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On the ecology of vectors

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Abstract—The strategies of vectors which are responsible for the dissemination and dispersal of parasites are shown to be a particular case of a more general bio-ecological phenomenon: the dissemination and dispersion of propagulae. Plant pollinization seed dispersal and parasite dissemination involve similar ecological relationships and the conservation of energy.

Keywords: vector; parasite; ecology; evolution.

1 Introduction

After the discovery of the role of vectors in biological cycles and in the transmission of parasites, a new and important field of ecological research was open to investigation. The obvious implication is that their control must be planned as an intervention in the complex ecosystems they are part of, which must be altered in a way as to provide lasting results, and to avoid unexpected medium- or long-term consequences we may come to regret later. Most often it is not a question of eradicating a species by direct action, but of suppressing ecological niches or modifying the structure of biotopes, through environmental manipulation or ecological engineering.

Finding a suitable host among the different species of a complex ecological community is no easy task and one which involves a considerable loss of energy. Dissemination by wind and water is hazardous. Vectors save time and energy by localizing suitable recipients of diasporae.

It is outside the scope of this study the redefinition and classification of biotic relationships (Starr); it merely intends to show certain types of associations under a particular point of view, to highlight their underlying common aspects. As a standard reference work on parasites and parasitism, the reader may wish to consult Rey(Rey, 1991).

Survival depends upon efficient mechanisms that permit the dissemination of diasporae inside the limits of the geographic and ecological distribution of organisms, reducing intra and inter-specific competition, and insuring its development in a favorable environment. Evolution depends, among other factors, on dispersal strategies into new habitats, crossing natural barriers, beyond geographical and ecological boundaries. Macro and microorganisms share similar requirements and frequently adopt similar solutions, in order to service. Sociobiologists feel tempted to generalize conclusion based on the observation of lower animals to include human behavior, but this discussion is beyond the scope of the present analysis.

The objectives of this article are: to highlight the basic similarities and differences that exist between the strategies for cross-pollination and zoochory, and those related to the transport of parasites from one host to another; to identify the general principles underlying these processes; and to demonstrate that the control of vectors must be planned as something distinct from a combat operation, but as the management of a complex selfregulated system that need to be fully analyzed and understood as a system, before changes are attempted.

Dissemination and dispersion of organisms may be passive. with the help of air (anemochorous) or water (hydrochorous) currents. Plants and animals may be transported in the hair of mammals, or clinging to the body of an animal, as some spiders which are carried by beetles. This type of association is called phoresia more complex mutualistic relationships require the passage of propagulae, diasporae, or cysts through the digestive system of an animal, to stimulate germination. Still more elaborate is the process of multiplication or development of a parasite in the body of a vector or intermediate host. Boucher *et al*. and Janzen have recently re-discussed the intimate nature and classification of mutualistic associations and the ecology of mutualism.

In 1976, Holmes recognized that the strategies used by parasites to reach the prey seem to be essentially the same as those used by animal dispersed plants or vector borne parasites. The literature vectors on plant pollination and dissemination is as large as that dealing with parasites and their vectors. But there are few studied focusing on the common aspects of the common subjacent biological processes.

In this article, plants receiving pollen and definitive hosts being parasitized, are referred to as receptors. The term vector is used to designate, collectively, pollinators zoochores, and intermediate hosts. In those instances where it is necessary to distinguish some particular aspect of each type of association, specific designations are used. Diasporae refer to propagulate, pollen, seeds, fruits, and early ontogenetic states of parasites, as eggs, larvae, miracids, cercariae.

A last warning is that we must be careful when interpreting apparently similar phenomena that resulted from separate evolutionary mechanisms.

The following terms and definitions are used throughout the text:

Abundance—Number of individuals in a population or community. Cf. density, frequency.

Accommodation — Range of amplitude of environmental factors that an individual tolerates . Physiological plasticity. Cf. Adaptation.

Adaptation—Range of amplitude of environmental factors a species tolerates. Statistical limits that condition its ecological distribution. Cf. accommodation.

Analogy—Superficial resemblance resulting from convergent evolution in organisms phylogenetically unrelated, which live in vicarious environments. Cf. homology(Haas & Simpson).

Center of origin—Area where an species originated or branched.

Density—Number of individuals per unity of area. Cf. frequency.

Diaspore—Egg, seed, or early ontogenetic stage of an organism capable of developing into a new individual. Cf. propagule.

