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SOME ECOLOGICAL ROOTS OF PEST CONTROL

BY

C. B. HUFFAKER

Division of Biological Control,
Department of Entomological Sciences,
University of California, Berkeley, U.S.A.

Development of pest management systems rests on relatively few major ecological principles and these underly the tactics and strategies available. Many are so self-evident that we often ignore their underlying significance. They are (1) the principle of inherent variation in the genetic properties of organisms; (2) the principle that an organism must be adapted to its environment and becomes so through its evolution; (3) the principle that all organisms require adequate nutrition; (4) the principle that to perpetuate their kind organisms must reproduce; (5) the principle that as organisms are born immature they must grow and develop; (6) the principle that life presents various compensations tending to correct for adverse occurrences; (7) the principle that most organisms derive their sustenance from other living organisms (predation); (8) the principle that organisms commonly suffer from depletion of resources by other organisms (competition among the same or different kinds of organisms); (9) the principle that cooperation serves many species well; (10) the principle that organisms must move about and do things (possess mobility and other behavior); and (11) the principle of holism and interactions among factors in ecosystems. Examples are given showing that advances in our knowledge in each of these basic areas are significant in developing ecologically sound pest management systems.

This paper was presented as a C. W. WOODWORTH Award address before the Pacific Branch of the Entomological Society of America, June 26, 1973. I do not here attempt to relate the fine achievements of Professor WOODWORTH in the areas of ecology and pest control, for this was done in excellent fashion by Professor RAY F. SMITH, the first recipient of this award. I will repeat a single sentence from SMITH's address, "Origins of Integrated Control", in 1971. He wrote, "In my view, the origins of integrated control and its philosophy can be traced clearly to a very modest and tolerant man who did so much for entomology and ecology at the beginning of this century and for which he has been little credited in recent times".

To emphasize this fact, although I have been interested in population ecology and natural control since about 1948, and although the originator of the accepted terminology for the two principal classes of mortality factors concerning natural control (i.e., the late HARRY S. SMITH) developed his views from work here in California, I was not aware until 1963 that C. W. WOODWORTH had antedated

SMITH and all others in expressing the clear distinction between these classes of factors. H. S. SMITH had worked closely with L. O. HOWARD and W. F. FISKE in his early career, and their more elaborated views of these factors, published in 1911, undoubtedly stood out in his mind over the briefer description of WOODWORTH published three years earlier, in 1908.

I refer to WOODWORTH's (1908) paper in *Science* which I first saw in 1963, and in which he described what H. S. SMITH termed in 1935 as "density-independent and density-dependent" mortality factors. WOODWORTH wrote:

"The various cause of death may be classed into two groups; first, those that destroy all insects in a certain condition or position, irrespective of the numbers present; and second, those that are more and more efficient as the numbers increase."

To honor this great and gentle man, I wish simply to scan some of what has been done since his time to forward the ideas and goals that he held to advance ecology and pest control as inter-related disciplines.

My topic, "Some Ecological Roots of Pest Control" is appropriate in honoring Professor WOODWORTH; it also happens to bring together my own areas of interest. I will not attempt a general description of why good pest control is actually applied ecology or why we must utilize ecological knowledge in its pursuit. These are elemental.

Rather, I wish to look at some ecological roots of pest control, some of them so obvious as to be taken for granted, sometimes without recognition of the connections. I consider just what are the major, total ecological principles that bear upon insect abundance and the potentials for pest control.

A pest is an organism that causes harm or annoyance to man. Here I will deal with insects primarily. But insofar as insects occur with other sorts of pests and with non-pests, as well, and may interact with them, or the control measures for one sort of pest may affect control of another, we must consider these interactions. This is the heart of ecology.

An organism is a pest only if it becomes abundant enough to harm man. Thus, we are concerned with numbers, or populations, of a species rather than its mere presence. This is basic to the concept of economic levels of a pest species. Central to any pest problem is its population ecology, involving the capabilities of the pest to survive and reproduce in the habitat, and the way in which any factor (s) inherent or extrinsic to the pest's physiology and behavior impinge on its success or failure.

The really basic ecological principles that are confronted are few. Those of most significance are the following, in coded expression: (1) variation, (2) adaptation, (3) nutrition, (4) reproduction, (5) growth

and development, (6) compensation and stability, (7) predation, (8) competition, (9) cooperation, (10) movements, and (11) ecosystem holism and interactions.

1. **Variation.** — INDIVIDUALS OF A SPECIES DIFFER FROM ONE ANOTHER INHERENTLY IN THEIR GENETIC PROPERTIES AND ALSO AS A RESULT OF ENVIRONMENTAL INFLUENCES ON THEM DURING THEIR DEVELOPMENT.

