

A reappraisal of the role of mosquitoes in the transmission of myxomatosis in Britain

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SUMMARY

Field experiments were made in southern England to re-examine the possibility that mosquitoes in Britain might feed on wild rabbits and hence be vectors of myxomatosis. Mosquitoes of several species were attracted to rabbits enclosed in cylindrical traps and in a trap in which the animal was placed in a wire mesh cage. Substantial numbers of mosquitoes were also caught biting, or attempting to bite, tethered rabbits which were not in cages or traps. Evidence that mosquitoes fed on wild rabbits under natural conditions was obtained from results of precipitin tests made on blood-smears collected from mosquitoes caught resting amongst vegetation. On a few evenings mosquitoes were seen to be attracted to healthy wild rabbits and apparently attempting to feed on them. Batches of two mosquito species collected from the field were infected with myxoma virus.

It was concluded that contrary to previous beliefs mosquitoes in Britain feed to a certain extent on wild rabbits, and therefore are potential vectors of myxomatosis. No attempts were made to assess their relative importance in the transmission of the disease, which in Britain is transmitted mainly by the rabbit flea.

INTRODUCTION

Mosquitoes are the primary vectors of myxomatosis in wild rabbits in Australia and they are recognized as vectors in France, and are considered to be important in causing summer epizootics (Fenner & Ratcliffe, 1965; Joubert, Oudar, Mouchet & Hannoun, 1967; Roubaud cited by Jacotot, Toumanoff, Vallée & Virat, 1954), but they are not considered to be vectors amongst wild rabbits in Britain. Their unimportance in the transmission of the disease in Britain, except possibly to domestic rabbits (Muirhead-Thomson, 1956*a*), is based almost entirely on investigations undertaken soon after the disease first appeared in Britain. None of the six sentinel rabbits exposed during March to October 1954 in a wood near Edenbridge in Kent contracted myxomatosis despite the presence of large numbers of rabbits suffering from the disease (Armour & Thompson, 1955). In the same area Muirhead-Thomson (1956*b*) concluded from field experiments that mosquitoes did not feed on wild rabbits.

The principal vector in Britain is the rabbit flea, *Spilopsyllus cuniculi* (Lockley, 1954; Andrewes, Thompson & Mansi, 1959), which until now has been considered

the only important vector. However, during recent ecological studies on mosquitoes in the Poole area of Dorset (Service, 1969*a, b*) it became evident that mosquitoes did in fact feed on rabbits. During the next 4 years further information was obtained concerning the ability of mosquitoes to feed on wild rabbits; results are presented here.

RABBIT-BAITED TRAPS

Cylindrical traps

Two metal cylinders about 35 cm. long, 25 cm. in diameter and with inwardly projecting wire mesh funnels at both ends were each baited with a rabbit and placed amongst vegetation on Brownsea Island in Poole Harbour, Dorset. Detailed results of these, and other trapping methods, have been given already (Service, 1969*b*); summarized results are that from 38 catches during June–September, 5 *Anopheles plumbeus* Stephens, 8 *Aedes punctor* (Kirby), 166 *Aë. detritus* (Haliday), 6 *Aë. cinereus* Meigen, 36 *Culiseta annulata* (Schrank), 205 *C. morsitans* (Theobald), 102 *Culex pipiens* L., 4 *C. torrentium* Martini and 448 *Mansonia richiardii* (Ficalbi) were caught. None of the adults of *Culex torrentium* and very few of those of *Culiseta morsitans* and *Culex pipiens* had fed on the rabbits in the traps. All three species are known to be avian feeders (Service, 1969*a*), and it is thought that they may have been attracted to the trap by a localized artificially high concentration of carbon dioxide or temperature. Several adults of the other species, which normally feed mainly on mammals, were shown by precipitin tests to have fed on the rabbits.

