catch was analysed for strontium-90 by the Health and Safety Laboratory of the U.S. Atomic Energy Commission; the results are shown in Table 7.

Taking into account the seasonal variation in fallout rate the mean annual rate of deposition of strontium-90 for Australia approximates to 1 mc./km.². Further work, now in progress, will establish this rate more definitely.

Comparisons of Australian Strontium-90 Levels with those in the Northern Hemisphere

The nearly uniform fallout of strontium-90 in Australia contrasts with considerable fluctuations observed in the United Kingdom and the United States, where the bulk of northern hemisphere measurements have been made. Nevertheless, rough average levels can be compared in those cases where data are available for the appropriate time (the United States does not measure sheep bones or cabbages).

The human bone results given in Fig. 2 show that the Australian levels are somewhat less than one-half those for the northern hemisphere. In the cases of milk and cabbages, comparisons with American⁶⁻⁹ and British⁴ data again indicate levels which are about one-half the northern hemisphere values while Australian sheep bone results for 1957 indicate levels less than one-half those in the United Kingdom⁴ at that time.

Australian soil-levels lie between one-fourth and one-third of those of the more densely populated regions of the northern hemisphere²⁷, while the open-pot measurements indicate a strontium-90 fallout rate of less than one-quarter that operative in the northern hemisphere.

Conclusions

(1) Within the sampling errors, and apart from some local variations noted, the levels of strontium-90 in the material examined are uniform throughout Australia. This indicates that the strontium-90 fallout over the continent arises from high-yield fission weapon tests overseas; as expected the contribution from local weapon tests is too small to be detected.

(2) The rate of deposition of strontium-90 and its accumulation in Australian soils are one-fourth to one-third those in the more densely populated areas of the northern hemisphere. The levels of strontium-90 in Australian human bone tissue and milk lie between one-third and one-half those in the northern hemisphere. This level is a little higher than would be expected from the fallout rate and the soil data, but the difference is not established statistically. If further experiments prove this difference to be real it would be hard to explain satisfactorily.

A similar difference between bone and soil-levels was reported by Kulp *et al.*²³ for other southern hemisphere samples and they considered that it might be due to the movement into the southern hemisphere of foodstuffs containing strontium-90 produced in the northern hemisphere. This explanation is unsatisfactory in the Australian case for the continent is self-sufficient in most primary production, especially of milk and cereals. Further results from the Australian survey should elucidate the position.

(3) The possible biological consequences to the population of Australia, of the fallout-levels reported in this paper, have been assessed by the Australian National Radiation Advisory Committee²⁸. The Committee concluded that the possible hazards are very small in comparison with those already accepted in technically advanced communities.

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EVOLUTION OF HOST-PARASITE RELATIONSHIPS

PROF. JEAN BAER (Neuchâtel) opened a symposium held by Section D (Zoology) at the recent British Association meeting in York on the "Evolution of Host-Parasite Relationships". He began by analysing an ecological survey of such relations. The survey

was limited to biting and sucking lice, fleas and worms parasitic in vertebrates, because the taxonomy and host-distribution of these parasites have been well studied, their life-cycles are usually complex and diverse and their host-relations show great diversity.

The host or host-group is comparable ecologically to an island, the parasites representing the endemic fauna, and the more isolated the island, or the more specialized the host, the higher is the degree of endemicity of its fauna. There is a great deal of evidence showing that both morphological and physiological specialization of the parasites is a consequence of their adaptive evolution to distinct groups of hosts.

A reliable impression of host-distribution can be derived from histograms of the numbers of genera of parasites in particular host classes, and from the individual distribution of each group may be deduced its probable age.

Mallophaga, for example, occur exclusively on birds and mammals, and have evolved more extensively on the former than on the latter. Monogenea are parasites on elasmobranchs, teleosts, amphibians and reptiles but are far more widely specialized on teleosts than on elasmobranchs and only very slightly on amphibians and reptiles. Cestodes occur throughout all the major groups of vertebrates; the greatest number of genera is found in birds and in elasmobranchs, whereas the largest number of genera of trematodes is found in teleosts even though trematodes have been reported from all the major groups of vertebrates.

