The rabbit flea and hormones

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The importance of the rabbit flea as a vector for myxomatosis led to attempts, at first unsuccessful, to breed the flea in the laboratory. This article describes the experiments with the rabbit flea that showed that the life-cycle of the flea is dependent upon the hormone cycle of the host.

In 1953, myxomatosis, a virus disease of native rabbits of South America, reached Great Britain, and within a short period it had killed between eighty and ninety million rabbits. In Australia, where the disease had been introduced in an attempt to control these destructive animals, it was spread by winged vectors, chiefly mosquitoes. It seemed more likely that the disease was carried in Britain by the rabbit flea (*Spilopsyllus cuniculi* Dale) [1], which does not occur in Australia but is present on all populations of rabbits on the mainland of Great Britain.

When it was proved beyond reasonable doubt that this supposition was correct, it became evident that further information was required about the rabbit flea. It was important to study myxomatosis with the object of obtaining a better understanding of the epidemiology of the disease [2], and also of big, insect-borne epizootics in general. In Australia, attenuated strains of the virus had appeared and the rabbits had evolved immunity and resistance to the disease. With a flea vector, would events follow a similar course in Britain?

In order to investigate these possibilities, we needed to breed the parasite, as well as the host, in the laboratory. The problem was tackled in two ways: firstly by observations made on fleas on wild rabbits; and secondly by observations and experiments carried out in the laboratory, using domestic rabbits. It is usually a fairly simple matter to breed fleas on captive hosts: for example, the oriental rat flea *Xenopsylla cheopis* Roths, the most effective vector of bubonic plague, presents no problem in this respect; all it requires to initiate copulation and egg-laying is a blood meal [3]. The hen flea *Ceratophyllus gallinae* pairs and is successfully fertilized even without a blood meal, and before it shows any signs of maturation. A slight rise in temperature is an adequate stimulus. The eggs develop subsequently after a blood meal on a bird, or even on a 'wrong' host, such as man. The rabbit flea, on the other hand, lived for months on the host in the laboratory, but did not mature, pair, or lay eggs. It was eventually discovered that this species appears to be an exception among insect parasites, since its breeding cycle is dependent on the hormone cycle of its vertebrate host. By this link the two cycles are perfectly synchronized in nature.

The principal experiments

When work on the life-cycle began, we were baffled by the fact that the fleas failed to breed, although they lived for many months, including those of the spring and summer, on our rabbits in the laboratory. Yet in the wild, we found the eggs and larvae in the rabbit's nest, which

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showed that they were breeding at the same time as their host. Was the laboratory failure due to the lack of some subtle factor found in nature, such as changes in temperature or humidity, or in hours of sunlight; or was it due to an increase in vitamins in the host's natural diet, or to the special conditions that existed in burrows? The fact that fleas of both sexes lived side by side, ingesting copious blood meals, and yet did not attempt copulation, gave us the first clue to the solution of this problem. It was postulated that some sudden change in the blood of the host was required to activate the male and trigger off the impulse to pair. A little reflection indicated that the sex hormones of the host fulfilled the theoretical requirements of such a factor. A. R. Mead-Briggs and A. J. B. Rudge [4] followed up this idea, and demonstrated that the ovaries of the female rabbit flea matured only on pregnant does. This discovery gave great encouragement to the hormone theory, and switched our attention to the female, rather than the male, flea.

The number of hormones that could be involved in such a trigger mechanism was obviously considerable, and it was necessary to design an experiment that would eliminate as many as possible of the irrelevant factors simultaneously, while confirming the role of the mammalian sex hormones in the maturation of the flea.

About 150 freshly emerged fleas were introduced on to a normal female rabbit, which was then mated to a sterilized (vasectomized) buck. Copulation between the rabbits induced ovulation in the doe, and a pseudo-pregnancy followed. The ovaries of the female fleas matured on the fourteenth day [5]. This simple but important experiment showed that the placental hormones and the foetuses could be eliminated from our calculations; yet at the same time it confirmed that the hormones concerned with pregnancy in the rabbit were also concerned with maturation of the female flea and with certain important physiological changes which took place simultaneously in the male flea. The next experiment involved injecting an extract of the entire anterior lobe of the pituitary gland (a commercial preparation, Ambinon B) into a castrated buck rabbit. The ovaries of fleas feeding on this rabbit matured (figures 5 and 6), and the parasites laid sterile eggs (figure 8) on the seventh day.