Dissemination—Propagation of diasporae (s. lato) inside the limits of distribution of the species. Cf. dispersion

Dispersion—Expansion into new areas: propagation of diasporae beyond the limits of the geographical distribution of the species. Cf. dissemination.

Ecological niche—Role or function of an organism in the trophic chain. Not to be confused with microhabitat.

Frequency—Quantitative distribution of an organism in an area. Pattern of ecological distribution.

Home range—Space used by an animal in the normal activities of searching for food, water, mates. Cf. territory.

Homology—Fundamental similarity among related organisms which indicates a basic ancestral structure. Cf. analogy.

Phoresia—Transportation of an organism by another.

Propagule—Vegetative reproducing bodies of plants.

Phytophagous—An animal that feeds upon primary producers as bacteriae, diasporae, branches, leaves, fruits, seeds, trunks. Herbivore.

Territory—Area defended by an animal against other individuals of the same species. We recognize feeding, breeding and living territories. Cf. home-range.

Vector—Used currently in medical, parasitological, and veterinary literature without a precise definition. It may designate indiscriminately the phoresic carrier, the intermediate host, and the vector (s. strictu) where a parasite multiplicities or molts (see International Rice Research Institute).

Zoochore—Animal that carry and disseminate (or disperse) plant diasporae.

2 Strategies

Biological strategies which are responsible for the success in the dissemination/dispersal of diasporae resulted from a long process of competition, cooperation, and natural selection. Some of the mechanisms invoked are homologous, with a common origin, some are analogous, exhibiting a superficial similarity, due to adaptation to similar ecological conditions.

As with protective resemblances(Avila-Pires, 1968) antagonistic selective forces may result in apparently identical situations. In the case involving vectors and receptors, the situation is similar to that involving batesian mimicry and mullerian convergence, as we shall see.

The biological factors or imperatives which are the main determinants of the phenomena we discuss in this article, are the following:

3 Competition and genetic variability

In the "Origin of Species", Darwin collated a large amount of evidence of the role of both intra-and interspecific competition in the evolutionary process. His theory of natural selection was based upon the observation of individual variations, both in domestic and in natural populations. He showed elsewhere the dangers of self-pollination of flowering plants, that would be explained later by the geneticists of the XXth century.

Ecological conditions that favors the planulae are not the same required by adult plants, and usually cannot be found in its shade. In animals, competition for food and shelter stimulate dissemination. Territorial behavior is also responsible for the search for suitable territories and home-ranges by the emancipated young, turned into potential competitors. Those are the main factors that force emigration from the vicinity of the nest and consequent dissemination, even if the distances traveled are reduced. Kennedy showed that these distances are usually smaller than one imagines.

4 Dispersal

Plant and animal dispersal was a key element in Darwins' theory, and the subject matter of two chapters in the Origin. The theory of the centers of origin was also discussed by A. R. Wallace, who proposed the biogeographical regions we accept today. Dispersal as geographical isolation depends on the existence of suitable active or passive means of transportation. Individual range of accommodation, and specific range of adaptation allow organisms to bypass barriers and to colonize new habitats. The theory of island biogeography has been successfully applied to the special case of parasite dissemination and dispersal.

Holmes remarked that with the exception of many of the ecotoparasites, parasites once established, cannot move out and search again. In this respect they are similar to plants or to sessile animals; therefore, strategies of host selection may be expected.

Parasite dispersal depends upon the movements of their hosts. Kennedy reminds us that vectors have small home ranges and that even if the host or vector undertakes extensive migrations, as do many birds, a restricted period of egg release may result in the parasites being confined to a small area of the host's range.

5 Energetic economy

Energy saving mechanisms is vital for arrival. The energy obtained from food is consumed in the course of normal physiological activities, including the search for food itself. When the English tried to control tse-tse flies, in the attempt to eradicate African trypanosomiasis be killing the antelopes which were their sources of food, they discovered that you did not need to decimate the last animal to succeed in reducing the fly populations. Even when the density of hosts was suitable, their low frequency required a fly to spend most of its energy in search for a blood meal(Muirhead-Thomson). Breeding consumes a lot of accumulated energy, in pre-nuptial rites and combats, in copulation, in the defense of territories, during the gestation period, and for caring, protecting, and feeding the young. The more eddicient the mechanisms that guarantees the survival of the offspring, the saller the number of youngs that are needed to insure the species survival Passive dissemination of diasporae, by wind or water, subject them to considerable risks. Predators, adverse environmental conditions as temperature, pH, flux velocity, and reduction of viability with the passing of time, are some of the factors of risks.

