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The Use of Attractants and Repellents in Vector Control

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A great many stimuli—auditory, visual and chemical—attract or repel insects and some of these play an essential role in maintaining the life of the individual or perpetuating the species. The author examines the modes of action of attractants in nature, particularly in relation to blood feeding. The predominant mechanism of attraction to an odour source (e.g., in host finding) appears to be positive anemotaxis. Success in locating the source is influenced by wind conditions and by the visual acuity and field of view of the insect. The author considers the physical and chemical properties of materials that have been widely used as attractants and repellents and indicates the unsatisfactory nature of present theories to explain their action. Possible applications of attractants in vector control include their use in traps, baits and sprays, while repellents are mainly of value for personal protection. Increased understanding of the mechanism of action is likely to lead to the development of much more effective materials and to their wider application.

INTRODUCTION

Although attract and repel are etymological opposites, meaning to draw to and to drive back, they are not entomological opposites. In the lives of most insects and many other animals there are two essential attractions, to sources of food, and to repositories of the germ cells—males to females, females to egg-laying sites. The range over which these may act is at least metres and may be kilometres. Repulsions, on the other hand, are essential only in the lives of comparatively few animals: skunks, stink bugs, bombardier beetles, and the like. Although a skunk may be detectable from a distance of a kilometre, neither it nor any other animal actually repels or drives away others for a distance of more than a metre or so, and usually the action is restricted to centimetres or even millimetres.

The term " repellent " is commonly used for stimuli which merely inhibit or neutralize attraction or which in some other way bar the expression of this. I shall use it in this general sense, but would draw your attention to the plea of Dethier et al. (1960) for a revision of terminology in this field. In this context, reference may be made to the controversy that arose during the Second World War over the effectiveness of pyrethrum as an ingredient of antimalarial " repellent " creams. The question was whether this material could be depended upon to knock down a mosquito before the injection of saliva had begun. The answer was that it could not. But it was surely taking a liberty to refer to this material as a repellent.

Attraction is necessarily much more specific than repulsion, both in the kind of animal which it affects and also in the kind of behaviour it elicits. Both attraction and repulsion are most commonly used in relation to chemical stimuli but may also apply to visual and auditory stimuli. Attraction to lights is familiar enough and that to moving objects is well recognized. Certain yellow lamps which are claimed commercially to repel insects in fact merely offer minimal attraction for a given luminosity to man. Attraction to auditory stimuli is familiar in nature, e.g., stridulation as a means of bringing the sexes together. A practical application of this has been attempted in the use of audio-frequency oscillators to attract female mosquitos. Auditory stimuli have also been used to repel, as in the use of klaxon horns to prevent locusts from alighting. This may depend on a resonance effect. Thermal and moisture stimuli can also attract or repel. This paper will be restricted to a consideration of chemical attractants and repellents, but it should be remembered that these other possibilities exist. Some of the

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principles I propose to enunciate for chemicals also apply to other stimuli.

BEHAVIOUR TOWARDS FOOD

Most vectors of public health importance are blood feeders, and of these many of the more important ones are winged and find their source of food while flying. An understanding of the mechanisms of host-finding and subsequent feeding is essential to further progress in the use of attractants and repellents. The future potential of these materials in vector control depends on this. The limit of usefulness of the heroic empirical testing of thousands of materials (King, 1954) has been reached.

Now the process of host-finding and feeding can be divided into a number of phases (Kalmus & Hocking, 1960). A resting mosquito, for example, must first be stimulated to fly and its flight must be directed into the general vicinity of the host; it must then explore for the body—and often for an accessible part of the body—and settle on this, then probe the skin for a suitable place to feed, then pierce and suck, then withdraw and again take off.

More is known perhaps about host-finding in mosquitos than in other vectors, and this knowledge has been briefly summarized in the following table:

A SUMMARY OF MOSQUITO BEHAVIOUR IN RELATION TO BLOOD FEEDING

Behaviour stage	Stimuli
1. Take-off	Diurnal changes in light intensity Mechanical: disturbance of vegetation Visual, odour, CO_2, change in air movement
2. Host finding	Positive anemotaxis triggered by odour (lysine, CO_2?, alanine)
3. Settling	Visual—movement, shape, warmth and moisture
4. Probing	Surface temperature, contact chemical stimuli (through tarsi and labellae)
5. Feeding	Adenosine-5-phosphate: probably mechanical, fluid flow
6. Take-off	Repletion—probably scolopidia registering tension in membranous areas of integument

These data have been obtained from work with many different species, mostly perhaps with *Aedes aegypti* L. Although the emphasis varies in different species, they seem likely to prove of fairly general application to mosquitos.