The genes possessed by the individual determine its capacity to cope with conditions encountered, while the pool of genes possessed by the population determines both its capacity to cope with prevailing conditions and to adapt over time to changes in conditions.

Except for isolated situations, most species present a considerable spectrum of genetic variability. A wide spectrum of genetic stocks of natural enemies and of crop plants or wild germ plasm for use in crop plant breeding are thus available for pest control. The relative neglect in modern plant breeding of the high degree of pest resistance inherent in the large number of varieties of rice grown formerly in the Orient poses a real threat to the current success of the Green Revolution (SMITH, 1972). The existence of these varieties implies some selection for adaptation, not only to climate and cultural conditions, but to pests as well. When some 10,000 world varieties of rice were grown under "traditional" culture in the Philippines, the highest yielding variety was one already popular among Filipino farmers (WORTMAN, 1968). A final loss of many hundreds of varieties already possessing resistance to various insects, nematodes and plant diseases could prove unredeemable.

The wide spectrum of variation in a species of natural enemy has been demonstrated by PAUL DEBACH and associates in their studies of the genus *Aphytis*. RAO & DEBACH (1969) found that *A. lingnanensis*, as formerly known, consists not only of three sibling species, but also of two semi-species exhibiting various degrees of reproductive isolation. Such strains or sibling species commonly exhibit sharp differences in capacities to effect control of their hosts in given situations; one may be superior in one situation and another elsewhere. Also, *A. maculicornis* exists in Eurasia as several "strains" or as yet indistinguishable sibling species, many of which were introduced into California for control of olive parlatoria scale (HAFEZ & DOUTT, 1954). Only the Persian *A. maculicornis* proved effective (HUFFAKER & KENNETT, 1966).

There is perhaps no better illustration of the resident genetic plasticity in a species than that demonstrated in the development of resistance to insecticides by various insect pests. GEORGHIOU (1972) noted that over 225 examples are now known and that past work indicates that resistance "almost invariably develops". He noted also that, "with the possible exception of the cyclodienes, resistance

to the organochlorine, organophosphorus and carbamate insecticides appears to be based on the same or similar backgrounds of ancillary genes"... and thus the substitution of one insecticide for another tends to preserve or even enhance the resistance.

2. **Adaptation.** — AN ORGANISM MUST BE SUITED TO ITS ENVIRONMENT, INCLUDING OTHER ORGANISMS, AND BECOMES SO THROUGH ITS EVOLUTION.

Adaptation is the "granddaddy" principle of biology. The result is a blend of current environmental fitness and a sufficient genetic plasticity to remain adaptative to changes in conditions.

Adaptation to the climate is an *a priori* requirement. Behavior has recently taken on new meaning in this adaptation. The choices made by mothers in moving to habitats and selecting places to oviposit are now taken as much more important than formerly. The mothers react to signals associated with favorable situations and not unfavorable ones. There are, of course, shortcomings; suitable places may remain uninhabited and inimical ones may receive doomed offspring. Totally unadapted species will not exist and poorly adapted ones only hazardously so, or confined to the most favorable places. Major pests are well adapted in this respect. So are many other species which would be major pests except for the good adaptations of their natural enemies.

Commonly, a pest will have a broader geographic range than any of its more effective natural enemies and these may each be best adapted and most effective only over a portion of the total range of the pest. Often, we find that an effective genus of natural enemies may comprise a cluster of species, with different ones dominant in different specific areas (WILSON, 1943). An example is that of the weed St. Johnswort of Eurasian origin which has been introduced into North and South America, Australia and Africa and where its biological control by introduction of its native phytophagous insects has been variably successful, or a failure. In Europe and North Africa, various species of *Chrysolina* occur, with variable degrees of influence on it there. Three of these were introduced into other world regions where the weed had invaded. *C. quadrigemina* has been more effective in environments comparable to those where this species is predominant in Europe, i.e., in the Mediterranean area. *C. hyperici* can compete with *C. quadrigemina* only in areas too cold for the latter in winter; hence, it is most effective in west Canada which has a climate nearer that of west and north Europe where *C. hyperici* predominates.

Often it is not due to lack of adaptation to climatic or edaphic conditions but to poor biotic adaptation that a species does not thrive. The two may be interrelated. A given natural enemy may simply be a better searcher in low host density situations and thus displace a competing species even better adapted to the climate. An

intermediate situation exists for *Aphytis maculicornis* and *Coccophagoides utilis* introduced to control olive scale in California. *C. utilis* is clearly the best adapted climatically ; *A. maculicornis* barely survives the hot dry summers. Yet the latter is so much superior in searching for and parasitizing scales during favorable periods, and has a sufficiently higher intrinsic power of increase, that it is clearly the dominant and most effective parasite on a year-around basis (HUFFAKER & KENNETT, 1966).