It was now necessary to find out if maturation was stimulated in the flea by one of the six main polypeptide or protein hormones—such as prolactin, luteinizing hormone, and thyrotrophic hormone—of the anterior lobe, or whether the stimulus was provided by these hormones acting on target organs in the rabbit, such as the gonads and the adrenal glands, which in turn secreted the relevant steroids, such as progesterone, the oestrogens, and the corticosteroids. In a typical experiment, an ovariectomized rabbit was injected with luteinizing hormone. Since the target organs—the ovaries—had been removed, any response on the part of the fleas would

have indicated that it was this polypeptide hormone itself which was influencing maturation. In the normal entire doe, the luteinizing hormone would have stimulated the corpora lutea of the ovaries to secrete progesterone, and the response of the flea could have been to either hormone. The luteinizing hormone failed to elicit any response and could henceforth be disregarded as a primary factor causing maturation. All the experiments consisted basically of a series of trial and error assays, using freshly emerged fleas, various hormones, and castrated, ovariectomized, and thyroidectomized hosts, and hosts in which the temperature and blood pressure had been raised or lowered artificially. Eventually it was shown [5] that the most effective hormones controlling maturation in the rabbit flea are the corticosteroids (figures 5 and 10), produced by the adrenal glands under the control of the adrenocorticotrophic hormones, secreted in their turn by the anterior lobe of the pituitary. Oestradiol also exerts an influence on maturation and the ovarian cycle in the flea. Furthermore, large doses of thyroxine (a hormone secreted by the thyroid gland in response to the thyrotrophic hormone from the pituitary gland) when injected into the rabbit can induce maturation in the rabbit flea [5]. But since it was also found that the parasite can mature and lay eggs on thyroidectomized rabbits, it seemed fairly likely that thyroxine acts indirectly, by boosting the metabolism and stimulating the adrenal glands to secrete more corticosteroids. However, a maturing flea normally develops an accelerated defaecation rate, and this was not shown by those reared on the thyroidectomized rabbits, nor by those fed on rabbits given very small doses of hydrocortisone. It is therefore obvious that in nature more than one hormone is involved, directly or indirectly, in the maturation of these fleas.

Up to this stage we were still under the impression that the effect on the parasites was produced by the hormones through their effect on the rabbit. Thus we assumed that the rise in the hormone levels in the host affected its metabolism, which in turn might have raised its blood temperature, blood pressure, the level of antibodies in the blood, or some other factor in the blood stream, or even the smell or skin texture. Any of these factors, it was thought, might trigger off the secretion of the fleas' own hormones, which were presumably required, as in other insects, for maturation and the control of reproduction.

In order to throw some light on this aspect of the problem it would have been useful to feed the fleas artificially, through a membrane, adding the various hormones one at a time to their diet, instead of keeping them on a living animal. The rabbit flea, however, is not a good subject for membrane feeding, and the hormones were therefore sprayed directly on to the fleas, which were subsequently introduced on to castrated buck rabbits. It was thus shown that the corticosteroids, and to a lesser degree the oestrogens, exert a direct effect on the rabbit flea. The sprayed fleas mature and lay eggs (displaying the associated 'maturation' changes in the salivary glands, gut, and defecation rates); in addition they remain gravid for relatively very long periods (figure 3). Presumably the hormones are absorbed slowly but continuously through the cuticle. It also became clear from these experiments that, quite apart from the quantity of mammalian hormones absorbed by the flea, nutrition plays an important role in maturation. Hormone-sprayed fleas that fed steadily matured more rapidly and, attained a larger size, than those whose feeding was interrupted or disturbed for one reason or another.

Behaviour of rabbit fleas

The experiments with hormones gave us a clearer understanding of the behaviour of this highly adapted parasite. When freshly emerged rabbit fleas first find a host, they spend about three weeks on the rabbit's muzzle and cheeks, feeding at the base of the whiskers. They then move to the ears, where they fix themselves to the skin of the host by their serrated mouthparts. During the spring and summer months they remain in small groups of about 10–150 specimens in this position, causing a slight but definite irritation to the host's skin (figure 1); if the weather becomes very cold they shift to more protected sites where the fur is longer [6].