The surprising thing revealed by these data is the number of different stimuli involved in host-finding—the complexity of the process. This is responsible for much of the confusion and difference of opinion to be found in this field, for not all authors have specified which of the many stages of host-finding they refer to when they talk about attraction and repulsion. As examples of disagreement, Bässler (1958) has claimed that carbon dioxide receptors are to be found on the maxillary palpi. While most authors agree that carbon dioxide is important in attraction, Rahm (1958a) has shown that palpi play no part in attraction from a distance. Kellogg & Wright (1962) consider carbon dioxide to be purely excitatory. Haddow (1942), Van Thiel & Laarman (1953), Brouwer (1958), Rahm (1958c), Ismail (1962), and Kalmus & Hocking (1960) have shown that individual odour, as distinct from moisture, is important both in attraction and in host selection. Kellogg & Wright (1962) claim that it plays no part. As Dethier (1947) has pointed out, many materials attractive at low concentrations are repulsive at higher.

It is noteworthy that the stimuli involved become more and more specific as we proceed from stage to stage. Almost any stimulus will serve to start a blood-hungry mosquito flying from its resting place in vegetation or hut; the threshold of intensity gets progressively lower as blood-hunger increases. At the other end of the process, so far as we know at the moment, a single chemical substance, adenosine-5-phosphate, present in the blood is not only sufficient to maintain sucking activity, but it will also override most other stimuli at quite high intensities: a mosquito may continue to feed when its abdomen is cut off, when it and the host are submerged in water or in quite dense smoke, and even when part of the body is painted with insect repellent.

The second stage, host-finding, is perhaps the subject of more confusion than any other. The old idea that odour attracts through a diffusion gradient of concentration dies hard. In the field, even under calm still conditions, an odour gradient with intensity varying inversely with the distance from the source is unlikely to be established for more than a very few centimetres. With a warm-blooded source, convection currents will limit this still further. It is manifestly absurd, no matter what faith one may have in the miraculous abilities of insects, to suppose that at distances of a kilometre or more from a source, the two antennae of an insect could detect differences in concentration of an odour gradient.

Although much of the evidence is circumstantial, the predominant mechanism of attraction to an odour source in the field seems to be clearly established as one of positive anemotaxis triggered by the odour (Schwinck, 1954). Any source of odour in the field gives rise to a cone of odour extending downwind from it, under favourable conditions for one or more kilometres. The shape and nature of these odour beams have been neatly calculated by Wright (1958) from formulae developed by Sutton (1949) for war gases. On encountering an odour beam, an insect flying in a random manner with a high rate of change of direction heads into the wind and continues to fly upwind as long as the odour stimulus is received. Adaptation to the odour is offset by increasing concentration as the source is approached. If the odour stimulus is lost, there is a return to random flight with a high rate of change of direction. This behaviour may be regarded as a precision derivative of odour klinokinesis (Fraenkel & Gunn, 1940) and parallels closely that of an aircraft homing on a radio beam.

Maintenance of upwind flight requires, of course, visual contact with the ground. This rarely presents difficulties. The eyes of most nocturnal insects, and certainly those of mosquitos, are well adapted to vision in low light intensities (Sato et al., 1957), and the wide angles of vision, which permit an insect to look forwards and backwards at the same time, are very suitable for the maintenance of a track. Studies on optomotor reactions show insects to be very sensitive to any tendency to side slip (Kennedy, 1940; Kalmus, 1948). Watching insects in flight one gets the impression of an acute consciousness of wind direction. It seems clear that some mosquito species at least can maintain a track in weak moonlight and perhaps even in starlight at heights up to at least a metre above any terrain providing visual landmarks of average dimensions (Klassen, 1959).