3. **Nutrition.** — ALL ORGANISMS REQUIRE ADEQUATE NUTRITION. This self-evident principle has many aspects in ecology and pest control. The way in which food is secured is the basis of ecological classification of organisms. The nutritional requirements of all organisms have much in common but in such features as securement and biochemical aspects of utilization many differences are exhibited. Nutrition is central to the origin of many other adaptations or the form or degree of their expression.

The subtlety of nutritional attainment that may pertain is illustrated by the work of K. S. HAGEN. HAGEN (1966) showed that bacterial symbiotes in the larvae of the monophagous olive fly are essential in the utilization of the olive by this tephritid, for when he added streptomycin to a complete adult diet of this fly, they deposited symbiote-free eggs which hatched but all larvae died in the lst instar. CHRISTENSON & FOOTE (1960) had earlier visualized the potential of controlling fruit flies by killing their symbiotes.

It is well-known that adults of many insects utilize pollen, nectar, honeydews and like materials in oogenesis and that the destruction of abundant sources of such supplies adjacent to a crop may greatly reduce the incidence of these species in the crop subsequently, with a consequent benefit or detriment, depending upon whether a pest or natural enemy is thus affected. LEUIS (1967) was able to increase by 18-fold the parasitism of tent caterpillar pupae in orchards where an abundance of wild flowers were maintained as a cover crop. Workers in the USSR especially (RABB & STINNER, in press and KLASSEN, 1973) have emphasized this relationship. Parenthetically, this also illustrates examples wherein diversity of the plant cover is more favorable to better pest control, although this idea cannot be taken as a fixed principle or law (VAN EMDEN & WILLIAMS, 1974).

4. **Reproduction** (Representing population growth potential) — AS NO ORGANISM HAS IMMORTALITY, ALL SPECIES MUST REPRODUCE. In their population ecology we must deal with organisms' capacity for increase in numbers, r_m, which is the inherent capacity for increase of a population of stable age distribution under given physical conditions when competition and other biotic mortality factors are absent. The actual rate of increase, r, is the rate of increase that

pertains under any prevailing condition, and is a more real statistic for population assessment. The former, however, is useful in comparing the potentials of different pest species, or of a pest species and one of its natural enemies (remembering, however, as many do not, that the mortality of the prey caused by the predator reduces by that much - often a great deal - the necessity for the predator to match the prey in inherent capacity for increase).

A population is at a state of equilibrium if its natality equals its mortality. Obviously, the extent to which births exceed deaths or deaths exceed births determines population increase or decrease. Life table studies giving fecundity and survivorship data, combined with statistical determinations, enable us to evaluate these various population-growth or decline parameters in relation to various environmental factors that affect them (DEEVEY, 1947; BIRCH, 1948). The *equilibrium mortality* is exceedingly important in pest population increase or decline. It merits more attention.

The principle of compensation and stability, highly important at the physiological level, is also equally important at the population level. Thus the tendency for all organisms to increase in numbers by reproduction is compensatorily met through adversity consequential to the increase itself (as Professor WOODWORTH stressed in 1908). When the principles of reproduction and of compensatory resistance to reproduction are viewed together there emerges the fact of natural control — a consequent principle itself.

5. Growth and Development. — AS ALL ORGANISMS ARE INITIALLY IMMATURE THEY MUST GROW AND DEVELOP BEFORE THEY BECOME REPRODUCTIVE.

Insects vary tremendously in the nature of this growth and development as free-living individuals. Some are retained in the bodies of their mothers until developed to even advanced stages, while others hatch from the egg as precocious embryonic larvae.

The food required is again enormously varied and may need to be extensively searched for, or it may be made available by the deposition of the egg into or by an adequate supply of food. Rates of growth and development are correspondingly varied, but in the presence of adequate food are normally functions primarily of temperature but also of atmospheric moisture and wind. Accumulated day-degrees of temperature have long been recognized as a yardstick to the development or phenology of many organisms, both plant and animal. Now, with developments in modeling pest population dynamics, this fact is used to good advantage to express time as physiological time.

