GENE FLOW IN A CLINE

AMATHES GLAREOSA ESP. AND ITS MELANIC
F. EDDA STAUD. (LEP.) IN SHETLAND

H. B. D. KETTLEWELL

Genetics Laboratory, Department of Zoology, University of Oxford
and

R. J. BERRY

Royal Free Hospital School of Medicine, London, W.C.1

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1. INTRODUCTION

THE Caradrinid moth *Amathes glareosa* Esp. has a distinct melanic form (*edda*) in Shetland. This form decreases in frequency from 97 per cent. in the north of the 70-mile-long group of islands to about one per cent. in the south (Kettlewell and Berry, 1961) (fig. 1). The difference between the two forms is controlled by a single gene, and in North Shetland (Unst) the black form seems to have near-complete dominance. However, slightly lighter forms are sometimes encountered in the wild population, although we found it impossible to differentiate these from the darker forms with accuracy. The obvious assumption is that these lighter moths are heterozygous for the *edda* gene. Despite the difficulty of scoring, we can state confidently that under 15 per cent. of 12,818 *f. edda* from Unst were classifiable as being of the lighter form. In this area the Hardy-Weinberg expectation for the frequency of heterozygotes is 28 per cent.

By contrast in South Shetland, in the Orkneys and in Fair Isle where *f. edda* occurs at a low frequency, many of the specimens are paler than any found on Unst, the majority are light and none of the darkest ones are as black as those from northernmost Shetland. This can be accounted for by either incomplete dominance in the Southern populations in contrast to the North Shetland one or alternatively by a different gene-complex which produces a paler insect here in both the *f. edda* genotypes. It must be emphasised that never is there any difficulty in distinguishing *f. edda* from *f. typica* which is the only form occurring throughout the rest of Britain.

We have described the occurrence and intensity of the cline in *f. edda* in three papers (Kettlewell, 1961a, b; Kettlewell and Berry, 1961) based on field-work in Shetland in 1959 and 1960. This paper describes work done in 1961 and 1962 with the particular object of investigating an apparent barrier to gene-flow in the centre of the cline.

In 1960 we showed that the frequency of *f. edda* over most of the north of the Shetland Mainland (= the main island) was 50-60 per cent.; in the South Mainland, all the populations sampled contained less than five per cent. of the melanic. In the intervening Central Mainland the phenotype frequency decreased by 50 per cent. over a distance of about 15 miles. The simplest explanation for this state of affairs is a barrier to gene-flow separating populations living under different ecological conditions.

Now in Shetland *A. glareosa* is caught in numbers in two very different

FIG. 1.—Map of the Shetland islands showing the places where *Amathes glareosa* was sampled on more than one year, with frequencies of *f. edda* indicated.

types of habitat. Over most of the islands the maximum abundance of the species occurs on or close to areas of short heather. This habitat includes the specialised flora which grows on the serpentine on the eastern side of Unst and the southern part of Fetlar (Spence, 1957). In the extreme south of the Mainland *A. glareosa* abounds on sand dunes on which no heather is present. As early as 1959 we noticed that a valley where today arable land replaces heather (which is unsuitable for the ecological requirements of *A. glareosa*) crossed the critical part of the Central Mainland. This valley (the Tingwall Valley) runs north-east and south-west and varies from half-a-mile to two miles in width, and is the result of a limestone fault. It serves also as a wind funnel for the prevailing south westerly winds. Hence it seemed that this valley might function as at least a partial barrier to gene-flow.

Traps placed on the north and south borders of the Tingwall Valley at the end of the 1960 season produced small catches of moths in which the frequency of *f. edda* fluctuated widely on different nights, but in a way suggestive that the frequencies of the morphs on either side of the valley were inversely proportional to each other (Kettlewell, 1961*b*). The overall frequency of *f. edda* in this area was about 20 per cent.: in other words the Tingwall Valley was in the middle of the steep cline in frequency between the North and South Mainland.

2. METHODS OF INVESTIGATION

The object of the experimental work in 1961 was two-fold: to determine the frequencies of *f. edda* at a number of sites in and near the Tingwall Valley, and by releasing marked insects on both sides of the valley, to discover the range of flight of individual moths and the extent to which moths crossed the valley. Mercury vapour traps were set at sixteen sites: two of them two miles to the north* of the valley, five of them in heather along the north border of the valley, three in the centre of the valley (two of these caught no *A. glareosa* and have been omitted from figures and tables), five along the south border, and one two miles to the south (fig. 2). The numbers of the two morphs caught each day in each trap were recorded.