Unless the rabbit becomes pregnant, these fleas cannot breed; the chances of their finding a pregnant host are increased by their tendency to transfer to other rabbits that come into close contact with their own host, especially during copulation, play, mutual grooming, or resting together in a confined space, such as a burrow. Fleas tend to mass on pregnant does [7], and our experiments suggest that the raised level of hormones induces them to fix more firmly, and that once they have found such a host, they do not readily detach themselves. During the last ten days of the rabbit's pregnancy, the level of hormones in the host's blood rises sufficiently to initiate the process of maturation in the fleas. This involves a series of profound changes (figures 5 and 6) in the whole organism, which include increased development and enlargement of the salivary glands; an overall increase in size of the gut, with proliferation and growth of the cells lining the midgut; secretion of yolk and maturation of the oocytes; secretion of an egg-shell coating material in the pedicels of the ovarioles; development of the spermatozoa; and increased defecation rate. In the male these changes, although well marked, are not so dramatic as in the female. Thus the salivary glands and cells lining the midgut do not reach the size of those in the female, and the maximum defecation rate of the male is one blood squirt every four minutes—the normal rate is one every fifteen to thirty minutes—whereas in the female, during the last days of the host's pregnancy, it can attain a rate of one squirt per minute. Yolk formation in the female is definitely dependent on the hormone levels associated with the breeding cycle of the rabbit, but it is not yet clear exactly how far sperm development can progress on a non-pregnant adult host.

It is interesting that the level of the hormones in the blood of the host controls not only the process of yolk formation, but also the speed of development and the number of eggs ripening simultaneously. Thus, in nature, there is a gradual and steady development linked to the increasing volume of corticosteroids in the circulation of the pregnant doe, but this can be accelerated by injecting hydrocortisone or corticosterone, or massive doses of oestradiol, into the rabbit.

In nature, the fleas do not pair on the adult rabbit. Fleas may often be observed laying eggs while still fixed to the prepartum doe, but these eggs will be sterile (figure 2). A few hours after the rabbit has given birth, the fleas detach themselves from the ears of the doe and

move into the fur on her face and head. As the adult rabbit tends the newborn ones, the fleas transfer to them, and pairing then takes place. It has been found that whereas a small injection of hydrocortisone into the host will induce the fleas, especially the females, to fix more firmly to the host, a bigger dose causes them to detach themselves and run about freely in the fur on the host's head. It is therefore likely that there are hormone changes in the blood of the doe some hours after she has given birth which account for the changes in the behaviour of the fleas.

Once on the newborn young, the fleas feed avidly. They spread themselves somewhat generally about the body, but prefer the sacral region, and the back and flanks above the tail. Pairing occurs after a few hours. The factor that induces copulation of the fleas is at its maximum in the day-old rabbit, and thereafter wanes, until it disappears when the young are 7–8 days old.

It is now known that the corticosteroid level in the blood of the newborn young rabbits is considerably higher than in the pregnant doe [8], but although this high level is presumably responsible for the increase in the speed of maturation of fleas observed feeding on newborn young [9], it is not responsible for pairing. Fleas do not, for instance, pair on shaved 8-day-old rabbits that have had their corticosteroid level raised above that found in a day-old rabbit. The factor, whatever it may be, influences the female to stimulate the male and then accept copulation. A male flea which has not yet fed on the newborn young, and in which sperm have not reached their maximum stage of development, will nevertheless succeed in copulating with an immature female, providing she has already spent some hours feeding on the baby rabbit. Yet a male flea, either fixed, or free alongside fully matured females on a pregnant doe, or on a rabbit whose corticosteroid level has been greatly increased with injections, makes no attempt to pair. It seems possible that the female flea, after feeding on the newborn young rabbit, becomes receptive herself, and releases a volatile attractant which stimulates the male and draws him to her. His approach to her at this stage is very characteristic: he follows a markedly zig-zag course and then quickly slips beneath her and tips up the abdomen. Both sexes feed while pairing.

At this time the defecation rate is at its maximum. The liquid blood which is passed out of the anus gradually dries and it ultimately falls into the nest. Here it becomes an important element in the diet of the larvae that will eventually develop in the nest debris.

