The Genetics and Population Dynamics of Porcellio scaber (Latrielle)

by

D.G.M. WOOD-GUSH
B.Sc.(Rand.) Dip. Genetic.(Edin.)

Submitted to the University of Edinburgh as a Thesis in fulfilment of the requirements for the degree of Doctor of Philosophy.

Institute of Animal Genetics.
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"For though there are animals which have no attractiveness for the senses, yet for the eye of science, for the student who is naturally of a philosophic spirit and can discern the causes of things, Nature which fashioned them provides joys that cannot be measured".

ARISTOTLE - De Partibus Animalium I.
INTRODUCTION

Since the publication of the works of Darwin and Wallace, the theory of evolution has influenced Man's philosophy and intellectual thinking more than any other biological doctrine. Today, it is the focal point of biology, and for its exposition relies on mathematics and many diverse sciences. Among these is Population Genetics. This is concerned with the genetic variability present in a species and the selective forces operating, and the effects of these forces on the fitness of the species. The interaction of these factors, however, appears to be largely governed by the state of subdivision or population structure of the species. A study of evolution in a particular species therefore involves a study of its population structure and its genetic variability. In this work both aspects are attempted, using the Isopod Porcellio scaber (Latrielle) as material.

The first part of this work is devoted to the study of the population structure of this species. In introducing this work, the theoretical importance of population structure is considered and some pertinent experimental data are discussed to ascertain the extent to which the theory is supported/
supported by fact, and to examine the techniques suitable for the study of natural populations. Pertinent studies on the life history of the species and the experiments dealing with population structure are then given.

The second part deals with the geographic variability of *P. acaber* over part of its range. This study was performed to get an indication of the amount of genetic variability possessed by the species; to ascertain what characters are under differential selective forces and to detect any incipient speciation that might be discernible.
THE REVIEW OF LITERATURE - PART I

A. The theoretical importance of population structure

The theoretical considerations of evolution are facilitated by that fact that Mendelian inheritance allows the pertinent phenomena to be represented by mathematical models. Fisher, Haldane and Wright have dealt with the mathematical theory of the subject, and have considered a wide variety of genetical circumstances, but as Haldane (1935) has inferred, this mathematical approach to the subject is only the beginning of a new branch of applied mathematics. They have dealt only with genes that are fully penetrant, and principally with those whose presence or absence is easily discernible in the phenotype of the organism. The consideration of characters dependent on a large number of genes has been confined mainly to the study of livestock improvement, although Mather (1943) and Lerner and Dempster (1948) have attempted to show that methods used in this field of genetics are germane to the study of evolution in natural populations. The importance of population structure has been emphasised mainly by Wright and his theories are summarized on the following/
To deal mathematically with the diverse agencies operative in evolution, a common basis is necessary and it is provided by the concept of gene frequency. Wright (1949, 1949a, 1950a and other papers) has listed the factors causing a change of gene frequency on the basis of immediacy and determinacy. It is apparently exhaustive and in the term selection he includes differential viability, differential maturity, differential fecundity and differential emigration.

His list is given below:

A Immediate Change

1. From systematic pressures ($\Delta q$ determinate in principle)
   a. Recurrent mutation
   b. Intrapopulation selection
   c. Recurrent immigration and crossbreeding

2. Fluctuations ($\delta q$ indeterminate $\Delta^2 q$ and $q$ determinate in principle)
   a. In systematic pressures
   b. From accidents of sampling

3. From unique events (wholly indeterminate)
   a. Mutation favourable from the first
   b. Unique selective incident
   c./
c. Unique hybridization

d. Swamping of mass immigration

e. Unique reduction in numbers

B Secular Change in System of Coefficients

1. From causes within species (control by new peak genotype)

2. From changes in external environment

   a. In home territory

   b. As that of new territory

Wright (1949a, 1950a) envisages two aspects of evolution: the multiplication of species and the transformation of species. In both these aspects he stresses the importance of ecological opportunity, such as the opening up of a new territory with many unoccupied niches, and emphasises that the species most capable of taking advantage of such a situation is one having a vast store of potential genetic variability. On this basis he has considered many models of population structure and their effects on the transformation of a species through the action of one or more of the agencies listed above. His conclusions, derived by means of mathematical deduction, emphasise the importance in evolution of Population Structure, a term which he (1950) has defined to include population numbers, composition/
composition by age and sex and the state of subdivision of the population.

In a large population in which there is complete random-mating or panmixia he (1949a, 1950a) maintains that most genes will reach equilibrium under steady external pressures, and evolution is best provided by unique mutations favourable from the start or from hybridization. However a permanent environmental change might also stimulate evolution. If the population size is small, changes may be accomplished by the random fluctuations of gene frequencies to new points of equilibrium, but if the population is very small, random fixation of genes will overcome the conservative forces of selection and degeneration is the most probable result. He then considers a species subdivided into populations which are semi-isolated from one another. In such a species there will be differentiation due to local environmental differences; genetic drift without complete fixation can occur if the effective population size and the migration coefficient bear a certain relationship to one another \(\frac{1}{2n}\) and \(m\) of the same order). Furthermore inter-population selection will add to the genetic variability of the species. He has discussed the advantages/-
advantages of a sub-divided population more fully in a non-mathematical paper (1950) but it is unnecessary to recapitulate the points here.

The ideal population structure as envisaged by Wright (1931, 1932 and other papers) is one in which the species is large but subdivided into many small local races, each breeding largely within itself but occasionally cross-breeding. A balance between mutation and reverse mutation, selection due to local conditions, cross-breeding and effective population size will ensure a store of potential genetic variability. Such a population can exist spatially in two forms: the local populations may conform to an island pattern or the species may be dispersed evenly over an area but still contain much local differentiation due to isolation by distance (Wright 1940, 1943). Each individual has its origin at a particular place and its parents are assumed to have been drawn from positions at certain distances from this place, and their parents from places of comparable distances. In an evenly distributed species the points of origin of the parents can be in any direction from the point of origin of the offspring, which means that these distances would have a variance in latitude and longitude. Ancestors of/
of generation k would be drawn from position sk times the distance moved by the parental generation. The parents may be considered as if drawn at random from a territory of radius R and effective population size N. The ancestors of generation k may then be considered to have been drawn similarly from a territory of radius KR and effective population size KN. If the parents were drawn from an area with an effective population size of approximately 100, then there is considerable fluctuating local differentiation. If N is larger than 1000 the results are equivalent to panmixia.

The importance of the effective population size has been emphasised and a definition of the term is warranted. It is smaller than the apparent population size (Wright 1931 and other papers) and is composed of the breeding members of the population only, and thus it is dependent on the age structure and sex ratio of the population. The whole concept of population size is built on the theory of the rate of loss of heterozygosis, and where there is a disparity between the sexes it is nearer to the smaller numbers. Also if the population numbers fluctuate the effective population size is closer to the minimum number than to the maximum number. Where these fluctuations are cyclic/
cyclic and generally cover a known number of generations the approximate effective population size can be found (Wright 1940).

A great deal of publicity has been given to the criticism of Wright by Fisher and Ford (1947). Much of this criticism appears to be unwarranted. They state that he claimed "Subdivision into isolated groups of small size is favourable to evolutionary progress". Wright (1948) replied to this stating that he had not claimed this and that he considered genetic drift to be merely one of a number of agencies capable of affecting gene frequency at those loci at which selection pressure was not appreciable. He has been criticized further by Fisher and Ford (1950) and by Mather (1943) but the settlement of these controversies must come finally from practical and not theoretical work.

Wright has brought together into his formulae a large number of phenomena capable of affecting the gene frequencies of populations so that their relative importance in a particular case can be assessed. His list appears to be fairly exhaustive and important among the phenomena is population structure, for the efficiency of the other agencies is affected by it. Thus stands the theory/-
theory, but is it borne out by experimental data? Is population structure so important under natural conditions? In the light of our present knowledge these questions cannot be answered and controversies on these theoretical considerations continue. In the next section of this introduction several apposite published experiments dealing with natural populations will be discussed. It will be seen that it is not easy to assess the population structure of species and although a great deal of ingenuity has been employed, we still know very little about natural populations. Attention is paid mainly to experiments using ecological techniques, for at this stage of our knowledge suitable techniques are important, and any knowledge we can gain about natural populations is of value. Although most of these experiments are extremely valuable, in no case are the data sufficient to test rigourously the theoretical considerations.
POPULATION STRUCTURE

B. Experimental evidence

When Wright delivered his address "The Roles of Mutations, Inbreeding, Crossbreeding and Selection in Evolution" at the Sixth International Congress of Genetics in 1932, there was very little experimental evidence on the nature of animal populations. To illustrate the point that species are divided into local races, he cited, inter alia, Crampton (1925), Jordan (1908), Osgood (1909), Schmidt (1917).

The majority of these papers do not give any critical data on the population structure of any of the colonies investigated, but merely record the fact that localized differences are apparent in the particular species under discussion. A resume of some work by Crampton will suffice to illustrate this criticism. He investigated the gastropods of the genus Partula on the island of Moorea. These species had been investigated by Garrett during the years 1861-88 and Crampton made collections in 1907, 1909, 1919 and 1923, gathering very large numbers (30,000 on his last visit). The island is divided into numerous valleys and he claims/-
claims that passage between these valleys is possible. In the species *P. taenita* (Mörch) populations from different parts vary in shell length, thickness of shell and in some populations the colour of the shells is different. No evidence as to the genetic basis of these characters is given, and the species is recorded as being ubiquitous on the island, so that no rigorous conclusions about the effective population size of the various colonies can be drawn. The species *P. naturalis* (Pfeiffer) is divided into two subspecies *alternata* and *vexillum* by Crampton. *Vexillum* had spread throughout the island during the period of investigation. In the old habitats the animals have dextrally coiled shells, but in the recently colonized areas the shells are sinistrally coiled. The genetics of this character have been fully analysed and Crampton's observation is interesting from the point of view of Natural Selection but affords little confirmation on the crucial problem of population structure. The species *P. mooreana* (Hartman) is described as a polymorphic species that has extended its range during the period under review. Its forms possess shells that differ in their banding. One of these forms with 3 narrow pale brown revolving bands decreased in frequency. The species *P. mirabilis*
mirabilis (Cramton) and P. dendroica (Cramton) each have several colour varieties that inhabit different valleys. Three distinct colour patterns were found amongst several hundred specimens of the species P. tohiveana that had been taken from a fairly restricted area.

Similarly Crampton found several colour types of the species P. olympia within a confined space.

These last four examples are more pertinent to the problem of Population Structure. The phenomena described are more easily explained by genetic drift, but although it is the most facile explanation it is not necessarily the correct one, and any description of the population structure of a species from these data must be extremely speculative.

Since 1932 much work, similar to the work quoted above, has been published. Generally it describes genetic divergence between populations, and small population size is invoked to account for the divergence. Granted that genetic drift is a possible cause, it cannot be considered seriously until something is known about the structure of these populations. Therefore, such papers will be neglected in this review and attention will be paid/-
paid only to the main papers that contribute directly to our knowledge about the structure of natural populations. Furthermore, the main emphasis of this review will be on those experiments which employed ecological techniques, for it is only with a very limited number of species that elaborate genetical techniques can be employed for these studies.

Dobzhansky and Wright together with several coworkers (1941, 1942 and 1943) have tackled the problem with great ingenuity, but their technique can only be used with very few species. Therefore, their experiments and others of the same type will be described only briefly. They investigated the population structure of *Drosophila pseudoobscura* in the Southwestern United States and Central America. These investigations were based on the premise that in large panmictic populations, lethal genes will be present in frequencies that are directly related to the mutation rates of such genes. In a species subdivided into small populations the frequencies of these lethal genes will vary considerably; in some populations they will be higher, in others they will be less, than in a large panmictic population. The premise depends upon these genes being entirely recessive or having a uniform/
uniform selective value in the heterozygote throughout the area under investigation. In practice another difficulty is encountered, for in these experiments no tests were made for pseudo-allelism which could easily vitiate the premises made, as the actual number of alleles are small. Furthermore, nothing is known about mutation rates under natural conditions or of selection on animals heterozygous for lethals and semi-lethals under the dynamic conditions of a natural habitat. Therefore their calculations of the population size include some assumptions that are by no means proven. These shortcomings are readily admitted by the authors, but the value of their experiments is very great. Similar techniques were used by Ives (1945) and Dubinin (1946) with D. melanogaster. The results of these experiments are summarized below.

In the Death Valley Region of the Southwestern United States, mountain ranges that support D. pseudoobscura populations are separated by stretches of desert. Eleven such populations were sampled and the effective population size of each locality was shown tentatively to be less than 2500. Another experiment was carried out at 3 ecologically different localities on Mount San Jacinto. In contrast to the previous experiment, these/
these localities were connected by a continuous sheet of forest. The effective population size of a station or sampling point was estimated as being about 50 flies, but such a point was found not to be substantially isolated from neighbouring stations. These results were confirmed by a later experiment (Dobzhansky and Wright 1943). The treatment of the data was more refined and more attention was paid to the temporal and spatial distribution of the lethals and their alleles. This experiment showed that the effective density of flies was 50 or 10000 square meters - a finding consonant with the earlier figure. They also calculated the size of the panmictic unit and concluded that the parents of most individuals are drawn from a circle with a radius of 250 meters, which would mean an effective population size of 500-1000 individuals.

Dobzhansky (1941 p177) found that the percentage of 3rd chromosomes carrying lethals and semi lethals was higher in populations of D. pseudoobscura from Mexico and Guatemala than in the Death Valley populations. The mutations rates had been found to be the same under laboratory conditions and therefore he concluded that the differences in the frequencies were due to differences in selection or effective population size. He decided that the/
the effective population size was larger in Central America, for the species is able to breed throughout the year while in the Death Valley region populations undergo regular reductions in size. This is very plausible, but until more is known about the ecology of this species, Dobzhansky's conclusion must be accepted with reserve.

_D. melanogaster_ is an exotic species in the U.S.A. and Ives (1945) studied populations from Florida and Massachusetts using the same techniques as Wright and Dobzhansky. He found that the population sizes of this species in both these areas was very large. In the U.S.S.R. Dubinin (1946) found that certain lethals were concentrated in certain populations and he attributed this to genetic drift. If these results are taken at their face value it would appear that the population structure of this species is different in the areas investigated by Ives and Dubinin.

Experiments of an ecological nature were also employed by Dobzhansky and Wright for obtaining data on natural populations. In their earlier experiments they had been unable to assign any definite value to the migration constant. Experiments were therefore performed on Mount San Jacinto with _D._/
D. pseudoobscura to obtain information on dispersal rates (Dobzhansky and Wright 1943). Genetically marked flies were released in a field which contained baited traps at regular intervals and placed in the form of a cross. The flies were marked with 3rd chromosome recessive gene, orange, and their vigour was increased by using only F₁ hybrids from two inbred orange lines. The authors maintain that they were capable of competing with wild type flies under natural conditions, for evidence was obtained that they bred in the wild and also their behaviour was no different from that of wild type flies marked with paint. Four experiments were performed in different parts of the area. Dispersion was found to be greatly affected by climatic and micro-environmental conditions. In the last three experiments which were carried out in the warmer weather, the flies reached average distances of more than 200 meters in a week or less. Experiments carried out with D. melanogaster and D. funbris showed their rate of dispersal to be considerably less than that of D. pseudoobscura. The authors suggest that this might be due to their different ecology.

Another experiment using the same marker gene was performed by them (1947) at Mather California/
California. Flies were released at various periods from July until nearly mid-August 1945 and trapping was carried out until September and was resumed again in June the following year. They again found that the movement of flies was closely correlated with temperature and that at the period of maximum activity of the flies, the average distance moved was about 120 meters per day. The 1946 trappings showed that 95% of the offspring of the released flies were to be found within a circle with a radius of 1.76 kilometers from the point of release.

Dubinin and Tiniakov (1946) have criticised the use of laboratory mutants as markers in field experiments and in a similar experiment with D. funebris, they used an inversion that had been obtained from a natural population. An approximate total of 100,000 flies were released in June 1945, and a month later samples of flies captured at the point of release gave frequencies of the inversion and the standard gene arrangement that were in accordance with the Hardy-Weinberg Law, thus showing random breeding in that area. Sixty days after the release of the flies, the inversion was recovered a kilometer away, again in frequencies approximating the Hardy-Weinberg Law, but with a slight preponderance/
preponderance of heterozygotes showing the fitness of the marker used. However, in calculating the rate of dispersion the authors have erroneously assumed two generations to be necessary to obtain frequencies fitting the Hardy Weinberg Law. This gives a greater rate of dispersion than was realized. Dobzhansky and Wright (1947) pointed this out and claimed that the rates of dispersal of D. funebris in this experiment resemble those of D. pseudoobscura.

The basic assumption of these experiments, that the behaviour of genetically marked flies is the same as that of the wild type flies, is debatable, but the data have given valuable information on the ecology of the flies that is extremely pertinent to the problem of the population structure. They have exposed some of the biological complexities underlying the population constants of theoretical population genetics, and have stressed the strict dependence of the population structure of Drosophila species on the ecological factors of the habitat.

Among the pioneers in this type of work were the Timofeeff-Ressovskys. They carried out a series of experiments with Drosophila species near Berlin. One of the experiments (Timofeeff-Ressovsky N.W. and E.A. 1940) aimed at obtaining information on the cruising range of D. funebris and D. melanogaster. It is essentially the same as the dispersal/
dispersal experiments described above and is subject to the same criticisms. However, the results gave very different figures for dispersal rates. In three experiments *D. funebris* dispersed over an area of 70 meters by 90 meters in a period of a fortnight. In a similar series of three experiments with *D. melanogaster*, the flies reached a maximum dispersal of 100 meters by 100 meters although the results of the three experiments were not uniform. These experiments however, indicate variable population constants in different parts of the species range.

In another series of experiments (Timofeeff-Ressovksy N.W. and E.A., 1940a) estimations were made of the population numbers of *D. funebris*, *D. melanogaster* and other *Drosophila* species, mainly from the *obscura* group, near Berlin. Baited traps were set in the form of a reticulate quadrat with distances of 10 meters between traps. Genetically marked flies were released and the traps were examined daily for a period and the numbers of marked and unmarked flies were recorded. From these data an approximation of the total population can be obtained by multiplying the total number of marked animals released by the numbers of/
of unmarked animals captured, and dividing this figure by the number of captured marked animals. This method has several possible sources of error: the traps may attract animals from other areas, and the mortality and capture frequencies of marked and unmarked flies may vary particularly if the marked flies are of a different species to the sampled population.

The picture obtained by the workers showed the population numbers to fluctuate seasonally with peak periods at different times for the different species. However the data did not allow any estimates on the effective sizes of the populations. No information was obtained on the minimum population reached during the course of the year, nor was it certain that the flies collected formed what was normally a panmictic unit. Furthermore nothing was known of the sex ratio and the age structure of these populations and the effect of these factors on fertility.

Jackson (1933) investigated the size of an isolated population of *Glossina morsitans* in East Africa. Flies were marked with paint and released on several successive days and then the area was sampled for marked and unmarked flies. Estimates/
Estimates of the population size were made, and allowances for deaths during the course of the experiment were made in the following manner: To maintain the species at a constant size, each female would have to produce two offspring. This would take a month of imaginal life, therefore he assumed that 3% of the population would die each day of the experiment. Unfortunately the figures he gives are only for males as the female is not easily trapped, but allowing for a 1:1 sex ratio he assumed that this area of 2½ square miles supported a population of 3000–4000 flies. These data were obtained in August, a month of maximum activity.

In later work (Jackson 1936, 1940 and 1943) this technique was considerably refined and more was learned about the dispersal of flies and of the ratios of natural population. It was found that flies have regular ambits which are determined by the vegetation. Movement within these ambits is frequent and rapid, but a slow constant movement from the ambits exists. Old males (i.e. males that have fed) rarely go on long journeys but the average weekly movement is half a mile. The ambits of the females appeared to be larger, as larviposition takes place in areas unfrequented by males. It also/
also appeared that females are longer lived than males so that the normal sex ratio deviated from a 1:1 ratio. The last paper (1943) dealt with records covering the period from January 1935 - May 1940. These records reaffirmed the data on dispersal, but showed no seasonal fluctuations in population size. However, a sharp drop in the fly population was found from 1935 to 1936 and was not confined to the experimental area only. Figures from March 1939 until May 1940 showed the density to be 15.3 old males per square mile with probably twice as many females. Although Jackson was not specifically examining the population structure of G. morsitans, his work shows how much information on the effective population size can be obtained by purely ecologically investigation.

Dowdeswell, Fisher and Ford (1940) used the same principle as Jackson to estimate the size of a population of the butterfly, Polyommatus icarus (Rotl). The site chosen for this experiment was Tean island in the Isles of Scilly, for it was fairly certain that the population was effectively isolated. Making empirical allowances for deaths and emergence, they estimated that during the fortnight from August 26th to September 8th, about 450-500 insects died including 100 that had emerged during that period and/
and that the imaginal population had decreased from 350 to a very small number. The effective population size on this island is probably very small; this species is described by South (1906) as commonly having 2-3 broods per annum in the South of England, therefore it is probable this experiment only included a late phase in the population cycle and that the effective population size at the beginning of the breeding season is fairly small. Marked animals in the experiment were reported to disperse themselves over the species habitat so that it is possible that the population is panmictic. A possibility which is supported by the fact that during the time of the experiment it was found that the species was highly specific in its vegetational preferences, and since there is a certain amount of individual variation in times of flowering among plants, not all the plants of the relevant species would be available to the butterflies at the beginning of the season. This would induce movement amongst the early butterflies, and this factor coupled with the highly developed sensory organs of the Lepidoptera would lead one to expect panmixia in such a population.

Another isolated lepidopteran population was investigated by Fisher and Ford (1947). A colony/-
colony of *Panaxia dominula* (L.) covering an area of 20 acres was inspected by the authors and a number of coworkers over a period of several years. Many pertinent observations were made on the ecology and life history of the species, and estimates of the population size were made annually from 1941 to 1946, using the same method employed on Than Island. Two colour varieties, apart from the normal form, are present in the population, and these varieties, *medionigra* and *bimacula*, are considered to be the heterozygous and homozygous expressions of the same gene, although both are very variable in expression. Records of the *medionigra* gene have been kept since 1939 when its frequency was 9.2%. In 1940 it rose to 11.2% then dropped the next year, and from 1941 until 1946 it averaged 5.2%. The authors conclude that the fluctuations in the *medionigra* gene are due to fluctuations in natural selection and not to random fluctuations expected from a periodic reduction of the population size to a small number. Wright (1948) has replied to this and pointed out that the fluctuations in gene frequency can be accounted for by either postulate. He states that the only significant change in gene frequency occurred between 1940 and 1941 and although no figures for the/
the population size are available for 1940, the moth was reported as being scarce during that year; therefore the change in gene frequency can be accounted for by a small breeding population during that year. He also indicated that a large difference between the apparent and real effective population size may be due to the survival of brood mates to the imaginal stage, rather than the survival of a random sample of larvae and pupae. This colony is one of the best recorded natural populations and it is to be hoped enough data will soon be available to settle the controversy.