All undamaged moths were marked on the underside of the wings by a spot or stripe of cellulose paint (Dowdeswell, Fisher and Ford, 1940; Kettlewell, 1961*b*), and approximately equal numbers of each form released on each side of the valley. Distinctive marks were given for each day, and also to moths released on the north and south sides. The moths were released at one of two release sites (fig. 2), each of them between one quarter and one half-mile from the nearest trap. Moths were usually marked on the day of capture and released onto heather at early dusk, about 9 p.m. Much of the bird predation on the moths took place during the hours of daylight (Kettlewell, 1961*b*), and it was hoped thereby to minimise this. The weather, with particular reference to wind strength and direction in the night, was recorded every morning.

At the same time that we were working in the Tingwall Valley, we were also carrying out investigations on behavioural problems in *A. glareosa*

* Strictly speaking the north and south borders of the Tingwall Valley are south-east and north-west facing slopes. However as the main axis (and populations of *A. glareosa*) of the Shetland Mainland runs north and south, we have written throughout of the Tingwall Valley as if it ran due east and west.

(Kettlewell, Berry, Cadbury and Phillips, 1969). This resulted in the collection of frequencies of *f. edda* from a number of localities in the South Mainland, which are included here. Although it had been hoped to continue the work in the Tingwall Valley in 1962, *A. glareosa* was comparatively uncommon in that year, and only frequency data are reported.

FIG. 2.—Map of the Tingwall area (the valley proper is shaded) showing the percentage frequencies of *f. edda* in 1961 (except for sites 6 and 18 which were only sampled in 1960). Sampling sites numbered as in table 2.

3. RESULTS

Five localities were sampled for *A. glareosa* in more than one year. The frequencies of *f. edda* in the different years are collected in table 1 to give information on the stability of the cline from year to year.

In 1960 we found that on Unst, the northernmost island, the frequency of *f. typica* rose towards the end of the hatching period, and we concluded that this was probably due to *f. edda* hatching earlier than *f. typica* here (Kettlewell, 1961*b*). Since in the Tingwall area we are dealing with fairly small differences in *f. edda* frequencies between localities, it was important to know the extent of any secular changes in frequency. Hence we have tabulated the frequencies of *f. edda* according to the dates of catching (tables 1 and 2). It is normally possible to catch *A. glareosa* in Shetland from about 10th August to 9th September. We have divided the data into three groups, each referring to approximately ten days of catching. Out of 46 possible com-

TABLE 1

Frequencies of f. edda at sites sampled on more than one year

Site	Year	% frequency of <i>f. edda</i> in period			Numbers caught over whole period of trapping			Overall % frequency of <i>f. edda</i>
		Up to 19th Aug.	20-29th Aug.	30th Aug. on	<i>f. typica</i>	<i>f. edda</i>	total	
1. Baltasound	1959	96.6 (948)	97.2 (1591)		77	2462	2539	97.0
	1960	97.2 (4957)	97.2 (5080)	96.5 (621)	302	10356	10658	97.2
2. Hillswick	1959			82.6 (23)	4	19	23	82.6
	1960	75.9 (87)			21	66	78	75.9
	1961	75.1 (366)	76.5 (234)	75.1 (305)	222	683	905	75.5
	1962	80.9 (194)	75.8 (331)	74.3 (304)	195	634	829	76.5
4. Vatster	1961		38.4 (125)	35.0 (60)	116	69	185	37.3
	1962	53.3 (15)	25.9 (54)	38.8 (67)	88	48	136	35.3
10. Catwalls	1960			24.4 (135)	33	102	135	24.4
	1961	17.5 (40)	21.2 (184)	20.5 (200)	337	87	424	20.5
	1962	36.4 (11)	28.0 (25)	20.0 (90)	97	29	126	23.0
29. Scousburgh	1959	2.9 (34)	4.6 (65)		95	4	99	4.0
	1960	6.3 (16)	3.3 (274)		280	10	290	3.4

Figures in brackets indicate the sample size.

The sites where moths were caught have been numbered from north to south (see figs. 1-3).