Development may in some species be enormously delayed naturally (17 year cicadas) or may be greatly prolonged by lack of food, low temperature, or aridity. Dermestids may molt successively 20

or 30 times. Adverse conditions are often met by the special adaptation of diapause. When this occurs with irregularity it poses special problems in assessing generation mortality. The efficiency of a parasite may be affected by the diapause or non-diapause condition of a host, or by its own capacity to develop a synchronizing diapause.

It is by exploiting knowledge of insect growth and development that the hormonal chemicals and their analogs have been suggested as the "3rd generation insecticides". It is yet too early, however, to become highly optimistic here. The concept of using hormone analogs has been around since about 1956, yet we are not too far along toward putting them to use for crop pest control. Many are photolabile and break down under ultraviolet light when applied to crop plants. The two basic types are the molting hormones and the juvenile hormones. Analogs of both have been found in some plants, the former especially in the ferns, and the latter especially in conifers. While it has been suggested that the relative restrictiveness of phytophagous species attacking the ferns, for example, or certain conifers, may be due to the effects of these substances in the plants, this relationship has not been demonstrated. Their lack of specificity, generally, is a real problem, because many non-target arthropods, including natural enemies, are likely to be affected with their use in agroecosystems. Ecdysone analogs are not readily absorbed through the insect body wall nor in most cases through the digestive system, but ROBBINS *et al.* (1968) and EARLE *et al.* (1970) reported digestive absorption of one formulation by the cotton boll weevil, and inhibition of larval development and egg production. Continued work may point to considerable possibilities. The juvenile hormone analogs do penetrate insect cuticle, are more easily synthesized and apparently have a brighter future as potential insecticides (ROBBINS, 1972; NASSAR *et al.*, 1973; STRONG & DIEKMAN, 1973), if ones exhibiting adequate specificity can be developed. There is, however, no assurance at all that resistance, e.g., to entry into the insects, may not be developed.

6. **Compensation and stability.** — COMPENSATION TENDING TO CORRECT FOR ADVERSITY IS A FUNDAMENTAL PROPERTY OF LIFE. It operates at the physiological, population, and community levels. The human body's compensation by a rise in temperature serving to counter an infectious invasion illustrates the former. The increase in plant growth of neighboring individuals or rise of a new plant when a member of a plant community is killed, illustrates the latter.

This principle is now being utilized in modeling the cotton ecosystem wherein the growth and production of cotton bolls forms the basic model, and sub-models are then superimposed relating to various insect pests (etc.) that would affect boll set and yield (GU-

TIERREZ, in press). By determination that cotton grown under given conditions develops bolls up to a "ceiling" level and compensatorily drops bolls above that level, it has been shown that much of the boll drop caused, e.g., by *Lygus* bugs constitutes meaningless, or merely compensatory, loss of bolls, but not of yield in some situations.

Growth, development and reproduction produce population increase potentials in favorable habitats that must be met by adversity of some kind if populations are to stay within bounds. It is the consensus that phytophagous insects do not commonly exploit their host plants in natural situations to the point of great severity. For those species highly adapted to the climate, it would seem that other, biotic factors, must account for this. Yet biotic factors do not act in isolation from the abiotic factors but in relation to them. Thus, "natural control" is viewed as resulting from the combined action of all factors of the environment, but in the long run necessarily comprising at least one factor which increases in intensity of action as density increases and relaxes in intensity with decreasing density. The greater the degree and constancy of action of density-independent factors, the less is required of density-dependent factors for regulation to occur. Spreading of the risk is a stabilizing trend but even ANDREWARTHA & BIRCH (1972) recently seem to admit that at least over long periods of time, a truly density-reactive factor is required.

Much has been said about the heterogeneity of the environment in respect to population and community stability. While some sorts of heterogeneity in some situations certainly increase the chances of a pest species being kept under stable control by its natural enemies (HUFFAKER *et al.*, 1963; FLAHERTY, 1969; STERN *et al.*, in press), the so-called "principle" that greater diversity implies automatically greater stability remains unproved and can be misleading. For some pests, existence of a complex of natural enemies is a good safeguard against outbreaks, as for spider mites in situations where a potentially highly effective type of controlling natural enemy is rendered ineffective on occasion. The quick responsiveness, functionally and numerically, of other mite predators may serve to suppress outbreaks or intercept their development. In such cases, as with the olive scale situation (HUFFAKER & KENNETT, 1969), two or more natural enemies are better than the best one alone. Yet, a single highly efficient natural enemy can be entirely capable of maintaining a stable low density equilibrium indefinitely, and this usually implies little chance for other natural enemies to affect the situation materially. Many examples of good biological control fit this pattern. Moreover, as WAY (1966) has noted, increased vegetational diversity near crop areas may result in *more* pest species and *more frequent* problems. But this and other forms of diversity can, on the contrary, result in *better* biological control and *reduced* problems. Each situation

requires special analysis; generalizing is unjustified (VAN EMDEN & WILLIAMS, 1974).

