

POPULATION VARIABILITY IN A DOMESTIC STORED PRODUCT PEST, THE PARTHENOGENETIC PSOCID *LIPOSCELIS BOSTRYCHOPHILA*: IMPLICATIONS FOR CONTROL

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Abstract—The small (1mm long), wingless, psocid, *Liposcelis bostrychophila* (Badonnel) (Psocoptera, Liposcelidae), is found throughout the world and is frequently a pest of farinaceous food stores. Since the early 1940's, when this insect was recorded for the first time in southern England, it has spread to virtually all parts of the UK where it is now a major cause of consumer complaints in some areas of the food industry.

L. bostrychophila is parthenogenetic and, for its size, relatively long lived. It displays considerable adaptability to deal with local or temporary situations. Adults have a wide temperature tolerance, a very catholic diet and an ability to go for long periods without food. In good conditions they maximise reproductive output whilst in poor conditions their egg output reduces or stops whilst their longevity increases. These two alternatives are readily switchable in fluctuating conditions. In addition they show some tolerance to pyrethroid insecticides.

Parthenogenesis is essentially a clonal mode of reproduction and yet there is a considerable degree of variability in the biologies of individuals of the same clonal line. Advantageous traits, resulting from random mutations, will be readily incorporated into the genotype of a parthenogenetic species and so spread rapidly, at least on a local scale. At the individual level allozyme variations can be seen within and between populations from different localities in the UK. These are being used to attempt to identify particular features of this liposcelid's biology.

The problems of controlling *L. bostrychophila* are discussed in the light of this population variation.

INTRODUCTION

The booklouse, *Liposcelis bostrychophila* (Badonnel, 1931) was discovered in the UK in the early 1940's (Broadhead and Hobby 1944) as a contaminant in insect cultures. It belongs to a little studied insect order, the Psocoptera, more commonly known as 'psocids'. For about 20 years following its original discovery in the UK this insect was primarily of taxonomic interest (Broadhead 1950, 1954) but the early 1960's saw the beginnings of an increase in psocid related complaints in a wide range of food and non-food products (Turner 1986, 1987). Today *Liposcelis bostrychophila* is the major cause of consumer complaints in flour products.

Originally from Africa, *Liposcelis bostrychophila* has become a pest species in temperate regions by developing a close association with man and his dwellings in the UK, Europe and elsewhere. In the UK, it lives solely within buildings and has not been recorded from natural outdoor situations.

Within the last ten years the growing numbers of psocid related complaints has prompted a variety of initiatives starting with the Society of Food Hygiene Technology (eg. Dodd, 1981) which explored, through its members, the scale of the problem. Research at King's College, London started in 1986 with funding from the Agriculture & Food Research Council and continues with support from the food industry.

Liposcelids are all wingless, more or less 1mm long and of varying shades of brown in colour. Their bodies are dorso-ventrally flattened and the hind femora are also flattened and look characteristically fat when viewed from above ('*Liposcelis*' means 'fat thighs'). This body form enables them to crawl into extremely narrow crevices and to enter most forms of unsealed or slightly damaged food packaging.

The importance of identification cannot be too strongly stressed. There are a number of psocopterans that are associated with man and his dwellings. They are often called booklice but this term is now very misleading and should be abandoned. Some of the larger psocopterans (eg. *Lepinotus*, *Trogium*, *Ectopsocus*) are comparatively easy to recognise whilst others, particularly the liposcelids pose considerable difficulties without access to good high power microscopical facilities. There are 14 species of the genus *Liposcelis* in the UK and the majority are found in close association with man (Table 1).

Table 1. The *Liposcelis* species found in the UK. These species are, with two exceptions (†), associated with man. Data extracted from Broadhead (1964) & Lienhard (1990). The numbers in brackets after the specific name indicates the common-ness ranking of the species in the food industry context whilst those without numbers have not been seen (Turner pers. obs.).