TABLE 2
Frequencies of f. edda at sites bordering or near the Tingwall Valley

Site	Relation to Tingwall Valley	% frequency of <i>f. edda</i> in period			Numbers caught over whole period of trapping			Overall % frequency of <i>f. edda</i>
		Up to 19th Aug.	20th-29th Aug.	30th Aug. on	<i>f. typica</i>	<i>f. edda</i>	total	
1960: 3. South Nesting	North	39.3 (56)			34	22	56	39.3
6. Breiwick	South border		12.9 (31)		27	4	31	12.9
10. Catwalls	North border		24.4 (135)		102	33	135	24.4
20. Scalloway	North border		19.1 (47)		38	9	47	19.1
18. Burn of Dale	South		21.4 (154)		121	33	154	21.4
1961: 4. Vatster	North		38.4 (125)	35.0 (60)	88	48	136	35.3
5. Wormadale	North	25.0 (16)	37.1 (35)		34	17	51	33.3
9.	North border	26.0 (50)	20.9 (115)	28.0 (193)	267	91	358	25.4
10.	North border	17.5 (40)	21.2 (184)	20.5 (200)	337	87	424	20.5
13.	North border			19.8 (253)	203	50	253	19.8
14.	North border	23.8 (21)			16	5	21	23.8
16.	North border	28.0 (25)	23.1 (65)		68	22	90	24.4
North border samples combined		23.5 (136)	21.4 (364)	22.4 (646)	891	255	1146	22.3
17.	Centre							
7.	South border	10.0 (20)	29.6 (27)	20.1 (154)	142	39	181	21.5
8.	South border		41.2 (17)		28	9	37	24.3
11.	South border	22.2 (18)	23.7 (76)	15.9 (63)	53	10	63	15.9
12.	South border		23.1 (52)	23.9 (117)	161	50	211	23.7
15.	South border			13.3 (15)	53	14	67	20.9
				26.9 (78)	57	21	78	26.9
South border samples combined		18.8 (136)	25.5 (145)	22.3 (273)	352	104	456	22.8
19.	South	17.8 (73)	22.4 (85)	13.5 (37)	158	37	195	19.0
1962: 4. Vatster	North	53.3 (15)	25.9 (54)	38.8 (67)	88	48	136	35.3
10. Catwalls	North border	36.4 (11)	28.0 (25)	20.0 (90)	97	29	126	23.0

Figure in brackets indicates sample size.

parisons where sampling was carried out during more than one ten-day-period at the same site, only one overstepped the bounds of conventional significance ($\chi^2_1 = 5.17$, $P < 0.025$ between the first two sampling periods for trap 7 in the Tingwall Valley in 1961). No "significant" differences were found for the eleven comparisons where sampling was carried out during both first and last sampling periods.

TABLE 3
Frequencies of f. edda at sites in the S. Mainland

Site	Year	Numbers caught over whole period of trapping			% frequency of <i>f. edda</i>
		<i>f. typica</i>	<i>f. edda</i>	total	
21. Easter Quarff	1961	137	23	160	14.4
22. Fladdabister	1962	137	0	137	0
23. Cunninsburgh	1960	96	3	99	3.0
24. Sandwick	1962	111	3	114	2.6
25. Channerwick	1962	247	4	251	1.6
26. Bigton and Ireland	1962	222	13	235	5.5
27. Levenwick	1960	173	2	175	1.1
28. Clumlie	1962	119	3	122	2.5
29. Scousburgh	1959	95	4	99	4.0
Scousburgh	1960	280	10	290	3.4
30. Boddam	1960	4105	80	4185	1.9
31. Sumburgh	1962	120	2	122	1.6
Foula	1963	24	0	24	0
Fair Isle	Hardy 1961	40	15	55	27.3
Rousay (Orkney)	Ffennell 1961	17	3	20	15.0
Orphit (Orkney Mainland)	Lorimer 1967	66	16	82	19.5
Orphit (Orkney Mainland)	Lorimer 1968	153	19	172	11.0
Binscarth (Orkney Mainland)	Lorimer 1968	37	22	59	37.3

Table 3 lists data on the frequency of *f. edda* in the South Mainland (fig. 3).

A total of 1682 (533 *f. edda* and 1149 *f. typica*) marked moths were released in the Tingwall Valley in 1961: 847 on the north side and 835 on the south (table 4). The sex of released individuals was not recorded. At the beginning of the hatching period, males greatly outnumber females.

FIG. 3.—Map of the South Mainland of Shetland showing sites sampled for *Amathes glareosa* (numbered as in tables 2 and 3), giving the percentage frequencies of *f. edda*.