Diver (1940) gives details of several populations of snails belonging to the two species, *Cepaea hortensis* (Mull) and *C. nemoralis* L. Shells were collected from various parts of the British Isles. The average number of *C. hortensis* shells per colony was 79 and only six colonies yielded more than 500 shells. However the value of these figures is doubtful for it is not known what proportion of the actual population was constituted by these shells. Populations of this species are commonly found in hedgerows and have a linear distribution there. One such population occupied a 45 yard strip, and brown shelled animals were found/-
found in samples from the first 25 yards but not in samples from the next 20 yards. Diver assumes that this is due to restricted population size, but more recent work by Cain and Sheppard (1950) indicates that shell colour in snails may have a high selective value, so that Diver's suggestion cannot be accepted without reservations. In *C. nemoralis* the average population sampled appeared to be somewhat larger although the evidence is drawn purely from the number of shells collected. Two localities were sampled in which the population numbers reached six and seven figures, but Diver assumes that the subpopulations or breeding units are fairly small. However, no rigorous proof on this point is available.

In the vertebrates, rodents and birds have been studied both genetically and ecologically, but there is surprisingly little information of the size of the breeding unit. Blair (1946) estimated the total number of *Peromyscus palionotus leucophagealua* on Santa Rosa Island, Florida. A small area of the island was sampled and its population was estimated by means of trapping, marking, releasing recapturing. This area was 1/150th of the area of the island and assuming a uniform distribution of/
of the species over the island, the total population was estimated to be approximately 12000. Blair assumes that the figure is near the maximum number and states that occasional hurricanes must reduce the number greatly. His data however, do not permit any conclusions to be made on the size of a panmictic unit on the island.

Similar samples of apparent population size are available from the work of ornithologists. Perry (1951) gives the numbers nesting pairs of gannets (Sula bassana) in the various gannetries found in the British Isles. These numbers vary from 470 pairs to 17000 pairs. The young birds migrate and reputedly return to their birth places in their third year, but whether this is invariable is not known. Adult birds supposedly return to the same breeding sites and it is probable that within a gannetry there is panmixia.

Dobzhansky (1941 p169) pointed out that the territorial habits in birds restricts the size of the breeding unit. He cites the work of the American ornithologist, Nice, who worked on the song sparrow Melospiza melodia and, the work of Erickson who worked with the green tit (Chamaea fasciata). Miller (1947) investigated the work of/—
of these ornithologists more closely and presented their work in the following way: The song sparrow has a territory of 50-85 meters in diameter; males occupy the same territory in successive years; females return to the same territory in 37% of the cases and in 30% of the cases settle in the neighbouring territory. In a check area of 500 x 800 meters, one third of the young males settling there had been born in the area and two thirds of the young males came from outside the check area. Assuming a "balanced" viability, then two thirds of the surviving young from the check area must have settled outside it. However, from Nice's data it appears that very few birds settle more than 400 meters away from the parental nest.

Miller assumes this to be the size of the panmictic area and from the data calculates the effective population size in the experimental area to be about 150 in a 'normal' year with fluctuations over several years from 65-215. Miller points out that in a period of successful reproduction the size of the panmictic unit may expand. On the other hand it is feasible that in years of food shortages the surviving young on returning to the breeding grounds maybe forced to disperse more than is customary.

From/-
From Erickson's work on the Wren-tit, Miller drew quite a difference inference, although this bird is a less powerful flier than the song sparrow. The territories range from 50-100 meters in diameter and are occupied by the same individuals throughout the year for a period of several years. However in a check area of 300 x 300 meters no young that had been banded in it settled there although a number of other unbanded young did. Miller supposes that the distance between the place of birth and place of settlement is about 600-700 meters. Assuming this to be the radius of the panmictic area, the effective population size calculated from the data is 500, which still allows a certain amount of genetic drift. These interpretations by Miller are only rough approximations and are only applicable to the particular check areas and the particular times at which the data were collected. Nevertheless they show that ecological data, if intelligently collected and applied, can give satisfactory estimates of the effective population size.

DISCUSSION OF LITERATURE

From the papers cited it is evident that in the twenty years since Wright's address to the Sixth/-
Sixth International Genetics Congress, comparatively little evidence has been obtained on the sizes of natural populations, although so much theory rests on such findings. Information on gross population numbers is rare and data on the size of breeding units are even rarer. However, from these experiments several generalizations emerge. The population structure of a species is by no means constant either temporally or spatially, and in both planes it is intimately connected with the environment of the population. It is far from certain, at this juncture, that small populations are the most common. A species with a wide distribution, can probably be viewed as a mosaic of populations differing in size and dispersal. Furthermore the mobility of the species is not correlated with the effective population size of its colonies. A species with a good means of dispersal does not necessarily have only large panmictic populations nor are its populations likely to be larger than those of a less mobile species. This was demonstrated by Miller's treatment of the data of Nice and Erickson. However these generalizations scarcely test the theoretical considerations forwarded by Wright and others. We are still no nearer to assessing/.
assessing the importance of such phenomena as genetic drift and will be unable to do so until we know more about animal populations and their structure. Similarly the magnitude of Natural Selection can only be gauged when we know more about the population in which its operation has been witnessed. The occurrence of cataclysmic events must have the profoundest effect on the evolution of species and in this respect it may seem pointless to study the population structure. Nevertheless consider a species, stricken by some calamity, possessing a score of resistant individuals. Under one type of population structure these individuals might be so dispersed that they can never mate. In an "island" type of population structure they are likely to be in the same isolate and will be able to mate. Furthermore in some cases these cataclysmic events may correspond to Wright's "ecological opportunity", and cannot detract from the value of studying the structure of natural populations. But this brings us to the core of the problem of evolutionary studies: they are ultimately dependent on field studies for their elucidation, and no quick returns can be expected. Slow diligent examination of natural populations appears/
appears to be imperative, and in this respect much field work has been too diffuse and not systematically planned. The overwhelming range of phenomena confronting a biologist in the field has been largely responsible for the uncoordinated results, but if we are ever to solve the enigma of evolution a systematic approach is necessary. This does not mean that the facts must be fitted subjectively to the given formulae, but that the effort must be towards some immediate goal. Therefore it seems profitable to investigate the points stressed by Wright, and in this way other vital clues may be found.

For the ideal study of population structure, a combined genetic and ecological study is necessary but it has been shown that purely ecological investigations have given very satisfactory results, especially when it is remembered that the majority of workers, cited above, were not interested in the effective population size. A section of this work is devoted to the study of the population structure of E. scaber, using ecological methods. This species suggested itself as very suitable for such ecological studies. It is easily collected during
the spring, summer and autumn. In winter it can be collected during dry sunny spells. Locally it displays a great deal of phenotypic variation. It is easily handled and its segmentation allows it to be marked frequently in such a way that the dates of recapture can be easily identified. Furthermore, its powers of locomotion are relatively poor so that vast areas are not necessary for ecological experiments. The details of the investigation include estimates of the population size of colonies from two different types of habitat; the age structure, sex ratio and survival rates in one of these populations are studied, and experiments dealing with population size are described. The effect of an abnormal morphological character in females on the population structure is examined. The results of these experiments have been interpreted in conjunction with studies on the life history of the animal. Finally at the end of this work, P. scaber is assessed as to its suitability for studies on evolution and population dynamics.
MATERIAL AND METHODS

In the review of literature, the experimental evidence showed that a knowledge of the natural history of a species is necessary for the study of its population genetics. Considering the wide distribution of *P. scaber*, relatively little is known of its ecology. Its habitats, distribution (in Britain) and colour varieties have been described (Collenge 1915, 1943, 1944 and other papers) but much of its life-history has not been described from adequate samples and little attention has been paid to geographic variability. Heeley (1941) studied the life history of *P. scaber* under laboratory conditions. His material was derived from the London area and in some respects his findings differ from those recorded here, presumably due to geographic variability. The ensuing section is devoted to observations and experiments necessary for the interpretation of the experiments that follow. All animals used for this purpose were collected from Edinburgh and the surrounding countryside unless it is otherwise stated.

The species *P. scaber* is a member of the Terrestrial Isopoda and belongs to the family Oniscidae. The order is especially interesting for
for evolutionary studies, for it contains both marine and terrestrial species, with the species Ligia oceanica (L) forming a link between the two types. The Terrestrial Isopoda whilst showing many affinities with the marine forms have adapted themselves successfully to life on land and are fairly ubiquitous despite the fact that they are restricted ecologically. They are generally negatively-phototropic and are limited to damp places. Nevertheless within this narrow range of niches a multiplication of species has progressed, the family Oniscidae alone, for example possessing 500-600 species (Vandel 1945).

In Scotland P. scaber is one of the dominant species of woodlice. Its main habitats are under stones and under the loose bark of old trees or logs. It is found wherever there is dampness and decaying organic matter. Buildings form a common habitat. Thus its present day distribution is largely governed by man. The planting, felling and transportation of timber and the construction of stone walls all influence its distribution. In Scotland the numerous "dry stane dykes", in some treeless parts form the main type of habitat. The species is easily collected during/
during the warmer months of the year and this consideration together with its relatively poor powers of locomotion, its polymorphism and its interesting phylogenetic status suggested that it would be useful in a study of evolutionary problems.

Morphology

The morphological structure of this species conforms with the general structure of Crustacea and Diagrams Nos. 1, 2 & 3 are provided to show the names of body parts. The ventral abdominal appendages differ in the two sexes. In the male the endopodites of the first pair of pleopods are elongated to form a pair of styles and the exopodite of the second abdominal segment is also elongated considerably. Another sexual difference (see Diagrams 2 & 3) is found in the slope of the remaining pleopods. In the male the posterior edges of these pleopods form acute angles with the longitudinal axis of the animal. In the females these angles are less acute. The posterior abdominal segment is modified and forms the telson, on either side of which is seen a uropod which is longer and more slender in the male. Further morphological differences between the sexes are discernible/-
Diagram 1 - The Dorsal view of an adult animal, showing the body parts referred to in the text.
Diagrams 2 & 3 - Ventral view of Male and Female abdomens.  

- $a$ = 7th pair of legs; 
- $b$ = lamella; 
- $c$ = 7th thoracic segment; 
- $d$ = 1st abdominal expodite; 
- $e$ = 1st abdominal endopodite modified to form copulatory style; 
- $f$ = 2nd abdominal expodite; 
- $g$ = pleopods modified for respiration; 
- $h$ = pleuron of 1st abdominal segment; 
- $j$ = pleopods (5 pairs); 
- $k$ = uropod.
discernible in the breeding season, for on the ventral surface of the thorax the female bears a brood pouch. This is formed by cotyledons originating near the base of each leg and which overlap with each other. In the nonbreeding female they are not seen. The male copulatory organ lies under the endopodites of the first pair of pleopods. The genital openings of the female are not normally seen but lie ventrally near the base of the legs of the fifth thoracic segment.

Polymorphism

The existence of different colour varieties in this species was recorded by Webb & Sillem (1906), Collenge and other naturalists. In Scotland the various colour forms are sympatric and this further suggested the use of P. scaber for studies on evolution. Four basic colours are found: brown, red, yellow and black. Brown, black and red self-coloured animals are found, but generally the colours are found in various combinations, giving rise to a wide range of colour forms. In addition a pattern is often, but no invariably, found. It consists of unpigmented patches on the/-
the dorsal surface at the junction of the terga and pleura.

In order to facilitate the description of populations collected in the field, a colour classification of the various phenotypes found in this region was drawn up and will be given later.

**Methods of Culture**

As with most new laboratory animals, culturing proved to be one of the largest obstacles in this work. In the beginning methods of culture suggested by Heeley (loc. cit.) were employed; animals were kept in petri dishes containing damp filter-paper and were fed on slices of carrot. However, as stocks increased this method was relinquished, for it was found that during summer the filter paper dried out very quickly and required daily attention. Also the large scale use of petri dishes is very expensive. Howard (1940) kept *Armadillidium vulgare* in 1 lb jam jars in which he placed dampened cotton wool, compressed to a depth of one inch. The animals were fed on leaves and twigs. This method was somewhat modified. A little sand was placed on the cotton wool after it had been sterilized at 140°C for one hour/-
hour, and all organic matter was similarly sterilized. These precautions were taken to kill the eggs of any predators that might be present in the material and to try to minimize the incidence of moulds which proved to be the biggest difficulty in the culture of these animals. A piece of potato was also added as it was found to be readily eaten by the animals. This method of culture was found to be suitable for adult animals, provided the jars were examined regularly, but jars containing a few young soon became very mouldy and the mortality was high. When the number of young was increased to minimize the chances of mould infestation the numbers of survivors was also very low owing to cannibalism.

Another method of rearing the young was then tried. They were separated and kept individually in 6 cm petri-dishes in which damp sterilized sand and a clean piece of potato was placed. This method was fairly successful with regard to mould, but the sand had to be changed every month. Furthermore many young animals escaped from the dishes even when these were kept closed by means of rubber bands. These difficulties have lead to a very high percentage of losses and have vitiated many/-
many of the experiments in this work, for the number of broods with high survival rates has been very small. Finally, in the last breeding season covered by this study another method was employed with some success. The young were kept individually in vials 2.5 cm in diameter and 7.0 cm deep. Damp sand was placed to a depth of 3 cm and potato was provided as food. The vials were closed by means of corks or wads of non-absorbent cotton wool. The vials were examined weekly when the food was changed and the sand dempned. All the vials as usual were kept in the dark, and the percentage of survivals in this medium has been fairly high. In all the methods used all the glassware has been thoroughly washed before being used again.

Temperature has been found to be exceedingly important in the rearing of these isopods. In a study of this nature it is imperative that the generation interval be short and that large numbers be quickly reared and scored for the characters under investigation. In this case it was intended to investigate the inheritance of the various colour forms. However, it was found that animals kept at room temperature grew very slowly and could not be scored with certainty at the end of/
of six months. Furthermore adult females kept at room temperature ceased to breed during the winter. When kept at 25°C, however, this hibernation was broken and the females bred readily, but the mortality of the young was very high at this temperature even if the most rigorous precautions were taken against mould infestation, and although the generation interval was decreased it was more than offset by the high mortality of the young. 18°C has been found to be the most successful temperature, especially with the new medium for young animals. The generation interval is shortened and the survival rates are fairly satisfactory. Unfortunately the space available at this temperature is limited in this laboratory, so that only a small percentage of the stocks could be kept at this temperature.

Another cause of mortality amongst the young occurs immediately after their liberation from the brood pouch, when they are liable to be eaten by the mother. In order to obviate this cause of death, gravid females were placed individually in large petri-dishes containing damp sand and large flat slices of potato which formed "refuge" for the young. These dishes were kept separately and were examined/-
examined daily. As soon as a brood had been liberated the female was removed.

A summary of the best methods of culture may be pertinent. Adult animals are kept in 1 lb jam jars containing a base of wet cotton wool to a depth of 1"-2". On this is placed sterilized sand and a piece of potato together with sterilized twigs and leaves. Young animals are best reared in 2.5 x 7.0 cm vials with 3 cm of damp sterilized sand and a piece of potato. The optimum temperature appears to be 18°C and animals are best kept in the dark. Regular examination of all cultures and changing of the food is necessary, which means that the maintenance of these animals is very laborious. However, with these precautions a fairly high percentage of young can be reared.
OBSERVATIONS ON THE LIFE HISTORY

1. Development

Heeley (loc. cit.) observed the growth stages and moultst in specimens of this species up to the age of approximately six months. Observations carried out in this study support his findings during this period of the life cycle, and will be summarized here. Within twenty hours of their liberation from the brood pouch, the young moult. Prior to this moult they are soft and too delicate to handle but after this moult they may be easily handled with a paint brush. The second and third moultts take place at approximately fortnight intervals and subsequent moultts at intervals of about three weeks. He found that the young moulted throughout the winter, but that will be discussed more fully later in this section. He observed several species, and found that the characters which are used as taxonomic criteria in distinguishing families are present when the animals are first liberated from the brood pouch, but those characters that distinguish species of the same genus are the latest to appear in ontogeny. The young of P. scaber only display the adult characters at/
at the age of 12 weeks, a factor which is important in field work.

2. Moultine

The process of moultine is preceded by a period in which white patches appear on the ventral thorax. These patches persist, on an average, for 6-7 days. The whole process has been described amply in the literature (c.f. Heeley) and need not be repeated here. However, in adult animals the rate of moultine during the warmer months of the year is important in population studies if any experiments are to be performed with animals marked with paint. The moultine rates at this time of the year differ between the sexes, for the female once possessed of a brood pouch does not moult until after liberation of the brood. In the male, however, moultine appears to be a regular process during the spring and summer. A number of males were kept under observation at room temperature from the middle of May until the end of August and the number of moultine per individual was recorded. Only information on those animals which were alive during the entire period is included in the data given below in Table 1.
Table 1 - Moulting rates in males in spring and summer

These data do not warrant statistical treatment but show that the males moult fairly regularly with an approximate average interval of one month between moult.

In order to obtain data on moulting during winter 27 animals were kept at room temperature. This group included 9 adult females that had had broods during the previous summer, 9 virgin females in their second winter and 9 young animals whose ages ranged from 7-9 months at the beginning of the experiment. The observations were carried out from mid-October until mid-April. Thirty-one mouls were observed during this/
this period showing an average of approximately 1 moult per animal during this six month period and of these 14 occurred in March and April. Only 2 animals moulted in the two months of November and December. Since conditions were warmer inside than outside, and food was available it seems very unlikely that moulting occurs under natural conditions in winter. The effect of temperature on moulting rates was observed by keeping 9 young animals aged between 7-9 months at 25°C. This experiment was started later than the other experiment but generally ran concurrently with it. During the period of the experiment 46 moults were observed against 10 moults in the 9 young animals kept at room temperature. Genetic differences are unlikely to account for this discrepancy, for the 18 young animals used in these experiments came from three broods whose members were divided equally between the two groups. Their earlier rearing had also been identical.

3. **Growth**

There is little information on the growth of isopods. Needham (1937 and 1943) investigated the subject in *Asellus aquaticus*, but only the work on *P. scaber* appears to be that of/-
of Heeley (loc. cit.) which deals only with young animals. It was necessary to know something of the nature of growth in this species for work that will be described later. Therefore experiments were designed to investigate this problem. These experiments are concerned only with body length and not with the growth of body parts relative to body length. Such experiments will be described in another section of this work.

a) Growth under laboratory conditions

A number of animals that had been born and reared at 18°C were moved to 25°C at the age of two months. Four of these survived more than a period of several weeks and measurements were carried out over a period of 13 months. Prior to measurement the animals were anaesthetized with carbon dioxide, generated from a Kipps apparatus. At the end of the rubber tubing leading from the apparatus a small length of glass tubing was inserted and clamped into a fixed position. The animal to be anaesthetized was placed in a small specimen tube under the glass tubing and the gas was allowed to fill the specimen tube. The animal after about a minute became extremely sluggish/
sluggish and would stay quite still in any position for four or five minutes. Deep anaesthesia was not desirable for the animals tended to curl up and exude a sticky colourless fluid. When ready, the animal was placed on a glass square and covered with a watch glass that had been cut down to a diameter of one inch. The glass square was then placed on the stage of a compound microscope which was fitted with a vernier scale that allowed measurements to be made to an accuracy of one-tenth of a millimeter. The length of the body was measured from the tip of the frontal lobe to the end of the telson, and if the animal is placed correctly these two points lies in the same plane. In order to obviate any mistakes in recording the length of animal, each one was measured twice and if a discrepancy occurred between the readings a third reading was taken.

To check the accuracy of this method of measurement, a repeatability test was performed at the start of the experiment. Ten animals were measured on 3 successive days and the data were subjected to an analysis of variance test. The total variance thus obtained contains three components: the variance between the lengths of different/-
different animals, the variance derived from the successive measurements of single animals, and a component of variance due to differences between days. Since there is no daily growth in these animals, any variance between days will be due to systematic errors in measurements. No such systematic errors are evident between days; there is no systematic increase or decrease in measurements on succeeding days, so this component has been neglected and is included in the error variance term. This error term gives a measure of the accuracy of the measurements, for its square root is the standard error of the measurements. The data are shown in Table 2 and the standard error of any of the measurements in the data is shown to be $\pm 0.189$ millimeters so that the technique is reasonably accurate for the purposes of the experiment.

Table 2/-
Measurements of Body Length

<table>
<thead>
<tr>
<th>Animal</th>
<th>1st day</th>
<th>2nd day</th>
<th>3rd day</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4.4</td>
<td>4.8</td>
<td>4.8</td>
</tr>
<tr>
<td>2</td>
<td>4.4</td>
<td>4.2</td>
<td>3.9</td>
</tr>
<tr>
<td>3</td>
<td>4.9</td>
<td>5.0</td>
<td>4.9</td>
</tr>
<tr>
<td>4</td>
<td>4.8</td>
<td>5.3</td>
<td>5.2</td>
</tr>
<tr>
<td>5</td>
<td>4.8</td>
<td>4.7</td>
<td>4.8</td>
</tr>
<tr>
<td>6</td>
<td>4.9</td>
<td>4.9</td>
<td>4.9</td>
</tr>
<tr>
<td>7</td>
<td>4.9</td>
<td>4.7</td>
<td>5.0</td>
</tr>
<tr>
<td>8</td>
<td>5.0</td>
<td>5.3</td>
<td>4.8</td>
</tr>
<tr>
<td>9</td>
<td>4.3</td>
<td>4.7</td>
<td>4.7</td>
</tr>
<tr>
<td>10</td>
<td>4.2</td>
<td>4.4</td>
<td>4.5</td>
</tr>
</tbody>
</table>

Table 2 - The measurement of body length in mm of 10 animals on 3 successive days

Analysis of variance of body length from data in Table 2

<table>
<thead>
<tr>
<th>Source of Variance</th>
<th>Sums of Squares</th>
<th>Degrees of Freedom</th>
<th>Mean Square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>3.11</td>
<td>29</td>
<td></td>
</tr>
<tr>
<td>Between Animals</td>
<td>2.39</td>
<td>9</td>
<td>0.265 = n \sigma_b^2 + \sigma_E^2</td>
</tr>
<tr>
<td>Within Animals</td>
<td>0.72</td>
<td>20</td>
<td>0.036 = \sigma_E^2</td>
</tr>
</tbody>
</table>

\[ \sigma_E = \sqrt{0.036} = 0.189 = \text{The Standard Error of any measurement in Table 2} \]

A similar check on the accuracy of the technique was carried out later with larger animals/
animals, and the results are given below in Table 3.

