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A RADIATION THEORY OF THE ASSEMBLING OF MOTHS

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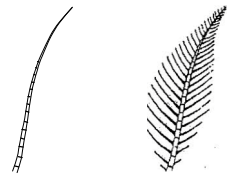
(Plate III) — [Figs. 3 & 5 — omitted here]

The ability of the females of certain species of moths to attract large numbers of males, often from long distances, is well known. It is possible that the phenomenon may be displayed, to a more or less extent, by all species of moths, although attention has naturally been focussed on-those species in which the sense is most highly developed. Possibly exaggerated reports have stated, that males have been attracted from distances of over ten miles. Certainly reliable experimental evidence is available, which indicates that marked males have flown in an almost direct line to a female placed one mile away (Imms, 1947). It is well-known among entomologists that only virgin females are suitable for enticing males in this way and that once a female has mated the attraction ceases. A further experimental fact, also well known to the collector, is that an empty box which has contained a virgin female can be used to attract males of the same species.

This last fact is probably largely responsible for the early belief that assembling was attributable entirely to an olfactory mechanism. Indeed subsequent observations produced further evidence in favour of such a theory. Scent glands, which are exposed in the virgin female moth, become retracted after mating. The antennae of the males of species which assemble most readily are invariably highly pectinated as shown in fig. 1(b) and fig. 5, a-feature which undoubtedly gives them a much larger area than that of a filiform structure (fig. 1(a)). The male antenna has been established as an olfactory receptor.



(a) (b)

FIG. 1
Forms of antennae. (a) Filiform; (b) Pectinate.

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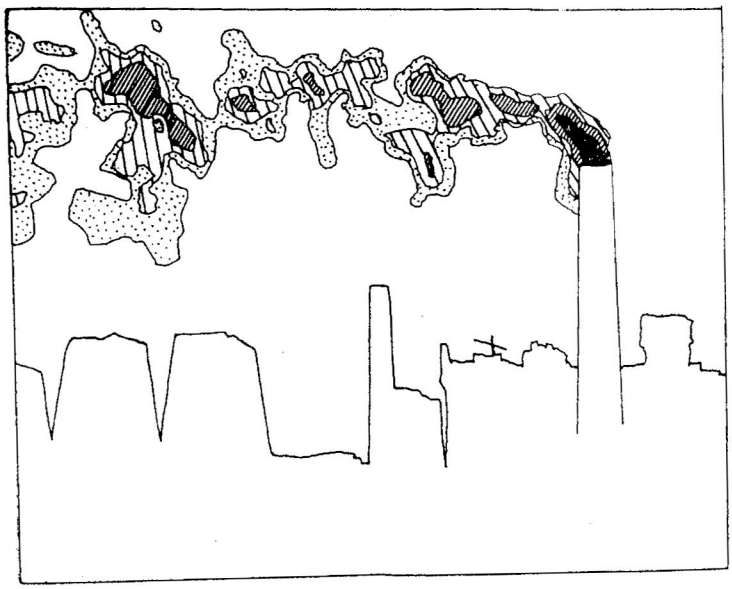
Any scientific theory remains good until the facts which it fails to explain become too numerous to be disregarded. In the light of such new evidence the theory is either discarded or modified. If the weight of evidence in favour of the theory is large, it is unlikely that it contains no truth, and it IS most probably only one facet of a much wider theory. There appears to be some evidence that the scent theory is not the whole truth in the case of the assembling phenomenon. In this paper, this evidence is discussed and a modified theory is suggested in which electromagnetic radiation plays a part.

FIG. 4



Density Contour Map of Fig. 3 (Plate III) [=*photo: omitted here*]

The Olfactory Theory

An olfactory mechanism depends on the transference of molecules of substance from the source to the observer, where they are in some way absorbed. To enable an observer to obtain an indication of the direction of a source of smell, two conditions must be fulfilled:

(a) There must be a particle density gradient increasing in the direction of the source.
(b) The observer must be able to move relative to the particles. This is to say that a field of particle density is essentially a *scalar* field.