The converse is true later in the season. The two sexes are not differentiated with ease. 65 (3.9 per cent.) moths (19 *f. edda* and 46 *f. typica*) were recaptured. Only one of these 65 crossed the valley. The majority of recaptures on both sides of the valley (46 out of 63) were trapped at sites to the south-west of the release grounds despite the fact that the winds during the mark/

TABLE 4
Summary of mark/release/recapture experiment in the Tingwall Valley

		Released on North side of Valley		Released on South side of Valley		Total
		<i>f. typica</i>	<i>f. edda</i>	<i>f. typica</i>	<i>f. edda</i>	
Number of moths marked and released		578	269	571	264	1682
Number of moths recaptured		25 ¹	13 ¹	21	6	65
% of moths recaptured		4.3	4.8	3.7	2.3	3.9
Direction and distance of movement between release and recapture	SW 550 yards	—	—	2	1	3
	SW 700 yards	1	1	1	1	4
	SW 880 yards	16	8	—	—	24
	SW 1050 yards	—	—	—	1	1
	SW 2290 yards	4	—	—	—	4
	N 700 yards	—	—	8	3	11
	E 1230 yards	1	3	—	—	4
	E 1410 yards	1	—	—	—	1
	E 2110 yards	1 (crossed valley)	—	—	—	1
Mean distance moved	SW	1140 yds.	860 yds.	680 yds.	770 yds.	
	N or E	1320 ² yds.	1230 yds.	700 yds.	700 yds.	

¹ Site of recapture of one moth not recorded.

² Omitting moth which crossed the valley.

TABLE 5
Relation between direction moved by marked moths between release and recapture, and wind directions during that period

	Direction of movement of moths between release and recapture	Number of nights when wind W, SW or S	Number of nights when N, NE or N
Number of night/moths flying between release and recapture	SW	140	51
	Nor E	30	13

release/recapture experiment were from the south-west on 12 out of the 23 nights of the experiment. The average time between release and recapture for any moth was 4.8 days: there was no correlation between wind direction during this time and site of recapture relative to release ground (table 5: contingency $\chi^2_1 = 0.22$, $P \simeq 0.6$).

The moth that crossed the valley was a *f. typica* and went from the north side to the south. It was recaptured 13 days after its original capture. In

this time it had moved a net distance of 2110 yards in a direction just north of east. On the night after release the wind was light north easterly; on the second night there was no wind; then followed a spell of ten days when the wind was from the south west, including five nights of fresh winds (force 5-6 on the Beaufort scale) and a night when a full gale (force 8) blew most of the time. Finally on the night of recapture there was a light easterly breeze.

From our data the chance of any one moth crossing the valley is about one-and-a-half per cent. Although the number of recaptures is too small to attach much importance to this value, it is clear that comparatively few moths crossed the Valley during the course of the experiments. This is substantiated by our failure to catch any *A. glareosa* in two of the three traps located in arable ground in the centre of Tingwall Valley.

4. DISCUSSION

Our work on *A. glareosa* was undertaken as a study of a non-industrial melanic situation in the hope that it might throw light on present day industrial melanism. Implicit in such a situation is the premise that the dimorphism is of long standing and relatively stable. Four years is too short a time to test adequately the constancy of a cline, but the data in table 1 show that the frequencies of *f. edda* remained unchanged at five localities during the years we worked in Shetland. Furthermore, the frequencies of *f. edda* were constant throughout the season at any one place (tables 1 and 2). The frequencies of *f. edda* are higher on the west coast than on the east. This is particularly marked in the South Mainland (fig. 3), but the same effect holds in the Tingwall Valley. This is consistent with a general finding throughout the Palaearctic that melanism in Lepidoptera is more pronounced on western shores than eastern ones. These facts mean that it is legitimate to seek meanings for observed local differences in gene frequencies.

This conclusion is important for the interpretation of *f. edda* frequencies in the neighbourhood of the Tingwall Valley. In this region four facts stand out:

- (1) The average gene frequencies on the two sides of the Valley are effectively the same (table 2).
- (2) Individual moths cross the valley infrequently (table 4).
- (3) The frequency of *f. typica* drops 10 to 15 per cent. as one proceeds northward in the two or three miles *immediately to the north of the valley* between Vatster (No. 4) or Wormadale (No. 5) to Catwalls (No. 10) ($\chi^2_1 = 17.9$, $P = < 0.001$) (table 2 and fig. 2).
- (4) The mean movement of marked individuals on each side of the Tingwall Valley was of the order of half-a-mile (table 4), independent of wind direction (table 5), which means that considerable gene mixture was continually taking place within the two relatively isolated populations. Fairly intensive selective pressures must be occurring to maintain the observed gene frequencies.