On 14 August 1962, I was able to observe the behaviour of *Aedes dorsalis* (Meigen) with binoculars before and shortly after sundown. There was a southeast wind of about 3 km/h blowing over a level stretch of short grass with widely scattered groups of small trees and shrubs. In any direction, mosquitos could be seen in random flight at distances up to 12-15 m and heights up to 1.5 m above ground. To the north-west, at distances up to 10 m, several were seen to make upwind turns, usually reaching me in one almost straight flight and landing usually low down on the downwind side.

I suspect that with a stationary host, sight becomes important at a distance of about 2 m; there is also perhaps a tendency to move down the wind velocity gradient, that is, across the wind, into the lee of the body of the host. These reactions provide a safeguard against overshooting, and may be very important when the host is moving too. The visual stimulus of a moving object appears to be more important in larger insects with better developed eyes, such as horseflies and tsetse-flies.

Wingless blood-sucking insects have mostly a simpler habitat and hence a simpler behaviour problem. For many of these, temperature gradients and perhaps warm air currents replace the odour-beam phenomena.

ATTRACTANT AND REPELLENT MATERIALS AND THEIR ACTION

In the search for insect attractants, the sources explored have been those which function in nature: components of the preferred food material, sex attractants, and components of oviposition sites. An example of the first of these is the discovery by Brown (1961a, 1961b) of a component of blood, lysine, which is attractive to mosquitos. It is interesting to note that protein hydrolysates have proved to be generally attractive to insects, especially Diptera, and much use has been made of them in agricultural entomology (Steiner, 1952; Lockmiller & Thomas, 1957a, 1957b). So far as I am aware, there has been no successful exploitation, in the field of vector control, of the other two possible natural sources of attractants, but it is interesting to note that moisture, which often functions as an attractant to oviposition sites, also plays a role in attraction to a source of blood.

The early repellents for blood-sucking flies were naturally available plant products, such as oil of citronella and oil of camphor, but these have no specific role in the life of blood-sucking flies in nature. Being highly odorous materials to man, they were supposed to act through the olfactory senses of insects, and investigators in search of new repellents were presented with the conflicting requirements of high volatility for olfactory effect and low volatility for prolonged protection. The advent of dimethyl phthalate (Granett, 1942) and many similar materials with low vapour pressure and much less pronounced odour threw some doubt on the validity of this assumption. Although it is now clearly established that these materials produce at least a part of their effect in the vapour phase (Kalmus & Hocking, 1960, and others) it does not follow that the olfactory sense is involved.

Two properties are so commonly found in repellent materials that one may suspect they are in some way connected with repellent action: they irritate the mucous membranes of man, and they are plasticizers of many paint films and plastics (Ihndris et al., 1955). Wright (1958) has claimed that there is a correlation between repellency to mosquitos and high infra-red absorption at or near 460 cm^{-1}. Water shows this property and this led him to suggest as an *experimentum crucis* that repellents should be attractive at very low humidities. This has not been shown. Wright also advances, as a part of his hypothesis, a theory of olfactory perception based on infra-red absorption and derived from that proposed by Ramsay (1882). More recently, Wright (1962) has suggested that absorption in a broader band extending to a lower frequency, about 200 cm^{-1}, is the important property. The correlation between this property and repellency, however, has not been clearly demonstrated, and the theory could not explain attraction from a distance of more than 15-30 cm.

A third property of repellents—toxicity to insects—is possessed by many modern materials. Many insecticides, too, are repellent and no firm line can be drawn between the two groups of materials; but caution is necessary in drawing teleological inferences.

The observation by Kalmus & Hocking (1960) that the inhibition of flight by tarsal contact was interfered with by mosquito repellents led to a hypothesis that these repellents act in a non-specific way by simply inactivating receptors with which they come in contact. This is supported by recent work by Khan (unpublished communication, 1962) which shows that repellents interfere with sugar feeding, mating, and oviposition responses as well as with blood feeding. On the other hand, nerve impulses picked up from the ventral nerve cord of a cockroach when the cerci are mechanically stimulated are almost unaffected by painting the cerci with repellent (Reddy, unpublished communication, 1962). Perhaps this is because muscle proprioceptors or some other internal sensilla are involved.

A further possibility which, so far as I know, has not been tested is that repellent substances are impervious to materials such as lysine, alanine, and arginine, and also perhaps, in part, to carbon dioxide, although they apparently do not affect the evolution of moisture (Gouck & Bowman, 1959).