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In the idealised example illustrated in fig. 2(a) a source S is situated in still air, so that the natural diffusion of the emitted scent particles produces a field of particle density as shown, the lines on the figure being contours of equal density. A wandering observer who chanced into such a field, and was immediately interested in locating the source, would do so in the least possible time by moving at right angles to the contour lines, just as if he were climbing a hill and the contour lines were lines of equal height. Such a path is shown by the full line AS in fig. 2(a). If the observer can only respond to the first derivative of intensity, he will proceed by the process of trial and error turning either left or right as soon as he observes that the density is decreasing as he moves. Examination of the conditions of the field, shown in fig. 2(a), reveals that his path will be along the dotted line AS since he will tend to continue in one direction until the density no longer increases.

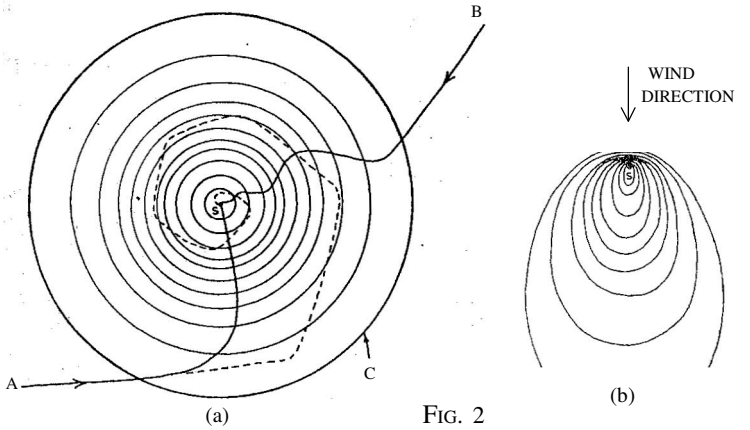

FIG. 2

If the observer has two separate receptors which record independently, the results .can be compared and he will discover the line of greatest slope by maintaining signals of equal strength in the two receptors. He can only direct himself to the extent that he can measure the difference between the signals. His path is shown as ES on fig. 2(a), the deviation from course necessary to cause an error becoming smaller as the density gradient increases. There is clearly a contour such as C outside which the density gradient cannot be detected. The problem is analogous to that of a two-footed creature climbing a hill blindfold.

Fig. 2(b) shows a field of particle density resulting from a source placed in a stream of air moving with laminar flow. The boundary contour is displaced asymmetrically with regard to the source and the observer is unlikely to locate the source from very far up wind of it. <115>

The air of the countryside is not likely to flow in lamina fashion. Hedges, trees and the ground itself produce turbulence to a very high degree. Fig. 3 gives some indication of the field of smoke density across a landscape, whilst fig. 4 is an attempt to draw the density contour map of fig. 3. It is apparent that an observer is likely to make many deviations from the direct line in finding the source, for each time he "mounts a false hill" and reaches its summit, he must set out in a random direction and refuse to be influenced by that hill for some time following, if he is to avoid climbing it a second time. He may be unlucky and turn his back on the source in descending a false hill. The field density pattern will change continuously as it drifts across the landscape. The evidence on assembling points strongly to the fact that a long-distance approach by a male is made in almost direct line and it has been established that males will assemble from both up and down wind.

This is the first piece of evidence which is difficult to explain by olfactory means.

The Evidence of the Empty Box

The empty box experiment establishes beyond doubt that males are attracted by some *substance* which may be detached from the female and still remain active. Furthermore, it is sufficiently powerful to be attractive even though it may have been obtained from a female in an unnatural manner in a box where, as some entomologists would describe it, "the condition would have a psychological effect on the female". The likelihood that the male is attracted by the *smell* of the empty box must surely be near to 100%. This being so, it becomes difficult to explain how a female, which has been putting out scent whilst at rest on the ground, can fail to attract males immediately after pairing, for such is the experimental evidence. The surrounding herbage as well as the air for a mile around must be full of her scent, and yet attraction ceases on pairing.

In view of these facts, which must throw grave doubts as to the validity of the olfactory theory, experiments were carried out using a species known to assemble readily.

Experiments with the Vapourer Moth

The common Vapourer *(Orgyia antiqua* L.) has a wingless female. It lives in colonies, despite the fact that in each generation the larvae walk considerable distances. The males have well-developed antennae and fly by day. Such qualities make the species ideal for experimental studies. Females can be transported from a colony to a locality well away from other specimens and males released where and when desired. The first two experiments yielded the following confirmation of reports which have already been published elsewhere. (1) Males will assemble to a virgin female both up and down wind. (2) A virgin female will attract males released 100 yards away. Once fertilised, a female can no longer attract males from 100 yards. <116> The second result is particularly interesting in view of the apparent conflict with the empty box experiment. The latter was repeated using female Vapourers and yielded the well-known, result.