The preceding items justify the need to improve the methods of transport of diasporae to insure survival, until they reach a suitable place for colonization and further ontogenetic development.

6 Transportation

As we saw, anemochory and hydrochory are the least efficient means of transportation, although some morphological and physiological adaptations may reduce the risks involved. Winged or filamentous seeds, putrefaction-resistant fruits that remain viable when immersed in the water of lentic environments, as the fruits of some palm trees which are single-species dominants in the tropics, are good examples. A good example is provided by a tropical plant from the family of the fig-tree. Its seeds are transported by bird-vectors, and are dropped among the branches of another tree. The seeds germinate, and the roots grow down the trunk of the host until they reach the ground. Eventually, the fig tree will constrict the host to death. McDiannid *et al*. studied this instance of biotic relationship, which is most pertinent to our discussion.

On the other side of the scale, true vectors not only offer a proper internal environment to diasporae, but also able to identify suitable receptors. Mechanical vectors offer examples of phoresia, endophoresi, and inquilinism. Tabanid flies that carry Trypanosoma evansi, a flagellate protozoan and blood parasite, the agent of surra, are mechanical carries, infecting the mammals they feed upon. House flies and roaches are carries of fungi and bacteria(Martin); Pulex irritans, the house flea, may occasionally transport Yersinia pestis, a bacterium responsible for bubonic plague, from one infected papient to a healthy person. To Rickleffs, most mutualistic relationships probably evolved by way of host-parasite interactions, while Allee, quoting Hulf, admits that malarial protozoans indicate that their major phyletic evolution(megaevolution) has been more clearly tied to that of insect vectors than to their vertebrate host.

Transportation is also related to feeding behavior. Holmes agree that parasites use two types of food-web relationships-the feeding patterns of vectors , usually bloodfeeding invertebrates, or the relationship between predatory definitive hosts and their prey, the intermediate host. In each case, the evolution of the parasite is dependent upon the characteristics of the intermediate host, in much the same fashion as a plant which depends upon an animal for dispersal of its seeds.

7 Homologies and analogies

Similar biological needs led to the adoption of similar adaptation involving both vectors and receptors, as we shall see.

7.1 Trophic relationships

Holmes was aware of the generality of processes involving the behavior of vectors (s. lasto), but his analysis deserves a few comments and corrections. He wrote that Levin and Kerster (1974) have pointed out to general adaptations in such plants: they synchronize their fruiting period with the time of the greater activity of the vector, and they provide a nutritional reward for the vector. Van der Pijl 1969 has emphasized two more: they locate their fruit in the region of the greater activity of the vector (or devise adaptations so that it will fall there), and they provide the fruit with attractants adapted to the sensory mechanisms used by the vector. Parasites also use these adaptations.

Holemes' analysis is most pertinent and enlightening, but we must consider that it is probably the vector's activity that depends on the fruiting season, or else, both are dependent upon the same environmental factors. This is more likely a case of co-evolution than of unilateral adaptation.

As far as trophic relationships are concerned, the following categories can be recognized:

—Between pollinizers or zoochores and receptors: mutualism

—Between pollinizers or zoochores and pollen or seeds: phoresia

—Between vectors and receptors: vector parasitism

—Between vectors and parasites: phoresia or parasitism

Where plants are concerned, their own reproductive processes are involved. The relationships between pollen or seeds and the host-plant are distinct from those between hosts and their parasites. This is a typical example of converging evolution, where similar procedures derives from distinct evolutionary forces. The pollinator or zoochore benefits the host-plant, while the vector(s.s.) benefits the parasite, to the disadvantage of the host. For the plants in the donating and in the receiving end, the survival of the vector is important, and for the vector, the seeds and pollen are not harmful, and sometimes, beneficial, as food. Parasites, on the contrary, impair the vector, change its behavior, and frequently cause its death, or make it vulnerable to the host. In certain cases, though, parasites stimulate community mechanisms in the host, protecting it from further infections.

Another difference lies in the fact that plants compete for the diasporae, as proved by Clements & Long. Vector(s.s) compete for their hosts, and there is a limiting population-density that permits success. When the number of tabanid flies trying to feed on a horse is too large, none will succeed, as the host reacts to the mass attack.