The fleas leave the body of the young rabbit after pairing and generally lay their eggs in the bottom of the nest. The egg, larval, and pupal stages are completed in about 30 days, by which time the nestling rabbits have usually left the breeding place. At the age of approximately three weeks, baby rabbits become unattractive to fleas. This is an adaptation that avoids both over-infestation and the risk, as far as the parasite is concerned, of 'killing the goose'. If, however, the doe has a second litter in the same breeding place, which occasionally occurs, these young rabbits are battened on by the generation of hungry fleas already in the nest, and these can reach the egg-laying stage within two or three days. In nature, second brood nests of young have been found containing thousands of fleas; how much damage they inflict on the baby rabbits is not known.

Figure 1   A group of male and female rabbit fleas feeding on the inside of a rabbit's ear. Note the patches of inflamed skin where the fleas are attached. (× 7)

Figure 2   Fleas under the influence of mammalian hormones laying sterile eggs on the host. Note the blood spattering the hairs. This has recently been passed out of the anus of the flea. The striped appearance of the fleas is due to the distension of the gravid abdomen. (× 8)

Figure 3   Large gravid flea which has been sprayed externally with hydrocortisone. Note the relatively small male in the foreground. (× 15)

Figure 4   Section through part of an ovariole of a flea which has returned to the doe after egg-laying in the nest. The bright red nucleus is at the centre of a resorbing oocyte. The circular blue patch is one of the 'blue bodies', a connective-tissue attachment in the wall of the pedicel. After the eggs are laid, these frequently remain in the base of the ovarioles or ovaries of spent fleas and can then give an indication of the number of eggs already laid. (× 450)

Figure 5   Section through the abdomen of a flea that was feeding on a rabbit which had been injected with hydro-cortisone. The yolk globules in the developing oocytes are stained bright red. The greyish egg-shaped body is one of the salivary glands which enlarge under the influence of the hormones. (× 120)

Figure 6   Section through the abdomen showing elongation of the villi of the mid-gut epithelium. To the left are several developing oocytes. The pedicel of the ovarioles can be seen at the base of the mid-gut, showing its yellow secretion which is one of the earliest manifestations of maturation. This secretion can be detected in the lumen of the pedicels six hours after moving a flea from a normal buck on to a day-old rabbit. (× 170)

Meanwhile the parent fleas, after a period, which varies from 4–20 days, of pairing and egg-laying in the nest, return to the doe. This sudden desertion of the young in favour of the mother is not understood. It may be due to yet another change in the relative hormone levels in the blood of the two age groups, but this is speculation. Curiously enough, the fleas frequently return to the doe long before they are spent, the males with testes still containing many sperm, and the females with sperm still stored, apparently normally, in their spermathecae and with developing eggs in their ovarioles. But once the fleas are settled back on the doe, the eggs are rapidly resorbed and the young developing oocytes are arrested at an early stage, before yolk formation; the salivary glands in both sexes regress; and the midgut epithelium and the secretory epithelium of the pedicels return to the form seen before maturation. Females in which the changes have taken place reveal they have laid eggs by the presence of degenerating egg follicles (corpus luteum) in the ovarioles and of 'blue bodies', which are areas of connective tissue below the site of attachment of the proximal oocytes (figure 4). Should the doe become pregnant again, these fleas can, in response to the rise in the hormone level, commence a new breeding cycle, although their reaction is slower than that of virgin fleas. Since fewer males are found to be available at this stage, it is assumed that a fairly high proportion die in the nest after pairing.
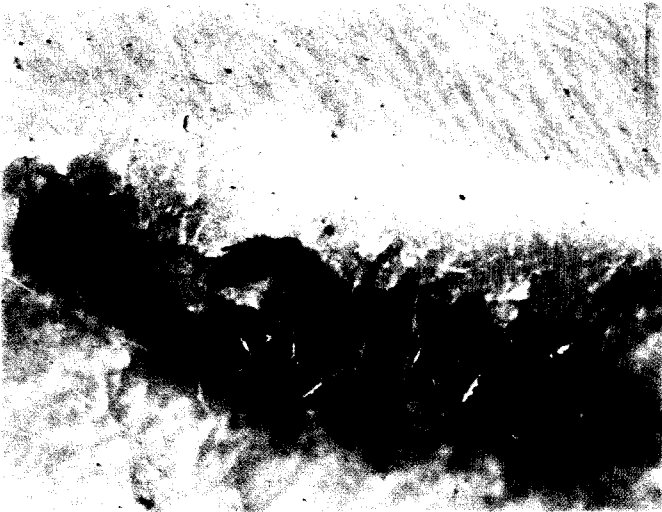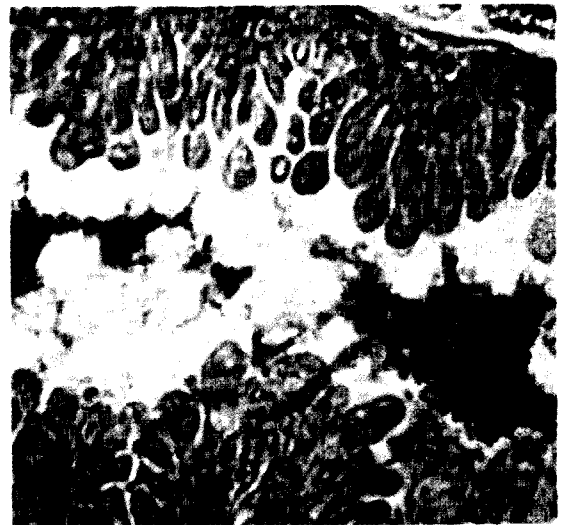
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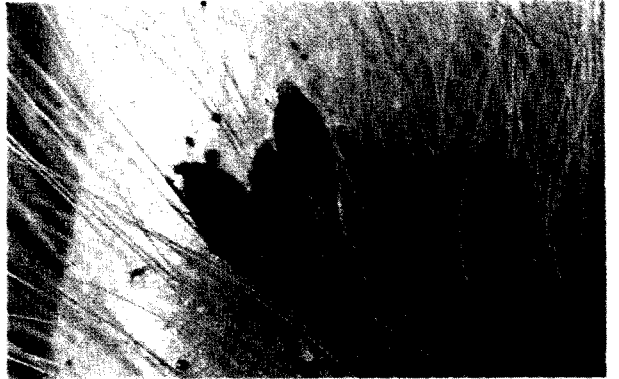
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Figure 7 Section through the testes of a freshly emerged flea. The sperms are still relatively undeveloped, and the 'heads' are undifferentiated and confined in their hyaline cysts. (×530)

