradation of some sites due to erosion, help to justify such culls. However, at the same time, the vegetation of herring gull colonies is of intrinsic ecological interest, as an example of an unusual type of plant community—a plant community controlled and determined by an animal population.

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