Strip cutting of alfalfa and strip rows of alfalfa in cotton can alleviate pest problems. The former method retains natural enemies in the alfalfa fields, while the alfalfa strips in cotton attract and hold immigrating *Lygus* bugs in the alfalfa where they do little damage, thus protecting the cotton (HAGEN *et al.*, 1971; STERN *et al.*, 1964, and in press).

The degree to which crop plants are protected from insects by their own compensating resistance capabilities is probably far greater than commonly thought. Professor DAVID PIMENTEL (personal communication) considers that this has served not only to give plants a degree of immunity to severe damage but that a functional generation to generation genetic feed-back between plant and insect populations accounts for the fact our plant species in natural situations are seldom damaged severely by insects. While I disagree with this general explanation, certainly in our plant gene pools a great potential exists for developing more resistant varieties. Also, degrees of resistance or tolerance to a pest could render effective an otherwise inadequate natural enemy complex. Contributive stress on the pest species by climatic and edaphic factors, even if no density related protective features are involved, can likewise render otherwise ineffective enemies effective.

Cultural practices can intensify the climatic and edaphic stress. In any event, natural enemies of plants, and the complex of higher level action of their natural enemies on *them*, present a very complex natural control picture. Most plants have not evolved resistance to the whole complex of phytophagous species that were their former potential attackers. Rather, there have arisen specialized phytophagous forms that have kept pace with the plant's efforts toward resistance. Such species, or very mobile ones, constitute our major pest problems for many crops. We are indebted to their natural enemies that these specialized phytophagous species are largely kept under control in nature.

7. **Predation.** — BROADLY SPEAKING, PREDATION IS THE ATTACK AND FEEDING OF ONE ORGANISM UPON ANOTHER.

This is a highly successful means of obtaining nourishment. Predation may shape the morphology, physiology and behavior of exploiter, exploited, and "would-be" exploited species, and also of outlandish mimics, or cause complete extinction or preclusion of species, affecting distribution, cause suppression which is little related to population regulation, or serve directly as the population regulating mechanism, mediate interspecific competition and enrich the diversity, structure and stability of biotic communities (HUFFAKER, 1971).

Biological control as an applied practice is entirely dependent upon a clear understanding of predation. Some 120 pest species have been brought under some degree of permanent control by introductions of predators i.e, natural enemies (DEBACH, 1971). Use of natural enemies has been a cornerstone in every successful or developing program of integrated insect control.

The characteristics of a good biological control agent are: its adaptability to the varying conditions of the environment, its searching capacity (including mobility), its power of increase relative to that of its prey, its power of prey consumption, a high degree of prey specificity, life cycle synchronization and special behavioral traits affecting performance.

A good natural enemy need not be superior in all these respects; superiority derives from the integrated effects of these often interrelated factors. Searching capacity is of foremost importance. The value of power of increase may vary greatly from stable situations to unstable ones.

The emphasis in the literature on the functional response of natural enemies can be misleading. Although largely responsible for the numerical response, it is the latter, not the former, to which we must look for the main impact in pest control. Moreover, the fact that there exists in nature a complex of natural enemies that attack a given pest species means that a regulating total response potential may exist even if the total response of a given natural enemy species is inadequate.

Professor WOODWORTH, himself, first claimed that the effectiveness of a natural enemy cannot be ascertained simply by the percentage kill. Percentage kill must be related to many other factors to have any regulatory meaning. Also, the MORRIS (1959) or VARLEY (1963) techniques of assessment will not tell us just how effective a given natural enemy may be. This can only be shown experimentally by use of check-methods, promoted especially by PAUL DEBACH (DEBACH & HUFFAKER, 1971), or by actual introductions and comparisons (VARLEY *et al.*, 1974).

8. **Competition.** — THERE IS OFTEN EXHIBITED A MUTUALLY NEGATIVE INTERACTION BETWEEN TWO OR MORE ORGANISMS.

Conventionally, this competition has been considered to apply only where such organisms search for and require some common resource or other real thing that is in short supply. DEBACH & SUNDBY (1963) contended that competition may occur when no such resource is in short supply and they described results of experiments claimed to support that contention. HUFFAKER & LAING (1972) agreed with the former but disagreed with the latter claim. They elaborated the contention of HUFFAKER & MESSENGER (1964) that competition as above defined, and competitive displacement *can* result even when

no real resource is competed for. The mutually negative effect among its own individuals when increasing density of a prey (or host) population induces increasing stress by natural enemies is here considered competition. Otherwise, one individual of a species might succeed and another fail, or one species could "competitively" displace another through mutually negative interaction mediated by natural enemy action even when no shortage of a real resource, and by conventional usage, no "competition", were involved. There is competition for existence unmolested by enemies, for too many individuals interfere with that need just as too many individuals interfere with securement of food and abode.