Figure 8 Blood passing through the proventriculus of a flea into the mid-gut. Note the strong chitinous spines. (×560)

Figure 9 Section through the testes, showing sperm with heads differentiated but still only partly developed. Testes of fleas which are fully matured appear in section as a tight mass of sperm in which there are no spaces and in which it is impossible to trace the course of a single sperm. (×670)

Figure 10 Epithelial cells lining the mid-gut developing under the influence of ACTH, with which the host had been injected. (×440)

Figure 11 Section through the terminal portion of a developing egg seven days after an injection of 'Ambinon B' into the host. Note the egg-shell (chorion) is already well developed. The tiny holes at the anterior end are the micropyles. (×400)

It is striking that there is no spermatogenesis in the adult flea, and that when the flea emerges from the pupa, the testes already carry their full complement of sperm. Once used up there is no replacement. Although the flea's spermatozoa grow and develop while on the host (figures 7, 9), no new sperms are formed. The pattern is different for the female, since eggs can be developed from the germarium of each ovariole practically throughout the life of the adult.

Comparison with other species of flea

It is clear that the rather specialized breeding habits of the rabbit, combined with the specialized feeding habits of the rabbit flea, have placed a premium on the linking of the two sexual cycles. By their response to these hormones in the host, the fleas are guaranteed their breeding habitat. They are transported by the doe to her nest, which is frequently constructed away from the main warren, and by their reactions to the rise and fall in the levels of corticosteroid and other hormones in the host they are induced to leave the doe at the critical moments following parturition, and to lay their eggs in the nest with the newborn young. The food supply is thus guaranteed for their own developmental stages, which are spent in the nest.

In nature there are probably other parasites which respond to the sexual cycle of the vertebrate host, especially the internal worm parasites, but among fleas the most likely group in which to seek a parallel phenomenon are bat fleas of the genus Ischnopsyllus Westwood. In the spring certain species of bats leave their winter quarters and the females repair to special summer breeding roosts on their own. It has been noticed [10] that before the bats depart, the fleas crowd on to the females. This clue is well worth following up.

It was thought at one time that perhaps all fleas required a certain level of corticosteroids in the blood of their host for successful breeding, and that the only feature peculiar to the rabbit flea was that it had become geared to the higher levels characteristic of pregnancy. However, this surmise proved to be incorrect, since the oriental rat flea Xenopsylla cheopis Roths. will breed on hypophysectomized rats [11].