<table>
<thead>
<tr>
<th>Animal</th>
<th>1st day</th>
<th>2nd day</th>
<th>3rd day</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>8.8</td>
<td>9.1</td>
<td>8.7</td>
</tr>
<tr>
<td>2</td>
<td>7.7</td>
<td>7.4</td>
<td>7.3</td>
</tr>
<tr>
<td>3</td>
<td>6.7</td>
<td>7.0</td>
<td>6.8</td>
</tr>
<tr>
<td>4</td>
<td>8.9</td>
<td>8.6</td>
<td>8.3</td>
</tr>
<tr>
<td>5</td>
<td>8.8</td>
<td>8.9</td>
<td>9.0</td>
</tr>
<tr>
<td>6</td>
<td>8.1</td>
<td>8.1</td>
<td>8.4</td>
</tr>
<tr>
<td>7</td>
<td>9.6</td>
<td>9.4</td>
<td>9.3</td>
</tr>
<tr>
<td>8</td>
<td>7.7</td>
<td>7.5</td>
<td>7.5</td>
</tr>
<tr>
<td>9</td>
<td>8.1</td>
<td>8.3</td>
<td>8.2</td>
</tr>
</tbody>
</table>

Table 3 - The measurement of body length in mms of 9 animals on 3 successive days

Analysis of variance of body length from data in Table 3

<table>
<thead>
<tr>
<th>Source of Variance</th>
<th>Sums of Squares</th>
<th>Degrees of Freedom</th>
<th>Mean Square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>16.82</td>
<td>26</td>
<td></td>
</tr>
<tr>
<td>Between Animals</td>
<td>16.24</td>
<td>18</td>
<td>0.902 = ( n\sigma^2_b + \sigma^2_E )</td>
</tr>
<tr>
<td>Within Animals</td>
<td>0.58</td>
<td>8</td>
<td>0.072 = ( \sigma^2_E )</td>
</tr>
</tbody>
</table>

\( \sigma^2_E = \sqrt{0.072} = 0.268 \) = The Standard Error of any measurement in Table 3

The standard error of the measurements of larger animals is there \( \pm 0.268 \) mms which shows that the technique is still reliable. In Figs. 1, 2, 3 and/–
Figures 1 & 2 - The growth of two local animals kept at 25°C. Body length plotted against time.
Figures 3 & 4 - The growth of two local animals kept at 25°C. Body length plotted against time.
and 4 the measurements of body length are plotted against time. The distribution of points allows fairly accurate curves to be drawn. In all four cases growth appears to be fairly rapid up to a point which varies slightly with the individual but in these animals and under these particular environmental conditions growth appears to be rapid up to 10-12 millimeters and then slows down very markedly.

b) **Sexual maturity and growth**

That growth continues after sexual maturity is shown by the measurements of some breeding females recorded in Table 4. These females had all been fertilized in the wild and were collected in the autumn of 1950 and were measured then, and again after the 1951 breeding season. The exact age of these females are not known, but they had all been fertilized in the wild with the exception of five and therefore the remainder must have experienced at least two breeding seasons. Remembering the standard error of any measurement (±0.268) it is obvious that in the majority of cases the increase is a real one.

Table 4/-
Table 4 - The measurements of body length of females

The first measurement was taken in autumn 1950 and the second was taken after the 1951 breeding season.

* Local females

c) Growth at outdoor temperatures

In a previous part of this section it was shown that at 25°C moulting continues throughout the/
the winter and that at lower temperatures it is sporadic during this period. Therefore since moulting is necessary for growth in animals with exoskeletons, under natural conditions growth must cease altogether during winter. This was indicated by keeping a number of animals in individual jam jars outside during the winter. They were measured on 19th November and again on 30th April when spring was well advanced. The measurements are given below in Table 5.

<table>
<thead>
<tr>
<th>Animal</th>
<th>1st Measurement 19/11</th>
<th>2nd Measurement 30/4</th>
<th>Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>8.1</td>
<td>7.9</td>
<td>-0.2</td>
</tr>
<tr>
<td>2</td>
<td>6.3</td>
<td>6.9</td>
<td>0.6</td>
</tr>
<tr>
<td>3</td>
<td>7.2</td>
<td>7.3</td>
<td>0.1</td>
</tr>
<tr>
<td>4</td>
<td>5.8</td>
<td>6.5</td>
<td>0.7</td>
</tr>
<tr>
<td>5</td>
<td>7.6</td>
<td>7.8</td>
<td>0.2</td>
</tr>
<tr>
<td>6</td>
<td>5.7</td>
<td>5.8</td>
<td>0.1</td>
</tr>
<tr>
<td>7</td>
<td>8.8</td>
<td>8.5</td>
<td>-0.3</td>
</tr>
<tr>
<td>8</td>
<td>7.1</td>
<td>7.7</td>
<td>0.6</td>
</tr>
<tr>
<td>9</td>
<td>5.7</td>
<td>6.2</td>
<td>0.5</td>
</tr>
<tr>
<td>10</td>
<td>7.4</td>
<td>7.6</td>
<td>0.2</td>
</tr>
<tr>
<td>11</td>
<td>8.0</td>
<td>8.4</td>
<td>0.4</td>
</tr>
<tr>
<td>12</td>
<td>5.9</td>
<td>5.9</td>
<td>0.0</td>
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<tr>
<td>13</td>
<td>7.3</td>
<td>7.4</td>
<td>0.1</td>
</tr>
<tr>
<td>14</td>
<td>8.6</td>
<td>9.6</td>
<td>1.0</td>
</tr>
</tbody>
</table>

Table 5 - The growth of animals over wintering at outdoor temperatures
Five animals show significant changes, but since the second measurement was late, they had probably had their first spring moult. From these data therefore growth in winter appears negligible. The behaviour probably approximates those of natural conditions and if so the growth of animals in the wild plotted against time will give a very different type of curve to the ones shown in Figs. 1-4. Periods of growth will alternate with periods of biological inactivity. This does not necessarily mean that when growth is in progress it will differ in rate from the growth rates demonstrated, although this could possibly be true.

Ten animals that had been reared at room temperature were measured at the age of 58 weeks. The average length was 10.75 mm. At 25°C this length was reached by the animals at the average age of 40 weeks. The difference in the time taken by the two groups to reach this length corresponds roughly with the period of sporadic moultng at room temperature. Although the numbers are small and the animals were of different genetic origin and the comparison is extremely crude, it can be taken to mean that the growth rate curve of animals in the wild during the summer is similar to the growth/-
growth rate curve of animals reared at 25°C. If this is so, then animals which survive several seasons in the wild will grow rapidly over the earlier seasons and after that growth will slow down considerably.

4. Reproduction

a) Generation interval

The sexes may be distinguished when the animals are two months old, for the male styles are easily discernible then. The age of sexual maturity, however, varies considerably. Some of the factors affecting it are genetic and others are environmental. Evidence will be produced later in this work to show that animals do not breed until their third summer under natural conditions in southern Scotland, so that the point need not be laboured here. In another experiment also to be described later it will be shown that geographic races exist in this species that differ in their reproductive behaviour. With local animals temperature influences the breeding behaviour greatly. At 25°C two generations can be obtained in a year. At 18°C sexual maturity is reached in 10-12 months.
b) **Copulation**

Copulation by woodlice has only once been described in the literature. Schobl (1880) observed several pairs in coitus, but it is uncertain as to which species was involved. It is most probably *P. scaber* for the material contained a large number of this species. Three pairs of local animals were seen in coitus on the afternoon of April 23rd. The observations disagree with those of Schobl in many respects but this may be due to the fact that he observed copulation in a different species. Schobl paid little attention to the courtship behaviour except to report that the male ran around briskly and touched the female with his antennae. Of the actual copulation he reported that the male fertilized both genital pores of the female simultaneously. The observations reported here disagree with this last point.

Attention was drawn to a male which was mounted on a female with his styles swung out forming a right angle with his anterior-posterior axis. The female shook him off and he was placed in another dish with a female which had the pre-moultling white patches. After contacting her, he left her and stood about an inch behind her, moving his antennae.
She remained stationary and this position was held for 10 minutes or so. He then approached her right side and placed his head on her back at the junction of the 6th and 7th sterna. The female extended her body and the male beat his first pair of legs on her back. The position was held for 15-20 minutes. He then mounted her crosswise with the 5th and 7th legs of his left side on her 7th thoracic sternum and 2nd abdominal segment respectively, and his head on her 2nd thoracic sternum. The female then rolled on to her back and the male raised his styles so that they appeared like a funnel and inserted them on the right side of a ventral groove between the 5th and 6th thoracic segments. The groove appeared to extend across the ventral surface of the female, and the styles appear to function as a guide for the penis. Copulation lasted for 1-2 minutes and then the female broke away. After a few minutes the male came up to her left side and stood there. He then mounted her with the 5th and 7th legs of his right side on her 7th thoracic sternum and 2nd abdominal segment respectively. The female rolled on to her side and this position was held for some time while the female was seen to shudder occasionally. She pivoted round in this position several times and then/-
then rolled on to her back. The male again raised his styles and inserted them into the left side of the groove. The penis could be seen moving between the styles during coitus. The female broke off copulation.

The other two cases were similar in procedure and in one of these cases the male was still interested in the female 24 hours later. The groove in the female is not easily seen but one female was examined and found to be exuding a colourless substance from the groove. A male was introduced into her dish and immediately became interested in her. However, she at first refused him by kicking, but eventually he took his stand with his head on her back and started the leg-tapping.

Elaborate courtship behaviour is well known in animals. In the anthropods it has been recorded in Lepidoptera (Ford 1945 p95, Tinbergen 1951 p32) and there is a growing literature on the mating behaviour of Drosophila species (Rendel 1944, Spieth 1947 and others). This display has been interpreted as being necessary for the stimulation of the female. In this respect P. scaber does not appear to be exceptional for the leg tapping of the male can be considered to be stimulating to/—
to the female. It is very probable that since only 3 cases were observed that some of the details were missed and that the courtship in this species is more complex than described above. The importance of mating behaviour in the evolution of the genus Peromyscus has been stressed by Dice (1940) and it is liable to be found to be equally important in other genera. Another factor of interest in the cases observed here was that copulation took place between animals of approximately the same size. Therefore it is possible that a discrepancy in size might make coitus impossible. In a later experiment this possibility was tested but was not realized.

Copulation is necessary in P. scaber for the production of broods, but the female is able to store sperm from season to the next. No examples of parthenogenesis were found in scores of virgin females kept during the course of this study and Heeley reported likewise. Similarly Vandel (1925) who has investigated the reproduction of many species of Isopoda does not mention P. scaber as being parthenogenic. However, virgin females do occasionally form brood pouches but the eggs never develop and are lost with the exuvia at/—
at the next moult. The period that a female can store sperm appears to be at least 2 years.

c) The breeding behaviour in local animals

In order to learn something of the breeding behaviour of *P. scaber* in this area, 140 adult females were collected in late March before breeding could have started. The collection was done at several places in the Edinburgh area so as to provide a representative sample. Each female was measured, numbered and put into a separate jar, and the food was changed regularly. To obviate any effect of temperature they were kept out of doors throughout the period of the experiment which lasted until mid-September. In spite of this precaution they were found to be somewhat precocious in their behaviour compared to animals collected in the wild which constituted the controls. Nevertheless the results obtained from this experiment are considered to reflect fairly accurately the breeding behaviour in local populations.

C.1. The breeding season

The first brood pouches were formed in the middle of May and by the first week in June...
most females were gravid. The latest brood were liberated in mid-July. On the 15th July a whole population was sampled and 95% of the adult females were gravid but none appeared to have released their young, for until a female has moulted after liberating a brood, the cotyledons of the brood pouch remain conspicuous. From this it appears that the experimental females were precocious, and by the second week of August the number of wild females with brood pouches is negligible and the breeding period is virtually over. None of the experimental females formed a second brood pouch. Heeley (loc. cit.) speculatively claims that in this species in Britain, a female produces one brood in her third year, 2 in her fourth year and one in her fifth year. This does not appear to be the case in southern Scotland, for the females in this experiment displayed a wide range of body length measurements (Wide Fig. 5) which would indicate a wide range of ages.

C 2. The number of eggs deposited in the brood pouch

Once the brood pouches had been formed the females were divided into two groups each containing seventy females. The two groups had identical/-
identical environmental conditions, so far as could be ascertained. The first group were used to investigate the number of fertilized eggs present in the brood pouch. Five to seven days after the formation of the brood pouch, the female was killed with ether and the eggs were removed. They were then examined under a binocular microscope to see if they were fertile. Only a very small number appeared to be unfertilized, and they were not included in the following calculation. The data from this experiment are shown in Fig. 5. Considering the number of eggs alone the average number per female is 49.3 ± 2.51. However, a closer scrutiny of the data shows that larger females tend to have more fertilized eggs in their brood pouches and this is shown by the correlation coefficient of these two characters, for \( r = 0.922 \) which is highly significant (at the 1% significance level for 52 degrees of freedom \( r = 0.354 \)). This means that an increase in size is accompanied by an increase in egg number, and that the smaller females tend to have fewer eggs in their brood pouches. The regression of egg number on body length is given by the regression coefficient \( b = 11.47 \). Therefore if given the body size of
a female the number of eggs she will produce may be forecast from the regression line given in Fig. 5.

C3. The number of young produced by females

The second group of females were used to determine the number of young produced. As stated earlier their treatment was identical to that of the first group. However before the brood pouch was too advanced to be damaged by handling, the females were removed from their jars and placed in individual large petri dishes with large flat slices of potato that formed "refuges" for the young. The dishes were examined daily and as soon as the brood was released, the females were transferred to a jar and kept for further observation. The young were counted on the day following their liberation so that they could undergo their first moult. The data are shown in Fig. 6. From these data the mean number of young produced by these is 46.08 ± 2.69. As in the egg data a closer scrutiny shows that the number of young is related to the body length of the female and the correlation coefficient is 0.889 which is highly significant (a 1% level of significance for 47 degrees of freedom r = 0.37). Again a knowledge of the regression coefficient allows the/
Figure 5. The regression of egg number on body length in local females. For further details see text.

Figure 6. The regression of brood-size on body length in local females. For further details see text.
the number of young to be predicted from a knowledge of the females body length. This coefficient $b = 11.12$. The regression line is given in Fig. 6.

In these experiments there were no controls. For in the first experiment the age of the brood pouch of wild females cannot be gauged, and if earlier than 5-7 days there is a possibility that not all the eggs have descended into the pouch. This possibility is demonstrated by the fact that at 5-7 days not all the eggs are in the same state of development. This does not necessarily mean of course that they have not descended at the same time, for they might possess genetic differences that lead to different rates of development, but it does make the use of controls doubtful. Furthermore if the brood pouch is older some of the eggs carrying dominant lethal genes or homozygous for recessive lethal genes might have disintegrated. In the case of the second experiment it is impossible to handle females with advanced brood pouches without rupturing the brood pouches. Therefore it can only be hoped that these results approximate conditions in the wild.

If this is so and there is no selection against/-
against large body size, the results are interesting. It was shown earlier that growth can continue after sexual maturity and from this experiment it appears that the longer a female lives the larger will her later broods be. Although with increasing age growth appears to become very slow. This means that with an old female this increase in brood size will be small relative to her previous brood but in relation to the brood size of younger females in the same population, her brood size will be large. The evolutionary significance of this fact will be discussed more fully later.

5 Sex ratios in laboratory stocks

Howard (1940) in his work with Armadillidium vulgare found animals whose broods deviated significantly from the expected 1:1 sex ratio. de Lattin (1949) reports that a gene M in P. scaber that causes mottling of the dorsal surface of the animal and is connected to abnormal sex ratios. The normal form in the area investigated is black and this form produces a slight preponderance of males. In the mutant stock MM the frequency of males in the broods was considerably lowered. He later (1951) has changed the designation/-
designation of this gene to Ma and has found a large number of modifying genes that affect the colouring. He also reports other genes with similar colouring effects but which are distinctly different in other respects. Generally his later paper confirms the findings of his first paper and the Ma gene was found to be dominant for both characters, mottling and the increased percentage of females in each brood.

A large number of broods were reared at room temperature and at 25\textdegree C, and the offspring were sexed as soon as possible. The female parents of these broods had all been fertilized in the wild and members of all the phenotypic colour classes were present amongst them. The data from the broods reared at room temperature are given in Table 6. No unisexual broods were found. In Table 6 it will be noted that some of the numbers of survivors are too small for statistical treatment and so every two broods are added together. Thus 24 broods in the original stocks are treated as 12 broods in the $X^2$ test. The arrangement of the broods was quite fortuitous so that the addition did not vitiate the results in any way. The heterogeneity $X^2$ is calculated to/
to be 9.216 for 11 degrees of freedom. At the 5% level of significance for the same number of degrees of freedom $X^2 = 19.67$, so that it can be inferred that the broods do not differ in their sex ratios. The total $X^2 = 6.53$ for 1 d.f. ($P = < .02$) shows that the number of females present is significantly larger than the number expected from a 1:1 ratio.

Table 6/-
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Table 6 - Sex ratios of broods reared at room temperature. Females fertilized in the wild. On right hand side is the sum of every pair of broods. (see text)
Of the broods reared at 25°C one brood was unisexual and numbered 30 females. Another brood consisted of 24 females and one female. The remaining broods are given in Table 7 and for statistical treatment the very small broods have been added to other broods. The heterogeneity $X^2 = 25.34$. There are 19 degrees of freedom and $P > 0.1$, so that the broods do not disagree with one another. Again as in the room temperature stocks, there is a preponderance of females which is significantly greater than the expected number ($X^2$ for 1 d.f = 5.68 $P < .05$).

Since there is agreement between broods and their parental animals were of all colours it is unlikely that the genes described by de Lattin is present in this area; if it is present its expression is so modified that it does not affect the sex ratios to the extent described by him. In both populations there is a preponderance of females and this is probably due to the females being better able to survive laboratory conditions. This supposition however, can only be supported by a knowledge of the sex ratio at liberation from the brood pouch which cannot be assessed.

Table 7/-
Table 7 - Sex ratio of broods reared at 25°C. Females fertilized in the wild

Small broods have been added to the brood below and the results are given on the right hand side of the table.

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TOTAL 369 307
Further Ecological Observations

In a study of the population dynamics of a species, a knowledge of its food requirements, seasonal behaviour and predators is a pre-requisite.

Collenge (1942) examined the contents of the intestinal tracts of several specimens of P. scaber. He found mainly rotting vegetable matter, some algae and fungal spores and a very small amount of animal remains, probably those of mites and collembola.

The behaviour of P. scaber during the winter remains a conundrum. It is supposed that they burrow into the earth or crawl down earthworm tunnels or climb into the deepest crevices of the tree or log which they inhabit. Some local animals were found in February amongst some grass roots under a stone and they were quite comatose. On being introduced to a higher temperature they all revived. If the coldest winter months are spent in such a condition then their food requirements must be negligible during this period and deaths during this period must be due to causes other than starvation.

In the habitats that have been investigated in this area, the species is usually found with/-
with another isopod *Oniscus asellus*. The other invertebrate fauna of these habitats include *Collembola, Myriapoda, Arachnids of various types, Dermaptera, Diptera and Coleoptera*. Of these some of the Coleoptera are predators of woodlice and some of the animals here have been parasitized by a Tachinid fly. Thomson (1934) investigated the parasitization of woodlice by these flies and among 1290 specimens of *P. scaber* from eighteen localities an average of 10% were parasitized by these flies. Local animals have also been found to be parasitized by mites but whether this is even a direct cause of death to the host is unknown. A heavy infestation might lower the viability of the host and make it more susceptible to other hazards.

Several birds are known to be predators of woodlice. Collenge (1943) found woodlice remains in jack-daws, field fares, red breasts and lapwings. He also cites a statement from "The Report on the Little Owl" that woodlice are very common in the good remains of the Little Owl. Of the avian predators cited above this is the only nocturnal bird and since woodlice are also nocturnal
it is probably their chief avian predator. It is also possible that certain nocturnal small mammals may prey on them.

SUMMARY OF LIFE HISTORY STUDIES

In this section a resume of the development of the free-living individual was given. Experiments on moulting rates under various conditions were described. The growth of animals kept at 25°C was found to be rapid up to a point and then it slowed down. Growth was shown to continue after sexual maturity and animals kept out of doors over winter showed no growth during that period. Copulation and mating behaviour play were described. The breeding season in this area appears to be confined to the last weeks of July and only one brood appears to be produced by a female in a season here. The number of eggs and the number of young produced by a female are highly correlated with her body length. The sex ratios of the broods of local females do not vary significantly from one another under laboratory conditions. The food requirements and predators of the species were discussed briefly.
COLOUR INHERITANCE

Introduction

The presence of a colour gene has been reported in this species by de Lattin (1949) and genes responsible for colouration have been investigated in the related woodlice Armadillidium vulgare (Howard 1940). P. scaber in this part of its range is polymorphic for colouration. There are four basic colours - brown, red, yellow and black. They are found in various combinations and sometimes in characteristic patterns on the individual. In addition to colouration a type of marking or pattern is commonly found among these animals. This pattern consists of non-pigmented patches on the dorsal thoracic segments at the junction of the terga and pleura. In some animals these patches cover almost the entire length of each segment (see Diagram 3A), and in other animals they are barely discernible. In the classification drawn up below these marks are referred to as the basic pattern. The classification was drawn up from hundreds of specimens caught locally.

Colour Classification

Group Y/
Diagram 3A - Dorsal view of an animal showing the basic pattern marks at the junction of the sterna and pleura.
Colour Classification

Group Y

1. Yellow and Brown
   (a) less than 50% brown
   1) Basic pattern
   2) No basic pattern
   (b) more than 50% brown
   1) Basic pattern
   2) No basic pattern

2. Green Yellow and Brown
   (a) less than 50% brown
   1) Basic pattern
   2) No basic pattern
   (b) more than 50% brown
   1) Basic pattern
   2) No basic pattern

3. Yellow and Black

4. Yellow and Red and Brown
   (a) less than 50% brown
   1) Basic pattern
   2) No basic pattern
   (b) more than 50% brown
   1) Basic pattern
   2) No basic pattern

Group B

1. Wholly Black

2. Black and Red
   (a) less than 50% black
   1) Basic pattern
   2) No basic pattern
   (b) more than 50% black
   1) Basic pattern
   2) No basic pattern
Group R

1. Red and Brown
   (a) less than 50% brown
   1) Basic pattern
   2) No basic pattern
   (b) more than 50% brown
   1) Basic pattern
   2) No basic pattern

2. Red and Yellow
   (a) less than 50% red
   1) Basic pattern
   2) No basic pattern
   (b) more than 50% red
   1) Basic pattern
   2) No basic pattern

3. Red uniform
   a) Basic pattern
   b) No basic pattern

Group D

2. Common brown grey
   a) Basic pattern
   b) No basic pattern

4. Similar to D₂ but has traces of orange on uropoda, or telson, or pleura, or base of antennae
   a) Basic pattern
   b) No basic pattern

Group A

1. Albino

Thus an animal which is predominantly brown with a little yellow and which has the basic pattern is classified as \( Y₁b₁ \). An animal which is red and black/-
black, with red predominating and which lacks the basic pattern is classified as $B_2 a_2$.

This classification was found to hold for all the animals examined during the course of this work and it allowed populations to be quickly and adequately described, but it has no accuracy from the genetic point of view. The numerous phenotypic colour classes indicate that the genetics of colouration in this species is probably very complex, but in the ensuing data there is some evidence which may show the presence of at least one major gene, and undoubtedly shows that colouration in this species has a genetic basis.

Material and Methods

In order to determine the genetic basis of coloured phenotypes it is usual to mate animals of similar phenotypes and thus obtain lines breeding true for a particular class. Such an approach was attempted in this work. However, *P. scaber* did not prove to be very good material for this type of investigation. Firstly wild females cannot be used in these matings for they may be carrying sperm from previous matings, and so only females reared in the laboratory can be used. Nevertheless over 50 matings were set up. The second/-
second problem is that of temperature. If reared at room temperature the generation interval is very long and since the time available for this work was limited, 2 generations could not have been reared at room temperature. A small incubator at 20°C was available, but the space was very limited and so only a few animals could be kept at that temperature which appears to be fairly suitable.