Application of the competitive displacement principle has resulted in many improvements in pest control, especially in weed control! There are also many examples of displacement of a previously existing natural enemy by one later introduced, in every case resulting in a lowered density of the pest. The displacement appears to result from the new species having a higher capacity to find and parasitize hosts, thus lowering the host density so much that the former natural enemy could not find sufficient unclaimed or still utilizable hosts to survive. DeBach & Sundby (1963) describe such events in California involving, first, displacement of *Aphytis chrysomphali*, a parasite of California red scale, from coastal, then intermediate, and finally interior citrus groves of southern California, by a congener *A. lingnanensis*, and secondly, displacement of *A. lingnanensis* in interior areas, and more gradually, in some intermediate and even coastal areas as well, by another congener, *A. melinus*. With each stage of displacement improved biological control resulted. Huffaker & Kennett (1969) also described the displacement of a complex of natural enemies of olive scale on olives in California primarily by *Aphytis maculicornis*, with great reduction of the pest through there was left an open niche (spring generation scales) which made possible the establishment of still another parasite species, *Coccophagoides utilis*. These two species now co-exist, with *A. maculicornis* remaining the superior species but the supplementing action of *C. utilis* so adding to the combined control effect that the pest is now completely controlled in all unsprayed areas on all host year after year. Competitive displacement of a vector insect by a non-vector type is also suggested.

Intraspecific and interspecific competition are quite distinct; the former is inherently a regulating process whereas the latter is not. Decreasing density of a Species A commonly means a decreased chance of its recovery as a population so far as its competition with Species B is concerned. A decrease in numbers when all the competition is intraspecific, however, means automatically a lessening of the effects of that competition and improved chances of recovery.

KENNEDY (1972) has challenged the usual view of intraspecific competition as being too one-sidedly negative, with its emphasis on adversity and mutual deprivation. He describes how *behavior* in the sycamore aphid, even when the signal is increasing numbers and degree of crowding in this *gregarious* species, results in a positive result from the crowding. The "shortage of space" is brought on by their own gregariousness and then they respond to the mutual stimulation by cessation of reproduction and emigration. KENNEDY states, "So the increased mutual stimulation can be regarded... not only as a signal of current or impending adversity but also as a signal of the new, positive opportunities open to the population when there are enough individuals to spare for the hazardous operation of dispersal. The intraspecific response promotes further population growth in the very process of restraining it locally". It seems to me, however, that the process is nevertheless one of negative feedback — that this expansive potential would only be achieved if, in fact, the same or a greater degree of crowding did not exist in other places sufficiently to offset the disadvantages of all such local populations remaining on the original trees. KENNEDY's point simply accents the fact that all species must be capable of finding new resources as old resources are depleted and that traits may arise for anticipating shortages and reacting by emigration while sufficient numbers are at hand to sustain the losses of movement to suitable new resources.

9. **Cooperation.** — THE EVOLUTION OF COOPERATION, EITHER INTRASPECIFIC (SOCIALITY) OR INTERSPECIFIC (MUTUALISM) HAS SERVED MANY SPECIES WELL.

Evidence suggests that wolf properties determining size of areas defended and his territorial limitation of his own numbers were evolved at a level consistent with serving primarily as a dampening factor in the population control of major herbivores on which he fed in primitive environments (MECH, 1974).

Except for the social insects, dragonflies and a few others, territoriality among insect predators is little developed. Effective pest-controlling natural enemies are essentially non-territorial. Without such, they could not tend to maximize yield to themselves. The primitive unrelaxed form of regulation holds — through reduction of prey density to the minimum essential to survival of the predator (NICHOLSON, 1954; HUFFAKER, 1971). This means control at non-economic densities in many situations.

The principle of interspecific cooperation, however, is well represented in the insects. It is well known that ants and a number of hompterous insects enjoy a mutually beneficial cooperation, the ants deriving nourishment from the honeydew produced by aphids and scale insects, for example, and in turn protecting them from natural

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enemies, or even culturing underground "gardens" of fungi and husbanding their benefactors upon them (e.g. FLANDERS, 1958). For many of these examples the ants do not actually "culture" the honeydew producing species and, in fact, may drive away natural enemies of other insects in which the ants have no interest whatever, producing pest problems in both honeydew producing species and others as well (DEBACH & HUFFAKER, 1971). The field entomologist must therefore be alert to the possibility of problems of either category.