Further experiments were now performed, the results of which threw considerable light on the apparently conflicting phenomena of the fertile female and the empty box. It was found that if males were released at a distance of 10 feet they would immediately assemble to (a) an empty box, (b) a fertilised female, (c) a dead female, (d) eggs, (e) an empty female pupal case. If released 100 yards away they were *not* attracted by any of the subjects (a) to (e) above, unless by chance, after a long period, they wandered into close proximity.

This evidence suggests strongly that there are two distinct phenomena — the long range and the short range. The latter is almost certainly a scent process. The long range mechanism appears to be quite different. One other interesting observation was made during the experiments. When males were being attracted from a long distance over open field they could be seen coming in an almost direct line until they were within some 10-15 yards of the female. Their flight then changed to a path similar to BS on fig. 2(a) suggesting the size of the contour C where the mechanism of the assembly changed over.

The following theory was formulated in an attempt to explain the long range mechanism.

(To be continued.) <117>

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(Continued from page 117)

A Radiation Theory of Assembling

This theory was first inspired by observation of the similarity between radar "antennae" and assembling male moth antennae. Fig. 5 [missing photo] and 6 illustrates this similarity. The structure of the man-made aerial (fig. 6) is the result of careful calculations, which were made in order to give the aerial high sensitivity, directive properties and so on. These calculations demand that the shape of the structure conforms to certain mathematical laws, for example the spacing and length of the dipoles is related to the wave-length of the radiation to be received.

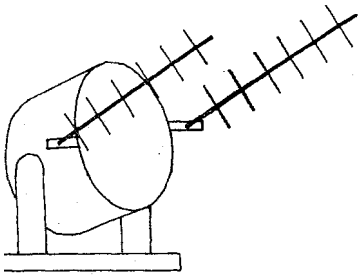

FIG. 6
Fishbone aerial arrays on a radar controlled searchlight.

One cannot examine antennae such as those shown in figs. 1 and 5 without being impressed by the geometry of their structure. The olfactory theory maintains that the purpose of the pectinations is to increase the surface area. It seems odd that such orderliness in shape, size and arrangement of pectinations should have evolved if area is the only consideration. Even more intriguing is the fact that if the antennae really are electromagnetic aerials, then the spacing of the pectinations indicates an operating wavelength in the far infra-red band (0.2-0.02 mm.). Such radiation is just beyond the range which can be generated electronically. It is a common radiation, being emitted by hot bodies, but investigation of its properties is very difficult. It will not affect a photographic plate and there is no known *solid* through which it will pass. Some work has been carried out on the far infra-red by Arkadiewa (1924) using coarse diffraction gratings. The difficulty in obtaining evidence in support or otherwise of a radiation theory is to devise an experiment, which will enable a female to put out scent but not radiation, or vice-versa. The latter appears to be virtually impossible in the absence of a permeable solid for the long infra-red. Two experiments have been carried out in which attempts were made to screen from radiation. <=133>

In the first, virgin females were placed in a box made from wire gauze of extremely fine mesh (1,000 wires per inch). Such material would allow scent particles to pass through it and at the same time act as an effective screen to electromagnetic waves well into the infra-red. Evidence that the scent was emerging was forthcoming in that males were attracted from short range. There was no evidence that any males were attracted from a long distance to the gauze box.