Host-parasite relationships as expressed by the number of genera of parasites associated with a given group of hosts also imply that the age of the parasites, that is, the time when they first adopted parasitism as a way of life, varies considerably. For example, fleas, lice and Mallophaga are unknown from hosts other than birds and mammals and it is extremely unlikely that such parasites existed before their hosts themselves appeared in late Cretaceous times. Monogenea and cestodes were already most certainly associated with the precursors of modern sharks and appear to have accompanied the aquatic ancestors of the land-dwelling vertebrates. Moreover, ectoparasitic Monogenea have only been able to survive by seeking refuge within the mouth cavity, oesophagus and urinary bladder of their hosts, and since their life-cycle restricts them to an aquatic habitat, they are associated with vertebrates such as amphibians and freshwater tortoises. On the other hand, tapeworms living invariably within the gut of their hosts have evolved together with the latter and, as their life-cycles also became adapted to terrestrial intermediate hosts, it is natural that these parasites occur in land-dwelling vertebrates, that is, in reptiles, birds and mammals.

These parasites of vertebrates were discussed ecologically, separately as ectoparasites and as endoparasites, and as to whether the larval forms had a free-living stage or not. The ectoparasites with no free-living stage were the Mallophaga and the Anoplolepta, and with a free-living stage, the terrestrial Siphonoptera, and the aquatic Monogenea. The endoparasites were those with a gradual metamorphosis, the nematodes, which might or might not have an intermediate host, and those in the metamorphosis of which distinct stages occurred, the trematodes, cestodes and Acanthocephala, all of which had at least one intermediate host.

An analysis of the results from an ecological approach to host-parasite relationships clearly shows the presence of two factors responsible for host distribution, namely, (a) the physiological requirements of each of the stages of the life-cycle; (b) the degree of morphological differentiation of the in-

festive larval stage. These factors, being inherent to the class to which the parasite belongs, must have been acquired genetically and are therefore subject to mutation and to evolutionary pressures.

Each successive stage of any life-cycle does not necessarily have identical physiological requirements, but the more highly specialized the latter the greater the degree of intimacy between the parasite and the host. In trematodes, for example, host-specificity for the first intermediate host is more pronounced than in any of the subsequent stages, whereas in tapeworms the greatest degree of intimacy occurs with the definitive host. In trematodes and acanthocephalians the infestive larval stage is already a completely formed young worm that only needs to mature and to grow to become adult. Since the distribution of these parasites in their definitive hosts mostly follows the ecological pattern, it is probable that the physiological requirements of the adult worms are not highly specialized. On the other hand, the infestive larvae of monogeneans and tapeworms on reaching the definitive host must undergo further metamorphosis before acquiring adult characters. The necessary conditions appear to be very strict and the more considerable the metamorphosis the greater the degree of host-specificity, the latter following the phylogenetical pattern. Although there is, as yet, insufficient evidence for parasitic nematodes, it seems, however, that there might be a specific mechanism that triggers the final moults of the infective larva.

Free-living flea larvae require strict conditions as to temperature and degree of humidity, implying that their physiological requirements may be rather specialized. But the legendary mobility of adult fleas and their resistance to starvation enable them to survive, but not necessarily to reproduce, by practising the art of host-hopping.

During their entire life-cycle, biting and sucking lice remain attached to the host. So it is not astonishing that their physiological requirements appear to be highly specialized as regards hair and feather structure. In birds, their host distribution appears to reflect principally the latter.

Summing up the effects of both external and internal factors responsible for parasite relationships we find that parasites do not select their habitat but that the latter is imposed by ecology. The resulting distribution, however, also reveals another selective mechanism, namely, the degree of physiological and morphological adaptation of the parasites themselves.

Prof. W. E. Kershaw (Liverpool School of Tropical Medicine), in discussing the evolving human filariae, suggested that it was more pertinent to consider their present evolution rather than what had happened in the past. This was possible because of precise information of those pathogenic human parasites which it had been necessary to obtain urgently in order to devise economic and practicable control measures. Their complicated life-cycles involved man, possibly other animals, and usually multiple species of vectors, each vector with its own sequence of environments. The parasite, therefore, should be regarded as one component of a parasite-host-vector complex. The true evolving entity was therefore not the parasite but the complex, which was evolving as were the separate components, and it was behaviour rather than structure which was critical.

Loa loa, a parasite responsible for the recurrent and crippling so-called Calabar swelling, occurs in West and Central Africa. There were two parasite-

host-vector complexes, an infection occurring in man and transmitted by two species of the vector genus, which bite during the day, and another occurring in three or more species of monkey which are adapted to different but related species of the vector which bite during twilight and at night. Both parasites were very closely related and differed only in their general dimensions and in their adaptation to different vectors. Each was well tolerated by the different vertebrate hosts and equally well transmitted by all the related vectors in the laboratory, but little interchange between these two populations occurred in Nature.