<i>Liposcelis bostrychophila</i>	(1)
<i>corrodens</i>	(2)
<i>pearmani</i>	(3)
<i>pubescens</i>	(4)
<i>brunnea</i>	(5)
<i>decolor.</i>	(5)
<i>mendax</i>	(6)
<i>entomophila</i>	(7)
<i>albothoracica</i>	
<i>paeta</i>	
<i>paetula</i>	
<i>bicolor</i>	†
<i>myrmecophila</i>	†
<i>obscura</i>	*

* One record only

Of the liposcelids in table 1, *L. bostrychophila* is the species overwhelmingly found in psocid related complaints. More than 99% of over 300 complaint specimens seen and identified between 1989 and the present were *L. bostrychophila* (Turner, unpublished).

It appears to be a species that is relatively common in domestic situations in the UK. Turner and Maude-Roxby (1989), in a survey of 863 domestic kitchens, showed that about 15% (14.4–16.5%) of them harboured *L. bostrychophila*, in most cases without the knowledge of the householder. In contrast, where psocid surveys have been carried out in manufacturing plants and warehouses, *L. bostrychophila* is usually absent whilst the other species, numbered in table 1, are more frequently found (Turner, unpublished).

For its size, *L. bostrychophila* is long lived. On poor quality food such as skimmed milk powder adult longevity is considerably greater than on yeast or wholemeal flour. One skimmed milk fed female survived for 53 weeks (Turner and Maude-Roxby unpublished) matching the maximum longevity recorded by Broadhead and Hobby (1944) also on poor grade food. In contrast egg output is increased if food quality is high to about 110 eggs per female per lifetime compared with only about 40 eggs per female per lifetime on poor food. This trade off, coupled with a considerable tolerance of starvation (Turner and Maude-Roxby 1988) makes *L. bostrychophila* extremely adaptable as a stored food pest.

Unlike all the other liposcelids found in the UK, *L. bostrychophila* is parthenogenic, no males or sperm have ever been seen or induced (Goss 1954). Since every adult is an egg-producing female, this species has a far greater reproductive potential than the other liposcelids which are all bisexual.

Parthenogenesis and variability

Without the fusion of haploid male and female gametes parthenogenesis removes the usual mode for the production of variation in a population, since there is no way that genetic characteristics of one individual can be combined with those of a second to give a rise to a third (White 1973).

Parthenogenesis is a mechanism that provides the potential for rapid population growth, of genetically fit individuals in relatively constant conditions. In the summer-time aphids become parthenogenic and the advantages to the aphid populations of this strategy are well known to any gardener or agriculturalist. In the more changeable climatic conditions of autumn and winter, aphids replace the genetic conservatism of parthenogenesis for the far more variable phenotypes produced by sexual reproduction to increase the chance of survival in less predictable environments (Greenwood and Adams 1987).

It is also seen as a mechanism for extending the species range, aiding colonisation by removing the need for both males and females to make it to a new area. A single female transported by accident to a new and favourable site will be able to found a new population there. Consequently parthenogenic species typically have wide distributions (White 1973). Where both parthenogenic and sexual forms are known of the same species there tends to be a far greater degree of

Table 2. Variability in egg production within and between populations from different places in England (identified by a population code no.) of *Liposcelis bostrychophila*. The adults were kept individually and provided with surplus food in constant conditions (either 20°C or 30°C and 75%r.h) during this time. They were examined and reprovisioned weekly. (Data from N. Ali unpublished.)

Pop. code	Egg output of individuals for the first 6 weeks of adult life					
	Temp. °C	n	Range	Mean	Variance	S.D.
1	20	13	23-39	31.69	24.73	4.97
2	20	13	2-17	8.77	24.69	4.97
3	20	14	22-49	35.14	69.98	8.37
8	20	13	9-37	20.31	79.90	8.94
10	20	14	17-55	35.93	77.92	8.83
16	30	13	42-100	84.92	259.91	16.12
18	30	13	40-99	75.77	278.36	16.68
lab. culture	30	15	28-86	57.87	237.84	15.42

parthenogenicity in the populations at the edge of the distributional range than at its centre. This has been illustrated in the case of psocids by Mockford (1971).

In common with other female Psocoptera, *Liposcelis bostrychophila* is diploid and has 18 chromosomes. Normal unfertilised psocopteran eggs have 9 chromosomes but those of *L. bostrychophila* are diploid with 18 chromosomes (Goss 1954). It would appear that during gametogenesis the reduction division stage of meiosis is lost thus retaining the full chromosome complement but the exact mechanism is unknown. Lewis and John (1963, p.340 onwards) describe the variety of known apomictic processes and discuss the genetic consequences of suppressing one of the meiotic divisions. They conclude that heterozygosity can be maintained but with the loss of variation.