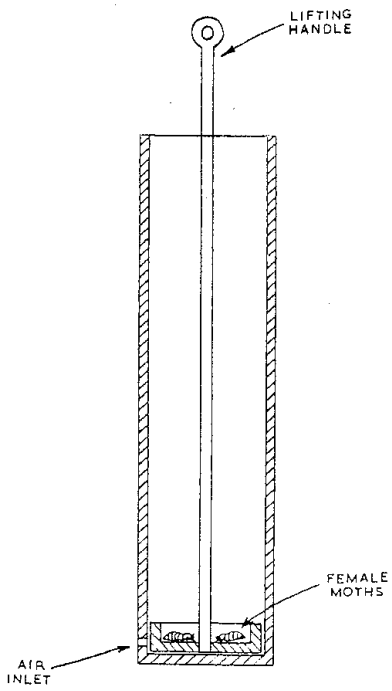

FIG. 7

The second experiment made use of the apparatus shown in fig. 7. A brass tube 15" long, having a small hole near its base, contained a tray connected to a rod, capable of being lifted out of the cylinder. The tray was a reasonably close fit inside the cylinder. Six virgin females were placed in the tray and the apparatus was set up about 100 yards from a colony. Every half-minute the tray was raised to the top of the cylinder by means of the rod, thereby forcing a column of contaminated air out into the atmosphere. In this way, any scent put out by the females was dispersed as if the females were in the open. The metal tube acted as a screen to any radiation, except for a narrow cone vertically above the tube which males were only likely to encounter accidentally. During a three-hour period three males located the tube. On the next day, in similar weather conditions during the same three-hour period, the same six females placed in the open attracted 64 males, each of which was captured before could mate. On the third day, no females at all were used, but observation was kept of the number of males which strayed within 20 feet of the locality accidentally. The number in fact was four. <=134+>

The evidence from these two experiments is encouraging but not conclusive, since it is a negative result which might obtain for a number of reasons. At the same time there appears to be a complete-lack of positive evidence that males have been attracted from long distances by anything but a virgin female. Haller *et alii* (1944) made attempts to isolate the chemicals responsible for the attraction, and the final extracts made for the purpose of luring males were obtained from the abdomen of the female. No reference to the range from which the males were attracted is mentioned in this reference.

Such is the present state of the evidence. Clearly there is scope for further investigation. It is interesting, however, at this stage to examine one further aspect of the behaviour of moths in relation to the possible effects of radiation.

Attraction to Light

The mechanism of the attraction of an artificial light for most moths has never been explained. To show that a light, which shines more on one side of an insect than on the other, produces stimuli which cause muscles to operate in such a way as to turn the insect towards the source is not a *basic* explanation of phototaxis. Several entomologists have speculated about the possible effects of radiation. Laidlaw (1951) asks: "Why do night-flying moths, which avoid daylight radiation, exhibit such a strong attraction to artificial light and ultra-violet? Is it confusion of light radiation with some other invisible sexual stimulus?"

Certainly there appears to be some sexual discrimination in light attraction, for of the total specimens attracted to lights, by far the majority are male.

If the radiation theory proposed in section (3) is to be used to explain light attraction there is one fact which is difficult to explain. The wavelength suggested by the geometry of the antennae is such that the effective radiation will not pass through glass, whereas moths are readily attracted to indoor lighting through closed windows. Furthermore, ultra-violet radiation is even more effective than the visible range.

The following extension of the radiation theory attempts to explain the various phenomena of light attraction. When electro-magnetic waves are propagated through a space containing molecules of substance, inelastic scattering occurs, during which process a small fraction of the incident radiation is converted to radiation of a longer wavelength. By this, process ultra-violet and visible 'light may generate infra-red radiation by their passage through an atmosphere containing water vapour. <=135>
Such might, be the explanation of attraction through glass. The visible light passes through the glass before scattering takes place due to the water vapour molecules in the atmosphere in the vicinity of the moth. The intensity of the scattered radiation is proportional to the intensity of the visible light at the point where scattering takes place and a sense of direction is thereby obtained. The effect on the moth may be similar to the optical effect which can be observed from a street lamp on a very foggy night. An observer approaching the lamp is aware of a general increase of "luminosity" of the fog before he actually sees the lamp itself.

Certain phenomena, well known to collectors, suggested the above explanation. All species of moth in which the antennae of the male are highly developed are readily attracted to lights. The males of species which are known to assemble from long distances have well-developed antennae. It is much easier to attract moths to light on a damp evening than on a dry one. Many collectors' books refer to the fact that many of the species with well-developed male antennae may be found most readily in damp places. It is possible that this is only due to the greater attraction for lights in the presence of water vapour.

It remains to explain the reason why a small percentage of the light visitors are female. The pectinations present in the female antenna are rudimentary in form, but it is possible that the radiation effect is so strong that even rudimentary organs experience some effect.

During the experiments on Vapourer moths some interesting observations were made for which no explanation can be offered, and yet the behaviour of the insects in this instance was such as to suggest some connection with the assembling process. These observations are included here in the hope that by bringing them to the notice of readers, other similar phenomena might be recalled which might throw further light on the problem.