The lack of distinctiveness in *f. edda* frequencies in the separated populations immediately to the north and south of the Tingwall Valley is the opposite of the finding of Creed, Dowdeswell, Ford and McWhirter (1959) at a long-established boundary between two populations of the Meadow Brown butterfly, *Maniola jurtina*, in Cornwall. They found that differences

between the populations were intensified at the boundary between them. In their situation, however, there was no physical barrier between the populations, so allowing the free production of the illadjusted intermediate types.

The similarity between the north and south Tingwall Valley frequencies is paralleled by the similarity of frequencies across the three miles wide sound between the Shetland Mainland and Yell, the next island to the north (Kettlewell and Berry, 1961), except that no sudden frequency change is found immediately to the north of this sound. Indeed it is easier to account for the similarity of *f. edda* frequencies in such separated populations than it is to explain the rapid change in frequencies occurring over the three miles immediately to the north of the Tingwall Valley. This is apparently an area which is ecologically uniform and favourable to *A. glareosa*. There are no obvious differences in the heather habitat between Catwalls (No. 10) and Vatstar (No. 4), except that the former is on the edge of a large area of short heather liberally mixed with *Molinia* extending down the slope of the valley. The region between the two sites (and stretching over a large area to the north) has a fairly complete heather cover (average height 7 in.) with many small tussocks (maximum height *c.* 12 in.). This habitat is uniform except for deeper heather in sheltered stream beds. Despite this, there was an increase of 15 per cent. in *f. edda* frequency between Catwalls and Vatster. This is particularly remarkable in context since there was no phenotype frequency change over the Tingwall Valley itself, and the frequency of *f. edda* dropped only about 30 per cent. in the 30 miles between the north of the Mainland and Vatster (Kettlewell and Berry, 1961). The change in *edda* gene frequency between Catwalls and Vatster is much less than that of the phenotype frequency (8.7 per cent. as compared with 14.8 per cent. for the latter), which may mean that an effect of the gene unrelated to the *edda* phenotype is important in these circumstances. However a change of gene frequency of 9 per cent. over $2\frac{1}{2}$ miles when individual moths not infrequently fly half this distance bespeaks of an intensive pressure of natural selection.

The obvious hypothesis to explain the frequency change to the north of the Tingwall Valley is that there is considerable northward movement of moths across the valley from the large pool of *typica* genes to the south, particularly since the southern Shetland moths fly more frequently than those to the north of the valley (Kettlewell, 1961*b*, 1963, and see below). It would be reasonable to assume that a high frequency of *f. typica* might be at a disadvantage in the "northern" population, and hence there would be a rapid fall in *f. typica* frequency as incomers are eliminated. The difficulty about this interpretation is that there is no experimental evidence that many moths fly across the Tingwall Valley. If the frequency change to the north of the valley is maintained entirely by immigration from the south, the majority of the moth population on the north border of the valley would have to be composed of immigrants. Even the possibility that occasional large-scale incursions of moths from the south take place under certain weather conditions is contra-indicated by the observed constancy of phenotype frequencies at Catwalls (No. 10) over three years and Vatster (No. 4) over two (table 1).

Furthermore the stimulus for flight in males is mainly concerned with finding a mate; in females it is for ovipositing on or near to its food plant. Both sexes search for flowers on whose nectar they feed, particularly heather (usually *Calluna vulgaris*) but also ragwort (*Senecio jacobaea*). In all these

situations the stimuli are olfactory, and consequently the flight direction must be up-wind. In a wind-funnel such as the Tingwall Valley, there can be little encouragement to cross the valley other than in exceptional circumstances.

In our previous description of the cline in *f. edda* (Kettlewell and Berry, 1961), we discussed various factors that could be operating to maintain it.

At its northern limit the high frequency of *f. edda* is governed to a major degree by intense selective bird predation (Kettlewell, 1961*b*). Observations over three years in and around the Tingwall Valley lead us to believe that little bird predation occurs there. The gulls (mainly *Larus canus*) apparently feed chiefly on *Tipulidae* in the meadows.