Sufficient space was available at 25°C and most of the matings were kept at that temperature. The generation interval is shortened considerably, but there is a very high mortality rate among young, for they seem ill-adapted to such a high temperature. Also the cultures tend to become very mouldy. Although extreme care was taken, the mortality in the F₁ animals was so high and the labour involved so great that only the F₂ cultures in the incubator were eventually kept. The F₁ and F₂ animals were kept individually in 1 lb jam jars on the standard medium and the food was changed regularly. Some of the F₂ animals were reared in specimen tubes on sterilized sand and fresh potato, others were kept in small groups in 1 lb jam jars containing bark and potato. de Lattin/-
Lattin does not state at what temperature he kept his stocks. The medium used by him differed from this one in that he included Daphnia and yeast. However, it would seem from these experiments that the differences in the results was due to the temperature at which the experiments were performed. If these experiments had been done at room temperature they would have taken longer, but the survival rate of the young would have been higher. Also it is very probable that the animals used by de Lattin were quicker maturing, for evidence will be produced later to show that animals from more southern latitudes are quicker maturing. The animals used in this study included local animals Shetland animals and animals from the South of England.

Results

A detailed analysis of the genetic colouration is impossible from the data at hand, but the evidence presented below show that colouration in _P. scaber_ does have a genetic basis. Nine examples are presented fully in order to study the inheritance of red colour through 2 generations.

Example 1/-
Example 1

\[ P_1 \: \text{♀ Brown and Red} \times \text{♂} \]

\[ \downarrow \]

\[ F_1 \: \text{Segregation} \]

\[ 13 \: \text{Non Red: 3 Reds} \]

\[ \downarrow \]

\[ F_1 \: \text{Mating} \: \text{♀ Brown} \times \: \text{♂ Brown} \]

\[ \downarrow \]

\[ F_2 \: \text{Segregation} \]

\[ 6 \: \text{Non Red: 4 Reds} \]

Example 2

\[ P_1 \: \text{♀ Brown and Red} \times \text{♂} \]

\[ \downarrow \]

\[ F_1 \: \text{Segregation:} \]

\[ 13 \: \text{Non Red: 3 Reds} \]

\[ \downarrow \]

\[ F_1 \: \text{Mating} \: \text{♀ Brown} \times \: \text{♂ Brown} \]

\[ \downarrow \]

\[ F_2 \: \text{Segregation} \]

\[ 6 \: \text{Non Red: 1 Red} \]

Example 3

\[ P_1 \: \text{♀ Brown and Red} \times \text{♂} \]

\[ \downarrow \]

\[ F_1 \: \text{Segregation} \]

\[ 13 \: \text{Non Red: 3 Reds} \]

\[ \downarrow \]

\[ F_1 \: \text{Mating} \: \text{♀ Brown} \times \: \text{♂ Brown} \]

\[ \downarrow \]

\[ F_2 \: \text{Segregation} \]

\[ 2 \: \text{Non Red: 3 Reds} \]

Example 4

\[ P_1 \: \text{♀ Red and Black} \times \text{♂} \]

\[ \downarrow \]

\[ F_1 \: \text{Segregation} \]

\[ 10 \: \text{Non Red: 5 Reds} \]

\[ \downarrow \]

\[ F_1 \: \text{Mating} \: \text{♀ Brown} \times \: \text{♂ Brown} \]

\[ \downarrow \]

\[ F_2 \: \text{Segregation} \]

\[ 10 \: \text{Non Red: 2 Reds} \]
### Example 5

<table>
<thead>
<tr>
<th>P1</th>
<th>♀ Brown and Yellow x♂ ?</th>
<th>♂ Red and Black x♂ ?</th>
</tr>
</thead>
<tbody>
<tr>
<td>F1 Segregation</td>
<td>6 Non Reds: 12 Reds</td>
<td>10 Non Reds: 5 Reds</td>
</tr>
<tr>
<td>F1 Mating</td>
<td>♀ Brown x♂ Brown</td>
<td></td>
</tr>
<tr>
<td>F2 Segregation</td>
<td>3 Non Reds: 3 Reds</td>
<td></td>
</tr>
</tbody>
</table>

### Example 6

<table>
<thead>
<tr>
<th>P1</th>
<th>♀ Brown and Yellow x♂ ?</th>
<th>♂ Brown and Yellow x♂ ?</th>
</tr>
</thead>
<tbody>
<tr>
<td>F1 Segregation</td>
<td>6 Non Reds: 12 Reds</td>
<td>7 Non Reds: 0 Reds</td>
</tr>
<tr>
<td>F1 Mating</td>
<td>♀ Brown and Red x♂ Brown</td>
<td></td>
</tr>
<tr>
<td>F2 Segregation</td>
<td>3 Non Reds: 0 Reds</td>
<td></td>
</tr>
</tbody>
</table>

### Example 7

<table>
<thead>
<tr>
<th>P1</th>
<th>♀ Brown and Yellow x♂ ?</th>
<th>♂ Brown and Red x♂ ?</th>
</tr>
</thead>
<tbody>
<tr>
<td>F1 Segregation</td>
<td>6 Non Reds: 12 Reds</td>
<td>5 Non Reds: 0 Reds</td>
</tr>
<tr>
<td>F1 Mating</td>
<td>♀ Brown and Red x♂ Brown</td>
<td></td>
</tr>
<tr>
<td>F2 Segregation</td>
<td>8 Non Reds: 3 Reds</td>
<td></td>
</tr>
</tbody>
</table>

### Example 8

<table>
<thead>
<tr>
<th>P1</th>
<th>♀ Brown and Yellow x♂ ?</th>
<th>Brown x♂ ?</th>
</tr>
</thead>
<tbody>
<tr>
<td>F1 Segregation</td>
<td>6 Non Reds: 12 Reds</td>
<td>9 Non Reds: 4 Reds</td>
</tr>
<tr>
<td>F1 Mating</td>
<td>♀ Brown and Red x♂ Brown</td>
<td></td>
</tr>
<tr>
<td>F2 Segregation</td>
<td>1 Non Red: 3 Reds</td>
<td></td>
</tr>
</tbody>
</table>
Example 9

F₁ ♀ Brown and Yellow x ♂ ?  ♂ Brown and Red x ♂ ?

F₁ Segregation
6 Non Reds: 12 Reds 5 Non Reds: 0 Reds

F₁ Mating ♀ Brown x ♂ Brown

F₂ Segregation 1 Non Red: 4 Reds

In these examples red may be interpreted as being recessive to non-red. In all the examples save 6, 7 and 8 both F₁ animals may be heterozygous for red and their progeny may be expected to segregate on a basis of 3 Non Red to 1 Red, if there is a single gene difference between red and non red and if non red is dominant. On a first inspection the examples 1-5 fit this hypothesis but example 9 does not, and is not included in the heterogeneity test below.

<table>
<thead>
<tr>
<th>Example</th>
<th>Non Red</th>
<th>Red</th>
<th>(\chi^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. 1</td>
<td>6</td>
<td>4</td>
<td>1.20</td>
</tr>
<tr>
<td>No. 2</td>
<td>6</td>
<td>1</td>
<td>0.42</td>
</tr>
<tr>
<td>No. 3</td>
<td>2</td>
<td>3</td>
<td>3.26</td>
</tr>
<tr>
<td>No. 4</td>
<td>10</td>
<td>2</td>
<td>0.44</td>
</tr>
<tr>
<td>No. 5</td>
<td>3</td>
<td>3</td>
<td>2.00</td>
</tr>
</tbody>
</table>

Total 27 13

Total \(\chi^2 = 7.32\) for 5 d.f.
Pooled \(\chi^2 = 1.20\) for 1 d.f.
Heterogeneity \(\chi^2 = 6.12\) for 4 d.f. \(P > 0.10\)

The/
The hypothesis must also be tested against the data in examples 6, 7 and 8. In these samples the $F_1$ females are red. If the males are heterozygous for red then the number of Non Red $F_2$ animals to Red $F_2$ animals should fit a 1:1 ratio. The numbers from these examples fit this ratio as is shown below, but they are so small and very untrustworthy, for if added to the other data they would have not changed the picture in the previous test.

<table>
<thead>
<tr>
<th>Examples</th>
<th>Non Red</th>
<th>Red</th>
<th>$X^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. 6</td>
<td>3</td>
<td>0</td>
<td>3.0</td>
</tr>
<tr>
<td>No. 7</td>
<td>8</td>
<td>3</td>
<td>2.2</td>
</tr>
<tr>
<td>No. 8</td>
<td>1</td>
<td>3</td>
<td>1.0</td>
</tr>
<tr>
<td>Total</td>
<td>12</td>
<td>6</td>
<td></td>
</tr>
</tbody>
</table>

Total $X^2 = 5.2$ for 3 d.f.
Pooled $X^2 = 2.0$ for 1 d.f.
Heterogeneity $X^2 = 3.2$ for 2 d.f. $P > .05$

In another 8 broods in which the phenotypes of both parents were known, red offspring appeared in the $F_1$, thus agreeing with the hypothesis that non red is dominant to red. No $F_2$ were raised in these broods so that they are not included.

Discussion/-
Discussion

The data presented are very meagre and do not really allow any conclusions to be drawn. Although other hypotheses might fit the data equally well, it is tentatively suggested that a non red and red segregate as a pair of alleles. The evidence that non red is dominant to red is strong but may be vitiated by 2 possibilities.

1) Animals might darken with age so that the parental generation although classified, as say, self brown might have displayed a little red when young. This was guarded against in the F1 and F2 by classifying them as late as possible.

2) The animals in these tests came from different parts of Britain and it is possible that alleles of different strengths exist in this species. This would tend to give an indication of differential penetrance in different broods.

The inheritance of yellow seems to be more complex from an analysis of the nine examples above. The numbers of yellow animals varied considerably from brood to brood and did not seem to fit any set ratio. However, no yellow offspring appeared in any family that did not have an animal carrying yellow in the previous 2 generations. Therefore/-
Therefore it too undoubtedly has a genetic basis.
The inheritance of the self coloured brown type
could not be investigated, but this type appears
to be dominant to the others for red and yellow
coloured offspring were present in the offspring
of animals of this phenotype.

It seems unlikely that the entire range
of colour polymorphism in this species is determined
by simple genetic means, for it is possible that
some colour phenotypes are determined by large
numbers of genes or possibly by such phenomena as
translocations. A detailed investigation however,
requires large numbers and these are only possible
if the culture methods are satisfactory. The
difficulty in Scotland is to find a suitable temper-
ature for the local animals, for otherwise the
generation interval is too long. From these data
it is evident that too high a temperature is dis-
astrous. The best temperature appears to be 18-
20°C, but this will not allow more than one genera-
tion per year with local animals, and such a rate
of breeding is scarcely suitable for the investiga-
tion of complex genetic systems.
POPULATION STRUCTURE

1) A woodland population

Introduction

In *P. scaber* body length and age are related, and since there is no growth during the winter months, the different age groups in a population should be distinguished by measurement. If the population sample is unbiased, data can be obtained on the generation interval and survival rates in the different age groups. Furthermore, this type of sampling should allow one to compare the colour composition of adjacent populations and to assess the amount of movement between these populations. In this experiment these facets of the population structure were investigated by sampling the woodland population. Sampling was done by removing whole logs to the laboratory and examining their fauna. In order that the sampling should be reliable it is essential that the woodland be small and uniform so that environmental variation should be minimal and that the woodland should possess enough logs of suitable size to give adequate samples at different times of the year. Initially there was some difficulty in finding a suitable/-
suitable wood.

**Material and Methods**

The woodland in which this work was done, is a mixed plantation of elm, beech and oak. It is situated on the crest of a long low hill. It is about fifty yards wide and 300 yards long. On account of its position and shape, there are no obvious differences in humidity, temperature or light intensity in any part of the wood. Some years ago, a certain amount of "thinning out" was done and a number of the smaller logs were left scattered over the floor of the woodland. These logs provided the material for this study and collections were made in autumn 1951 and in the spring and summer of 1952. Once a log was selected it was placed in a large bin and removed to the laboratory. It was then put in a bath full of water and the animals were removed from it. This method of recovering the fauna of a log is very satisfactory for animals of 5 mms or larger but is uncertain for smaller animals. It efficiency was tested in the following way. After a log had been soaked but while it was still damp, it was gradually burnt in a fire. This was done by slowly burning/-
burning the one end of the log and thus allowing any surviving animals to escape from the other end. Only two woodlice and several spiders were recovered so that the soaking method was assumed to be accurate enough for the purposes of this experiment. The animals thus recovered were measured, sexed and classified for colour. From these data information was obtained on the following components of population structure:

1) Generation interval and age structure
2) Sex ratio during breeding period
3) Mortality rates
4) The state of subdivision of the population

Results

1) **Generation interval and age structure**

It was shown in a previous section that in *P. scaber* age and size are related, although after a certain time, growth becomes very slow. Also it was shown that there is not likely to be any growth during winter and since the breeding season is short, size differences should exist between different age groups in the same population. The distribution of body length measurements of animals/
animals in three logs are shown in Figs. 7, 8 and 9. Unfinished groups \( A_1^{\varphi\varphi}, A_1^{\varphi\var}, A_2^{\varphi\var}, \) and \( A_2^{\varphi\var} \) are found in Figs. 7 and 8. These groups show the presence of very young animals in the populations. These animals were not measured but merely recorded as being present for they were not easily recovered from the log and also not all of them could be classified as \( P. \) scaber with any degree of certainty. Nevertheless, their presence is important for identifying the age groups in the population. These groups \( A_1^{\varphi\var}, A_1^{\varphi\var}, A_2^{\varphi\var} \) and \( A_2^{\varphi\var} \) represent the animals born in the breeding season of 1951. In Fig. 9 there are no such groups, for this population was collected in July 1952 and by this time the young from the 1951 breeding season had all grown and acquired the adult morphology of the species, and in that Fig. are represented by curves \( B_3^{\varphi\var} \) and \( B_3^{\varphi\var} \).

In Fig. 7 which represents a population collected in autumn 1951, the males are represented by 3 non overlapping groups, \( A_1^{\varphi\var}, B_1^{\varphi\var}, \) and \( C_1^{\varphi\var}. \) The females of this population overlap as do the \( B \) and \( C \) groups of both sexes in the spring population (Fig. 8). However in the summer population (Fig. 9) the \( B \) and \( C \) groups for both sexes are discrete.
Figure 7 - The body lengths of animals collected from the autumn log. The top histogram shows the distribution of male measurements and the lower one the female measurements. The "A" groups show the presence of young animals. The shaded areas denote animals whose positions are doubtful. They cover 0.5 mm on either side of the mid point between the groups of B_1\sigma^f and C_1\sigma^f for the standard error of a measurement is ± 0.26. The shaded area in the female histogram is taken from the male data (See text).
Figure 8 - The body lengths of animals collected from the spring log. The top histogram shows the distribution of male measurements and the lower one the female measurements. The "A" groups show the presence of young animals. The shaded areas denote animals whose positions are doubtful. These areas are derived from Figure 7 (see text).
Figure 9 - The body lengths of animals collected from the summer log. The top histogram shows the distribution of male measurements and the lower one the female measurements. Note the absence of any "A" group animals. The shaded areas are obtained by measuring 0.5 mm on either side of the midpoint between the groups B3 and C3, for the standard error of a measurement is ± 0.26.
Even where overlapping does occur, there is a real size difference between the two groups. It will be recalled that the standard error of a measurement in this range is ± 0.268, so that the number of animals whose position is doubtful is very small.

To return to the male distribution groups in the autumn population in Fig. 7; these groups may be interpreted as representing three classes of animals.

1) Those born in 1951 (Curve A₁♂)
2) Those born in 1950 and still sexually immature (Curve B₁♂)
3) Those born before 1950 and now adult (Curve C₁♂)

As stated above the A₁ males are identified by their pre-imaginal morphology. Proof that the C group animals are the breeding animals and the B group animals are the immature non-breeders is given in two ways. Firstly, 30 young females from the B₁ population were kept in individual jars during the ensuing winter and summer at outdoor temperatures, 15 of these animals survived the entire period, and none of them produced any young, although 3 developed virgin brood pouches. This indicates that they had not been inseminated in the previous breeding season. The information of virginal/
virginal brood pouches shows that some were definitely sexually mature in the summer, but the production of these brood pouches does not seem to be common in mature virgin females. In fact it appears to be only a small minority of virgin females that form them. Therefore it is most probable that all these females were sexually mature in the summer of 1952, and their lengths by this time were well within the C₃♀ group in Fig. 9. A second point supporting this was given by the summer population in Fig. 9. More than 95% of the females in group C₃ had brood pouches and none of the females in B₃ group had a brood pouch. In laboratory experiments no great difference between the growth of males and females has been noticed and so it is presumed that the B group males, like the B group females are immature sexually.

Summarizing the data available it is found that the population from the autumn can be presented by three groups when their body length measurements are plotted. Age and body length are related except in older animals. The breeding season is confined to a short period in this area and growth over winter is unlikely. Therefore size differences may be expected between animals born in different seasons and reared in the same environment.
The females in the B groups have been shown to be sexually immature and the C group females are adult. These data are taken to mean that there is an age difference between the B and C group animals. An alternative explanation is that the C group animals are the faster growing animals. This means that in the period six months an animal would have to grow more than 7.5 mms allowing for no growth in winter. Such growth is only possible at 25°C with optimum food conditions. Individual variation in growth is common but it has not been observed to exceed the range of any B or C group. The most feasible explanation then is that the 3 groups represent three age classes.

For most of the year the P. scaber population in Southern Scotland consists of three groups. Those born that year, a non-breeding group and a breeding group. The only exception is in summer shortly before the breeding season when only two groups are found. Both these have the adult morphology but one is a breeding group and the other is a non-breeding group. Animals enter the B group at the end of their first year and enter the C group at the end of their second year. The C group cannot be accurately interpreted for/-
for it was shown under experimental conditions that growth slows down and the interpretation of age from size becomes inaccurate. However, it will be shown that the C group contains animals that have bred for more than one season. To repeat the salient points of this section; the generation interval in this woodland population has been found to be at least 2 years and for most of the year, except for a short period before the breeding season the population consists of 3 groups - young animals morphologically immature and two groups of morphologically adult animals, but one group of which is sexually immature.

2) **Sex ratios**

The sex ratios of the populations collected from the three logs are given below and in toto do not deviate from a 1:1 ratio.

<table>
<thead>
<tr>
<th>Season</th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autumn Log</td>
<td>204</td>
<td>177</td>
</tr>
<tr>
<td>Spring Log</td>
<td>197</td>
<td>184</td>
</tr>
<tr>
<td>Summer Log</td>
<td>196</td>
<td>235</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>597</td>
<td>596</td>
</tr>
</tbody>
</table>

These numbers are made up of males and females of all age groups and what is really wanted is the sex ratio of the breeding animals during the breeding season. This information is provided from/-
from the groups $C_3^{00}$ and $C_3^{00}$ in Fig. 9. The sex ratio of breeding animals in this population $140^{00} : 149^{00}$, which is entirely normal and would indicate that in this particular population no genes as described by de Lattin (loc. cit.) are at work. This finding depends upon the assumption that the logs sampled are equally attractive to both sexes. It is possible that part of the population are on the forest floor. An area of the forest floor was examined and some $P. scaber$ were found under occasional pieces of bark but they were not very numerous and included both sexes, so it is unlikely that there is a differential distribution of the sexes in this woodland.

3) Mortality rates

An estimation of the mortality rates in this woodland from the data obtained from these logs rests on several assumptions.

a) The selective forces at work in these log populations of $P. scaber$ are equal throughout the woodland, apart from subtle nuances. This is a very difficult, if not impossible point of prove, but it can be discussed from the available knowledge. Selection can be divided into intra- and inter-specific/
inter-specific selection. Intra-specific selection includes competition for food, habitat space and sexual selection. The logs used in this experiment were not of the same wood and of the same approximate size. They all appeared to be of approximately the same state of decay and their fauna appeared to be identical. From this cursory examination it appears that the amount of food available in these logs would be the same, for as stated earlier, the main food appears to be rotting vegetable matter, algae and fungal spores together with a little animal matter. The equality in the amounts of food available is supported by the fact that these logs all of approximately the same size, supported nearly the same number of animals.

Inter-specific selection includes predators, and competition with species that overlap ecologically. Since the logs all supported the same fauna it does not seem likely that inter-specific competition varies from log to log. In a woodland of this size it is also unlikely that the number of kind of predators are likely to vary from one part to another except if a log happens to be near a predators nest. No nests could be seen in the area from which the logs were collected.
Fisher and Ford (1947) reported that a virus attacked the Lepidopteran species that they were investigating. It is likely that virus and bacterial diseases affect P. scaber but in a woodland of this size and shape it is unlikely that they would long remain endemic to any particular part of it.

These points do not prove that selection is of equal intensity throughout the wood, but indicate that it can possibly be so. However, selective forces will vary with the seasons and from year to year but it is suggested that the data from these logs may be considered to be seasonal observations on the same population and to reveal the seasonal variations in selection.

b) A second necessary assumption is that there is no differential emigration or immigration from the logs by any particular age group. It was mentioned earlier that a few P. scaber were found in the forest floor. These groups included all age groups and both sexes. Shortly after the breeding season in late August, several boards were distributed over a part of the forest floor which was covered with leaves and twigs to see if P. scaber young were to be found wandering on the floor. Several boards yielded many young specimens of Philoscia sp. which is easily distinguished from P. scaber.
scaber at that age, but none of the young Isopoda could possibly have been P. scaber. Therefore it seems likely that the populations sampled are true reflections of what occurs in the wild.

c) The final assumption is that the populations observed were neither expanding nor decreasing in size apart from minor fluctuations.

Considering the male population of the autumn log, it is found to consist of 56% young non-breeding males and 42% adult breeding males. These numbers do not include animals in the range 8.2 - 9.3 mm as the two groups may overlap in this region due to the standard error of measurement (± 0.268). By the spring time the relative proportions of these two groups have altered showing a large relative mortality of adult males in the winter. The two spring groups B₂♂♂ and C₂♂♂ are not discrete and a division between the groups is somewhat arbitrary. However, since very little growth takes place in the winter and since the ranges of sizes of the two populations are very similar, it was decided again to neglect animals in the 8.2 - 9.3 mm section. Thus in this spring population the C group males form only 15% of the male population and the B group males form 85% of the/
the male population. At the height of the breeding season the non-breeding males (those less than 6.2 mm) number 29% of the male population and the breeding males from 71% of the population. If this population is not being increased by immigrants, it appears to be declining, at a first glance. The immature to adult ratio in the summer is 30:70 and in the autumn is 50:50 which means a minimum decline of 40% in the adult male population. However, if there is no differential mortality in the two age groups in the late spring and early summer, then the adult males in the summer will contain a number of males from a previous season. The figure for the adult males in the spring population was 15% and if some of the males in the 6.2 - 9.3 mm range are included, the figure can be increased to approximately 25%. Therefore the summer male population will consist of 30% immature males, 18% males breeding for a second or subsequent time and 50% will be breeding for the first time. These percentages however, do not allow the population to maintain itself in this experiment the immature males fall short by 10-20%. The possible causes of this will be discussed later.