Paradoxically, against this background of parthenogenetic characteristics, *L. bostrychophila* shows, sometimes considerable, variation both between and within clones. This variability can be seen in a range of areas.

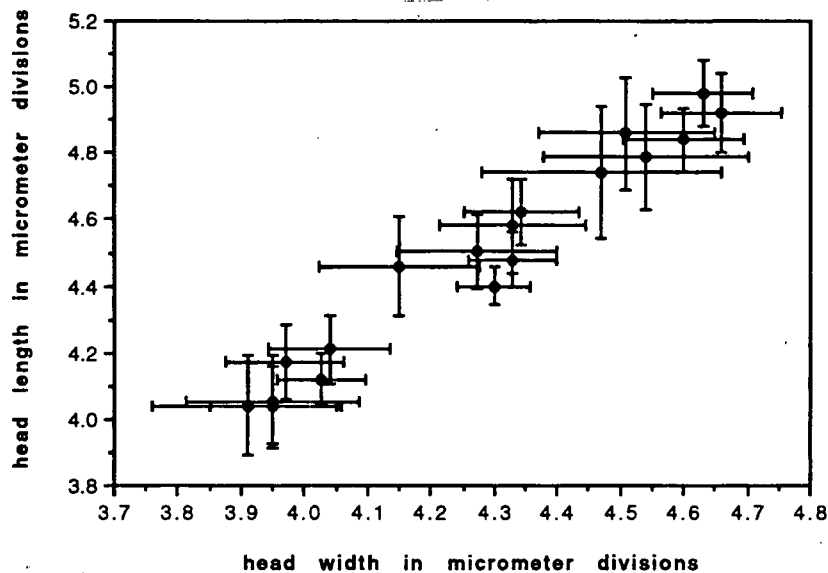


Figure 1. Morphometrics of *Liposcelis bostrychophila* populations. the measurements are max. head width (posterior to the eyes) and max head length (vertex to clypeus edge). The cluster of points at the bottom left are all laboratory cultures (either mixed age samples on a complete diet or those fed solely on flour, yeast or skimmed milk powder). The other points are for a variety of 'wild' populations from different parts of England. Each point is the mean of 40 individuals chosen at random from the cultures. The error bars are ± 1 S.D. One micrometer division = 0.057mm. (Data from Turner and Maude-Roxby unpublished).

a) *Fecundity*. Table 2 presents some data on the egg laying of a series of individuals, drawn from different populations, during the first 6 weeks of adult life.

For any population there is considerable individual variation in egg output, as seen in the range and variance figures, and some populations produce markedly less eggs than others. Notice the lower individual reproductive output of the laboratory strain in comparison with the 'wild' populations. The laboratory strain has been at King's College for at least 8 years and originated from a colony kept at MAFF, Slough, for an unknown period before then.

b) *Size*. *Liposcelis bostrychophila* populations differ in mean size as measured by head dimensions. Figure 1 shows the mean head morphometrics (width posterior to eyes and length from anterior edge of clypeus to vertex) of a series of populations which had been kept in culture in the laboratory for a minimum of 3 and a maximum of 24 months. There is a considerable but continuously overlapping variation within and between populations but no trends with regard to geography or how long they have been in laboratory conditions.

c) *Diet*. Psocids have been found infesting a wide variety of premises and foods as well as some non-food situations (eg. O'Farrell & Butler 1948, Obr 1978, Turner 1987, Sinha 1988, Dodd 1990). Turner (1987) analysed the correspondence on psocid complaints which had been received by the British Museum (Natural History) for the 20 year period 1955 to 1985. In this survey 46 different foods had been affected and the majority of these were cereal based. Foods vary in their nutritional value for psocid development, but in some cases, eg. complaints of psocids in salt, there is no nutritional value and the psocids were clearly just contaminants from elsewhere in the vicinity.

