

AN ECOLOGICAL STUDY

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(Part of Presidential Address, delivered 16 February 1963)

The study of the Mollusca may take many forms, all interrelated and all of importance. Molluscan morphology and taxonomy are very properly the province of the professional biologist, and the erudite papers produced on these subjects may prove discouraging to the amateur, who is often anxious to do something more than collect shells. There is one aspect of the study, however, in which the amateur may come into his own and that is molluscan ecology.

The father of molluscan ecology was the late Professor A. E. Boycott, whose papers on the land and freshwater Mollusca of the British Isles (1934 and 1936) will ever remain classics in their particular field. These great works were based on studies of the parish of Aldenham, in which he lived, and on presidential addresses he gave before the Hertfordshire Natural History Society, a body of amateur naturalists. He and Charles Oldham, who was for ten years Secretary of that Society, and for twenty-two years Treasurer of the Conchological Society, were both amateurs in the best sense of the word. It is true that Boycott had a scientific training, in that he was a pathologist of some eminence. He was introduced to ecology by his friend and neighbour, Professor (now Sir) Edward Salisbury, and it is probably true to say that he knew very little about ecology when he began its study. His papers were the results of careful observation and recording and a logical interpretation of the facts.

While few can hope to achieve the stature of Boycott, he would have been the first to agree that his work was incomplete, as all scientific work must be incomplete, each new discovery leading to another. There is, therefore, much to be done in the ecological field, and every contribution, however small, is of value.

The following is the record of a very simple exercise in ecology, designed to show the sort of thing that can be done by the veriest beginner. The molluscan world is but a small part of a much larger one, and molluscs must be studied in relation to the flora and fauna of that larger world, while the soils on which that larger world is based also play an important part. An endeavour has been made to show something of these relationships, and it is hoped that this study will encourage more people to venture into the realms of ecology, which are both stimulating and rewarding.

The counties of Bedfordshire, Hertfordshire and Buckinghamshire meet at a point some three-quarters of a mile south of the village of Dagnall. A mile to the north of this point is Whipsnade Zoo in Bedfordshire; a little more to the south is Ashridge Park, with the Bonar Law College, in Hertfordshire; and two miles to the west are the Ivinghoe Hills in Buckinghamshire. These hills may be described as a bastion of the Chiltern Hills as they stand out from the main chalk mass, with lower ground on three sides.

There is an isolated mass of chalk consisting of Beacon Hill, 750 feet, with a long spur to the east known as Gallows Hill, and two knolls, each over 700 feet, to the south of Beacon Hill. Between the two knolls is a deep gully; the more northerly knoll is joined to Beacon Hill by a saddle. The road from Ringshall in the south winds round the western side of Beacon Hill, dropping quickly to the Tring-Dunstable road, which runs from east to west along the foot of the escarpment and follows the ancient Icknield Way, the oldest road in Britain. South of the Beacon Hill mass and the road is Steps Hill, which rises gently to over 800 feet at its highest point. All is National Trust property and typical chalk country. To the north of the escarpment is a narrow band of the Upper Greensand, beyond which the great Oolitic plain stretches away to the Lias in the far distance. On the summit of Beacon Hill is a flat pear-shaped area, the site of a prehistoric camp, with a tumulus within. Beside the old stands the new, the stone block of a trigonometrical station. There is another tumulus on the southernmost knoll.