The mutualistic relationship by which microorganisms (symbiotes) are maintained in the digestive tract of certain insects and in turn serve an essential role in food utilization by their hosts is represented by wood feeding insects such as termites with their protozoan symbiotes, and by certain fruit flies and symbiotic bacteria referred to above.

10. Movements. — ALL ORGANISMS MUST BE ABLE TO GET ABOUT AND DO THINGS (FINDS MATES, FOOD, HOSTS, EAT, OVIPOSIT, ETC.).

We know less about the behavioral movements and how to quantify and predict them than perhaps any other basic principle of comparable significance. Our ability to assess the importance of movements is very limited for highly mobile species. Mark and recapture techniques of evaluation of the control capabilities of natural enemies apply mainly to the less mobile species of pests and natural enemies.

Nature's great chemical messengers, the pheromones, present avenues not only to learning about pest and natural enemy movements, but also as a means by which we can monitor pest populations more accurately and apply insecticides much more wisely as to place and timing. Also, the horizon to direct control through pheromone trapping or mass confusion is envisioned.

Behaviorists are reshaping old concepts of insect movements. Up to 20 years ago it was considered that strong fliers like butterflies and locusts could maintain directional flights for hundreds of miles, while the weak ones like gnats and aphids simply drifted passively with the wind (KENNEDY, 1972). While much new evidence suggests that even such strong fliers as locusts move as swarms with the wind (and this has survival value in taking the locusts to the point(s) of wind concurrence and rain), new studies emphasize the role of behavior in *initiating* and *timing* the flights and in *determining their end.* Yet, according to KENNEDY it appears that the research chemists have been avidly synthesizing sex pheromones before they know anything about the behavior of mate finding. KENNEDY writes that, the chemists' expertise and pertinacity, although highly admirable, serves only to "...show up the emptiness on the behavioral side". The work of SHOREY (1973) has emphasized that a "sex attractant" may indeed orient an insect to its mate, or, under other conditions

signal it to move in the opposite direction by switching on an orientation to wind or light. Thus, while some optimism about the use of pheromones, not only for monitoring, but as a direct control tactic, seems justified, the chemical horse again seems about to run away with the biological wagon unless much more intensive *behavioral* studies are done. While successes may be had without them, frustration and failures may be averted with them, writes KENNEDY.

Greater knowledge of insect behavior and movements also offers a means out of the current dilemna in which insect control finds itself in urgently requiring narrow-spectrum specificity in insecticides with little chance that industry will develop physiologically selective chemicals. However, we may find it possible, through close study of insect behavior and other aspects of insect biology and ecology, to obtain the essential ecological specificity, even with current physiologically broad-spectrum materials (SMITH, 1970).

11. The holism and interactions of ecosystems. — ECOSYSTEMS EMBRACE MANY INTERRELATED FEATURES AND MUST BE VIEWED AS WHOLES.

Ecosystems exhibit a holism, capacities of compensation and ecological interactions among the natural factors acting therein and with the artificial control measures we apply to control crop pests in them. To attempt patterned pest control decision-making for a complex of pests of a crop, we need to develop equations expressing these interrelationships among the principal pest species, their natural enemies, soil and weather conditions, the main crop production processes and economic relationships (SHOEMAKER, 1971).

The first principle of integrated control is stated in the dictum: "Consider the ecosystem" (STERN *et al.*, 1959). This rests upon the basic principle of interrelatedness of ecosystem factors. Although complex and difficult of analysis, modern pest control must understand and deal with these interrelationships; otherwise we will continue to fly blind just as preventive calendar date entomology has been flying blind for too long now. Economic entomology, the farmer and society at large have had enough of this flying blind and relinquishing to the organic chemist the duties of biologists. Insect problems are first of all practical field ecology problems and must be solved by ecologically minded entomologists.

We can see one facet of this complex of interrelationships in ecosystems by considering the ecology of pesticides interference. As indicated in the works of Professor WOODWORTH, whom I honor in this presentation, and of his great mentor, STEPHEN A. FORBES, when we apply an insecticide we inevitably do far more than affect the target species. These other effects include : (A) direct toxic effects on natural enemies; (B) indirect effects on natural enemies : 1) by severely reducing the target species serving as hosts or prey, 2) by

direct or indirect reduction of necessary alternate hosts or prey, 3) by reduction of species supplying subsidiary foods, and 4) by direct poisoning of subsidiary foods; (C) stimulation of pest reproduction; (D) the eliciting of pest species counter reaction by development of resistance to the pesticide; (E) rise of competitively suppressed species through reduction of superior competitors; (F) destruction of pollinators and other beneficial organisms; and (G) combined effects of any of these (HUFFAKER, 1971 b).