A factor certainly of more importance to the cline in the Tingwall area is the flight habit difference which we demonstrated between moths of both morphs from the northern population (the majority of which are *f. edda*) and moths from the south (the majority of which are *f. typica*) (Kettlewell, 1961*b*). This difference is one in which the individuals from the northern population fly on fewer nights than those from southern Shetland, regardless of whether they are released in north or south Shetland. Since the northern and southern populations seem to meet at the Tingwall Valley and since the habit difference is one between whole populations, rather than between morphs (Kettlewell, 1963; Kettlewell, Berry, Cadbury and Phillips, 1969), this behavioural difference must be a major contributing factor to the maintenance of a cline in the Tingwall area.

Clarke and Sheppard (1966) have argued that the melanic polymorphism of the Peppered Moth (*Biston betularia*) in North Wales and Liverpool is stable and not transient, since no populations contain more than 98 per cent. of the dominant melanic form and the selective disadvantage of the typical form appears to be over 50 per cent. in such areas. In other words, physiological factors as well as visual selective predation are involved in the maintenance of *f. carbonaria* of *B. betularia* (*q.v.* Ford, 1937; Kettlewell, 1955). Such factors must also be involved in the *f. edda* cline which has been in existence much longer.

In work which has been much quoted in evolutionary literature, Sumner (summarised 1932) studied a cline in *Peromyscus polionotus* in Florida. On an off-shore sandy island a light-coloured cryptic form occurred. The mice on the nearby mainland were also lighter than the typical form, but were considerably darker than those on the island. The two forms differed genetically at a number of loci. The typical mainland form was not found nearer than 100 miles to the coast. Sumner showed that there was a rapid change of morphological characters between coastal and inland forms twenty miles from the coast, and a further change in pigmentation characters another twenty miles inland. There was no obvious gradient in soil colour inland away from a narrow littoral fringe of sand, and Sumner could find no differences in the environment of the mice which could explain the cline. Consequently he was forced to conclude that the "expanding coastal population pressed inland, displacing and absorbing the inland form, until its advance was halted by the centrifugal pressure of the latter" (Sumner, 1929). If this explanation is correct, the rapid changes in frequencies in the *P. polionotus* cline are unlikely to be due to the same causes as the ones operating in the part of the *A. glareosa* cline immediately to the north of the Tingwall Valley since this would require there to be a continuous population of moths over

the valley from the south of the Mainland. However, all Sumner's results cannot be explained by migration pressure of cryptic individuals, and a full interpretation of the cline in *P. polionotus* will have to include the same sort of behavioural and physiological considerations that are involved in the *B. betularia* and *A. glareosa* clines.

The Shetland population of *A. glareosa* is effectively divided by the Tingwall Valley. It is tempting to speculate that the northern population has forfeited some physiological advantage by incorporating allelomorphs concerned with crypsis and flight adaptation into its gene complex (although it would be expected on theoretical grounds that physiological disadvantage and cryptic advantage would have become separated in a long-established cline: e.g. Ford, 1965). This could explain why moths with the putative southern population gene-complex might be only slowly eliminated in the area of little bird predation immediately to the north of the Tingwall Valley.

The work described here indicates once again the intense selective forces so often found in wild populations, and shows the value of studying parts of a cline where the advantages and disadvantages of physiological, ecological and colour differences which have arisen at different ends of the cline, can be compared.

5. SUMMARY

1. The frequency of the melanic *f. edda* of the Noctuid (Caradrinid) moth *Amathes glareosa* decreases in 70 miles from 97 per cent. in the north of the Shetland Islands to approximately 1 per cent. in the south.

2. This decline is fairly constant except for a region in the Central Mainland (= main island) where the phenotype frequency drops from 35 per cent. to 13 per cent. over 8 miles.

3. The middle of this region is crossed by the Tingwall Valley which consists largely of a habitat unfavourable to *A. glareosa*; yet the frequencies of *f. edda* on each side were identical.

4. Mark/release/recapture experiments over a period of four weeks in 1961 showed that the valley was crossed rarely (of 1682 marked moths released, 65 were recaptured but only one had crossed the valley).

5. The mean net flight distance of recaptured individuals was approximately half-a-mile, yet the frequency of *f. edda* drops 15 per cent. over 2½ miles immediately to the north of the Tingwall Valley.

6. The constancy of gene frequencies throughout the cline from year to year, indicates that differences in frequencies between areas are maintained by fairly strong selective forces.

7. Since bird predation in the Tingwall region is light, it is suggested that these may be concerned with behavioural and physiological requirements for maintaining the integrity of co-adapted gene-complexes.

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