Apart from the Camp site, several well-worn paths and the gully, the whole area is clothed with long grass. Steps Hill is dotted with small hawthorns (*Crataegus monogyna*) and wayfaring trees (*Viburnum lantana*). There are many fine plants of *Arctium lappa* and *Taraxacum officinale*. On the southern side of the Beacon Hill mass are widely scattered dwarf hawthorns. On the northern escarpment there is a fairly close hawthorn scrub with much larger trees along the top of the slope, becoming more scattered and with smaller trees lower down. In spring the whole area is dotted with cowslips (*Primula veris*). By June there are masses of *Helianthemum chamaecistus*, and in August the dominant plant, apart from the grasses, is *Centaurea scabiosa*. There are patches of *Hippocrepis comosa*, *Ononis repens*, *Campanula rotundifolia* and an occasional *Carlina vulgaris*. Plants which appear to be confined to the southern side are *Anacamptis pyramidalis*, *Scabiosa columbaria* and the rare and beautiful *Gentianella germanica*. *Thymus pugelioides* (?) grows amongst the short grass of the gully. Over all flits the dainty chalk-hill blue butterfly. A particularly interesting area, though a small one, is situated by the road just before it turns westward between Steps Hill and the main mass. Here is a roughly circular patch of herbage about 25 feet across, consisting of *Heracleum sphondylium* growing to six feet in height, with *Artemisia vulgaris* and *Urtica dioica* up to four or five feet. The two last occur nowhere else in the area, and the first has but a few scattered plants just outside this patch.

While the snail population of the Ivinghoe Hills is very large, the number of species found during the summer and autumn of 1962 was no more than twelve, and one of these was represented only by dead shells. Four species, *Helix* (*Cepaea*) *nemoralis* L., *Hygromia* (*Trichia*) *liberta* (Westerlund), *Monacha cantiana* (Montagu) and *Helicella itala* (L.), occurred in vast numbers. *Abida secale* (Draparnaud) was common and in some places abundant. *Pupilla muscorum* (L.) and *Ceciloides acicula* (Müller) were widespread but needed looking for. *Oxychilus cellarius* (Müller) and *Retinella* (*Aegopinella*) *nitidula* (Draparnaud) had

a scattered and sparse distribution, and that of *Helicella* (*Cernuella*) *virgata* (da Costa) was most interesting. *Helicella* (*Candidula*) *caperata* (Montagu) yielded only two specimens. *Pomatias elegans* (Müller), dead and very old, three shells only, was found in a mole heap. It seems probable that this species has long been extinct on the Hills, though it has been found living on lower ground to the west. It prefers broken chalk in which to burrow. The thick mat of grass roots would make this difficult and would also break up the chalk into finer particles. It may even be that these shells are relics of the days when the Chilterns were covered with forest.

The most abundant snail was *Monacha cantiana*, which was ubiquitous. It was found everywhere in great numbers, except on the Camp site, which seemed to be devoid of snails. There was little variation in size, though the finest were found in the hogweed patch.

The three species of *Helicella*, all typical of chalk country, provided an interesting contrast. *H. itala* was almost as abundant as *M. cantiana* on the southern slopes of the Beacon Hill mass, was much scarcer on the northern side, and was not found at all across the road on Steps Hill. Like all the *Helicella*, it reaches maturity in the autumn, when large shells were plentiful. There was some variation in the width of the bands and var. *lutescens* was as common as the banded form.

The case of *H. virgata* gives rise to some speculation. It is a species most frequently associated with the short downland turf, but at Ivinghoe, as in so many places, this short turf is no more, due to the disappearance of the rabbit. Around the hogweed patch, where some years ago it was fairly common, only four specimens were found in the course of several visits. Of these, one was var. *albicans*, white with a single peripheral band, the other three being var. *albida*, pure white. Further to the north seven specimens were taken over a much wider area. Of these, four were typically banded shells, the others being var. *albida*. On the northern slopes *H. virgata* lived in only one place, a wide track ascending to the top of the escarpment, with the turf kept short by the passage of many feet. Here it lived in some numbers. A random sample of some 70 shells was taken, of which only six could be said to be typically banded. Fifteen were var. *lutescens*, some with a reddish colour round the aperture, 24 were var. *albida* and nine var. *albicans*. The rest had a single band, white above and coloured as *lutescens* below, a striking form. There were no snails in the long grass beside the track. It would seem that, owing to changing conditions, *H. virgata* is a waning species in the Ivinghoe Hills. The only two specimens of *H. caperata* were found at the hogweed patch, one typical in the middle, the other, var. *ornata*, in the long grass outside.