Baited suction traps

Because some types of animal-baited traps, including the design just described, may not give representative samples of the mosquito species normally feeding on the bait animals, a new type of trap was designed to present a rabbit under more natural conditions (Plate 1). This consisted of a cage measuring 38 × 38 × 50 cm. with the four sides and top covered with 1 in. wire netting and was baited with a rabbit and placed about 35 cm. from the ground amongst scrub vegetation in Monks Wood Nature Reserve, Huntingdon. One end of a 1.75 m. length of 25 cm. diameter flexible tubing rested on top of the cage, while the other end was connected to the top of a 9 in. (23 cm.) diameter Johnson–Taylor suction trap (Johnson, 1950). The fan of the suction trap operated on a repetitive cycle of 7 min. off and 3 min. on. This allowed host-seeking mosquitoes to be attracted to the rabbit, after which they were sucked into the collecting magazine situated at the base of the suction trap. An electrical timing device allowed metal disks to drop and segregate the catch into 50 min. samples. Because mosquitoes in the area were most active at night the trap was operated from 1600 to 0900 hr. B.S.T.

Since unbaited suction traps have been used successfully to sample mosquito populations (Service, 1969*c*), the trap was operated on 8 nights without rabbits to discover whether those caught represented just randomly flying mosquitoes or those definitely attracted to the rabbit. Only two unfed *Aë. cantans* were caught in these unbaited catches, whereas in 20 catches during June–August, 1970, with a rabbit, 383 *Aë. cantans*, 88 *Aë. geniculatus* (Olivier), 1 *Aë. rusticus* (Rossi), 77 *An.*

plumbeus, 1 *An. claviger* Meigen and 5 *Culiseta annulata* and 18 *M. richiardi* were collected. All were females and most were unfed, but a few blood-fed adults of *Aë. cantans*, *Aë. geniculatus* and *M. richiardi* were caught. Precipitin tests on 9 *Aë. cantans*, 3 *Aë. geniculatus* and 1 *M. richiardi* showed they had fed on rabbits.

Segregation of the catch into 50 min. intervals showed that 77% of *Aë. cantans*, 62% of *Aë. geniculatus* and 71% of *An. plumbeus* were attracted to the rabbit between 1740 and 2010 hr. Only 10% of the mosquitoes caught were collected after 2100 hr. Mosquitoes appeared to feed on rabbits mainly in the early evening, at a time when they are active above ground.

TETHERED RABBITS

In Australia Myers (1956) collected mosquitoes attracted to rabbits by lowering cone-shaped traps at intervals over rabbits firmly pinioned to a board. Although the rabbits were not enclosed in traps they nevertheless had very little freedom of movement. To try and catch mosquitoes attracted to rabbits presented in a more natural manner, a rabbit was tied by 1 m. length of lead to a tree and visited at 10 min. intervals so that any mosquitoes attracted to it could be caught in aspirators. Such bait rabbits had considerable freedom of movement. In the first series of 9 catches on Brownsea Island, 7 *An. plumbeus*, 7 *Ae. punctor*, 164 *Aë. detritus*, 15 *Culiseta annulata*, 12 *M. richiardi* and 1 *C. morsitans* were caught (Service, 1969*b*). In four new catches in a small copse at Arne Peninsular in Dorset, 108 *Aë. cantans*, 57 *Aë. punctor*, 28 *Aë. cinereus*, 6 *Aë. detritus*, 4 *Culiseta annulata*, 11 *An. claviger*, and 18 *Aë. geniculatus* were caught. This gave further evidence that British mosquitoes are attracted to rabbits.