Here, I emphazise in the strongest terms, however, that even though pursuing the proper goal of maximizing natural control factors and minimizing use of the more pollutive and disturbing chemicals as we seek better insect control, we will have to continue to rely heavily on chemicals in the foreseeable future. We simply are not likely to obtain other solutions for all of the pests on very many crops. Chemicals present the most reliable *immediate* solution to a problem. But, of course, we are threatened with their mounting ineffectiveness if we do not act to prolong their useful life by reduced and strategic usage.

Another important facet of this interrelatedness is seen in the consideration of economic injury levels. Actual injury to a plant by a pest may depend upon its numbers, stage of development, phase of growth, and the cultural conditions of the crop and its inherent resistance or tolerance, soil and weather conditions, and the degree to which a given population at an early stage of development may be killed by natural enemies, weather adversity, etc. The degree of economic injury is also dependent upon the supply-demand condition for the crop, the direct and indirect costs of taking remedial action, and the capacity of the crop to compensate, prior to harvest, for actual damage at a given time.

Among the most active researches relating to insect populations have been those providing means by which we gain better insight into the processes in host-parasite or predator-prey systems, and the actions of various mortality factors on field populations. The life table technique provides a means of cataloguing the actions of the various mortality factors and the reproduction of a given generation. Once this basic information is gathered, two rather distinct methods of using such data have been advanced, that of R. F. MORRIS in Canada and that of G. C. VARLEY in England. WAY (1973) complains, however, that neither of these methods have "yet proved their practical value in controlling pests". DEBACH *et al.* (in press) also point out that check-methods and carefully performed *experiments* appear to be more productive in some respects. While such life table and key factor techniques indeed provide insights, we must not spend a disproportionate effort in these areas, for the problems of designing and maintaining pest management programs are far more complex

and greater in scope than these techniques are designed to handle. Moreover, the extensive studies on host-parasite models have not been applied to the analysis of, and used in prediction of, pest numbers in the field in a single case. Perhaps this is because they are commonly conceived as an interaction in a "microcosm", whereas field populations present extensive sub-population groupings and unaccounted-for movements (HUFFAKER & STINNER, 1972). The recent theoretical studies of HASSELL & MAY (1973), however, offer serious suggestions which may prove useful in making natural enemy introductions(see VARLEY *et al.*, 1974).

The problems are site individualistic and often highly concerned, not only with unique adaptations to climate, but with highly specialized behavior and physiology and biotic factors which we know little about. We will not be assured of predicting the success of a parasite we are to introduce simply by performing a life table or key-factor study of its performance in the home of origin. The different biotic factors, as well as subtle differences in physical conditions affecting behavior and performance, may be quite different. It is not justified that introductions be delayed for many years while such extensive studies are carried out (DEBACH & HUFFAKER, 1971).

The need for basic individualistic and practical studies to develop integrated control schemes will remain great (WAY, 1973). Not life tables, nor host-parasite models, nor systems analysis, will do these things for us. Such individualistic studies are a part of must both precede and run concurrently with other approaches utilizing an analysis of the whole system, with stress on main areas and promising tactics (e.g., nature's own system: natural enemies and host plant resistance) which previous individualistic and practical research has indicated as rewarding. Systems analysis is used also to point to gaps in research findings, the two approaches thus to go hand in hand. It boils down to this: The problems posed when we consider all aspects of crop production as related to methods of control of a diverse complex of pests, are too complex to handle reliably without the aid of a quantitative, patterned procedure for decision-making. The farmer has had to be his own systems analyst. Scientists must do a better job for him. With luck, good coordinated ecological research from all relevant disciplines, and an eye always to the practical, we can do so.

RÉSUMÉ

Quelques principes écologiques de la lutte contre les insectes nuisibles.

Dans cet article nous donnons des exemples montrant que contre des insectes nuisibles, toute lutte écologiquement satisfaisante est fondée sur nos progrès dans la connaissance de onze principes fondamentaux d'écologie. Nous discutons les principes concernant la variation génétique, l'adaptation, la nutrition, la reproduction, la croissance et le développement, la compensation vis-à-vis de facteurs adverses, la prédation (y inclus le parasitisme), la compétition, la coopération, la mobilité et les interactions de facteurs dans un système global.

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