APPLICATIONS OF ATTRACTANTS AND REPELLENTS AND FUTURE PROSPECTS

Very little use has so far been made of attractants in the direct control of vectors of public health importance, but this possibility is beginning to receive attention. It would be interesting to see how the performance of a moving-stripes light-trap could be improved by adding a supply of lysine to it and reversing the air flow. Doubtless the air speed would have to be reduced. Light-traps of all types are, of course, attractants, but their value has lain more in the estimation of populations than in the control of them.

Another possible application for attractants is as spray additives in order to counter the repellent properties which many spray ingredients have been shown to possess (Hocking & Lindsay, 1958; Hocking, 1961). It is possible, too, that economies in insecticides, desirable for many reasons, can be effected by using attractants, or repellents *(Pest Control,* 1958), to concentrate insect populations.

While repellents are most widely applied directly on the skin, many other applications are possible. Space repellents were suggested by Ginsburg as long ago as 1935 but do not seem to have had more than occasional use. Materials that have high repellency but have been rejected for use on the skin because of irritation or other toxic effects may prove of value when used in this way, or as additives to protective air currents (Hocking, 1960). Used on the skin or in the clothing or both, present-day repellents that have been developed on an *ad hoc* basis are nevertheless extremely valuable. Tremendous improvements can be expected with increased understanding of how these materials work.

The lesser attractiveness to mosquitos of new-born infants and of women may be useful clues in the search for a repellent for oral administration. The claim that thiamine taken orally exerts a repellent action (Shannon, 1943) seems to be unfounded where mosquitos are concerned (Wilson et al., 1944; Rahm, 1958b), but in the case of fleas (Eder, 1945) the question is still open.

There are three stages of blood feeding where a repellent can usefully act, each calling for different properties. A repulsive odour can interfere with attraction through the sense of smell; an irritant action through chemical perception can prevent landing and probing; a true taste repellent may prevent the consummation of probing as piercing and, if present in the blood, may inhibit actual feeding. Only when these properties can be measured separately will it be possible to seek correlations with chemical structure. This may allow the development of better materials for each stage and their formulation into an ideal repellent.

Both attractants and repellents offer a way of partly circumventing the problems of resistance to insecticides. An individual insect, for example, which does not respond to its natural attractant to man when this is used in a bait or a trap is unlikely to feed on man anyhow. If it feeds at all, it is likely to feed on some other host, and the result would thus be selection for zoophily. Similarly, extensively used repellents tend to force insects to select other hosts. Mosquito species, at least, readily develop strains with particular host preferences (Mattingly et al., 1951).

RÉSUMÉ

Un grand nombre de stimuli audio-visuels, et surtout chimiques, exercent sur les insectes des effets d'attraction ou de répulsion; certains de ces stimuli sont indispensables à l'existence des individus ou à la perpétuation de l'espèce. L'auteur examine, notamment à propos de la prise des repas sanguins, les divers modes d'action des facteurs naturels qui ont un pouvoir d'attraction. Chez l'insecte en quête d'un hôte par exemple, l'anémotaxie positive s'est révélée être le mécanisme principal qui attire vers la source émettrice d'une odeur définie. Le repérage de cette source s'effectue avec plus ou moins de succès selon le régime des vents, l'acuité visuelle de l'insecte et l'étendue de son champ de perception. Les substances ou matières qui ont été largement utilisées pour leurs effets attractif ou répulsif sont ensuite examinées au point de vue de leurs propriétés physico-chimiques; l'auteur indique en passant que les théories actuelles donnent une explication peu satisfaisante de leur action. Il discute la possibilité d'appliquer sur une plus vaste échelle les produits à effet attractif à la confection de pièges, d'appâts et de pulvérisations qui seront destinés à lutter contre les vecteurs, tandis que les produits à effet répulsif sont plus particulièrement réservés à la protection des personnes. En tout cas, il est à prévoir qu'une compréhension meilleure de ces mécanismes d'action permettra de mettre au point des substances ou matières à efficacité accrue qui recevront des applications multiples et étendues.

