like to leave with you in regard to the use of pesticides, whether it be for the purpose of improving the general welfare of man through agricultural pest control, or through the control of insects transmitting diseases. We have been bombarded in the past with many adverse press stories regarding the hazard to public health caused by the application of these materials.

Everyone who is connected with the use of pesticides has a responsibility for the proper application of these materials. The records have proved that much of the criticism and a great deal of the hazard comes from improper use of these products. A great deal of the misuse of pesticides can be overcome by reading the labels on the materials and following directions specifically. The continued adequate supply and wide choice of these materials depends in great part upon responsibility in their proper use.

As a representative of the National Agricultural Chemicals Association, I wish to extend to you an invitation to consult our Association about any situation or problem which you may have concerning the use of pesticides. Our industry is doing everything possible to promote the proper use of its products and offers its services to expand the use of pest control in agricultural and public health fields.

MOTIVES BEHIND MOSQUITO FLIGHTS

MAURICE W. PROVOST

Biologist, Division of Entomology, Florida State Board of Health, Jacksonville

I'm sure if I were in the audience instead of here, I'd be asking why in the world does this man want to talk about motives, of all things, in mosquito flights. Let me tell you why, at the outset. We are working with migratory mosquitoes in Florida. We are learning many things about our salt marsh mosquitoes. But when asked about our findings, we frequently make ourselves difficult to understand—not because we talk in terms too technical or anything of the sort, but mainly because many features of migratory behavior which we take for granted, being continually concerned with them, appear differently to others. What I mean is that the very great differences between migratory flights and other mosquito flights which we are so accustomed to observing seem not to be equally appreciated by others. The best examples of this are questions asked about "flight range" of salt marsh mosquitoes—a matter which strikes us as meaning little when it is expected to mean something quite concrete. It's only because migratory flights differ from other flights chiefly in motivation that I'm led to talk of motives. We just want and need to understand one another more clearly.

When we speak of motives, we must put ourselves in the subject's boots. It's not easy to put yourself in a mosquito's position, but with a little imagination and perhaps a lot of daring, it can be done. Our guess is that a mosquito is always in one or the other of two opposite states: either it is at ease or it is uneasy. In us, being at ease or not depends on more than strictly biological conditions; but in mosquitoes purely biological factors can explain either their actions or their feelings. It is difficult for us to refrain from projecting our consciousness and our thinking into the behavior of an insect. Most of what we do, at least in our sober moments, has a purpose. No one would seriously claim an insect thinks, and no one could *prove* it is even conscious. Yet many do not hesitate to say that mosquitoes act with a purpose—that is, with a beforehand knowledge of what they are about to do. This is pure delusion; the insect is a living automaton.

By motives in mosquitoes, therefore, we

understand not an emotion as found in us, and, still less, an act of will. We mean simply a state of nervous tone, an altogether mechanical state of affairs in the nervous machinery. When all the parts it serves are satisfied, that machinery may be said to be in equilibrium and the mosquito is at ease and resting. If then any unsatisfaction develops, any physiological need or want in any part, the machinery is out of equilibrium and the mosquito is uneasy. This state of uneasiness gears the machinery in such a way that the mosquito becomes active and searches for whatever stimuli will guide it to the satisfaction of the need. This active seeking of stimuli is called appetence. Examples of appetential behavior would be a hungry female searching for a blood meal, a gravid female looking for a place to deposit its eggs, or a mosquito of either sex looking for a resting place. This concept of appetence is nothing new, and it is accepted by most students of animal behavior. Something very much of the same sort lies at the base of human behavior, although in us there are psychological complications so great that appetential behavior is relegated to the subconscious.

Now, let us consider two case histories of flight in the salt marsh mosquito, *Aedes taeniorhynchus*. It was just past sunset, down at the edge of a large puddle in a salt marsh. Female 1 was leaving her birthplace and female 2 was biting the observer. Number 1 had struggled out of her pupal case at noon. Her first weak flight was a matter of a few inches from the water's edge to the base of a grass clump. She idled away the hot afternoon hours there in the moist shade. As the sun set, she stirred a little. She started climbing. The darker it got the higher she climbed until she was perched at the very tip of the grass culm. Suddenly she let go, flew straight up a few feet, then levelled off in a bee-line to the northward. Within twenty feet of the grass she was invisible in the dusk, but within a short time she would be miles away. At about the time she left, female 2 bit the observer on the forehead. It was her first taste of blood. Ten miles away and three days ago, she had emerged from a marsh much like this one. Somewhere along the line she had mated. When female 1 was emerging at noon, this female 2 was resting on the ground in the shade of dead sea-grape leaves some 200 yards away. There she stayed idle until the sun turned red, preparing to set. She became restless and flew away. Her flight was more leisurely than number 1's and not straightaway but zig-zag and up and down. When she came close enough to the observer watching number 1, she set her course and made straight for his forehead, where he first became aware of her.