Malayan filariasis caused recurrent lymphatic inflammation and fever and often resulted later in the disabling permanent swelling of the limbs and the genitals known as elephantiasis; one form occurred in the north-west (periodic) and the other in the south and east of the Peninsula (non-periodic). The parasites responsible had only trivial structural differences, differing mostly in behaviour. In the 'periodic' form the larvae were rarely found in the blood during the day, being most numerous at night. In the 'non-periodic' form, the larvae were apparent during the day and night in similar numbers. The larvae of these two forms behaved differently in the blood, they had different groups of vectors, and though both could be transmitted easily to cats, one form is not so well adapted to animals and occurs naturally only in man; whereas the other form is well adapted to animals and occurs naturally in man, in several species of monkey, in the domestic cat and in the pangolin.

In addition to these two infections in man, one of which is shared with many animals, there was a further and separate parasite which behaves a little differently from the other two, was transmitted by vectors somewhat different from the others and occurred in a very large range of animals, including the dog, the domestic cat, two species of wild cats and the civet cat, the tiger, the pangolin, the moon-rat and the slow loris, and could be transmitted experimentally to man and to the domestic cat. It had so far been found in the State of Pahang.

Work in East Africa had disclosed a fourth parasite, occurring in animals but not so far in man, closely related in structure to the two forms of human filariasis in Malaya and to that described in the State of Pahang occurring in a large range of animals. There were four related parasite-host-vector complexes, one of which had separated from the other three and was so far believed to be restricted to East Africa, and three occurred in Malaya. These three in Malaya are now evidently undergoing further divergent evolution, though their overlap is still very considerable.

Onchocerciasis caused skin changes and was associated with blindness in Central America and in tropical Africa. In the Americas, the adult worms occurred in nodules in the head and neck and eye changes were common, while in Africa they occurred on the lower part of the trunk and the legs, and eye changes were less common and occurred mostly in old-standing infections, so that they were once thought to be due to different parasites. In Africa the distribution of the larvae in the skin had a very clear pattern both on the surface and in depth, and in early infections these larvae were limited to the legs. Only when exposure to the infection had been repeated for many years did the concentration of larvae rise and were they to be found in the upper parts of the

body. While similar precise information was lacking in the Americas it seemed likely that the larvae were most numerous in the head and neck. The vectors in Africa bit on the ankle and leg, and in America on the head and neck. These two different parasite-host-vector complexes have the same host and the same parasite, but differ in their manifestations because of the different behaviour of the two different groups of vectors.

The fundamental research undertaken to make it possible to devise economically practicable control measures has disclosed evolution in progress.

Dr. C. A. Wright (British Museum, Natural History) discussed the relation between trematodes and molluscs. The problem of speciation in the digenetic trematodes had received little attention. Isolation of some kind is an essential factor in the evolution of new species, and it is suggested that the part played by the molluscan intermediate host is of considerable importance in the speciation of flukes. The effective geographical range of a parasite is that area where all of the hosts necessary to the completion of the life-cycle occur together. The ecological requirements of most molluscs are such that a species is seldom uniformly distributed throughout its range but is broken up into separate populations between which there are varying degrees of isolation. These populations serve as the foci for the completion of fluke life-cycles and it is around these centres that the gene pools are formed from which new species may arise. There are three main factors in the maintenance of the purity of the gene pool, the geographical isolation of the locality, movement of the definitive host and the longevity of the adult parasite within that host. The third factor may partly offset the second for, if the parasite matures quickly, lays its eggs and dies, there is less chance of the eggs reaching other centres where the cycle could be completed even if the definitive host is very mobile.

The importance of host-restriction in the parallel evolution of host and parasite is of great significance, and the degree to which this phenomenon is shown in the relationship between larval flukes and their molluscan hosts is far greater than it is between the adult flukes and their vertebrate hosts. In those flukes which have a free-swimming miracidium there are at least two ways in which new fluke-mollusc relationships may occur. In the process of host-location by the miracidia the first stage is a response to physical stimuli which bring the larvae into the region of the host-habitat. Thus, the substitution of a different mollusc having the same ecological requirements as the normal host may result in the adoption of this new host if its tissues provide an acceptable environment for further development of the larvae. The last stage of the host-finding pattern by miracidia is a response to a chemical stimulus. Paper chromatography has shown the presence of species-specific substances in the body-surface mucus of freshwater snails and it is possibly these substances which enable miracidia to discriminate between potential hosts. It has now been shown that there exist differences in the composition of the mucus of snails of the same species from different populations and this may have great significance in the evolution of new mollusc-fluke relationships.