Corticosteroid levels in the host

The only insect known to be sensitive to the corticosteroids in the blood of the host is the rabbit flea, which responds to the minuscule dose of 16 μg of hydrocortisone injected into a 10 lb rabbit. The flea's reactions and behaviour on the host indicate that there is a steady rise in the level of corticosterone in the rabbit's blood during the last 10 days of the host's pregnancy, possibly a further short rise in the first few hours following parturition, and thereafter a decline to normal prepartum levels. The flea also indicates (by rapid maturation and restlessness) that the level of corticosteroids in the blood of the newborn rabbits must be at least twice as high as in the doe, and that in 3–5-week-old rabbits, on the contrary, it must drop to a lower level than at any other time of their lives. Since our experiments showed that the flea is much more sensitive to hydrocortisone than corticosterone, its behaviour on the baby rabbits suggests that perhaps hydrocortisone may be present in the young (one to six days old), although it has not hitherto been detected in measurable quantities in adult rabbits.

We have often noticed that when the young are born dead or are feeble—and about 50 per cent of winter litters are non-viable—the fleas fail to leave the doe after parturition. This suggests that the hormone level in the blood is not raised sufficiently to stimulate detachment from the ears of the host. It is possible that hormone imbalance may be one of the factors adversely affecting the young rabbits in the winter litters. Furthermore, it has been found that the ovaries of fleas feeding on rabbits suffering from myxomatosis [14] also mature, even though the rabbits are not pregnant. This may be due to a stress reaction in the diseased host which in turn raises the level of the corticosteroids in its blood.

Mechanism of action

It is, of course, not known how the mammalian hormones produce their effect on the rabbit flea. The investigation of maturation—the secretion of yolk and the various changes which culminate in egg production and fertilization—has revealed that a very complex system controls these activities in insects. V. B. Wigglesworth has concluded [12, 13] that neurosecretory cells in the brain (protocerebrum) and suboesophageal ganglion, the corpus allatum and corpus cardiacum, and the ovary, are all involved in this process. They influence one another by nervous stimuli, by neurosecretions carried along nerve pathways, and by humoral factors circulating in the blood. He pointed out that the relative parts played by the different elements in this system vary from one insect to another.

One of the most important factors involved in insect maturation is the secretion of the so-called juvenile or yolk-producing hormone, the action of which is reproduced by farnesol [13]. It has been found that, in nature, a wide variety of stimuli, ranging from distension of the abdomen with blood, to the act of copulation, can initiate the secretion or release of stores of this hormone into the body tissues. It may well be that in the rabbit flea there is a direct relationship between the mammalian hormones and the secretion and release of the juvenile hormone, or possibly of the hormone from the neurosecretory cells of the brain. When the corticosteroid level in the blood of the host is high, it would seem that the juvenile hormone levels are also high, and that these fall off correspondingly

167

when the mammalian hormone is withdrawn or when its level in the blood is reduced. Fleas sectioned after they have spent a period of 6–24 hours feeding on the newborn young, in which the corticosteroid levels are at a maximum in the rabbit, demonstrate that various changes associated with maturation are occurring simultaneously in different organs. However, experiments have also shown that not all the organs in the flea respond to the same levels of hormones. Thus, for example, relatively low doses of corticosteroids result in yolk formation and ovariole secretions, but much higher levels, characteristic in nature of those associated with the last days of pregnancy and the first day of life, are required to produce the highest defecation rates in the fleas. Furthermore, small doses induce them to feed steadily, whereas very large doses make them restless and intermittent feeders. This in turn slows down maturation.

It is, of course, possible that this flea has now progressed so far along the parasitic road to dependence that it has lost the power of secreting its own hormones and has to make use of the mammalian hormones themselves. This is unlikely, since, during the larval stages, the flea requires secretions of the juvenile hormone without which the insect would undergo precocious metamorphosis [13]. It is extremely improbable that the larval fleas would have to rely for their supply of this hormone on the blood of the host, passing out of the anus of the parent flea. It seems more reasonable to suppose that the flea can still secrete its own juvenile hormone but that its release is under the influence of the hormonal blood levels of the rabbit. This is certainly one of the more interesting aspects in the life of the rabbit flea and is worthy of investigation. Unfortunately, since the advent of myxomatosis and the reduction in the numbers of its host, the

rabbit flea has become relatively scarce. Furthermore, it is not easy to handle, and these considerations make an early solution of the problem rather unlikely.