By definition, number 1's flight was non-appetential, and number 2's appetential. When number 2 left the sea-grape leaves at sunset, she was hungry. She didn't smell blood the minute she left; she left, searching for that smell. She was in a state of appetence and flew about looking for a clue. Her flight was not oriented by the smell of blood or breath but by something inside that said: "keep flying until you cross the scent of a warm-blooded mammal." When she came close enough to the observer, her antennae tingled to the odor that then oriented her straight in his direction. Things were a lot different with number 1. When she left the top of that grass spear, she was not hungry. She had brought with her from the pupal stage enough food reserve to yield energy for quite awhile yet. She didn't need anything badly enough to unease her. But when the illumination had dropped to a certain point, she couldn't resist the urge to fly. Once on the wing, this urge was satisfied as long as she flew. There was nothing inside telling her to search for this or that stimulus; there was no appetence, she was comfortable and content just flying. Without anything inside nagging her on and thereby orienting her flight, she simply took the path of least resistance, environmentally speaking, and so made a bee-line in whatever direction and at whatever speed the environment dictated. *She was migrating.*

I hope you'll overlook the simplifications used in painting this picture. Actually, every least phase of animal activity is fantastically complex when examined for causes. It may seem presumptuous even to talk of causes without knowing more of what in fact happens. Nevertheless, we must suppose a little now, just for the sake of better understanding one another. Investigations of mosquito flight are multiplying fast, and I'm afraid we are rapidly reaching rampant confusion unless we take stock of what we already know and agree on some fundamental facts. Some of us are working with non-migratory and others with migratory mosquitoes. This is a difference so great that our findings appear contradictory. We would do well to seek agreement on what constitutes migration in mosquitoes and what it implies. After a considerable study of what others have written about insect migration, I am led to believe that it differs from other flights only by its lack of appetential motivation. Let us see, now, what ensues from such a basic premise.

In insects, migration is movement away from the terrain of normal satisfaction of biological needs. It is associated with outbreak production and it is characterized by the unidirectional flight of individuals. In butterflies and locusts, an enormous amount of investigation has shown that migrations are not directed at any special goal but are merely the result of a locomotory drive channeled by environmental circumstances. What little we know of mosquito migration gives no support whatever to any other explanation but the same one. Whether the locomotory drive replaces or suppresses the usual appetential flights does not matter; what matters is that it exists as an all-consuming impellation which maintains the insect in flight without special motivation and therefore at the mercy of environmental orientation.

Every intensive study of insect migration has come up with essentially the same patterns of events. First of all, the necessary locomotory drive is released only at certain times in the individual insect's life. Secondly, the weather sets a limit to the exercise of the locomotory drive. These two factors together, one physiological and the other ecological, set a time limit to an individual insect's migratory flight. This time limit then establishes the distance limit in combination with whatever ground speed is allowed by the insect's flight powers and the wind. And finally the direction of the migratory flight is determined by the accident of weather and terrain as affecting the insect's peculiar reactions. If all this is so, you might say, a supposedly migratory insect may either migrate or not migrate, may go north, south, east or west, may fly 5 miles an hour or 20, and may migrate 10 feet, 10 yards, or 10 miles! This is exactly the case; migration is but the expression of an average.

There is no need to consider migration as a very special kind of behavior. Neither is it logical to presuppose a special migratory instinct or that basic mechanisms for migration exist in certain species and not in others, for in either case the physiological and morphological specializations assumed would be too fundamental and unique to criss-cross the genealogical lines the way they must. Even if facilitated in some cases by certain adaptations, migratory behavior must be a phase of normal behavior latent in entire families or orders but varying among species only in the extent of its exercise. We do not yet know to what extent even *Aedes aegypti* may migrate. The longer the locomotory drive persists and the more its interval is atune with weather characteristics that will allow its exercise the more migratory is the species. Given a species that has these properties to the extent that salt marsh mosquitoes have them, we may certainly speak of that insect as a migratory mosquito. But we must not let this label misguide us. To what extent a particular brood of that migratory mosquito species will migrate, if at all, is something else again. This will depend on the topography, which in its particulars will vary about every breeding area, and on the weather, which also will vary in its particulars with every emergence.

There's no telling in advance where or how far an individual salt marsh mosquito will migrate from its site of emergence. We can talk only of averages. For instance, with *Aedes taeniorhynchus* we may be able some day to say: (1) in the female the locomotory drive is released for 48 hours, (2) the average weather will allow the female to exercise its locomotory drive during 6 of those 48 hours. We would then have the average migratory period for the species: 6 hours. We may then learn that the average ground speed of migration is two miles per hour. Thus we would conclude that the average length of migration is 12 miles. Narrowing this down to a certain area, we may be able to say that from *this* breeding area, average weather conditions will channel the average flight northward for 12 miles.

All this talk of averages may be very unsatisfying to the man looking for something concrete to guide his mosquito control planning. But it won't help to contradict nature. If averages it is, then the thing to do is find ways of using averages. It will do little good to hold on to rigid rules and definitions that have no meaning in reality. One such unrealistic rule is that every mosquito species must have what is called a "flight range." It's true that in species where the dispersal is almost altogether appetential, there may be a fairly constant limit to dispersal from breeding areas which can be called a flight range for the species. With such species the flight range may vary directly with the intensity of breeding; and the adult density may decrease regularly with distance from breeding area. These concepts are all based on dispersal by appetential flight, so characteristic of the much-studied anophelines. But such generalizations cannot be applied to migratory species where one long non-appetential flight has more to do with the final dispersion than the thousands of short, appetential flights made later. With highly migratory mosquito species the concept of flight range, with every one of its connotations, has little meaning and less application. Dispersion in mosquitoes, therefore, is by random scattering in search of blood, oviposition sites, resting places or whatever else the insect requires. This applies to all mosquitoes. But the thing to remember is that in some species this appetential dispersal was preceded by a migratory flight which may have transplanted the entire population many miles before it even began the normal or appetential dispersal. From the standpoint of total dispersion from the breeding area, it therefore makes a huge difference whether or not migratory flights are involved.

I hope I can close on another note than did the mosquito biologists who reported: "The large amount of experimental work which we performed has on the whole added to the pre-existing confusion." There is no denying the existing confusion on mosquito dispersal. Whenever a topic is confused and fellow-workers fail to understand one another, it is usually because something fundamental is being overlooked. In the case of mosquito flights, I feel certain the fundamental fact overlooked is their motivation.