Dr. Theresa Clay (British Museum, Natural History) made some suggestions about the evolution of host-parasite relationships in the Mallophaga of birds. It was possible that the breaking up into

non-breeding units by the birds during their evolution would result in isolated populations of Mallophaga and was analogous to the situation found on a group of continental islands the populations of which had become isolated by the disappearance of land connections. Later secondary infestations of Mallophaga from one host group to another are analogous to the trans-oceanic colonization of oceanic islands. Successive colonizations and the occupation of the different ecological niches on the body of the bird could explain the number of different genera and species of Mallophaga found on one host species. During the time that the Mallophaga were still partly free-living and before they had developed any close adaptation to life on the bird or to a particular bird species, interchange of host was presumably more frequent. Thus, although birds within an order or sub-order are usually parasitized by related mallophagan faunas which have presumably evolved on these orders, the origins of related mallophagan faunas on different orders are difficult to assess. In the affinities between mallophagan faunas of the birds¹, a diagram meant to demonstrate factually these affinities and not necessarily to suggest affinities between the host groups, the similarity of the mallophagan faunas of the Procellariiformes and those of the Charadriiformes, for example, may show no more than an ecological relationship, members of both orders living in the same environment. The fact that in general the species on the two orders are now well differentiated suggests that, if this distribution is due to secondary infestations, it could not have been recent and supports the theory that establishment on a new host took place mainly in the early days of the evolution of host and parasite.

Mr. P. F. Mattingly (British Museum, Natural History) stated that the complete restriction of human and simian malaria to anopheline vectors suggests that this group may originally have evolved

mainly as feeders on mammals. Bird malaria, on the other hand, was carried exclusively by culicine mosquitoes which might thus have originated as feeders on birds. The fact that human filariasis was carried by both anopheline and culicine mosquitoes suggested that it may have entered the system comparatively recently. The comparative physiology and biochemistry of blood-meal utilization in mosquitoes had been very inadequately studied. This was a particularly promising field for research which might throw light on many problems.

Prof. G. C. Varley (Oxford) believed that host specificity needed careful definition. Not only must both host and parasite be accurately identified, but also those cases where a parasite can only complete part of its development must be distinguished. Published lists unfortunately often gave equal emphasis to unique records and to regular parasite relationships.

Prof. Baer considered that the relation between a parasite and a group of hosts, related by ecology or phylogeny, was biologically significant, whereas the relation between one parasite and one host meant little.

Prof. Baer believed that the biochemical approach to species determination should be encouraged in the way that Dr. Wright was applying it to snails, and that isolated proteins and carbohydrate fractions from hosts and parasites might be used.

Dr. J. Sandground (New York) described his experience with onchocerciasis in Guatemala and in the Gold Coast, and referred to his demonstration some twenty years ago that the parasites in the New and Old World were identical. He believed that much more work remained to be done in onchocerciasis before the infection could be understood adequately and before control would be easy.

WILLIAM KERSHAW

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ANIMAL CLOCKS

THE significance of rhythmic activities in animal physiology is becoming increasingly evident to-day. For this reason, the symposium on 'animal clocks' held in York on September 4, by Section D (Zoology) of the British Association for the Advancement of Science, was well timed. During the morning sessions, Dr. L. Harrison Matthews, section president, was in the chair.

The first speaker, Prof. F. A. Brown, jun. (North-western University), described recent research carried out in his laboratory. In 1948 he had established that the frequency of the rhythm of colour change in fiddler-crabs was independent of temperature over a 20-deg. C. range. Later it was shown that this 'indicator' process was itself regulated by a more fundamental rhythmic element and that two control centres were involved. Although the concept of an autonomous clock is retained by most investigators, Prof. Brown now postulated that the periodisms which comprise basic biological clock systems are imposed by environmental changes even in conditions hitherto presumed to be constant. This hypothesis he supported by a detailed statistical analysis of data obtained by means of an automatic recording respirometer from organisms as unrelated as fiddler-crabs and potatoes which

had been hermetically sealed in constant conditions including pressure, for several days at a time.

Although other speakers did not agree with this view, all must have been stimulated to look more carefully at their own data. Unfortunately, it has so far proved almost impossible to devise a really critical experiment that will differentiate between an innate clock mechanism and one derived from exogenous sources, since it appears possible, by analogy, to alter the position of the hands of the clock relative to the works. Just as it is difficult to conceive of a distance-judging mechanism independent of space, so a clock system presumably requires some fixed points of reference.

In a paper on the influence of the environment on the cyclical biting-behaviour of mosquitoes, Dr. A. J. Haddow (director of the East African Virus Research Institute) pointed out that every species so far studied has shown a 24-hr. periodicity. In some, this is merely nocturnal or diurnal, but in others most of the activity is confined to one or two short and precisely delimited periods. These, while usually very constant for a given environment, may be entirely different in another. Further, they may show very striking differences at different levels