REFERENCES

Bässler, U. (1958) *Z. vergl. Physiol.*, **41**, 300

Brouwer, R. (1958) *Geurverschillen bij de mens als oorzaak van interindividuele verschillen in attractie voor malaria muskieten* (Thesis, Leiden)

Brown, A. W. A. (1961a) *Nature (Lond.)*, **189**, 508

Brown, A. W. A. (1961b) *J. econ. Ent.*, **54**, 317

Dethier, V. G. (1947) *Chemical insect attractants and repellents*, Philadelphia, Blakiston

Dethier, V. G., Barton-Browne, L. & Smith, C. N. (1960) *J. econ. Ent.*, **53**, 134

Eder, H. L. (1945) *Arch. Pediat.*, **62**, 300

Fraenkel, G. S. & Gunn, D. L. (1940) *The orientation of animals*, Oxford

Freyvogel, T. A. (1961) *Acta trop. (Basel)*, **18**, 201

Ginsburg, J. H. (1935) *Science*, **82**, 490

Gouck, H. K. & Bowman, M. C. (1959) *J. econ. Ent.*, **52**, 1157

Granett, P. (1942) *Insect repellents.* US Patent No. 2,293,256.

Haddow, A. J. (1942) *Bull. ent. Res.*, **33**, 91

Hocking, B. & Lindsay, I. S. (1958) *Bull. ent. Res.*, **49**, 675

Hocking, B. (1960) *Bull. ent. Res.*, **51**, 135

Hocking, B. (1961) *Bull. ent. Res.*, **52**, 1

Ihndris, R. W., Gouck, H. K. & Bowen, C. V. (1955) *Effect of promising insect repellents on plastics and paints*, US Department of Agriculture, Agricultural Research Service, Publication ARS-33-37

Ismail, I. A. H. (1962) *Acta trop. (Basel)*, **19**, 1

Kalmus, H. (1948) *Physiol. comp. et oecol.*, **1**, 127

Kalmus, H. & Hocking, B. (1960) *Ent. exp. appl. (Amst.)*, **3**, 1

Kellogg, F. E. & Wright, R. H. (1962) *Canad. Ent.*, **94**, 1009

Kennedy, J. S. (1940) *Proc. zool. Soc. Lond.*, **109**, 221

King, W. V. (1954) *Chemicals evaluated as insecticides and repellents*, Washington, D.C., US Department of Agriculture (*Agricultural Handbook* USDA 69)

Klassen, W. (1959) *The influence of the North Saskatchewan river valley on the dispersion of* Aedes (Thesis, Alberta)

Lockmiller, N. R. & Thomas, M. J. (1957a) *Bett. Fruit*, **51**, 6

Lockmiller, N. R. & Thomas, M. J. (1957b) *Agric. Chem.*, **12**, 34, 120

Mattingly, P. F., Rozeboom, L. E., Knight, K. L., Laven, H., Drummond, F. H., Christophers, S. R. & Shute, P. G. (1951) *Trans. roy. ent. Soc. (Lond.)*, **102**, 331

Pest Control, 1958, **26**, 16

Rahm, U. (1958a) *Z. Tropenmed. Parasit.*, **9**, 146

Rahm, U. (1958b) *Schweiz. med. Wschr.*, **88**, 634

Rahm, U. (1958c) *Rev. suisse Zool.*, **65**, 779

Ramsay, W. (1882) *Nature (Lond.)*, **26**, 187

Sato, S., Kato, M. & Torium, M. (1957) *Sci. Rep. Res. Inst. Tohoku Univ., Ser. D.*, **23**, 91

Schwinck, I. (1954) *Z. vergl. Physiol.*, **37**, 19

Shannon, W. (1943) *Minn. Med.*, **26**, 799

Steiner, L. F. (1952) *J. econ. Ent.*, **45**, 83

Sutton, O. G. (1949) *Roy. met. Soc. Quart. J.*, **75**, 335

Thiel, P. H., van & Laarman, J. J. (1953) *Docum. Med. geogr. trop.*, **6**, 156

Wilson, C. S., Mathieson. D. R., & Jachowski, L. A. (1944) *Science*, **100**, 147

Wright, R. H. (1958) *Canad. Ent.*, **90**, 81

Wright, R. H. (1962) *Canad. Ent.*, **94**, 1022