Considering the female population from the autumn log, it is seen that the two groups $B_1\,\ddagger\ddagger$ and/
and $C_1^{\varnothing \varnothing}$ overlap. To rectify this, the same procedure as was used in the case of the males is again adopted. No animals in the range 8.2 - 9.3 mm, are included in the calculations. This is quite arbitrary and may be erroneous but the error is unlikely to be very large for growth does not appear to differ in the two sexes. The immature females form 68% of the autumn population and the adult females 32%. In the spring population the immature females comprise 79% of the population and the adult females 21%. But if some of the females from the 8.2 - 9.3 mm range in this spring population are included the percentage of adult females is increased to approximately 25%. In the summer population the immature females form 36% of the population and the breeding females 64%. If there has been no differential mortality a quarter will be old breeding females and 48% of the total female population will be breeding for the first time.

As in the case of the males there is a discrepancy between the immature females and the females breeding for the first time, such that the population cannot maintain itself. However, when it is considered that this analysis is derived from three different populations it is unlikely that exact agreement is to be found. It seems most probable that the discrepancy between the immature and the newly breeding females and males is due to
experimental and sampling errors, but one cannot entirely preclude the fact that it maybe due to fluctuations in the population size of the woodland that may occur from year to year. The main experimental error is probably due to the fact that larger animals are more easily found than smaller ones. Nevertheless the "goodness of fit" of these figures from these log populations would seem to support the theory that the environmental conditions do not differ greatly from log to log.

There does not appear to be much differential mortality between the B group females and the C group females during autumn, winter and spring, but the breeding females suffer their greatest losses as a group after the breeding season - a factor that has been born out in laboratory stocks. Summarizing these findings it appears that in this woodland the breeding females in a population will contain 20-30% females who are not breeding for the first time. Some of the males and females in these populations are likely to be several years old and to be enjoying a isopodan ripe old age.

One of the interesting features of P. scaber is the high correlation between the body length/
length of the female and the number of young per brood. Age and size are also correlated and it has been shown that some females breed for at least two seasons. This means that their second and subsequent broods will be larger than the population average. This may mean that there is selection for longevity or for large body size. If there is selection for longevity this type of reproductive activity is very efficient for selection against genes that are late in expression. A gene of this nature is the one responsible for Huntington's chorea in man (Fraser Roberts 1940 p37). The majority of carriers are affected after the age of 30 and many are affected after the age of maximum reproductive potential. If however, fecundity increased with age in man then such genes would be more exposed to Natural Selection.

So far only the relative mortality rates between the B and C group animals have been considered. Since the actual number of breeding females in the summer log is known and since their body lengths have been recorded, it is possible to estimate the number of fertilized eggs and young they would produce from the regression lines in Figs. 5 and 6 respectively. These calculations of/-
of course, will only give some indication of the mortality rates up to the age of sexual maturity. If the population possesses a lethal gene at high frequency which kills the animals in the embryonic stage, the mortality will be recorded here as mortality of the young liberated animals rather than as egg mortality. Nevertheless it is assumed that the results will give an adumbration of the average course of events.

The breeding females in Fig. 9 can be expected to produce 4,748 fertilized eggs and to liberate 4319 young. This means that 429 zygotes would have died in the maternal brood pouch; a loss of 9%. If this is a stable population, the number of breeding animals must remain fairly constant from year to year. In this population 214 animals were breeding for the first time. Therefore of the 4319 young liberated 214 should survive to breed in two years time, which expressed as a percentage is 4.5. Therefore of the 4748 fertilized eggs produced 9% die in the maternal brood pouch, 86.5% die before sexual maturity and mostly in the first year of life. Of the remainder approximately one quarter can be expected to reproduce again. Therefore 3.5% of the initial 4748/-
4748 die after breeding once and 1% breed more than once. The mortality figures given above will include emigrants and the survival figures will include immigrants. If the population is not moribund or not growing these two factors, emigration immigration, should equal one another, on the average and so not affect the figures.

These figures are somewhat similar to ones quoted by Bodenheimer (1938), describing mortality rates in a population of the desert locust (Schistocerca gregaria). The population was kept in large cages at moderate to sub-optimal conditions. Mortality during the egg state was 16.5% and 64.3% during the larval stages. Only 4.4% of the males and 4.5% of the females reached sexual maturity. These mortality rates were recorded under artificial conditions and their relevance to natural conditions is doubtful. However, the low survival of animals to the breeding age is to be expected in species where a large number of young are produced. Of interest though is the percentage of deaths in the egg stage of P. scaber compared to the locust which oviposites. It is also small compared with the pre-natal mortality of the vole Microtus agrestis. Ranson (1941) found/
found that at least 21.07% of the embryos died in pre-natal life. Emlen (1940) investigated the mortality rates in the California Quail. Three types of plumage are distinguishable: juvenile, immature and adult. The juvenile plumage is lost at 2-6 months and the immature at 11-17 months. His data on mortality rates was obtained from many sources and over a period of many years. The general picture that emerged is summarized below. Survival from potential egg to 12 months is 8.5% and survival from first spring to second spring is 50%. The survival to the age of one year when presumably sexual maturity is reached is somewhat higher than the survival of P. scaber at sexual maturity (4.5%), and the survival to their second year is also higher in the quails, being 50% as against 25% for P. scaber.

4) The state of subdivision of the woodland population

This woodland must contain tens of thousands of specimens of P. scaber. These gross population figures, while of some value, do not give any information on the size of the natural breeding unit. It is very difficult problem to answer/-
answer but a number of facts will be presented; none of which by itself is conclusive, but which when taken together agree in their indications.

a) The distribution of colour classes in the woodland

The various phenotypic colour classes have been described and colouration has been shown to have a genetical basis, although its inheritance could not be analysed from the available data. In the following experiment the relative frequencies of the colour classes in two log populations are compared. Only animals 7 mm's and longer were used so as to avoid any mistakes in classification.

Two oak logs of equal size and state of decay were sampled within a week. The distance between them was less than 30 feet. The results of the comparison which were highly significant are shown below:

<table>
<thead>
<tr>
<th>Colour Class</th>
<th>1st Log Frequency</th>
<th>2nd Log Frequency</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brown</td>
<td>25</td>
<td>35</td>
<td>60</td>
</tr>
<tr>
<td>Red &amp; Brown</td>
<td>44</td>
<td>38</td>
<td>82</td>
</tr>
<tr>
<td>Yellow combined with other colours</td>
<td>67</td>
<td>28</td>
<td>94</td>
</tr>
<tr>
<td>Total</td>
<td>136</td>
<td>101</td>
<td>237</td>
</tr>
</tbody>
</table>

Table 8 - The relative frequencies of different colour types found in two adjacent logs
\[ \chi^2 = \frac{n_T^2}{a_{T1} a_{T2}} \left[ \sum \left( \frac{a_{1i}^2}{n_1} \right) - \frac{a_{T1}^2}{n_T} \right] \]

= 13.169 for 2 degrees of freedom \( P < 0.01 \)

This type of distribution of the phenotypic classes is taken to indicate a similar distribution of genes and may be due to one of two reasons.

a) Differences in the selective forces in the two logs

b) Genetic drift due to small population numbers

The selective value of the various colours might lie in their ability to conceal the animals from predators. However, it is unlikely that this is the cause of the difference between the two populations, for the logs were equally exposed and of the same state of decay and of the same type of wood. Also they lay on the same type of background. The type of predator is unlikely to differ over a distance of 30 feet. Their selective value may be concerned with the physiology of the animal and the difference between the two log populations may be due to subtle differences in the micro-habitat. This is difficult to prove or disprove. Grosser habitat differences are unlikely for/
for both logs contained the same fauna. However, all that can be said at this juncture is that there is a differential accumulation of genes in two sub-populations thirty feet apart.

b) Ecological observations

The number of breeding animals of the logs that were sampled have been well within the limits required for the operation of genetic drift, but the degree of isolation of these logs has not been examined. In the following section this problem will be discussed.

The frequencies of the various age groups within the logs that were examined did not hint at large scale migration. All age groups were present in proportions that indicated stability and the possibility of equal selective pressures within logs. If the population was in a state flux these conditions would not have been realized. The placing of boards on the forest floor yielded no P. scaber although other isopods and anthropods were found under them. This would indicate that these animals do not roam widely in this forest. Furthermore, experience with these animals shows them to be generally sedentary. This is difficult to/
to prove under natural conditions, for in capturing
and marking animals in the wild, the habitat can
be so damaged as to make the animals vacate it
entirely. Occasionally a suitable natural habitat
is found that allows animals to be removed without
injury and without losing any of its attractions
for them. A stop cock watch in the grounds of this
institute proved to be suitable. It remained
attractive to the animals for sometime after dis-
turbance and the lid could be replaced without
injuring any of the animals. Capturing and
marking was carried out over a period of 4 days
and during this period

5 animals were captured once
6 " " " twice
3 " " " thrice
1 animal was captured four times

This habitat was a few feet from a building and
probably formed an "outlier" of a larger population,
but the results indicate that within these popu-
lations there is not much movement even after being
disturbed. Of course conditions might differ
considerably between this type of habitat and a
log, but the indications are that P. scaber is not
very mobile, and that inter-population movement is
not likely to be on a large scale under normal
conditions.

c/
c) The recovery of mutations by inbreeding

In a species which is subdivided into very small breeding units, semi-isolated from one another inbreeding must be fairly common practice. This would mean that a number of animals would be homozygous for mutations, and if these mutations affected the morphology of the animals, they would be easily discernible in an examination of the population. If however, there was selection against these animals, the small breeding units would become purged of such mutations in time and the mutations would be present only in frequencies consonant with their mutation rates. In a parnictic population selection against the homozygotes would be just as stringent, but assuming that the heterozygote is as fit as or nearly as fit as the wild type, the frequency of the gene would be higher than in the sub-divided populations, for the heterozygotes would shelter it and the chances of two heterozygotes mating would be less than in a population sub-divided into small breeding units. Therefore the recovery of mutations may be used to draw inferences about the breeding structure of a population.

A colony from a tree was collected and found to contain 18 adult breeding females. All the animals...
animals seen were collected, but it is not known whether this population was a single breeding unit or whether it was merely part of a larger population. However, the progeny of 4 of these females were sib-mated. Spencer (1947) has shown that the chances of recovering a mutant from a wild population with different numbers of $F_1$ matings. With one $F_1$ mating the chance of recovering a mutant carried by one parent is 25%; with 2 $F_1$ matings it is 44% and with 3 $F_1$ matings it is 56%. It was intended to have 2 or 3 $F_1$ matings from each of the 4 females; 2 were obtained from each of 3 females and only one from the fourth female. Therefore, the chance of recovering a visible mutant is 44% in the case of the three females and 25% in the case of the fourth. No aberrant animals were found when the animals were examined after attaining their adult morphology. Three broods were small but this was probably due to their dams being very small when mated. The losses in these broods and contemporaneous and identically treated outbred broods are shown below. No statistical treatment of the data appears necessary as the losses in both groups are of the same order. Firstly in Table 9 are given the losses suffered during/
During the period from the counting of the brood to the separation of the young into individual vials. The counting was done 24 hours after liberation and the separation 48 hours later. Table 10 gives losses incurred during the period from the separation into individual vials until the animals were finally examined.

### Table 10

<table>
<thead>
<tr>
<th>Pre-Separation Losses</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inbred Broods</td>
</tr>
<tr>
<td>Brood</td>
</tr>
<tr>
<td>-------</td>
</tr>
<tr>
<td>a</td>
</tr>
<tr>
<td>b</td>
</tr>
<tr>
<td>c</td>
</tr>
<tr>
<td>d</td>
</tr>
<tr>
<td>e</td>
</tr>
<tr>
<td>f</td>
</tr>
</tbody>
</table>

Table 9 - The losses in inbred and outbred broods from 24 hours after liberation to 72 hours
Table 10 - The losses in inbred and outbred broods from the age of 72 hrs. until the attainment of adult mortality

* Not included in Table 9 owing to uncertain data but losses were apparently small.

In only one inbred brood (No. f) does the proportion of losses exceed that of the outbred broods, therefore it does not seem likely that these inbred broods contained a higher than average frequency of lethal or poor viability genes. The sex ratios were normal in all but one brood (No. a) in which 6 females survived. However, since the size of the brood at birth was 22 it is likely that the mortality in both sexes was very high. This experiment is/
is far from satisfactory for the chances of recovery of visible mutants are never very high and the number of P1 females sampled is very small. However, the chances of obtaining lethal genes in these broods would probably be greater than the chances of finding a visible mutant, for in Drosophila melanogaster which is the best known genetically of all animals, genes adversely affecting viability are far more common in natural populations than visible mutations (cf. Dobzhansky 1939). In these broods the percentage of mortality is no greater than in outbred broods and the size of the brood was generally what was to be expected from the size of the F1 females, although no strict measurements were taken. In other words the results of this experiment, such as they are, support the theory that P. scaber in a woodland type of habitat generally exists in small breeding units.

Gordon (1936) examined the problem of heterozygosis in free-living populations D. melanogaster and D. subobscura. Collections were made when the flies were most abundant. In D. subobscura he examined the descendants of 17 females in 1934 and obtained a frequency of autosomal recessives of 0.636 - 0.149. In D. melanogaster in the same year he examined the descendants
of 9 wild females and obtained a frequency of autosomal recessives of $0.924 \pm 0.251$. As already stated these collections were made when the fly populations were at a peak and so the number of wild females tested must have formed a very small proportion of their population. Since this is one of the probable drawbacks of the *P. scaber* experiment, the comparison between the results of the two experiments is the more striking.

Sansome and La Cour (1935) investigated the genetics of the polymorphic grasshopper *Chorthippus parallelus*. They found no mutants beyond those visible in the free-living populations. Gordon discusses this point and compares it to his own findings. He offers two possible reasons for this difference. There may be a difference in the mating system; *C. parallelus* maybe more inbred.

The second suggestion rests on the theory of Fisher's which suggests that in polymorphic species the heterozygotes are fitter than either the homozygotes. In such cases there will be little dominance and thus no shielding of the mutants against selection. This theory however, need only be applicable to those loci which are concerned with the polymorphic character, and dominance may be expected at other loci.
loci. *P. scaber* is polymorphic for colouration but structurally it is very uniform so that dominance maybe expected at the "non-colour" loci even if this theory is correct, and the first reason tendered by Gordon seems to be the most germane to the present experiment.

**Discussion**

In the foregoing sections evidence has been accumulated to discuss the state of subdivision of this woodland population. It has been shown that the relative frequencies of the colour classes which have a genetic basis differ in 2 log populations less than 30 feet apart. This may be due to genetic drift or to differences in selection. Even if the differences in selection are responsible it would indicate some type of barrier between the two populations. The ecological evidence produced showed *P. scaber* to be "ortskservativ" as Timofeeff-Ressovsky has described species which normally do not move much. It seems unlikely from this evidence that there is much movement between populations. Furthermore, movement between logs would not make the migration coefficient very large for two adjacent populations would most likely/-
likely resemble one another in genetic properties, and for "m" to be large the migrants must have genotypes representative of the species at large (cf. Wright 1940). Therefore from this evidence it seems as if P. scaber breeding units in this type of habitat are generally small under normal conditions. The inbreeding experiment, whilst inconclusive in itself, agrees with the possibility of small population size. While none of these approaches can be taken as proof positive that P. scaber lives in small breeding units in this woodland they seem to indicate it. The effective population size can also be influenced by two earlier findings. The fact that the breeding population will include approximately 20-30% animals who are not breeding for the first time, increases the chances of inbreeding in a population and thus can affect the effective population size. Furthermore, the long generation interval may also affect the size of breeding units. Every population contains sexually immature animals and these may compete with the breeding stock for food and space, and where these habitat factors are limited, the non-breeding animals will also aid to lessen the effective/-
effective population size. It can be argued that such competition might lead to more migration, but this is discussed later.

The size of the breeding population of the summer log was 289. From these observations of the woodland it seems unlikely that other population units are larger unless isolation by distance is operative. It is quite possible however, that some units may be smaller, but in the very small units it is possible that the ecological conditions may be so changeable that movement may be more common than in the logs where steady food supply and adequate humidity conditions exist. Under these conditions it is unlikely that the subpopulations will drift apart to any great extent, for in general the selective forces will be uniform throughout the woodland and in abnormal years populations probably mix a great deal.
2) **The population of a stone wall**

The "dry stane dykes" form one of the main habitats of *P. scaber* in Scotland. It is cogent therefore to investigate the population structure of such a habitat. In the following experiment the gross population size of a stone wall is estimated and is compared to the woodland habitat of the previous section.

**Material and Methods**

The stone wall used in this experiment lies in the middle of a golf course and is well isolated from trees or other walls. It is approximately 100 yards long and is generally in a state of good repair except for one patch about 10 yards long which is broken down and is probably capable of supporting a larger isopod population than equal lengths of wall in better repair. If the wall is examined on a fair day after rainy weather some *P. scaber* will be found lying at the base of the wall in the roots of the short turf there. To count these animals is a simple but laborious task, but the problem then remains; what proportion of the animals are still in the interstices of the wall? Perhaps the problem is best/-
best set another way; is there any chance of obtaining a valid assessment of the animals within the wall?

Cloudsley-Thomson (1952) working on the assumption that Terrestrial Isopoda are more active at night than during the day, tested the obvious differences between diurnal and nocturnal conditions on some laboratory specimens of *Oniscus asellus*. He concluded that darkness was the main factor affecting activity, but that in the majority of isopod habitats the factors investigated by him would not be important. In one of his experiments he placed animals in a chamber with a choice of light or darkness, and the experiment was replicated under different conditions of relative humidity. In all cases a certain percentage of animals chose light, although the percentage that did thus varied according to the relative humidity of the chamber and to whether they had been subjected to the dark prior to the experiment. What is important is that under a given set of conditions, a certain percentage of animals will endure light. Therefore if a number of animals are marked and released at points along the wall, a number will choose to remain outside in the light. Cloudsley-Thomson claims that the percentage that chose light depended/-
depended on whether they had been kept in the dark or not, but his results received no statistical treatment and only percentages are given so that this factor must be treated with reserve. Furthermore, under wild conditions this qualification might be completely valueless. The animals used for this purpose had all been kept in the dark as it was considered that conditions in the wall would be very dark. Edney (1952) has put forward another reason for the presence of isopods outside their habitats on hot days. He maintains that evaporation and convection are important factors in controlling the body temperature of Isopoda and Myriapoda and under certain conditions on hot days evaporation and convection may be greater outside the habitat, so animals will migrate out. This may be perfectly valid but these experiments were all done before 8 a.m. so that it is unlikely that the temperature at that time would be so high as to drive the animals from their habitats. It seems therefore that under suitable humidity conditions, a certain percentage of animals become fairly tolerant of the light and that this percentage can be determined by the use of a sample of marked animals. The best sample would be one drawn from the population under examination/
examination but unfortunately the capturing of animals under these conditions is very difficult and an adequately sized sample could not be obtained.

Results and Discussion

Thirteen points along the wall were chosen at random distances before going out to the wall, and these places were examined over a distance of a foot on either side of the wall, constituting in effect an examination of 13 random feet. At three of these points 120 adult marked animals were released, 20 of either sex at each point. The recovery of the marked animals 24 hours later at these points were 0, 8 and 3 giving a total recovery of nearly 10%. The number of wild animals found in the 13 feet at the same time was 10. Therefore along 300 feet one would expect 230 animals, provided these 13 feet are a good random sample. This point was checked later by taking counts at 10 feet intervals along the wall. This would constitute 30 feet of wall and 27 animals were found. If these 230 animals constitute the 10% light-tolerant section of the population, the total population must be somewhere in the region of 2300. This figure of course cannot be /-
be exact, for there are several errors. The broken part of the wall will contribute more animals than have been calculated. However, it is hoped that this figure gives a just approximation to the true gross population size. It is not certain whether the marked animals behaved as the wild ones do, but from Cloudsley-Thomson's work there is little evidence to indicate that they should act differently. Edney's suggestions do not seem cogent at the temperatures at which these experiments were performed. No external lateral dispersion took place as special attention was paid to this factor.

Does this population constitute a panmictic unit? Wild animals that were marked were never recovered except for one animal which was found a month later at the same place. She was a gravid female and so had not moulted. This would imply that some animals do not move much in this type of habitat. Movement in species must generally depend to a large extent on the ecological conditions of the habitat. Where conditions are unstable, animals are likely to move on, until they find more suitable conditions. Thus in the marginal ecological zones there is probably less inbreeding/-
inbreeding than in a stable environment where the members of a brood may live their whole lives without ever moving. Most probably it is the stable habitats that provide emigrants to settle in the marginal areas, and it is also probable that they generally do not receive many immigrants. In the case of _P. scaber_ the marginal habitats are under small pieces of bark, wood or small stones and in places that are liable to occasional exposure or flooding. Therefore within a major habitat such as a wood or stone wall it is suggested that there are relatively stable breeding units where inbreeding is common, together with the unstable populations which receive the surplus animals from the stable populations. A fair degree of cross breeding probably occurs in these marginal zones but the chances of survival of the young are likely to be very low.
A sexual abnormality and its effect on the population structure

Introduction

The occurrence of sex reversal in Crustacea is well known and the main investigations have been reviewed by Kleinholz (1942). The cases discussed by him describe the male undergoing changes in a female direction; many of the cases involve parasitization which is claimed by some workers to alter the metabolism of the male in such a way that it resembles the normal female metabolism. In Isopoda the cases of intersexuality have been reported in the species Armadillidium vulgare (Collinge 1946, 1947). The aberrant animals possessed small styles and one also had oostegites. Dissection of these animals revealed small ovaries and some tissue that could possibly be described as masculine. de Lattin (loc. cit.) has described a gene which reduced the proportion of males in broods, but it is not certain that this gene causes actual sex reversal at an early age. During the course of this work aberrant females have been encountered. They have possessed pleopods that resembled male ones, and the object of/-
of this experiment is to investigate the effect of this phenomenon on the population structure of the species. Firstly does this aberrancy in the phenotype of some females indicate true sex reversal? If so, does it mean that formerly fertile females can become functional males? If there is no sex reversal, does it indicate a state of unbalance in the reproductive system of the female that renders her sterile? If there is no sterility does it affect the size and sex ratio of the brood? Then again does it affect the reproductive potential of a female by influencing her chances of life? All these questions have a direct bearing on the population structure of a species. Furthermore it is necessary to know whether the character is determined by genetic or environmental means or by an interaction of both agencies. No attempt is made here to determine the relationship between this phenomenon and sex determination for the only concern here with its causation is to learn whether it has a genetic basis or not.

a) Description of the character

Diagrams of the normal male and female were/-
were shown earlier and descriptions were given in the text; these descriptions will be repeated briefly. In the male the endopodite of the first pleopod is long and pointed while the exopodite of the second pleopod is similarly elongated and the endopodite of this pleopod bears a long style, the appendix masculinus. In the female there is no elongation of these body parts. In the male the posterior edges of the pleopods 3-5 form an angle of approximately 45° with the mid ventral line of the animal; in the female this angle is approximately 70°. A further difference is afforded by the lamella which in the female forms a short isosceles triangle at the posterior end of the 7th thoracic segment. In the male it forms a chitinous plate covering part of the styles and part of the penis (Legrand 1941). These features constitute the main external structural differences between the sexes.