Helix nemoralis was abundant on Steps Hill and all the Beacon Hill slopes except in the hawthorn scrub, where it was decidedly scarce. Four large random samples, each of over 100 shells, were recorded during the autumn of 1962, three from various parts of the southern slopes and one from the northern. In all 22 band variations were found,

this not including shells of indeterminate banding, and there were two self-colours. There were quite remarkable differences between the shells of the southern and northern sides. On Steps Hill 68% were pink, 32% yellow; in the hogweed patch there were 95% pink and 5% yellow, and on the southern slopes of Beacon Hill the proportions were about the same as on Steps Hill. Of the northern sample only 44% were pink and 56% yellow. Over 40% of the southern shells were banded 12345, of the northern only 18.5%. The proportion of shells with bands fused or bands absent varied little, but of the shells having bands both fused and absent the figures for the south side were 2.2%, 8% and 4.4%, but on the north 25%. Again, on the south side 95% of all shells had brown lips and ribs; on the north only 24.3%, the rest being made up of brown and pink, brown and white, all pink and pink and white.

The finest shells, both in size and colour, were found at the hogweed patch, where 38% showed some fusion of the bands, the highest figure. One shell began as 12345, but after a repair on the body whorl, became (123)(45). Five plain pinks were found here, but only two in the rest of the area. As is often the case with this species, there was considerable variation in shape, from depressed to high-spined shells, but there was little variation in size amongst the southern shells. On the northern side there were considerable differences both in shape and size. Quite a large number of shells were small and high-spined, reminding one of var. *alpicola* of *Arianta arbustorum*. Two plain olive-brown shells, var. *olivacea*, were found on the south side.

There appears to be some question as to whether *Hygromia liberta* is a good species. Dr. H. E. Quick says there is no difference between its anatomy and that of *H. hispida*. However, another worker has recorded *H. liberta* from Ivinghoe, so that name will be used for the present. The shells were small, high-spined, densely hispid and with very narrow umbilicus; they occurred everywhere abundantly at the roots of grass. *Abida secale* lived with *H. liberta* in varying numbers, but the place for this species was the gully. On the north side, facing south, is short grass with little bare patches of chalk overhung with wild thyme. Under the thyme it was common to find up to eight or nine of these snails in a few square inches. On the south side, facing north, there is less thyme, and *A. secale* was less common than on the other side. It was also decidedly scarce on the northern slopes of Beacon and Gallows Hills. It has not so far been found on Steps Hill.

Ceciloides acicula was found on ant hills, as is commonly the case. Only dead shells were found, many of them quite fresh. This snail probably occurs with some frequency, but being subterranean in habit is not always easy to find. The untenanted parts of the ant hills proved too damp to delve into; the tenanted parts were occupied by very vicious red ants. The soil thrown up by moles seems to be too coarse to expose the shells, or it may be that the more violent mole action breaks them up. At any rate, none was found on mole

hills. *C. acicula* was also found on small bare patches of fine soil, possibly the denuded remains of ant hills. *Pupilla muscorum* was found in grass round these patches, and in damp weather, crawling about on the patches themselves. Both species occurred right up to the edge of the Camp site at the top of Beacon Hill. *Oxychilus cellarius* and *Retinella nitidula* were found in ones and twos all over the area at the roots of grass, but numbers were small.