In one case a population of *Liposcelis bostrychophila* was found infesting a bag of bran. The population was thriving in the bran but all attempts to get the population to grow in culture using the standard psocid food mix failed. Unfortunately the bran population also died out before it could be investigated in more detail. But it would appear that this population may have been specially adapted to live on bran, a substrate usually ignored by liposcelids with a range of other foods available to them.

The situations described above were produced in cultures with constant food supplies, constant temperature and constant humidity conditions so that the effects were genetic in origin. In different locations in the UK potential habitats for these liposcelids will vary. In an attempt to explore the potential genotypic and phenotypic elements in this variation this paper describes some first analyses of this variability on the basis of allozyme differences in *L. bostrychophila*.

METHODS

Supply of *L. bostrychophila* populations

Since November 1991, through contacts in the food industry, we have been sent live liposcelids which originate from consumer complaints. These founders, from locations all over the UK, range from singletons to occasionally more than a 100 individuals. They have been used to establish individual populations, all kept at 75% rh, room temperature and fed a mixture of flour, yeast, wheatgerm and milk powder. A total of 103 separate populations are now in culture each isolated in individual humidity chambers. The identity of every population has been checked and only one is not *L. bostrychophila*. (This single population, of *L. corrodens*, is not included in the analyses.) In addition, live *L. bostrychophila* were also available from 4 foreign sites, 2 from Thailand and one each from Indonesia and Ethiopia.

Allozyme methods

Enzymes were detected using the Helena (Helena Laboratories, Beaumont, Texas, USA) cellulose acetate electrophoresis system. Individual liposcelids were placed directly in the plastic sample wells and 5–8 μ L of a non-buffered solution, modified from Loxdale et al (1983), containing 0.25% sucrose and 0.5% Triton X-100 added. The liposcelids were homogenised directly in the wells using a specially shaped stainless steel rod. 1.25 μ L aliquots of the homogenate were transferred to the cellulose acetate plate. Ten individuals could be run on the same plate at the same time using these

methods. The electrophoretic runs were performed at constant voltage (150V) for 17 minutes using ice to cool the apparatus.

The methods used in this enzyme survey followed the protocols given by Richardson *et al.* (1986) with slight changes to the staining procedures as advocated by Helena Laboratories and Loxdale *et al.* (1983). Two individuals from the laboratory culture were run on every plate as a standard control. It had been established that this culture shows virtually no enzymatic variability between individuals. Where possible purified enzyme was also run on the plate to validate the staining methods.

RESULTS

Enzyme survey

L. bostrychophila homogenates from a number of populations were tested for the 34 enzymes listed in Table 3. Positive results were obtained for 16 enzymes and of these 4 showed polymorphism. The other 18 could not be detected using this system, either in homogenates of 1, or up to 5, individuals.

Further analyses will concentrate on these 4 polymorphic enzymes, esterases, glucose phosphate isomerase, mannose phosphate isomerase and phosphoglucomutase. This paper describes some data on the first of these, the esterases.

Esterase variability

When run on the cellulose acetate plates esterases from *L. bostrychophila* are revealed as a set of up to 4 equidistant slow bands together with a series of often very faint faster bands. Only the stronger

Table 3. List of enzymes tested for in *Liposcelis bostrychophila*. The +, ++, +++ score indicates the strength of the substrate reaction, - indicates no detectable enzyme level, P indicates polymorphic enzymes.