They are as follows: — The male Vapourer, having assembled to within a few inches of the virgin female, performs what is often called a "love-dance". The wings vibrate very rapidly and the insect appears to attempt to stand on its head as it gyrates on the ground. It was observed that males in flight showed a marked attraction for the panes of glass in windows and that they would press their heads against the glass and, although not so violently, would repeat some of the motions of a love-dance. This phenomenon was observed on many occasions. The only apparent difference between the light reflected from glass and the direct sky radiation is that it is possible that the reflected light has some degree of polarisation.

Conclusions

The radiation theory without the extension which attempts to explain light attraction is not very different from the well-known explanation for the glow-worm's light. The only difference is that the radiation from the female glow-worm is visible to us a fact which makes it very easy for us to observe the mating signal. <136>
It is an interesting speculation as to whether the assembling of male glow-worms would also have been explained at the present time as an olfactory mechanism, had the wavelength

of the radiation been just a little longer, putting the radiation just out of the visible band. The comparison between the glow-worm and the moth can be very striking. The female glowworms cannot fly so that long range signalling becomes essential. Such is the case with moths like the Vapourer in which the female is wingless. The female glow-worm can control the light emission and turn it off after pairing. So apparently can a female moth, and it seems unlikely that cessation of exposure of scent glands would prevent further attraction from the evidence of the empty box experiment. This one fact alone seems sufficient evidence in itself to cause doubts about the olfactory theory.

The problem of producing a conclusive experiment which would give a positive result is not so much one of being unable to produce the right kind of radiation as one of being unable to emphasise a selected wavelength, for infra-red of a variety of wavelengths is emitted by most objects. It seems likely that if the female emits a radiation to attract the male she does so in a series of pulses which would certainly be more easily detected than would an emission of constant intensity. The movements of the female abdomen, which are normally assumed to have the sole purpose of exposing scent glands, occur about 60 times per minute in the case of the Vapourer. Perhaps the most fruitful line of research in the future would be to build a sensitive bolometer, capable of detecting small quantities of infra-red radiation and to attempt to detect radiation from the female. If pulsations corresponding to abdomen movement could be detected the case would be proved. The construction of apparatus of the required sensitivity with a response fast enough to observe pulsations is difficult, but it is hoped that something of this nature will be developed within the next few years.

Acknowledgments

The author is indebted to Dr. W. D. Hincks and Dr. E. J. Popham of Manchester University and to Mr. G. S. Kloet for encouragement and much useful discussion leading to the preparation of this paper.

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LAIDLAW, W. B. R. 1951. *Trans. of Soc. Brit. Ent.,* **11**(2): 74 .

Notice

Readers are invited to submit comments on Dr. Laithwaite's interesting article. A selection of contributions will be published in a later issue of *The Entomologist.*

— EDITOR.

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1961 Response to the Editor's Invitation

Kettlewell seems to have been only immediate respondent within this *"The Entomologist"* journal — acting on the editor's invitation, see the opposite column.

The relevant references and Kettlewell's background paper are — in chronological order:

Kettlewell, H.B.D. (1946 Jan) "Female assembling scents with reference to an important paper on the subject". *The Entomologist* **79**(992), 8-14.

Kettlewell, H.B.D. (1961 Mar). "Radiation Theory of Female Assembling in the Lepidoptera". *The Entomologist*, **94**, 59-65.

Laithwaite, E.R. (1961 Apr) "A Reply to Dr. Kettlewell's Contribution on Assembling of Lepidoptera". *The Entomologist*, **94**, 95-99.

Recent References to Laithwaite's Paper

Traill, R.R. (2005c). *How Popperian positivism killed a good-but-poorly-presented theory — Insect Communication by Infrared.*
Ondwelle: Melbourne. www.ondwelle.com/OSM03.pdf
[A reconciliation regarding Diesendorf's attack upon Callahan's further development of such theories]

Traill, R.R. . (2008). *Critique of the 1977 debate on infra-red 'olfaction' in insects — (Diesendorf vs. P.S.Callahan).*
Ondwelle: Melbourne. www.ondwelle.com/OSM09.pdf
[Conference of the Australian Entomological Society (A.E.S.) — Orange, NSW, Australia; (30 Sep.2008)]

R.R.Traill, September, 2009

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Note: "<113>" = "The original page 113 ends here", *etc.*

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