PRECIPITIN TESTS

An alternative method to using traps for determining whether mosquitoes feed on rabbits is to identify by precipitin tests blood-meals of engorged mosquitoes collected from natural resting places. Lee, Clinton & O'Gower (1954) used the method in Australia to discover the species feeding on rabbits. Blood-fed mosquitoes were collected, therefore, by sweeping various types of vegetation in areas of southern England where rabbits were known to occur, and Dr P. F. L. Boreham kindly agreed to perform precipitin tests on the blood-fed mosquitoes caught. The following lists show the numbers of blood-meals positive for rabbit blood out of the totals tested from different areas. **Woodwalton Fen and Monks Wood, Huntingdon:** 25/26 *Aë. cantans*, 0/1 *Aë. annulipes*, 0/2 *An. maculipennis* complex, 4/4 *Aë. cinereus*. **Surlingham Fen, Norfolk:** 14/14 *An. claviger*. **Arne and Studland Heath, Dorset:** 7/77 *Aë. cantans*, 0/7 *Aë. detritus*, 0/11 *An. plumbeus*, 0/3 *Aë. geniculatus*, 1/16 *Culiseta morsitans*, 0/29 *M. richiardi*, 1/2 *Culex pipiens* or *C. molestus* Forskål, 3/149 *Aë. cinereus*, 0/195 *Aë. punctor*, 0/20 *C. annulata*, 5/40 *Aë. dorsalis*, 0/5 *An. claviger* and 0/6 *Aë. annulipes*.

Six hundred and fifty-five blood-smears from 14 species were tested and 58 of these from six species were positive for rabbit blood. It is just conceivable, though I consider it most unlikely, that these feeds on rabbits were from lethargic animals suffering from myxomatosis, and that mosquitoes cannot feed on healthy active

wild rabbits. A search for blood-fed mosquitoes was made therefore on Lundy Island which is 20 km. from the mainland of Devon, and which has a very large myxomatosis-free rabbit population. Unfortunately only 12 blood-fed *Aë. punctor* were found, but precipitin tests showed that six of these had in fact fed on rabbits; two of these had also fed on other mammals. It is inconceivable that all these had fed on the mainland on diseased rabbits, and subsequently dispersed to the island. Further evidence was therefore obtained of mosquitoes feeding on healthy rabbits.

NATURAL INFECTIONS OF VIRUS IN MOSQUITOES

In France myxoma virus has been found in wild caught adults of *Aë. caspius* (Pallas), *Aë. detritus*, *An. maculipennis* complex and *C. modestus* (Ficalbi); the first species being considered the most important vector of summer epizootics of myxomatosis in the Camargue area (Joubert *et al.* 1967). In England Muirhead-Thomson found natural infections in *Aë. cantans* and *Aë. annulipes* (1956*b*) and in *An. labranchiae atroparvus* van Thiel (1956*a*), and I have caught adults of *Aë. cantans* from Monks Wood and *An. claviger* from Surlingham which were found to be infected with myxoma virus by Dr J. Ross of the Infestation Control Laboratories of the Ministry of Agriculture, Fisheries and Food at Worpleston. As transmission by arthropods is apparently mechanical (Fenner & Ratcliffe, 1965) then any mosquito feeding on rabbits is a potential vector. The presence of the virus in mosquitoes only indicates that the species concerned are attracted to rabbits and can feed at least on those infected with myxomatosis.

DIRECT OBSERVATIONS

On Brownsea Island adults of *Aë. detritus* and *M. richiardi* were often observed feeding on tame rabbits kept out of doors in rabbit hutches. Because of the rabbit's movements and twitchings they appeared to have some difficulty in getting a complete blood-meal, and many were seen to probe at several sites before becoming replete. As observed in France by Jacotot *et al.* (1954) nearly all biting was restricted to around the eyes and nose.

It is difficult to observe mosquitoes feeding on wild rabbits, but on several evenings at Arne in Dorset and on one evening on Lundy Island mosquitoes were observed hovering over and settling on the heads of grazing rabbits. It seems reasonable to assume that they were attempting to feed on them.

DISCUSSION

The rabbit flea, an important vector of myxomatosis in Europe, is absent from Australia where the most important vectors are *Culex annulirostris* Skuse, *C. pipiens australicus* Dobrotworsky and Drummond, and *An. annulipes* Walker. The last mosquito is a particularly well adapted vector as adults rest during the day in rabbit burrows, and feed on rabbits both above and below ground (Myers, 1956). In England mosquitoes, including blood-fed specimens, have been found in a fox hole by Shute (Service, 1969*a*), but Muirhead-Thomson (1956*b*) was unable to

find any in rabbit burrows. I have examined rabbit burrows on many occasions but have found mosquitoes in them only once. This was during a very dry spell in the summer when *Aedes* species were resting in several burrows in Monks Wood. It rained heavily in the evening and none could be found on the following days. Normally adults of British *Aedes* species rest during the day amongst the shelter provided by grassy and scrub vegetation, but it is possible that they retreat to rodent holes during adverse dry weather. It is not known whether they feed on rabbits in their burrows.