Enzyme	E.C.number	Score
6 Phosphogluconate dehydrogenase	(1.1.1.44)	-
Acid phosphatase	(3.1.3.2)	-
Aconitate hydratase	(4.2.1.3)	+
Adenylate kinase	(2.7.4.3)	+
Alanine aminotransferase	(2.6.1.2)	-
Alcohol dehydrogenase	(1.1.1.1)	-
Aldehyde dehydrogenase	(1.2.1.5)	-
Aldehyde oxidase	(1.2.3.1)	-
Alkaline phosphatase	(3.1.3.1)	++
Aspartate aminotransferase	(2.6.1.1)	+
β Hydroxybutyrate dehydrogenase	(1.1.1.30)	++
Esterases	(3.1.1.1)	P +++
Fructose 1,6 diphosphatase	(3.1.3.11)	-
Fumarate hydratase	(4.2.1.2)	+
Glucose 6 phosphate dehydrogenase	(1.1.1.49)	-
Glucose dehydrogenase	(1.1.1.47)	-
Glucose phosphate isomerase	(5.3.1.9)	P +++
Glutamate dehydrogenase	(1.4.3.1)	-
Glyceraldehyde 3 phosphate dehydrogenase	(1.2.1.12)	+
Glycerol 3 phosphate dehydrogenase	(1.1.1.8)	-
Glycollate oxidase	(1.1.3.1)	-
Guanine deaminase	(1.5.4.3)	-
Hexokinase	(2.7.1.1)	+++
Isocitrate dehydrogenase	(1.1.1.42)	++
L iditol dehydrogenase	(1.1.1.14)	-
Lactate dehydrogenase	(1.1.1.27)	-
Malate dehydrogenase	(1.1.1.37)	++
Malic enzyme	(1.1.1.40)	++
Mannose phosphate isomerase	(5.3.1.8)	P ++
Peptidases	(3.4.11 or 13)	+
Phosphoglucomutase	(2.7.5.1)	P +++
Superoxide dismutase	(1.15.1.1)	-
Xanthine dehydrogenase		-
Xanthine oxidase	(1.2.3.2)	-

slow set of bands have been used to characterise the populations. Individual bands may be revealed as pale or intense.

The esterase patterns of a sample (average of 39; range 25 to 150) of individuals from each population were determined. Figure 2 shows the frequency of 11 recognisable esterase patterns among the 102 *L. bostrychophila* populations. The laboratory culture (run twice on every plate) has an esterase pattern similar to, but distinct from, pattern 10. It provided a constant reference to characterise the other patterns.

Except for 5 populations where two patterns were found, all individuals in a sample from the

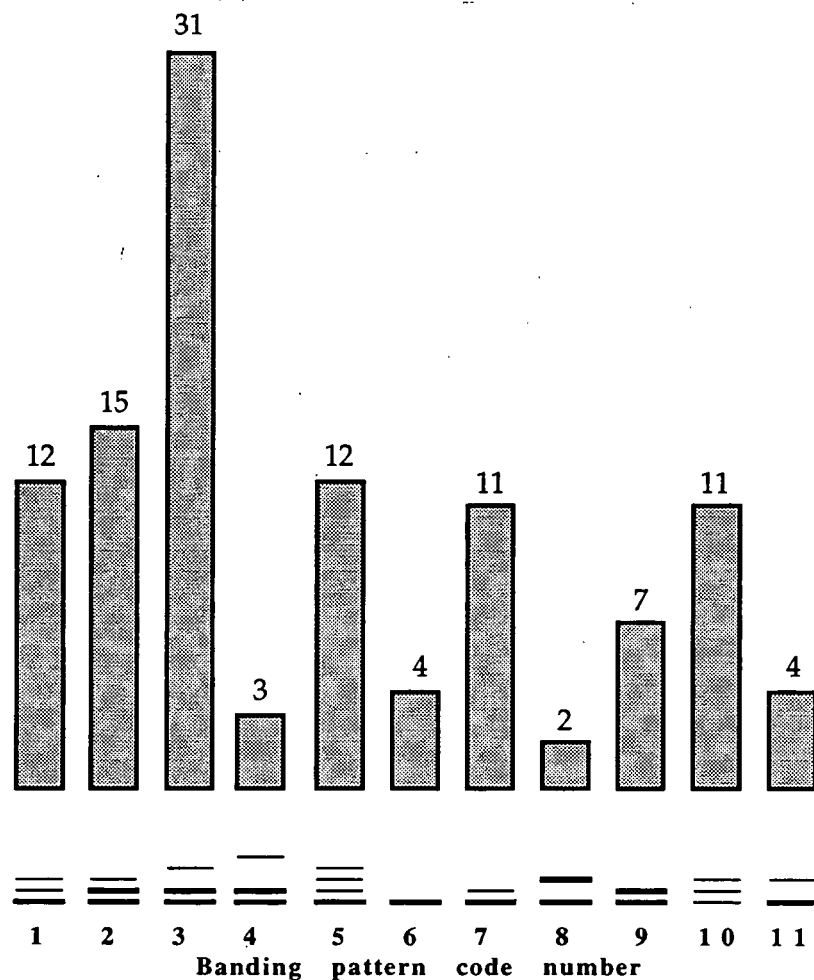


Figure 2. The frequencies of the 11 esterase banding patterns among the 102 populations of *Liposcelis bostrychophila*. The slowest band is uppermost. Optimum results for esterases were obtained using a 0.015M Tris-EDTA-borate-MgCl₂, pH7.8 buffer and post-coupled staining (Richardson *et. al.* 1986).