Acknowledgments

References

[1] Rothschild, M. 'Report to the Myxomatosis Advisory Committee'. 1953. (Private circulation.)
[2] Andrewes, C. H. *Nature, Lond.*, 174, 529, 1954.
[3] Suter, P. R. *Acta trop.*, 21, 193, 1964.
[4] Mead-Briggs, A. R. and Rudge, A. J. B. *Nature, Lond.*, 187, 1136, 1960.
[5] Rothschild, M. and Ford, B. *Ibid.*, 201, 103; 203, 210, 1964.
[6] Idem. 'Movements of the Rabbit Flea (*Spilopsyllus cuniculi* Dale) on the Captive Host'. 1st Cong. Parasitology, Rome. September 1964.
[7] Allan, R. M. *Proc. R. ent. Soc. Lond.* (A), 31, 145, 1956.
[8] Exley, D., Ford, B., and Rothschild, M. (In preparation.)
[9] Mead-Briggs, A. R. *J. exp. Biol.*, 41, 371, 1964.
[10] Hurka, K. *Acta faun. ent. Mus. nat. Pragae*, 9, 57, 1963.
[11] Rothschild, M. and Ford, B. *Proc. R. ent. Soc. Lond.* (C), 29, 35, 1964.
[12] Wigglesworth, V. B. *Endeavour*, 24, 21, 1965.
[13] Idem. In 'Advances in Insect Physiology', Vol. II, pp. 299, 302, 1964.
[14] Rothschild, M. and Ford, B. 'Reproductive Hormones of the Host Controlling the Sexual Cycle of the Rabbit Flea (*Spilopsyllus cuniculi* Dale)', XII International Congress of Entomology, London. 1965.

Book reviews

LATTICE THEORY

Introduction to Lattice Theory, by D. E. Rutherford. Pp. x+117. Oliver and Boyd Ltd, Edinburgh and London. 1965. 35s. net.

The aim of this elegant and well-written little book is to present the basic ideas of lattice theory to beginners in the subject. However, although the book demands no previous technical knowledge, a reader who is not already trained to receive modern abstract mathematics in general, and modern algebra in particular, is unlikely to make much of it. With this proviso, one can say that the job has been well done: the monograph deals briefly with a fair number of topics, above all the Boolean algebras and their various applications to formal logic and the theory of switching circuits. There are also accounts of Brouwer algebras, intuitionist logic, topology, and metric spaces. The author's claim to treat algebraic geometry as well as the rest is a very slender one: the whole lot is knocked off in a couple of pages. This may indeed be a

formalist's notion of what the topic comprises, but it is far from being a geometer's.

The general production of the book is excellent. For those who can take it, the work is warmly welcomed.   *L. Roth*

ELEMENTARY PARTICLES

The Eightfold Way, by Murray Gell-Mann and Yuval Ne'eman. Pp. xi+317. W. A. Benjamin Inc., New York and Amsterdam. 1964. Paper, $4.35; cloth, $8.80.

Over the last few years, our list of strongly interacting particles (the 'hadrons') has been increasing at a considerable rate with the continuing discovery of further particle states, and it has become clear that the hadronic states occur grouped in characteristic patterns of charge multiplets. These octet and decimet patterns correspond to a unitary (or SU(3)) symmetry for the hadronic interactions, and its recognition has been the most significant development to date in our knowledge of the hadrons and their strong interactions. This unitary

symmetry represents a generalization of the charge independence property (equivalent to an SU(2) symmetry) which has been known for nucleons and nuclear states for several decades.

This volume collects together a large fraction of the basic papers on SU(3) symmetry and its implications for elementary particle states. The papers are grouped into chapters, for example on the mass formula, supermultiplet assignments, the symmetry-breaking interactions, and on the SU(3) properties of the electromagnetic and weak interactions. The authors have prefaced each chapter by a few pages of introduction to set the scene and to direct the reader's attention to further papers which elaborate particular topics. Every scientist interested in the properties of the elementary particles will wish to have this important collection of papers on his bookshelf, close at hand for easy reference. The reviewer has found himself referring to it many times every day.   *R. H. Dalitz*