Results from experiments with baited and tethered rabbits indicate that British mosquitoes are attracted to rabbits, and direct observations on feeding and the identification of natural hosts by precipitin tests proves without doubt that mosquitoes do feed on rabbits. This conclusion disagrees with those reached by Muirhead-Thomson (1956*b*). Working in a wood harbouring large numbers of man-biting *Aedes* species, he found no evidence that they were attracted to rabbits either in, or outside, traps. He considered that the identification of blood-meals from wild caught mosquitoes would give the most convincing demonstration of any natural feeding on wild rabbits. Unfortunately he was unable to find any blood-engorged specimens. The reasons why the rabbit-baited traps of Muirhead-Thomson failed to attract mosquitoes and why he was unable to find blood-fed specimens is not understood. It is possible, however, that trap design and siting are important. I have found that within woods there are favoured, and often very selective, sites and types of vegetation in which mosquitoes rest during the day, and Muirhead-Thomson may have failed to locate these sites.

It is established from the present study that mosquitoes in Britain can feed on healthy wild rabbits, but their importance as vectors of myxomatosis depends on several factors. For example, examination of the results of precipitin tests indicates that rabbits were preferred hosts when there were few, or no, alternative larger hosts, such as domestic livestock (e.g. in Monks Wood and at Surlingham) but when these were present (e.g. at Arne) considerably fewer appeared to have fed on rabbits. The incidence of feeding on rabbits may therefore depend on the availability of alternative hosts. It is also possible that in areas where myxomatosis is present mosquitoes may find it easier to feed on comatose diseased rabbits than healthy ones, thus leading to a disproportionate number of feeds on diseased rabbits. A high percentage of mosquitoes will consequently become infected, but the frequency of transmission to healthy individuals may be lowered. On the other hand, because mosquitoes seem to need several probes on the same, or different rabbits, before getting a complete blood-meal the chances of transmission should be increased.

The time during June to September in England required for blood digestion and ovarian development is about 5–7 days for those species investigated (Service, 1968). It is not known whether there is any marked delay between the completion of ovarian development and oviposition, or between oviposition and refeeding, but it is generally assumed that these intervals are minimal in mosquitoes. If so, then adults will take blood-meals at about weekly intervals. Age grading techniques on British species have shown that large numbers of mosquitoes feed at least twice in

their lifetime, and a number feed four or more times. Because of this longevity and the fact that myxoma virus can remain infective on mosquitoes for nearly 6 weeks in the summer and possibly much longer in the cooler winter months (Andrewes, Muirhead-Thomson & Stevenson, 1954), there is ample opportunity for mosquitoes to become infected. Mosquitoes feeding through normal rabbit skin do not become infective but those feeding on primary lesions or on well-developed secondary lesions nearly always do (Fenner & Woodroffe, 1953; Fenner, Day & Woodroffe, 1952, 1956). Since mosquitoes mainly feed around the eyes and nose of rabbits, regions in which tumours and lesions usually occur, they therefore select the most infective areas.

There have been no detailed studies on the distances covered by mosquitoes in Britain, although there are a few records of individuals travelling at least 4–8 km. (Covell & Shute, 1962; Service, 1969*a*) and up to 5 km. soon after taking a blood-meal (Service, 1969*a*). It is likely that mosquitoes in Britain disperse greater distances. It is possible that the sudden re-appearance of myxomatosis in areas from which it has been absent for some time is due to re-infection by mosquitoes originating from areas harbouring the disease.

The above experiments have shown, contrary to previous belief, that in Britain mosquitoes feed on healthy rabbits. Therefore the possibility that they transmit myxomatosis to wild rabbits should be reconsidered.

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EXPLANATION OF PLATE

Plate 1. Suction trap fitted with flexible tubing for catching mosquitoes attracted to rabbits.