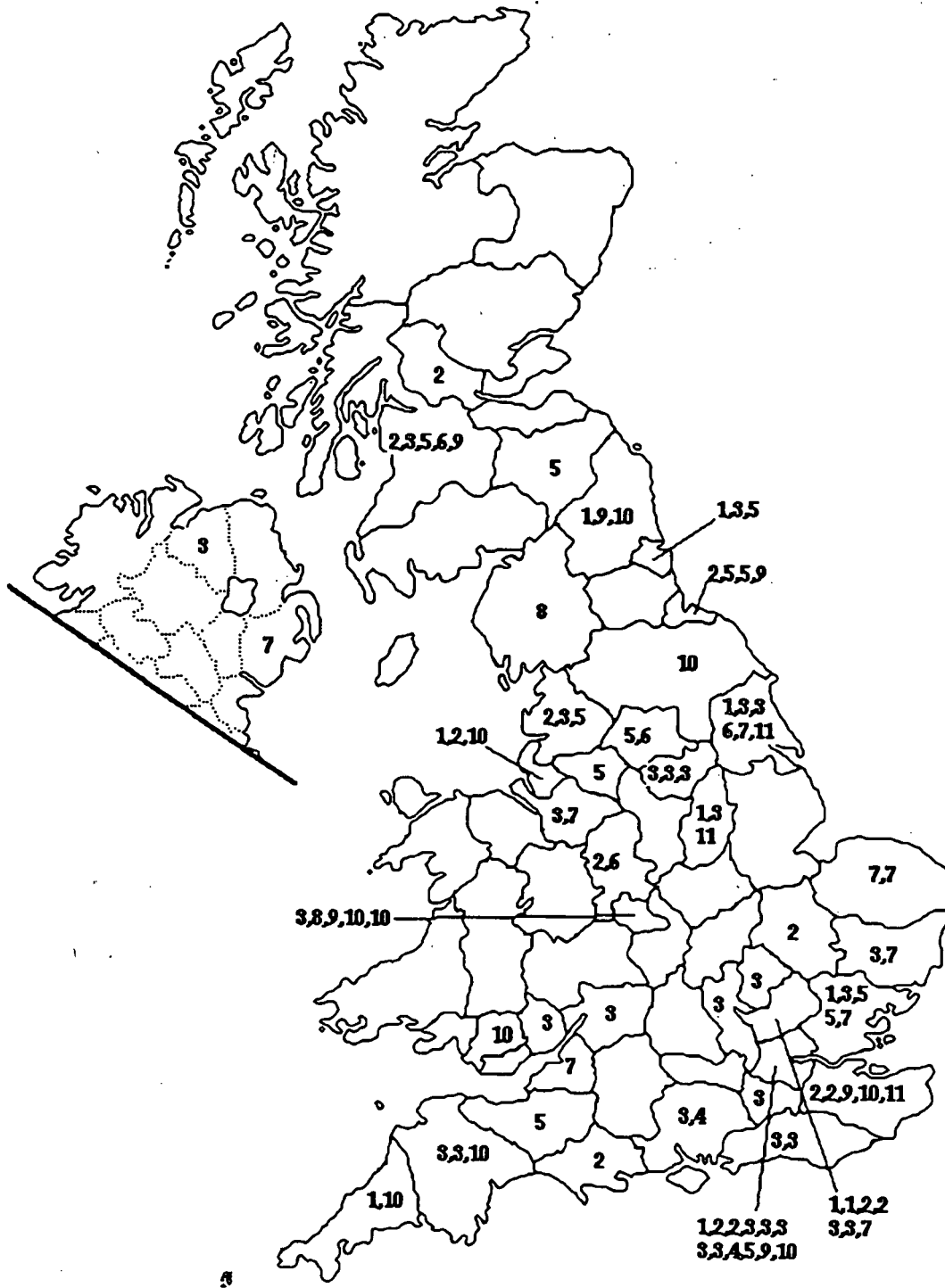


Figure 3. The geographic spread of the 102 *Liposcelis bostrychophila* populations identified by their esterase banding patterns (numbers refer to the patterns shown in figure 2). Six populations have no locality data and are of the following patterns:- 3,3,5,7,10,10.