In the initial stages, the aberrancy reported here is perceptible to an experienced eye only. One or two minute styles may be seen growing between the first pair of pleopods. They may or may not protrude beyond the posterior edge of the pleopods. An example of this type of aberrancy is/
are seen in Diagrams 4 and 5. In other cases the aberrancy is seen initially by the posterior points of the pleopods failing to coincide along the midventral line of the animal as shown in Diagrams 6 and 7. Finally the aberrancy may be noticed by the increased slope of the posterior edges of some of the pleopods. An example of this type is shown in Diagram 8, where the slope of the posterior edge of the second pair of pleopods is very marked.

An advanced case is shown in Diagram 9. Here the styles are well developed and all the pleopods have assumed a masculine appearance. The difference is striking and it seems doubtful if the early stages that have been described are in reality the fore-runners of such extreme masculinization. Later, the development of the character was observed in 4 females including the female in Diagram 9, to ascertain whether complete sex reversal can be accomplished.

The late development of the character

Speculations on the effect of complete sex reversal are of interest when considered in relation to inbreeding and sex linked genes and also in relation to selection and sex limited characters. To investigate the possibility of complete/
Diagram 4 - The ventral view of an abnormal female. A small style is seen between the first pair of pleopods. The seventh pair of legs have been removed.

Diagram 5 - The ventral view of an abnormal female showing a small style between the first pair of pleopods which do not coincide.
Diagram 6 - Ventral view of abnormal female.
The posterior points of the pleopods fail to coincide along the mid-ventral line of the female. The seventh pair of legs have been removed and the 6th right leg has been injured.

Diagram 7 - Another female showing the failure of the posterior edges of the pleopods to coincide along the mid-ventral line.
Diagram 8 - An abnormal female showing the increased slope of the posterior edge of the second pair of pleopods.

Diagram 8A - An abnormal female in a fairly advanced condition. The styles are well developed but the pleopods are not masculine.
Diagram 9 - An abnormal female in a very advanced condition (CA/36 in the text). The styles are well developed and the pleopods have a very masculine appearance. For further details see text. This photograph was taken after the animal had died.
complete sex reversal, 4 aberrant females were closely observed over a period of three months and measurements were taken of the growth of styles and the progressive masculinization noted. These females were originally from two Unst (Shetland) populations. A short description is given of each female as she appeared when first examined in the laboratory, and finally the growth of styles during the three months, April, May and June 1951 are given in Table 11.

**Female CA/64:** First examined 18th Oct. 1950. Two very small styles were seen between the first pair of pleopods. They appeared from the base of the 7th thoracic segment and did not protrude beyond the posterior edge of the first pair of pleopods. By the first week in April, the styles protruded beyond the posterior edge of the first pair of pleopods and had assumed the firm chitinous appearance of the normal male styles. Also the posterior abdominal segments had the steep masculine slope.

**Female CA/66:** This female was from the same Unst population as the previous one and was first examined on the same date. One small style, that did not protrude beyond the posterior edge of the first/-
first pair of pleopods, lay between those pleopods with its anterior edge immediately adjacent to the 7th thoracic segment. By 4th April, 1951, two styles protruded well beyond the posterior edge of the first pair of pleopods and the slope of the other pleopods, although not typically masculine, was steeper than is usual in females. 

**Female CA/68:** This female was from the same population as the previous two and was first examined on the same date. One style was seen between the first pair of pleopods with its posterior edge protruding beyond the posterior edge of these pleopods. On the 4th April, 2 styles were visible and both protruded beyond the posterior edge of the first pair of pleopods, but after a moult that ended on the 7th April only the left style was visible. 

**Female CA/86:** This female came from a different Unat population and was first examined on 24th November 1950. No styles were visible but the slope of the pleopods was distinctly masculine. On 4th April, 1951, two well developed styles were visible and the slope of the pleopods 3-5 was still very masculine. The styles were well chintinzied and are shown in Diagram 9. 

The growth of the styles in these females/
females during the 3 month period April-June are shown below in Table 11.

<table>
<thead>
<tr>
<th></th>
<th>April</th>
<th></th>
<th>June</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of</td>
<td>Right Style</td>
<td>Left Style</td>
<td>Right Style</td>
<td>Left Style</td>
</tr>
<tr>
<td>CA/64</td>
<td>6.0</td>
<td>4.8</td>
<td>8.0</td>
<td>7.0</td>
</tr>
<tr>
<td>CA/66</td>
<td>3.0</td>
<td>5.0</td>
<td>6.0</td>
<td>8.0</td>
</tr>
<tr>
<td>CA/68</td>
<td>0</td>
<td>4.5</td>
<td>0</td>
<td>5.0</td>
</tr>
<tr>
<td>CA/66</td>
<td>8.5</td>
<td>10.0</td>
<td>12.5</td>
<td>12.5</td>
</tr>
</tbody>
</table>

Table 11 - The growth of styles in 4 Shetland females. The units of measurement are micrometer units.

These observations show a steady increase in the apparent masculinity of these females, and prove that the initial aberrations are true indications of further possible changes. In these females, with the exception of CA/68, the changes involved not only an increase in the length of the styles but the slopes of the pleopods also became more masculine. In most aberrant females the styles appear flatter and softer than the male styles but in the cases of CA/66 and CA/64, the styles appeared to be hardened and to possess slight protruberances at the posterior ends as found in normal males. None of these females were dissected to find the presence of male tissue, but/-
but another female which was considerably more masculine than CA/68, but not as masculine as the others, was dissected. The ovaries were present and had not degenerated in any noticeable way, but tissue similar to the male testes was present. No. examination for sperm was carried out with this tissue. None of the four females lived to become functional males but it is uncertain whether this masculinization, per se, was the cause of their deaths. From this study it seems unlikely that the complete sex reversal of an adult female is ever effected under natural conditions.

The basis of the character

Most of the cases of sex reversal in Crustacea involved parasitization (Kleinholz loc. cit.). All aberrant females were examined for external parasites in this work, but only mites were found. However, these parasites were found on both normal and aberrant females in apparently equal numbers. Three aberrant and three normal females were examined for internal parasites. These females were of equal ages and had been reared under uniform laboratory conditions.

Squashes of the alimentary tract, ovaries and digestive/-
digestive glands together with the haemocoel were examined in all cases, but no parasites were found. This suggested that the characters had a genetic basis, and this hypothesis was duly tested.

However, since *P. scaber* is a slow breeding animal a detailed analysis of the genetics of this aberrancy requires much time, especially as the character can only be scored with certainty in the adults of one sex. Nevertheless it is possible to demonstrate that the character is genetically determined and not entirely dependent on environmental factors for its expression. If a character has a genetic basis animals carrying it should have a significantly higher proportion of offspring showing the character than an equal number of normal animals. This has been found to be the case in this aberrancy of the pleopods. The numbers unfortunately are small as classification for this character can only be carried out when the animals are fully adult, and not many offspring survived to the requisite age in either group. However, the broods of the abnormal females contained a significantly higher proportion of abnormal daughters than the control group. All the females were inseminated in the wild except the females/*-
females 1/2, 1/3 who were mated in the laboratory to a male which was possibly a sib.

<table>
<thead>
<tr>
<th>Female</th>
<th>Abnormal Females</th>
<th>Normal</th>
<th>Abnormal</th>
<th>Normal Females</th>
<th>Brood</th>
<th>Abnormal</th>
<th>Brood</th>
</tr>
</thead>
<tbody>
<tr>
<td>CA/60</td>
<td></td>
<td>4</td>
<td>1</td>
<td>CA/67</td>
<td>2</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>CA/93</td>
<td></td>
<td>0</td>
<td>1</td>
<td>CA/30</td>
<td>4</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>U/8</td>
<td></td>
<td>1</td>
<td>5</td>
<td>CA/47</td>
<td>6</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>1/2</td>
<td></td>
<td>2</td>
<td>5</td>
<td>CA/48</td>
<td>9</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>1/3</td>
<td></td>
<td>7</td>
<td>8</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>14</td>
<td>20</td>
<td>Total</td>
<td>21</td>
<td>5</td>
<td></td>
</tr>
</tbody>
</table>

Table 12 - The numbers of normal and aberrant daughters in the broods of 5 aberrant and 4 normal females

The fecundity of aberrant females

Complete sex reversal does not seem likely in the aberrant females of *P. scaber* described here, but their fecundity may be seriously impaired by their aberrancy. In order to compare the fecundity of normal and aberrant females, large numbers are necessary and it is imperative that the comparison should cover the whole reproductive span of the females. Unfortunately the numbers and time were not available for such a test, but the fecundity of these aberrant females can/-
can be measured indirectly.

In one collection of breeding females 14 were classed as aberrant and 30 as normal. Eight or approximately 66% of the aberrant females produced young while 21 or 70% of the normal females had broods, showing that the percentage of fertile females did not differ in the 2 groups. In order to compare the sizes of the broods of the 2 types of females, the figures have to be broken down further. This is due to the fact that brood size varies geographically: therefore a comparison of brood size can only be made between animals derived from the same locality. Table 12 shows the brood sizes of the two types of females derived from the same locality.

<table>
<thead>
<tr>
<th>Aberrant Females</th>
<th>Normal Females</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female No.</td>
<td>No. of Young</td>
</tr>
<tr>
<td>1</td>
<td>11</td>
</tr>
<tr>
<td>2</td>
<td>10</td>
</tr>
<tr>
<td>3</td>
<td>17</td>
</tr>
<tr>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>5</td>
<td>11</td>
</tr>
<tr>
<td>( \bar{x} )</td>
<td>10.6</td>
</tr>
<tr>
<td>( s )</td>
<td>2.06</td>
</tr>
</tbody>
</table>

Table 13 - A comparison between the sizes of broods of aberrant and normal females collected from the island of Unst.
In other populations sampled the number of aberrant females is too small to allow a similar comparison, but their brood size does not appear to differ from the normal females of the same population even where the styles are fairly large. The number of broods per season is a character that varies geographically and here again there does not appear to be any difference between the two types of females. Finally the total number of broods produced will be dependent on the age at which a female reaches sexual maturity and on her longevity. The aberrant females that were born and reared in the laboratory did not seem to be unduly late in reaching sexual maturity, but again the numbers available for comparison are extremely small. Five females, three normal and two aberrant, from the same population were all mated at the same time and all had brood pouches in their 17th month.

A direct comparison of the longevity of the two types of females was not possible in this work. It will be recalled however, that age and body length are correlated, so that there should be no difference in the sizes of the two groups of females from the same population. The sizes of the two types of females from two populations are given/
given in Table 14 and they do not appear to differ.

<table>
<thead>
<tr>
<th>Population A</th>
<th>Population B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aberrant ♀♀</td>
<td>Aberrant ♀♀</td>
</tr>
<tr>
<td>No.</td>
<td>Length</td>
</tr>
<tr>
<td>-----</td>
<td>--------</td>
</tr>
<tr>
<td>1</td>
<td>10.2</td>
</tr>
<tr>
<td>2</td>
<td>9.6</td>
</tr>
<tr>
<td>3</td>
<td>10.5</td>
</tr>
<tr>
<td>4</td>
<td>11.8</td>
</tr>
<tr>
<td>5</td>
<td>9.6</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
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<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>( \bar{x} )</td>
<td>10.3</td>
</tr>
</tbody>
</table>

Table 14 - The distribution of body length of aberrant and normal females in two populations

Summarizing the available data: there does not appear to be any difference in the size of broods of the two types of females nor in the number of broods per season. There does not appear to be any difference in the ages at which they reach sexual maturity. There does not appear to be any difference in the body lengths of the two types of females in two/
two natural populations and this may be interpreted as showing no differential mortality in the adults of the two groups. Therefore the aberrancy described here does not appear to affect the fecundity of a female if the masculinity does not proceed too far. If this happens the female dies. The majority of aberrant females examined however, were only slightly masculine and did not become progressively more so.

The sex ratios of progeny of aberrant females

The character may affect the population structure of a colony by altering the normal sex ratio. The broods of 3 aberrant females, one of whom had very large styles, were reared almost entirely without loss and sexed. The results are given below.

<table>
<thead>
<tr>
<th>Brood No.</th>
<th>Sex</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>8</td>
<td>5</td>
</tr>
<tr>
<td>2</td>
<td>6</td>
<td>10</td>
</tr>
<tr>
<td>3</td>
<td>22</td>
<td>16</td>
</tr>
<tr>
<td>Total</td>
<td>36</td>
<td>31</td>
</tr>
</tbody>
</table>

These results do not differ from the sex ratios of broods from normal females shown earlier.
The distribution of the character

It appears that the aberrancy described here only affects the fecundity of the females when the change towards masculinity has proceeded fairly far. However, in the majority of cases encountered, the females have remained only slightly masculine, and in these cases the aberrancy does not appear to have any deleterious effect, under laboratory conditions. Therefore it is not surprising to find the character widely distributed in natural populations. No local population appears to be entirely free of aberrant females, but their frequency is generally low. In a population from Kent, 3 out of 21 or 14% adult females were classified as aberrant; similarly a population from Peeblesshire had 4 aberrant females out of 39 (10%). On the island of Unst 48 females were classified as aberrant in a sample of 113 adult females (42%). All the collections from the Shetland Islands had high percentages of aberrant females and the data are presented in Table 15.

Table 15/-
<table>
<thead>
<tr>
<th>Island</th>
<th>Place</th>
<th>Size of Sample (Females only)</th>
<th>%age Aberrant ♀♀</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unst</td>
<td>Baltasound</td>
<td>41</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>Collaster</td>
<td>22</td>
<td>54</td>
</tr>
<tr>
<td></td>
<td>Virda Field</td>
<td>36</td>
<td>58</td>
</tr>
<tr>
<td></td>
<td>Innerskaw</td>
<td>14</td>
<td>43</td>
</tr>
<tr>
<td>Mainland</td>
<td>(Hillswick)</td>
<td>32</td>
<td>47</td>
</tr>
<tr>
<td>Bressay</td>
<td></td>
<td>28</td>
<td>26</td>
</tr>
<tr>
<td>Yell</td>
<td></td>
<td>15</td>
<td>66</td>
</tr>
</tbody>
</table>

Table 15 - The percentages of aberrant females in samples from 4 islands in the Shetland archipelago. All collections were made from confined areas.

These data show that the character is widespread in the islands. It is present there in higher frequencies than in the populations of Scotland proper, and this point warrants consideration.

Discussion

The differentiation of island populations is well known and a good example is afforded by the Shetland Wren (Huxley 1942 p176). Some differentiation of island populations can be effected by genetic drift if the initial population is sufficiently small and isolated. If genetic drift was the sole agency responsible for the present distribution of this sexual aberrancy in *P. scaber*, the character must have/-
have been introduced a long time ago, for the species is very common in the archipelago now. The present isolation of the Shetland Isopoda is probably not very complete. There is no timber on the islands and since the advent of man many woodlice must have been introduced with the timber importations alone. This process has been in progress for a great many generations of woodlice, and therefore if the aberrant females were inferior to the normal wild type female, the character should now have been replaced despite the earlier action of genetic drift. The fact remains that it is present today in very high frequencies in apparently large populations in the face of what must be a fairly high migration pressure, and therefore it seems most likely that the character has some local selective advantage either per se or the genes responsible are pleiotropic, and their other effects are sufficiently advantageous to balance any ill-effects of the sexual aberrancy. An analogous example has been investigated in D. pseudoobscura (Wallace 1948). In that species a character known as "sex-ratio" occurs. It is a sex linked genetic condition which causes the elimination of the Y chromosome and an additional division of the X chromosomes during spermatogenesis, thus resulting in/-. 
in entirely female broods from \(Sr\) (sex ratio) males. Its presence in a natural population is identified cytologically and its frequency varies spatially and seasonally. In experimental populations kept at 16\(^\circ\)C it was found that \(Sr\) was not eliminated but remained in the population at a low frequency due to the fact that \(Sr\) males were superior in fitness to the standard males. This superiority is offset by the \(Sr/Sr\) females being inferior to the standard females. These changes occurring in the experimental populations were interpreted as showing that the relative frequencies of the \(Sr\) and standard types are determined by natural selection. Thus a character that superficially would seem to be disastrous to a species may be maintained in the species without impairing the evolutionary chances of that species. It is submitted that the sexual aberrancy described here may be such a character: that it is maintained in the Shetland islands at high frequencies by Natural Selection.
Summary of experiments pertaining to population structure

The individual experiments have been discussed already and the general evolutionary significances of their findings is discussed at the end of this thesis together with the data from Part II. This section therefore is confined to a summary of the experimental data and the conclusions that were drawn in the discussions of each experiment.

In the studies on the life history of *P. scaber* it was found that body length and age are related. It was also found that there is no growth during winter. The breeding season in southern Scotland is short, and so the age groups in a population can be distinguished by measurement. Whole logs were removed from a small wood at various seasons and the woodlice were extracted and measured.

It was found that in the autumn the body lengths of the animals from a single log fall into 3 groups, one of which consists of young that were liberated some weeks previously and are morphologically distinct; the other 2 groups are distinguishable by size only. However, females from the middle group were found to be virgins, and in a log sampled/-
sampled in summer only the largest sized group contained gravid females. Growth appears to be of the same rate in both sexes. It was concluded therefore that the middle group are sexually immature animals which were born the previous year and who would mature sexually after their second winter. It was also found that in this population the sex ratio in the breeding group was normal during the breeding season. The data from these logs allowed the mortality rates to be estimated, depending on several assumptions. It was found that of the zygotes found in the brood pouch, 9% die there, 4.5% develop into sexually mature individuals, and 1% breed for more than one season.

It was concluded that the population of this wood is subdivided into small breeding units. This conclusion is based on three experiments, none of which is entirely conclusive in itself but which all agree in their general indications. Two logs were sampled within a week. They were 30 feet apart in the wood. Their populations were found to differ significantly in the relative frequencies of the different colour phenotypes which have a genetic basis. This difference could be due to genetic drift following upon small population size.

In/-
In a second experiment marked animals were found repeatedly at one place indicating that *P. scaber* is territorially conservative. In the third experiment some F1 animals from a population collected from a tree were inbred. No deleterious mutations were found and their fertility was equal to that of outbred broods. This can be interpreted as showing that inbreeding is common in *P. scaber* and so most of the deleterious genes have been exposed to Natural Selection and are present only in frequencies consonant with their mutation rates. The effect on the effective population size of the long generation interval and the survival of 25% (approximately) of the breeding stock each year is discussed.

The gross population size of a stone wall was estimated by releasing marked animals and recapturing them. Finally the effect of the habitat type on the effective population size were discussed, and it was concluded that within a major habitat there are probably two types of populations: those that are stable and in which there is probably inbreeding and those that are unstable and in which there is probably crossbreeding.

In some populations females are found that/
that possess abnormal male-like pleopods. This trait appears to be genetic. Its effect on the fertility of the females was examined to ascertain if it could affect the effective population size. However, the fertility of these females appeared to be normal. In the Shetland Islands the percentage of abnormal females is very high and it is suggested that the high frequency of the trait there is due to Natural Selection rather than to genetic drift.
Wright's two-fold conception of evolution has been mentioned: the transformation of species and the splitting of species. If the logic of this concept is accepted then it is probable that many species at our horizon in time are being split into two or more species. The best chances of observing this incipient speciation are afforded by a study of populations from different parts of the species range. In addition, such a study will indicate some of the genetic variability possessed by the species; it will throw into sharp relief some of the characters that are under selection and may give some indication of the efficiency with which the species is meeting these selective forces. An investigation into the geographic variability of a species therefore seems a necessary adjunct to the study of its evolutionary dynamics, and the second section of this work deals with a study of three populations of P. acaber from different parts of the British Isles.

Several investigations have shown that certain species are subdivided into geographic races/-
races which occupy discrete parts of the species range and in some cases form, spatially, a chain of geographic races or sub-species. These sub-species generally interbreed whenever they come into contact with one another. However, certain examples have been cited in which the races forming the extreme ends of the chain meet, and do not interbreed although connected by interbreeding races. Many such examples are cited by Huxley (1942 p243) and by Mayr (1942 p180). In some cases the barriers to mating may be ecological; in others differences in mating behaviour may prevent mating under natural conditions. These differences that result in a lack of stimulus to copulate have been termed ethological barriers by Mayr (1948).

The relevance of these cases to Wright's concept of evolution is that if the intermediate races of the chain were to be eliminated then the two sympatric races would be regarded as separate species. An example of this sort from the anthropoda has been reported by Forbes (1928). The butterfly Junonia lavinia is found in North, Central and South America and in the West Indies. Although there is much local differentiation, the species can be divided into three well-marked geographic races. The race coenia inhabits North America/-
America and in Mexico it meets the Central American race *zonalis*. In this part of the species range they interbreed but in Cuba they are sympatric and do not interbreed. He assumes that the two races have reached Cuba by different routes (via North and South America) and have become differentiated en route, but does not state the nature of the barrier between them.

Goldschmidt (1940) is antagonistic to the idea that new species may be formed from subspecies. His idea on the breeding barriers between species are very rigid and complete sterility or sterility of the hybrids are the only barriers he acknowledges between species. He therefore rejects sexual isolation or ecological isolation as being capable of forming an effective hiatus between species. He is of the opinion that subspecific differences are of a very different order to specific differences and that infra-specific differences are derived by genic rather than chromosomal differences which are responsible for inter-specific differences. However, as will be mentioned later, chromosomal variability has since been found at the infra-specific level. Nevertheless, his studies on the gypsy-moth *Lymantria/*...
*Lymantria dispar* (L.) are amongst the classical investigations into geographic variability (Goldschmidt (1934)).

*Lymantria dispar* is widely distributed in the palearctic regions. Two groups can be distinguished by the colour of the abdominal hair of the females. All the northern races have dark brown 'wool' and all southern forms have light yellow 'wool', but within these major groups numerous subspecies can be described by morphological features. Goldschmidt however, found that physiological characters were more important in differentiating the races and the pre-imaginal characters were more important than imaginal ones for the major portion of an individual's existence is passed in the pre-imaginal state. He found that the species can be split into a number of sex races that are characterized by different valencies of their sex-determining mechanisms. He also found differences in the length of time of larval development, the number of larval instars, the length of the diapause, growth and body size, larval pattern, amount of chromosomal material and velocity of differentiation of gonads.

The sex races were diagnosed in the following manner. If the females of one race when crossed with
with males of another produced daughters that were intersexual to any degree, the female race was termed a weak race and the male race a strong race. Different degrees of weakness were recorded by the intersexuality of the daughters which ranged from complete sex-reversal to low grade intersexuality. Strong races could also be graded, and races that produced normal daughters with both weak and strong races were termed neutral. Goldschmidt concluded that the genetic basis of this trait is dependent on the interaction between a cytoplasmic factor inherited through the females and a male-determining sex gene which is a member of a series of multiple alleles. The European and Russian races are all weak. Those in the Italian Alps, Russian Turkestan and Korea are half weak. However, across the Tsushima Straits from Korea, on the Japanese island of Kyushiu they are neutral minus. Further north in the southern part of the island of Honshiu they are neutral and moving north on this island, the races are all strong with varying degrees of strength. Finally on the northern island of Hokkaido the weakest race of all is found, and except for this anomaly there is a continuous gradation from Korea through the southern part of Japan/—
Japan and north east over the Japanese archipelago. Goldschmidt was unable to find any obvious adaptive value for this character.