Mention has been made of the association of *Abida secale* with wild thyme, and there were in the area several other obvious associations of snails with certain plants. In dry weather the best place to look for *H. nemoralis* on Steps Hill was under dandelion leaves, obviously because they gave good cover and, being fleshy, always kept fairly moist. The green leaves were never eaten, though the dead brown leaves underneath showed signs of attack. Elsewhere the greater knapweed provided the cover, with thick bushy plants a foot or more high. Later in the year when the leaves had died off *H. nemoralis* had moved away, but *T. cantiana* and *H. itala* could be seen clinging to the bare stems. Presumably a certain amount of decay had set in on the dead stems and food was thereby provided. *T. cantiana* fell off at the least touch, but *H. itala* clung much more tenaciously. In the hogweed patch *H. nemoralis* was found under the leaf canopy in summer. By October the hogweed had lost all its leaves, though the mugwort and nettles retained theirs a little longer. On the gaunt hogweed stems *H. nemoralis* sat out in the sunshine for all to see, many of the snails five feet from the ground. Very few were to be found on the mugwort and nettles. Again food was probably the deciding factor.

Apart from *Abida secale*, the gully has another claim on our interest, for in 1959 many specimens of the Sciomyzid fly *Ditaenia cineraella* (Fallén) were captured there. This may seem irrelevant in a paper mainly about snails, but the Sciomyzidae is a family of dipterous flies which are predatory or parasitic on snails. The larvae of these flies, generally referred to as marsh flies, feed on snails, some species eating only one snail and pupating within the shell, others eating a number of snails and pupating elsewhere. Being mainly inhabitants of marshes, the commonest hosts are freshwater pulmonates and members of the Succineidae, but some species will eat land snails.

In 1959 and again in 1960 Professor C. O. Berg, an entomologist from Cornell University, came to Rothamsted Experimental Station, Harpenden, as part of European tours in search of these flies. His first field trip in 1959 was with the author to Ivinghoe, and the first flies he took in Britain were *Ditaenia cinerella* in the gully. He was greatly surprised to find them in such a situation. Later he took them in Belgium, France, Austria and Italy, all in marshy places, and he quotes C. H. W. Pugh, 1957, as finding them in marshy places in Shropshire and North Wales. In 1960 Professor Berg took adult flies on sand dunes at Tenby, South Wales. P. Ardo, 1957, reports taking them on sand dunes at Orre, near Stavanger, Norway, so this fly does not seem to be particular about its habitat as long as snails are available.

Many dead snail shells were broken open both at Ivinghoe and Tenby in the hope of finding puparia, but none was found. The reason for this became obvious later. A number of living flies was sent by air-mail to Cornell. They not only survived the journey but laid eggs on the way, and from these flies were reared. The larvae proved catholic in their taste for snails, attacking American snails as avidly as they had British ones. Throughout the breeding experiments at Cornell they were fed exclusively on freshwater pulmonates, whereas their progenitors at Ivinghoe could only have fed on land snails. They are not, therefore, as many Sciomyzid flies are, host specific, i.e. confined to one species of snail. The host snails at Ivinghoe were not determined, though *Hygromia liberta* seems the most likely, with possibly *Helicella itala* and *Monacha cantiana*.

Ditaenia cinerella is also of historic interest. In 1917 H. Schitz reported rearing an adult fly from a puparium found in a snail shell. This was the first suggestion ever made that there was any connection between the Sciomyzidae and snails. Lundbeck, however, wrote in 1923, "I have the same species from flood debris. It is certainly no snail feeder, its presence in the shell being quite occasional." Professor Berg writes, "This must go down as one of the most obvious cases of faulty logic in the annals of biology. As if it followed automatically that every larva that kills a snail must pupate inside the shell. *D. cinerella* usually does not, as we found in rearing it."

It is of interest that Professor Berg found another Sciomyzid fly, *Sciomyza albocostata* Fallén, at Long Wood in 1959 and at Aldbury Common in 1960. These woods are only a few miles from Ivinghoe. These flies were reared on *Discus rotundatus*. The author is greatly indebted to Professor Berg for so willingly providing all this information.

Apart from the gentian and the flies, there is nothing remarkable about the flora and fauna of the Ivinghoe Hills. This study is in itself incomplete, as the list of molluscs probably is. Undoubtedly even a small extension of the area would reveal further species.

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