same population gave the same esterase pattern. The cultures of 4 of these 5 exceptions were originated from complaint material consisting of a number of individuals and so could have had founders of more than one genetic pattern, but a single complaint specimen from St. Helens, Merseyside, has produced a population in which pattern 2 and pattern 10 are present in the ratio 5:3 (sample size 40).

Individuals from the populations of *L. bostrychophila* started from specimens from the 4 tropical sites all showed the same esterase pattern. This pattern differed slightly from any of those from the UK. It most closely resembled the laboratory culture but was fainter and with the bands smeared together. It also had a slightly greater mobility than the laboratory culture, being positioned further from the origin.

There appears to be no obvious correlations between the esterase banding patterns and the source of the founding individuals. Figure 3 plots the source locations for the 102 *L. bostrychophila* populations to county identified by their esterase banding pattern. Geographical differences in environmental factors do not seem to exert any control on the esterase patterns. The overall coverage is patchy with no populations originated from large areas of the Midlands and Wales, but it does generally reflect the distribution of the greatest numbers of consumer complaints. On the current availability of material the Greater London area has the largest range of esterase variability with 7 types followed by Strathclyde and Humberside with 5 each.

DISCUSSION

The variation seen in the biology of populations of *L. bostrychophila* also exists in their genetics as indicated by differences in the esterase banding patterns. Esterases are difficult to interpret genetically because there is an unknown number of loci involved. This study has started with them because they are an important group of enzymes involved in the detoxification of insecticides (eg. Hassall 1982) and therefore may indicate differences in tolerance and resistance levels. Their complexity also provides good population indicators with a marked inter-population variability but little evidence of any within a population.

With the one remarkable population originating from a single individual from St. Helens there is evidence that some variation can occur in a parthenogenetically reproducing individual but in the other 4 instances where two variants were found, the original samples contained more than 30 individuals. It is therefore possible that these individuals came from different populations. However the situation is ambivalent since these 4 also only showed two polymorphs rather than a larger number.

Both the egg production (table 2) and the morphometric study (figure 1) indicate that the laboratory culture is less fecund and smaller than the 'wild' populations. Their esterase pattern is not identical to any of the wild populations assayed although closest to pattern 10 which itself constitutes only 10% of the variability seen. They are therefore possibly poor models of processes in the real world. It is well known that populations lose vigour in culture but this usually happens in sexually reproducing populations where the range of genetic variation is limited. With parthenogenetic species the only concern is related to the possibility of the incorporation of a chance mutation that would normally fail in the variability of the wild but is more successful in the constancy of culture.

The evident variation in esterases may explain the lack of experimental agreement in the tolerance of *L. bostrychophila* to pyrethroid insecticides. Pinniger (1984) initially suggested this species shows some tolerance to permethrin and this was explored at some length by Turner (1988; Turner et. al. 1991) who also suggested the mechanism for tolerance. Recalling the origins of the laboratory culture at King's College, it is worth noting that since Pinniger was reporting on work carried out at MAFF, Slough it is more than likely that his findings were based on the same stock culture of liposcelids as Turner. Dodd (1990) however has affirmed that deltamethrin and permethrin performed effectively against *L. bostrychophila* despite presenting somewhat variable data which lacked any error analysis. One explanation for the differences in experience of the efficacy of pyrethroid insecticides on *L. bostrychophila* may be due to allozyme variations between the stock cultures used.

This raises the obvious question as to how long, if at all, does it take for allozyme changes to occur in populations in culture? We are unable to answer this yet. At the time of writing the oldest 'wild' Populations have been cultured for 16 months (about 8–10 generations) and there has been no change in their esterase pattern over this time.

Currently our research is exploring the range and variability of the other polymorphic enzymes identified in Table 2. The population groups so identified will then be examined to see whether these changes at the genetic level correspond with variation in the biology, morphology and insecticide tolerance already noted.

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