Length of larval life on the other hand was considered by Goldschmidt to be adapted to the temperature of the habitat and to be in harmony with the period of vegetative growth. The number of larval instars was found to be genetically determined by three alleles which he called $T_1$, $T_2$ and $T_3$. All Eurasian forms contain only $T_1$ and $T_2$ and in Hokkaido, Korea and the northern most parts of the Japanese main island these alleles are also present. Further south $T_1$ is missing and in mid-Japan $T_3$ appears and is found further south, but in the island of Kyushiu all three alleles are present. No adaptive value for this character could be found.

The length of the diapause was gauged experimentally by transferring the eggs from a very low temperature to a temperature suitable for hatching and measuring the time until eclosion. He called this time the period of incubation. This technique has a short-coming in that the temperatures used in the experiment are not necessarily the temperatures experienced in the wild and so do not reflect/
reflect the nature of incubation there. However, genetic differences between races were found and very plausible inferences were drawn from the data. He found that the forms with the short incubation periods came from areas with long winters and slow springs so that a comparatively low temperature sum is required for hatching. Body size in this species, as in most organisms, is much modified by environmental conditions, but he found that underlaboratory conditions, size differences were discernible and that the distribution of races according to size is very similar to that shown by the number of larval instars which is indicative of the velocity of development, but the distributions are not identical. Three types of larval pattern are found. They are also distributed geographically. The adaptive value of this character is unknown, but Goldschmidt thinks that it is connected with some metabolic situation. The chromosome number is identical for all races, but when he compared the equatorial plates of the first meiotic division from individuals of different races, he concluded the amount of chromosomal material varied from race to race. This is a very crude method of comparison and may be influenced by age and other environmental conditions and also by the methods of preparation. Finally, when he plotted the absolute size/
size of the gonads against time, he found that the weak and half weak races have rapid gonad differentiation of the gonads, with the exception of one race. Goldschmidt concluded that the cytoplasmic factor F was in some way concerned with this character.

Tests of this nature reveal genetic differences between races, but do not indicate what really occurs under natural conditions so that in many cases the adaptive nature of the differences is hidden from the investigator. Nevertheless this type of investigation shows how important physiological characters are and how much more accurate than morphological characters they can be in assessing the infra-specific structure of species.

Goldschmidt refuses to consider the sex races in *Lymantria dispar* as being incipient species, because the crosses between races of different strengths give intersexual daughters only in one type of cross; the reciprocal crosses produce normal daughters. Furthermore, mutations occur within races that give intersexual daughters. However, it must be admitted that at present there is partial selection against inter-racial crossing which possibly can allow the various races to accumulate/-
accumulate greater differences that may lead to complete inter-racial sterility.

Another classical investigation into subspecific variability was executed by Sumner (1932). He worked with the American deer mouse of the genus Peromyscus, and the work has been continued by subsequent workers in the United States. The range of the genus includes most of the North American continent. In particular he investigated the sub-specific variability of the species of Peromyscus maniculatus whose range covers most of the North American continent and has 35 sub-species, some of which have discontinuous or checker board distribution. The characters used in the identification of these sub-species include linear measurements of the body parts and the colour of the pelts and the area of the coloured parts. He found that some sub-species differ so much that there is no over-lapping, while others differ in a few characters. In these cases the differences between characters are compared. Furthermore, within sub-species much local differentiation is found. All the sub-species of a species were infertile and the characters investigated appeared to be dependent on a large number of genes for their inheritance.
He found several examples of clines or character-gradients. Some of these concern body measurements and others concern coat colour. In one case coat colour was found to correspond closely with soil colour and later it was shown to serve as a protective measure (Dice 1947).

Dice (1940 and other papers) and Blair have continued the work with Peromyscus and have paid attention to the problem of speciation within this genus. Dice has found that all the subspecies of any species are inter-fertile in the laboratory, but that they frequently do not interbreed under natural conditions. The the Glacier National Park in Montana, a forest-inhabiting subspecies P. maniculatus artemisae meets a grassland race P. m. osgoodi and they do not interbreed. He maintains that that is partly due to habitat differences but in some places they share the same habitat and here he maintains they are kept discrete by differences in mating behaviour. He concludes that this type of barrier (sexual isolation) is one of the most important in forming new species in the genus Peromyscus. He also emphasises the fact that any population, provided it is sufficiently isolated, can be transformed into a/-
a new species. A necessary proviso to this observation, however, is that the population size must not be too small.

The examples quoted above have dealt with species that display external variability, but even in species whose external morphology is relatively uniform, geographic variability has been found. An example of this type is offered by *Drosophila pseudoobscura*. Dobzhansky and Sturtevant (1938) reported 12 different kinds of gene arrangements or pattern of banding in the third chromosome. Its sibling species *D. persimilis* which was formerly called *D. pseudoobscura* Race B and which is very similar morphologically was found to have six different kinds of gene arrangements in its third chromosome, although it was not investigated so thoroughly. In the *D. pseudoobscura* data, each gene arrangement was found to occur in a definite geographical area, but very often the populations are polymorphic for several of these gene arrangements. None was found to occur throughout the species range. Dobzhansky investigated the phenomenon more fully and later (1947) reviewed the data. He found that the population of any locality could be described in terms of the relative frequencies of different/-
different gene arrangements.

On Mount San Jacinto he examined three gene arrangements in the population. One of these remained constant at all altitudes, but the relative frequencies of the other two changed with altitude. Furthermore, over a long period he found that the relative frequencies of the three gene arrangements could change from month to month and they displayed a cyclic regularity at lower altitudes. The changes require high selective pressure to accomplish such drastic and relatively sudden changes in the composition of a population, and therefore to show that changes in the relative frequencies of the various gene arrangements can be affected by Natural Selection, Dobzhansky set up populations in special cages. These populations contained the three different gene arrangements at different relative frequencies. The cages were kept at different temperatures and under different lighting conditions. It was found that the relative frequencies changed at the higher temperatures until equilibrium was reached, showing that the heterozygote was the fittest under these conditions. These experiments do show that the different gene arrangements have definite selective values under the laboratory conditions and/-
and they do substantiate, to a certain extent, the suggestion that the seasonal changes in the relative frequencies of the different gene arrangements are adaptive responses in the population. However, they do not allow any estimation of the exact nature of the adaptation of the various gene arrangements.

Analogous fluctuations concerning morphological characters were found by Stalker and Carson (1947) in *Drosophila robusta* (Sturtevant). This species was chosen because it inhabits woods and is not affected much by man. Its distribution ranges from eastern north America to the Gulf of Mexico and north to Canada and as far west as Nebraska. The authors collected 45 strains from 22 widely separated localities, each strain being derived from a single female caught in the wild. The flies were reared under conditions that were as uniform as possible. No differences were found in the pre-imaginal characters examined, but differences in adult body measurements were found. These characters were wing length, wing width, greatest width of head, length of thorax and length of femur. It was found that individuals from colder climated are characterized by longer wings, narrower heads/-
heads, shorter thoraces and longer femora than those of warm climates. However, from the data given it cannot be said whether these differences are adaptations to climatic differences or to habitats factors that are correlated with climate.

In a further investigation Stalker and Carson (1949) found that there was a seasonal variation in the morphology of D. robusta. The material was collected from a deciduous wood in Missouri at different periods during 1946. The F2 flies were examined after being reared under apparently standard nutritional and temperature conditions, and it was found that the morphology of the flies changed towards a "southern" morphology during the warm part of the year. Since F2 flies were used the change must have a genetic basis. It was also found that flies from widely different geographic areas when reared under low temperature conditions had a significantly more "northern" phenotype than flies reared at higher temperatures; thus indicating that the genotype and the environment both act in the same direction in this particular case. The authors assumed that these changes in this wood were due to Natural Selection rather than genetic drift, but the proof is not rigorous.
The geographic distribution of the alleles at a single locus in man have been described by Boyd (1939). These genes determine the human blood group, A, B, AB and O, and consist of several alleles. At present they appear to have no selective value, but their relative frequencies vary geographically. The gene A has a high frequency amongst the aboriginal peoples of Northern America and South Australia and a miderately high frequency amongst the peoples of Europe. The gene A\(^B\) is generally missing in North America and has a low frequency in Europe, but reaches its highest frequency in Asia. Boyd (1950) tentatively uses the data on the distribution of these alleles to show the relationships between ethnic groups, and cites work in which this has been done. This method of assessing ethnic relationships, however, has several serious objections; if these alleles once possessed a fairly high selective value then their distribution would not necessarily reflect any relationships between human races; also if human populations were once small and semi-isolated then genetic drift might have been important in governing their distribution. However, when the data on their distribution are used with other anthropological/
anthropological methods as has been done by Mourant and Watkin (1952) the evidence becomes more plausible. These workers used blood group data together with anthropometry, philology, phonetics, ancient records and the similarity between domestic animals to show the relationship between the people of the western fringe of Britain and the Berbers and other people of the Mediterranean and Middle East.

Discussion of the Literature

The literature that has been reviewed in this section of the introduction is not meant to be exhaustive on the subject of geographical variability, but is meant rather to show what may be gained from a study of this subject and to emphasise its importance in studying the evolutionary dynamics of a species. In some cases possible examples of incipient speciation have been found. In others the differences between races have been of a smaller order, but they remain important in helping us to understand the evolutionary processes. In some species the variability appears to be largely morphological, although the physiological differences may be masked; in others the differences/-
differences appear to be largely physiological. From the Drosophila work it is apparent that even outwardly uniform species have much geographic variability, and the selective forces involved are large and sometimes reversible in direction. From the data on human blood-groups it is learnt that knowledge of the spatial distribution of genes may be employed usefully in the study of the evolutionary history of a species.

A section of this thesis therefore is devoted to the study of the variability between three populations of P. scaber from different parts of the British Isles. One population is derived from Southern England, the second from Southern Scotland and the third from the Shetland Islands. These populations have been kept in the laboratory for 2 years under conditions as uniform as possible. They have been compared for differences in morphology, colouration and reproduction. The data thus obtained are discussed to learn something of the differences in Natural Selection in the three areas, and to ascertain how much divergence has been effected between the populations. Finally in the general discussion this genetic divergence is related to the number of generations that the Shetland population has been separated.
The Comparison of Three Widely Separated Populations

Introduction

Much of the work on geographic variability has been done with birds and since they are very mobile animals, the areas involved in such studies generally are very large. In a less mobile species such as _P. scaber_ one might expect a comparable amount of variability in a very much smaller area. In this experiment three colonies of _P. scaber_ from different parts of the British Isles were sampled. They were from Sittingbourne in Kent, Dreva in Peeblesshire, and Unst, the northernmost island of the Shetland Archipelago. These localities are separated each by approximately 5° of latitude, but lie approximately on the same line of longitude. They differ in climate. Spring comes earlier and summer lasts longer in the south and higher temperatures are experienced there. The Shetlands do not have as great a difference between the mean maximum and mean minimum temperatures as the British Mainland. Other climatic differences include differences in the length of day, amount of wind and the relative humidity. These climatic differences/-
differences between the Mainland and the Shetlands have obvious effects on the vegetation and in the Shetlands no trees are found. This affects _P. scaber_ directly, for in the Southern localities the loose bark of trees forms a common habitat and it is possible that the greater variety of habitats available to the Southern populations might lead to greater genetic variability in those populations. To what extent the differences in the macro-climate are masked by the micro-climate of the habitat is unknown, and the indirect effects of these differences can only be guessed. A final consideration pertinent to the divergence of these populations is the isolation of the Shetland populations, for this factor, in itself, would lead one to expect differences in characters that were not under appreciable selection pressure. The two Southern localities also differ in macro-climate. No exact figures are available from Dreva, but the mean winter temperatures at Kelso and West Linton, which are nearby, are lower than those at Tunbridge Wells, the meteorological station near Sittingbourne. Also the advent of spring is somewhat later than in the south of England and the warm weather does not last as long.

These comparisons of the differences in the macro-climate of the three localities do not offer/
offer any suggestions as to which characters are likely to differ between populations, for the micro-climate of the habitat may be fairly uniform in the three localities. Therefore the comparison must be as wide as possible. Morphological and physiological characters must both be considered. Edney (1951) has demonstrated that the water-loss in the Isopoda is related to the temperature and relative humidity of the environment and therefore it is possible the populations might differ in those characters concerned with water conservation. Body size and surface area are two such characters and they were investigated in this experiment. Body colour might also have some physiological importance either per se or through the pleiotropic action of the genes determining it. However, the distribution of colour phenotypes in the woodland populations described in a previous section suggest that body colour might be one of those characters on which genetic drift might operate. It was also investigated in this experiment. Other characters that were considered were concerned with reproduction. The age of sexual maturity, the number of broods per season and the size of broods were all examined.
All these characters were investigated firstly in samples of animals collected in the wild and then again in their offspring which had been chosen at random and reared under uniform laboratory conditions so that the genetic differences could be distinguished. Finally some interracial crosses were set up to test for sexual isolation between races.

Material and Methods

The Unst collection consisted of 47 animals while the Dreva and Kent populations contained 46 and 40 animals respectively. The Southern populations were derived from single colonies while the Unst population was collected from three stone walls. No significant differences were found between the Unst animals and so they were treated as a single collection. The collections were made in the late summer and early autumn of 1950. The animals were sexed, classified for colour and measured. These measurements included body length, which, as previously defined, was the distance between the tip of the frontal lobe and the end of the telson. The lengths of the first and fourth thoracic segments were also measured.
for these segments as is explained later give a good indication of the shape of the animal and the area of the dorsal surface. Twenty-two Unst females, 22 Dreva females and 17 Kent females were retained for breeding. They were kept individually in 1 lb jam jars in an incubator in which the temperature varied between 68°-70°F. They were maintained on the standard medium in this incubator until July 1951 when the F₁ animals became too numerous for both generations to be retained in it.

When a female formed a brood pouch she was transferred to a large petri dish containing slices of potato that formed a refuge for the young. As soon as the brood had been liberated the female was transferred and after 48 hours the brood was counted and transferred to 1 lb jam jar. The young animals were put into a jar which there was a standard amount of potato, bark and leaves. This method of rearing the young allowed some difference in the early environment. Some broods consisted of less than 10 animals and the majority of broods were not multiples of 10. Therefore a number of jars contained less than 10 animals, but as the number of survivors per jar varied considerably, the original number of young per jar became/
became quite valueless. At the age of 60 days a number of randomly chosen animals were transferred to individual jars and measured. They were again measured at 330 days and also classified for colour and later mated.

**Results**

In this section each character is dealt with separately; the animals collected in the wild are compared and the $F_1$ generation is compared for the same character. Finally the genetic differences are discussed in order to ascertain what possible adaptive values the various characters may have. They are dealt with in the following order:

a) **Body measurements**

b) Body colour and pattern
c) Reproductive behaviour
d) Interracial crosses

a) **Body measurements**

The animals were measured for body length and the length of the first and fourth thoracic segments. Body length is a good criterion/"
criterion of general size and the other measurements may show any gross differences in shape that may exist. The fourth thoracic segment is the widest part of the animal. In local populations, some animals appear to be more square and less oval than others; this is due to the first thoracic segment being longer than usual. Therefore these two thoracic measurements should be good indicators of differences in body shape.

Table 16/
<table>
<thead>
<tr>
<th>Measurement</th>
<th>UNST</th>
<th>DREVA</th>
<th>KENT</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>P100</td>
<td>F100</td>
<td>F1♂♂</td>
</tr>
<tr>
<td>Mean Length of body</td>
<td>9.37 ± 0.24</td>
<td>9.87 ± 0.24</td>
<td>9.09 ± 0.16</td>
</tr>
<tr>
<td>Mean Length of 1st thoracic segment</td>
<td>3.67 ± 0.10</td>
<td>3.83 ± 0.10</td>
<td>3.39 ± 0.05</td>
</tr>
<tr>
<td>Mean Length of 4th thoracic segment</td>
<td>4.36 ± 0.13</td>
<td>4.41 ± 0.12</td>
<td>3.86 ± 0.02</td>
</tr>
<tr>
<td>Size of Sample</td>
<td>22</td>
<td>13</td>
<td>20</td>
</tr>
</tbody>
</table>

Table 16 - A comparison of the body lengths and lengths of two thoracic segments in adult females collected in the wild (P1♂♂) and their progeny that had been reared in the laboratory. The F1 were measured at a uniform age.
The body length measurements in Table 16 show that the Unat females are shorter than the others in both generations, while the southern females do not differ significantly from one another. The Dreva $F_1$ male sample is very small and therefore is not very reliable, but the Unat males are shorter than the Kent males. No $P_1$ males were included for the collections had been primarily concerned with obtaining females and the males collected were probably not a good random sample. The measurements of the first and fourth thoracic segments give very similar results to those obtained from the body length measurements. However, as Huxley (1932) has pointed out a difference in the linear measurements of body parts in different populations may be due to differences in absolute size. A straight comparison such as this is valueless therefore, unless the animals have the same absolute size, and the best method is to compare the relative growth rates of these body parts in each population. If the relative growth rate of the body part is identical in each population, then the differences in these body measurements are merely secondary effects of the differences in absolute size. This type of comparison has been used/-
used by several workers investigating toxonomic problems (Huxley 1932, Hersh 1934, Reeve 1940).

The $F_1$ animals from the three populations did not vary at all in their body measurements at the age of sixty days. (Vide Table 17). This indicates that the relative growth in early ontogeny is identical in the three populations and that any possible differences in relative growth must occur in the adult stage.

Table 17/-
<table>
<thead>
<tr>
<th>POPULATION</th>
<th>MEASUREMENTS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Body Length</td>
</tr>
<tr>
<td></td>
<td>Mean Length</td>
</tr>
<tr>
<td>UNST</td>
<td>4.34 ± 0.1</td>
</tr>
<tr>
<td>DREVA</td>
<td>4.51 ± 0.1</td>
</tr>
<tr>
<td>KENT</td>
<td>4.42 ± 0.18</td>
</tr>
</tbody>
</table>

Table 17 - The body measurements of F<sub>1</sub> animals at the age of 60 days. The two sexes are treated together.
The original formula employed by Huxley in problems of relative growth was \( y = bx^k \), but it has been much criticized (Reeve and Huxley 1945, Richards and Kavanagh 1945). No satisfactory theoretical basis for the formula exists; the visual method of fitting a line is very inaccurate and the different parts of an organ may not grow uniformly. Kermack and Haldane (1950) recommend the use of another formula. This formula employs the reduced major axis of the logarithms of the data, and the only stipulation is that the logarithms should be distributed normally. It obviates the visual fitting of a line to obtain the value of \( a \) (the present designation of \( k \)), and also dispenses with the use of a regression coefficient which when used necessitates the arbitrary choice of a dependent and independent character. It was impossible to test the distribution of the logarithms, for the data were not sufficient. However, to ensure that \( a \) was fairly constant in value in both populations, the logarithms of the value of \( x \) and \( y \) were plotted for two animals, one from each population. The points in both cases appeared to lie in a straight line, so it was assumed that \( a \) is constant during adult growth.
The formula recommended by Kermack and Haldane is given below:

\[
a = \sqrt{\frac{\log (1+V_y^2)}{\log (1+V_x^2)}} \left[ 1 - \sqrt{\frac{1 - r^2}{n}} \right]
\]

where and are the two measurements and

\[
r = p = \frac{\log (1+p^iV_xV_y)}{\left[ \log (1+V_x^2) \log (1+V_y^2) \right]^{\frac{1}{2}}}
\]

where \( l^1 \) if the correlation coefficient between the two measurements.

Table 18/
Table 18 - The relative growth coefficient values of the 1st and 4th thoracic segments in the two generations.
Despite the fact that both samples are liable to errors (Richards and Kavanagh loc. cit.), there is remarkably close agreement between the two generations and there is no difference between the values of "a" for the first thoracic segment in either population sample. (Vide Table 18). Furthermore, although the $F_1$ values of "a" for the fourth thoracic segment differ, in the $P_1$ data these two values are in agreement. It seems therefore that the differences in the measurements of the first and fourth thoracic segments are merely secondary effects due to differences in general size.

b) **Body colour and pattern**

Body colour might be expected to be either physiologically or ecologically adaptive, for it has been shown to be of adaptive value in other invertebrates, cf Dobzhansky (1941 p.195), Ford (1945a). Differences in the relative frequencies of the colour classes in the colonies may be expected therefore. Such differences however, do not prove that body colour is an adaptive trait, for genetic drift cannot be dismissed as a causation without further proof.
Using the usual classification the populations are found to be very different. A summary of the frequencies of the different phenotypic classes is given below.

<table>
<thead>
<tr>
<th>Colour Class</th>
<th>Unst</th>
<th>Derva</th>
<th>Kent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brown &amp; Orange</td>
<td>130</td>
<td>22</td>
<td>23</td>
</tr>
<tr>
<td>Brown</td>
<td>34</td>
<td>14</td>
<td>10</td>
</tr>
<tr>
<td>Black</td>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Red &amp; Black</td>
<td>0</td>
<td>9</td>
<td>2</td>
</tr>
<tr>
<td>Yellow &amp; Brown &amp; sometimes Red</td>
<td>12</td>
<td>25</td>
<td>5</td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td>180</td>
<td>70</td>
<td>40</td>
</tr>
</tbody>
</table>

Table 19 - A summary of the colour classification of the 3 populations collected in the wild.

A striking difference is the complete absence of red animals in the Unst population, for the 12 animals which were predominantly yellow carried no red. Also black animals were absent from the southern populations. In doing a statistical test the black and red and black classes are omitted for not only are the expected numbers very small and liable to invalidate the test, but the differences are so obvious as not to warrant statistical/
statistical treatment. A comparison of the remaining classes is shown below.

<table>
<thead>
<tr>
<th>Place</th>
<th>D4 Brown &amp; Orange</th>
<th>D2 Brown</th>
<th>Yellow &amp; Brown &amp; Red</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unst</td>
<td>130 (112.0)</td>
<td>34 (37.1)</td>
<td>12 (26.6)</td>
<td>176</td>
</tr>
<tr>
<td>Drev</td>
<td>22 (36.8)</td>
<td>14 (12.8)</td>
<td>25 (9.3)</td>
<td>61</td>
</tr>
<tr>
<td>Kent</td>
<td>23 (24.1)</td>
<td>10 (8.0)</td>
<td>5 (5.8)</td>
<td>38</td>
</tr>
<tr>
<td></td>
<td>175</td>
<td>58</td>
<td>42</td>
<td>275</td>
</tr>
</tbody>
</table>

\[ X^2 = 21.38 \quad \text{d.f.} = 4 \quad P < 0.01 \]

Table 20 - A contingency table comparing the relative frequencies of the different phenotypic colour classes in the 3 populations.

Although this contingency table shows that the populations differ significantly from one another, the classification employed does not show the subtle differences found. The D4 animals from Unst could generally be identified from the D4 animals of the other populations. Their brown colouring was very much darker than that of the others; the orange on the basal segments of the inferior/-
inferior antennae was very intense, whereas in the southern animals of this class it graded into red. Also the Unst population tended to be the most uniform and the Dreva population the most varied. The uniformity of the Unst animals and the distinctness of the brown and orange colouring was such that they could be classified as Unst animals on colour alone after some experience. Another point of interest about the Unst animals was that 11 of the 12 yellow animals came from a single colony so that that colour class is much rarer than one would suppose from an inspection of the contingency table. In the South it is a class that is predominantly female but three of the yellow Unst animals were males.

The $F_1$ animals were all classified for colour at the age of eleven months and the results are given below.

<table>
<thead>
<tr>
<th>Place</th>
<th>Colour Class</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(Brown)</td>
<td>(Brown &amp; Orange)</td>
</tr>
<tr>
<td>Unst</td>
<td>22</td>
<td>6</td>
</tr>
<tr>
<td>Dreva</td>
<td>12</td>
<td>1</td>
</tr>
<tr>
<td>Kent</td>
<td>28</td>
<td>12</td>
</tr>
</tbody>
</table>

Table 21 - A summary of the colour classification of the $F_1$ animals from the 3 populations.
These results show that the populations still vary very much from one another, but some of the classes are too small to be treated statistically. The southern populations remain more variable than the Unst population, and although the Unst population is still very uniform, its "type" has changed. In the $F_1$ 72% of the animals were $D_4$ but in the $F_1$ only 23% are $D_4$, the remainder being plain brown. Furthermore, the $F_1$ animals that are classified $D_4$ are indistinguishable from the $D_4$ animals of the other populations. They are no darker and their orange colouring grades into red, despite the fact that most of the breeding females of the Unst population were $D_4$. Therefore it seems likely that the distinctness of the Unst $D_4$ animals in the $F_1$ generation was enhanced by some environmental factor or factors. Nevertheless the change in the two generations might be due to errors in sampling.

Another difference between the populations was found during the classification of the $F_1$ animals. It concerned the basic pattern. This pattern consists of light patches on the dorsal thoracic surface at the junction of the pleura and terga. The size of these patches is variable; sometimes/-
sometimes they extend across the width of the thoracic segment; in other cases they are barely discernible. They were found to be very much smaller in the Unst animals as is shown below. In this classification those patches that covered less than a quarter of the width of the thoracic segment were classified as small.

**PERCENTAGE SMALL PATCHES**

<table>
<thead>
<tr>
<th>Generation</th>
<th>Unst</th>
<th>Dreva</th>
<th>Kent</th>
</tr>
</thead>
<tbody>
<tr>
<td>P₁</td>
<td>100%</td>
<td>31.6%</td>
<td>4%</td>
</tr>
<tr>
<td>F₁</td>
<td>85.7%</td>
<td>0</td>
<td>7.5%</td>
</tr>
</tbody>
</table>

Table 22 - The percentage of animals with small patches in the 3 populations. Data from both generations.

The findings are consistent in both generations of the Unst and Kent animals. The discrepancy in the Dreva animals may be explained by the fact that the F₁ animals were all derived from females with large patches.

c) Reproductive behaviour

Animal populations from localities with different/−
different macro-climatic conditions may differ in their reproductive behaviour. Adaptations to duration of the warm weather and to the availability of food supplies may produce different time of breeding. Longer growing periods may produce different rate of development. In *Lymantria dispar* differences in the duration of larval development were found by Goldschmidt (1934) to be correlated with the climatic differences of the localities where the races were collected. In order to investigate the differences in reproductive behaviour in the three populations, 17 females from the Kent colony and 22 from each of the other two populations were set up. Together with their offspring these females provided the material for the observations on the reproductive behaviour of the 3 populations.

1. **Differences in fertility and sexual maturity**

Considerable differences in the fertility of females from the three populations were found and persisted in the F₁. A number of the F₁ females were found to be virgins and only produced broods after males from their respective populations had been/-
been introduced. These females are included in the data below which shows that the percentage of fertile females was much higher in the Kent population.

**PERCENTAGE OF FERTILE FEMALES**

<table>
<thead>
<tr>
<th>Population</th>
<th>Generation</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$P_1$</td>
<td>$F_1$</td>
<td></td>
</tr>
<tr>
<td>Unet</td>
<td>41%</td>
<td>38.5%</td>
<td></td>
</tr>
<tr>
<td>Dreva</td>
<td>33%</td>
<td>50%</td>
<td></td>
</tr>
<tr>
<td>Kent</td>
<td>88%</td>
<td>100%</td>
<td></td>
</tr>
</tbody>
</table>

Table 23 - The percentage of fertile females in the 3 populations. Data from both generations.

The apparent discrepancy in the Dreva data may be due to the $F_1$ sample consisting of only 10 females whereas the $P_1$ sample contained 22 females. The comparatively low percentage of fertile females in the Northern populations may be explained in the following manner. The collections were made at the end of the summer and early autumn. In an earlier section of this work it was shown that in the Edinburgh area this is a period of maximum mortality amongst the breeding females. Therefore, a collection of females at this/
this period would include a number of immature females. Indeed this was found to be the case in all three populations, for a number of females proved to be virgins. Six females of each population that had not bred by May 1951, after seven months in the incubator, were mated to males from their respective populations. The 6 Kent females bred within 5-6 weeks after the males were introduced. Four of the Drea females bred but only in September - after a year in the incubator. None of the Unat females bred. These events may be explained by considering the Kent females to be quicker maturing than the others. This consideration is supported by the F₁ data. The majority of the F₁ females were mated in April 1952 when their ages ranged from 13-14 months. All the Kent females, which were the youngest, had broods regardless of the origin of the male to whom they were mated, but in the other two populations there was a certain amount of cannibalism. This does not usually occur in the breeding season if the animals are sexually mature. Thus the F₁ Kent females appear to be quicker maturing as a group than the northern females. However, it is possible that the lower fertility of the northern females was due to the lack/-
lack of some unknown but necessary environmental factor.

No difference in the age of sexual maturity was apparent in the F_1 males. Twenty F_1 Kent females were mated to 9 Unst, 2 Dreva and 3 Kent males, but there was no difference in the times that these females had their broods. It would appear therefore that the northern males are quicker maturing than the females.

2. Size of broods and numbers of broods

In estimating the size of a brood the usual precautions were taken to protect the young from being eaten by the female and counting was done as soon as the young could be handled safely, about 24 hours after liberation from the brood pouch. The results for the two generations of the Unst and Kent animals are given below.

<table>
<thead>
<tr>
<th>Generation</th>
<th>Unst</th>
<th>Dreva</th>
<th>Kent</th>
</tr>
</thead>
<tbody>
<tr>
<td>F_1</td>
<td>11.6 ± 2.2</td>
<td>-</td>
<td>38.2 ± 2.2</td>
</tr>
<tr>
<td>F_1</td>
<td>8.3 ± 2.5</td>
<td>36.3 ± 10.6</td>
<td>34.3 ± 2.6 (1st broods)</td>
</tr>
</tbody>
</table>

Table 24 - The average brood size in both generations of animals from the 3 populations. The Kent data are based on the first broods of females. For information on P_1 Dreva females see text.
The $P_1$ Dreva broods are not included as some of the $P_1$ females had their broods when they were not under daily observation and so the numbers recorded were probably smaller than the actual number. However, including these doubtful figures, the average brood size in the Dreva $P_1$ generation was $23.3 \pm 3.4$ but it is probably very similar to the $F_1$ average. Both southern populations have larger broods than the Unst females.

Inseparable from the factor of brood size is the number of broods per season. It was stated earlier that if females were kept at a high temperature, they produced more broods than at room temperature. The $P_1$ females were kept in the incubator from October 1950 until June 1951, and the temperature in this incubator was less than that at which local Edinburgh females increased their fertility. The $P_1$ females were then kept under observation at room temperature until September 1951, and any broods they produced in that period were recorded. The number of broods produced in that period is not necessarily a reflection of what occurs in the wild but it is a comparative measure of the fertility of the females. It will be seen in Table 25 that the Kent $P_1$ females produced more broods in a given time than the other/-
other $F_1$ females and similarly in the $F_1$. These results are interpreted as meaning that the Kent females have a quicker rate of reproduction than the others, and are more sensitive to temperature.

<table>
<thead>
<tr>
<th></th>
<th>Parental Generation</th>
<th>$F_1$ Generation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Unst</td>
<td>Dreva</td>
</tr>
<tr>
<td>No. of ♀♀ producing 1 brood</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>No. of ♀♀ producing 2 broods</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>No. of ♀♀ producing 3 broods</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 25 - The number of broods produced by females from the 3 populations under standardized conditions.

The male does not seem to have much influence on the number of broods produced, or the size of the brood produced. The 17 $F_1$ Kent females were mated to males of all races including 7 Unst males. Similarly the $F_1$ Unst and Dreva females that had broods had been mated to males of the different populations, endorsing the fact that the males did not have any discernible effect on brood size.

The/-
The second brood in the Kent population averaged 27.5 ± 2.6 and was no different from the first brood average of 34.3 ± 2.6.

The higher fertility of the Kent females in this experiment does not appear to be solely a consequence of their earlier maturity, for the P₁ and F₁ Unst females that bred were very similar in the sizes of their broods. Also a significantly larger number of P₁ Kent females had more than one brood compared to the other P₁ females. The general agreement between the 2 generations indicate that the Kent females are more fertile over a given period of time, in addition to being quicker maturing under the conditions of the experiment. No differences were found in the length of the period of incubation in the three F₁ samples.

d) **Inter-racial crosses**

Some successful matings were obtained in all the possible inter-population crosses made in this experiment. When the matings were set up it was considered that sexual isolation could be effected by any of the following reasons.

1) **The inability of the animal to copulate.**

When coitus was observed in this species it/
it appeared to take place between animals of similar size, and it was considered that the size differences between the Unst and the other populations might prevent copulation. In addition to this possibility, mating might not occur for other anatomical or psychological reasons. However, broods were produced by large Kent females mated to small Unst males.

2) The inviability of the hybrids. This possible type of isolation was also ruled out.

3) The sterility of the hybrids. Unfortunately the hybrids were still very young at the close of this experiment and this factor could not be tested.

Partial sterility might be said to occur if the normal sex determining mechanism was affected so that only unisexual broods were obtained from certain crosses. This seemed possible, for in this species some genetic factors are known to alter the normal sex ratios (de Lattin 1949, 1951). Unfortunately at the close of this experiment only in the crosses in which the Kent animal was the female were the animals old enough to be sexed. The results are given below and show normal sex ratios.

Cross (Parents)/-
Cross (Parents)          Offspring

<table>
<thead>
<tr>
<th></th>
<th>♂♂</th>
<th>♀♀</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unst ♂ x Kent ♀</td>
<td>10 : 13</td>
<td></td>
</tr>
<tr>
<td>Dreva ♂ x Kent ♀</td>
<td>4 : 14</td>
<td></td>
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<tr>
<td>Kent ♂ x Dent ♀</td>
<td>14 : 13</td>
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**Discussion**

Before discussing the significance of the population differences, the main ones are summarized below.

1) The Dreva and Kent populations were found to be larger in body size than the Unst animals.

2) The Kent females appeared to be quicker maturing and relatively more fertile than the northern populations. The Dreva females had significantly larger broods than the Unst females.

3) The male did not appear to have any discernible effect on brood size or the number of broods. The northern males mated more easily than the northern females. This is interpreted as showing that they mature earlier. However, the deficiency of some necessary environmental factor may have caused the northern females to be tardy in reproduction, but it seems unlikely.

4) /-
4) The population differed in the relative frequencies of certain colour classes, and some colour classes were missing from some populations. The Shetland population was the most uniform but the "type" colour in the P. Unst population appears to be influenced by the environment to a certain extent. A sample of P. scaber from the Bass Rock in the Firth of Forth has some animals resembling the Shetland animals suggesting that the typical Shetland colouration is influenced by some factor common to coastal localities.

Geographic size differences were found in Lymantria dispar but no adaptive significance could be found (Goldschmidt 1934, 1945). A study of the Carabid beetle Dicaelus purpuratus in the United States showed that it decreased in size from South to North (Park 1949). The author suggests that this a non-genetic trait due amongst other things to the difference in night-length in the two regions. The animal is nocturnal, and the northern populations have less time to feed in the summer than the Southern populations, if feeding occurs throughout the night. If body size in P. scaber is an adaptation it may be concerned with some nutritional factor, but this cannot be proved here.
In a previous section of this work it was shown that in adult females of local origin, kept out of doors, brood size was highly correlated with body length. The larger the body length of the female, the larger her brood. The same relationship has been found in this experiment. The larger the female the larger the brood. The Unst females being the smallest females produce the smallest broods. The Dreva and Kent females did not differ in body length nor in brood size, although the size of the Dreva sample was very small.

It is possible in these animals for large body size to be compatible with small brood size, and therefore it is theoretically possible that selection for small broods would not affect body size. Conversely it seems very unlikely that selection for small body size could be compatible with large brood size, unless the size of the egg decreased and with it the period of incubation. Therefore it is possible that selection in these populations has been concerned primarily with body size, and the difference in brood size have been secondary effects. Another possibility is that some factor, say availability of food, has led to the selection on both characters simultaneously.
in the same direction. This suggestion seems more feasible for the difference in the number of broods per female over a given period would indicate that there has been selection for differential fertility.

The number of broods produced in a given period further emphasised the differences in fertility. The Kent females produced more broods per female than the northern females in a given period. This finding is supported from other sources. Local females kept at room temperature only have one brood a year here in Southern Scotland, whereas animals from Southern England kept at room temperature there produced 2 broods in a season (Heeley loc. cit.). This raises an interesting point: does the greater fertility of the southern animals mean that there is greater interspecific competition there, and for the population to remain relatively stable numerically, more offspring have to be produced than in the north? Or is the greater fertility merely a reflection of the longer breeding season, and is the main limit to the expansion, intra-specific competition? A similar state of affairs occurs in the blackbird (Lack 1949). In Holland the average clutch size from 981 samples collected from March to July is 4.3/
4.3 and the average clutch size in Britain over the same period is 3.9. Lack offers no suggestions to account for this difference.

The relative colour uniformity of the Shetland population may be due to genetic drift or to selection. From the available data the exact agency cannot be named, but the fact that the Bass Rock and Shetland population, including samples from three other islands of the archipelago, resembled one another may indicate that selection is responsible.

From this study it appears that three characters are under differential selective forces in this part of the species range - size, colour and fertility. Two of these, size and colour, are common taxonomic criteria and together with the differences in reproductive behaviour ensure that the Shetland population of *P. scaber* has reached sub-specific status. Nevertheless from the available data it is very difficult to see exactly how speciation will be accomplished, if ever.
 Adult females were collected from Sittingbourne in Kent, Dreva in Peeblesshire and Unst in the Shetland Islands. These localities differ climatically.

These females were kept in the laboratory under standard conditions and broods were raised from them. The $F_1$ animals were kept under standard conditions and were measured, and classified at a uniform age.

In both generations the Kent and Dreva animals were found to be larger than the Unst animals. The Kent females appeared to be quicker maturing and relatively more fertile than the Northern populations. The Dreva females had significantly larger broods than the Unst females. It is suggested that body size and fertility have been under selection pressure acting in the same direction.

The population differed in the relative frequencies of certain colour classes. The Shetland population is the most uniform and it is suggested that the typical colouration of the Shetland animals is influenced by some factors common to coastal localities.

Since/-
Since the Shetland population differs from the Mainland populations in age, colour and reproductive pattern, it is suggested that it has achieved sub-specific status.
The evolutionary progress of a species depends upon its genetic variability and on the selective forces operating on it, while the interaction of these factors appears to be governed by the population structure of the species. This study of the genetics and population dynamics of *P. scaber* is concerned with its evolution, and has been presented in two parts. Firstly, experiments investigating the population structure of local natural populations were described. Unfortunately breeding experiments were unable to disclose any suitable genes for the study of gene frequencies in conjunction with the ecological studies on population size. Secondly, the geographic variability of the species over a part of its range was investigated. This study was undertaken to see whether the species possessed much genetic variability and how the species was meeting the selective forces operating in the different parts of its range. These individual experiments have already been discussed and in this closing section it is intended to use the data to conjecture some of the evolutionary trends in this species. The speculative nature of this discussion however cannot be overstressed.

In the experiment dealing with population/
population structure it was found that under natural conditions in southern Scotland the generation interval is at least 2 years. Work in the laboratory showed that this character is greatly modified by temperature and also there is some evidence that there are genetic differences for this character in populations from different parts of the British Isles. There is no doubt that in Scotland the long generation interval is due, in part, to the short growing season and to low temperatures, nevertheless the fact remains: for an organism of this size, the generation interval is very long. What is the evolutionary significance of a long generation interval? Simpson (1944 p62) was unable to find any general correlation between generation interval and speed of evolution. However, in this case a possible answer may be provided by a brief survey of the evolution of the Oniscidae. Webb and Sillem (loc. cit.) state that the remains of Isopoda occur in the old Red Sandstone (Devonian) of Herefordshire. The genera Armadillidium, Oniscus and Porcellio are found in tertiary deposits (Nicholson and Lydecker 1889). Vandel (1945) estimates that the Oniscidae now consists of 500-600 species. Therefore/
Therefore evolution in this group has been relatively slow and has resulted in a large number of small highly adapted groups. de Beer (1930) visualizes that such a group could have arisen by the process in which novel characters appeared late in ontogeny. Heeley (loc. cit.) found that specific characters were the last to appear in ontogeny. This coincides with de Beer's speculations on the mode of evolution of such a group. Therefore it is possible that evolution in the Oniscidae has proceeded by the appearance of novel characters late in ontogeny. Such a type of evolution could lead to selection for a longer period of development, and thus to a longer generation interval.

The mortality rates in *P. scaber* do not appear to be very different from those recorded in other species in which there is no post natal care of the young. One exception however, warrants repetition. It was found during the course of this work that the body length of a female increases after sexual maturity. Body length and brood size are highly correlated ($r = 0.889$). Therefore in general, the later broods of a female will be larger than her first brood, and since the majority of females in local populations are breeding for the/
the first time, later broods of a female will be larger than the average for the population. In short, older females tend to produce more offspring than younger females in this area. This may mean that there is selection for longevity in this area. This pattern of reproduction is very efficient for exposing to Natural Selection, those genes whose action is not expressed until the organism is relatively old.

A knowledge of the approximate generation interval and the amount of genetic divergence between the mainland and Shetland population allows some interesting speculations about the rate of divergence. The Shetlands were covered by the Scandinavian Ice Sheet which is estimated to have retreated from that latitude about 9000 years ago (Wright, W.B. 1937). It is also estimated that in the Pre-Boreal period about 10,000 years ago Britain became capable of supporting a complex vegetation and that during the Boreal Period 7-9000 years ago the climate was warmer than it is today. Pine and Beech were well established in Northern Scotland (Tansley 1949). Therefore it is probable that the Shetlands would have been able to support Terrestrial Isopoda about 7-8000 years ago. This is the maximum period that the Shetland population of P. scaber could have/
have been separated from the mainland populations, and would mean 3-4000 generations. During this period changes have been what Goldschmidt would describe as micro-evolutionary. Changes in size and reproductive pattern have occurred, thus allowing the Shetland populations the status of a subspecies. Has this been a slow rate of divergence? The Shetland wren has been accorded sub-specific rank and presumably could have been separated from the mainland population as long as the Isopoda, but it is doubtful whether such a comparison is really valid. Natural Selection in Shetland might prove to be very similar to that encountered on the mainland for one species, while in the case of the other special, it may be very different in the two areas. The degree of isolation might also be very different for the two species. Nevertheless, the rate of divergence of P. scaber has been as great as that of the Shetland wren. The maximum possible ages of some avian sub-species in Egypt have been estimated from a knowledge of the local geology (Moreau 1930). There are three races of the crested lark (Galerida cristata L.) in Egypt, differing from one another in colour. One race, which is much darker than the others, is confined to/-
to the lower Nile Valley with its very black soils. These soils are assumed to have become dark about eleven to twelve thousand years ago, thus placing a maximum age on this subspecies. A sandy coloured race inhabits the Sinai desert and southern Palestine. The soil in this area can only have reached its present colouration in the Post-Pluvial Period which is estimated as 5000 years. These examples assume that differentiation has taken place in situ and that the races did not emigrate into the areas in their present forms. Another example is provided by the graceful wren warbler (Prinia gracilis). A distinctive race of this bird inhabits Wadi Natrun which has been isolated by desert for about 4500 years thus placing a limit on the maximum age of this subspecies. An example of more rapid divergence is possible provided by the Faroe house mouse (Evans and Vevers 1938). It differs in colour, size and stoutness of hind feet. The authors assume that it could not have arrived in the Faroes before they were colonized by man about 1000 years ago. However, if this species has more than one generation per year, then the rate of divergence will have been no faster than that of P. scaber. In general these examples/
examples show that the divergence in P. acaster is of the same order as it is in some other polytypic species and that it possibly has been effected at the same rate.

The sexual aberrancy reported here shows how easily the sex determining mechanism of this species is disturbed. In this respect the observation agrees with the work of de Lattin which has been quoted several times. In fact, the sex determining mechanism of the whole group appears to be abnormal. In *Armadillidium vulgare* unisexual broods are an established feature of the reproductive pattern (Howard loc. cit.). Parthenogenetic species have been found in the related genus *Trichoniacua* (Vandel 1925). de Lattin considers the Isopoda investigated by him to be latent hermaphrodites. It is possible that bisexual reproduction is a relatively recent innovation into the order and thus it has not become perfected and as stable as it is in higher organisms. It is also equally feasible that in a group in which it has become stabilized, it can be relatively easily lost, and that this is what is happening to the Isopoda. If this is so, the evolutionary pattern of/-
of the group might resemble the patterns of some extinct invertebrates whose extinction was preceded by a spate of variability now seen in their geological records.

Finally the suitability of *P. scaber* as material for studies on evolution must be discussed. Ideally, for a species to be suitable it should be good material for cytogenetic and ecological study. From the first standpoint it should have a short generation interval, produce many young, require little laboratory space and a cheap food supply. It should have few diseases under laboratory conditions. It should be polymorphic or possess a number of mutant genes of good penetrance. It should possess a limited number of large chromosomes so that any cytological peculiarities may be detected. In most of these requirements *P. scaber* is poor when compared to a number of other invertebrates. It is true that its food requirements are cheap and that it requires relatively little space. Its polymorphism which was an initial attraction appears to be complex and a possible age effect may lead to pitfall. Genetic studies are hampered by the fact that females/-
females are able to store sperm, but its reproductive rate is the main difficulty. It has a deplorably long generation interval at room temperature, and the viability of the animals at higher temperatures is bad enough to offset any gain from the reduced generation interval. 18°C appears to be the best temperature but the generation interval remains in the region of 12 months. Furthermore at higher temperatures the cultures are susceptible to mould which means additional work. It may be that the Northern races are slower maturing and generally less viable than races from the European continent, for de Lattin has used _P. scaber_ for genetic studies. In _Lymantria dispar_ Goldschmidt (loc. cit.) found many races which were unsuitable for laboratory studies. Cytologically _P. scaber_ is bad material. Mr. W.R. Sobey made cytological preparations from male gonads and found the haploid number to be 28 but the chromosomes were too small for detailed cytological work. (Personal communication).

From the ecological viewpoint _P. scaber_ is better than a number of other invertebrates. It is very abundant and is easily caught. It is easily handled and marked. However, many of its habitats...
once disturbed have no attraction for it, and its habits are not easily observed in the wild. The fact that it cannot be attracted to traps also places a limitation on the type of work to be done with it. One of its greatest advantages for ecological work is the small area required for work. In general, though, the poor qualities of local races as cytogenetic material make them unsuitable material for comprehensive studies on evolution.
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ACKNOWLEDGEMENTS

I am indebted to the University of Edinburgh for a Post-graduate Studentship and to Professor C.H. Waddington, F.R.S. for facilities enjoyed in the Genetics Department.