7.2 Search and identification

Finding and recognizing a suitable receptor are two distinct aspects of an important survival problem, akin to the need to find and recognize food. Location is achieved often in an indirect way, when vectors are attracted or guided by features of the environment and not by the receptor. Hummingbirds are attracted by the flowers where the insects they feed upon are also feeding. Cercariae of schistosomes have a positive phototropism, and swim towards the surface, where they are able to find their hosts.

In 1923, Clements & Long published a remarkable book with the results of their observations and quantitative experiments on the methods used by pollinators to locate and recognize suitable plant species, or as they as in the introduction, to study the attraction of insects by flowers. They investigated competition among receptors, and based their conclusions on a detailed statistical analysis. Unlike Darwin, who did most of his observations on gardens, Clements & Long investigated the pollinating behavior in natural environments. They were able to establish the role and the relative importance of shape, color, grouping and distribution of flowers in the plant, as attractants and means of recognition by pollinators. Studies in the field of agriculture increased our knowledge on this subject and Smith published a good review of the processes of recognition in animals.

Macinnis collated the information on the methods used by parasites and vectors to locate and recognize suitable hosts. Vectors perform a more active role than plant diasporae. Certain parasites answer to stimuli to abandon the host at a ceratin moment: motor activity of the host and some stimuli of environmental factors, as light and heat act as signalizers. Larvae of Dracunculus abandon their host as they take to the water where Cyclops, their intermediate host is found. Circarie of schistosomes abandon their snail hosts stimulated by light. There is a growing litrature on this subject, and the few examples given here are sufficient to guide our discussion.

According to Macinnis, the main environmental factors which are capable of eliciting an answer from parasites are of a chemical or physical nature, as pH, heat, light, gravity, and chemical substances in the water. He says that not surprisingly, they are almost exactly the same as those that function within a host.

Our knowledge of the processes involved in the recognition by animals was increased also by the contribution of ethologists investigating reproductive behavior. Understanding the methods used by males and females of cryptic species to identify a partner has clarified some aspects of vector recognition behavior(Smith). Many parasites show a blind pattern of colonization. Shotgun dissemination is an wasteful process, in terms of energy. Scattered larvae penetrate blindly many unsuitable hosts, and die. A survey of schistosomiasis in natives of the Xingu region. In Central Brazil showed a high percentage of positive immune responses, in the absence of the infection or of the disease. Swimming in water where there are cercariae of schistosomes parasitic of fish and bird, these people suffer aborted attempts at colonization, which provoke an immune response, but no actual infection. Holemes mention the fact that in Cold Lake, Canada, Metechinorhynchus salmonis constitutes 70% of the parasite fauna found in *Catostomus*, which is not a viable host.

Although the specificity of the relationship involving vectors and hosts favors parasite survival, extreme specialization also involves the risk of extinction following occasional changes in the physical or biotic environment. This is why behavior is so important for the economy of ecological systems, as natural selection acts directly upon it.

7.3 Behavior

All those who study behavior of vectors in the field are aware that the presence of the observer influences the behavior.

Clements & Long proposed a number of interesting techniques for the quantitative analysis of the mutualistic behavior of insects and plants. They had several observers working simultaneously in different locations, including controlling sites. They analyzed the influence of pollen and nectar acquisitive behavior, and the efficiency of transfer from a plant to a receptor. They noted the influence of seasons, days, hours, of meteorological conditions as wind, clouds, temperature variation, of the grouping and spacing or frequency of plants and flowers and behavior of the vectors. They remarked that even the weather of the prevous day might have a profound effect upon insects: if it was rainy, unusually cold or warm, or windy. They noted that differences in vector behavior, in places only meter distant from one another, could be related to shade, exposition and distance from their respective nests. They showed that male and female pollinators had different patterns of behavior.

Success in the dissemination of diasporae demands synchrony in the timing of its development with its placing in a suitable site to be located by vectors. The flowering and opening of flowers must coincide with the periods of activity of the diurnal or nocturnal pollinators. So, bats vicariate birds by pollinating many tropical forest flowers that are open at night.

There is a seasonal synchronism, well marked in zones where seasons are well defined, which is governed by hormonal alterations, as those which are stimulated by photoperiodism and are thus responsible for reproduction. There is a circadian floral rhytm, and the vectors have their own alternate programmed periods of activity and rest. The case of Wuchereria bancrofti is always remembered because of the impact caused by its discovery and due to its peculiarities. The microfilariae remain in the internal circulation during daylight and migrate at night towards the peripheral veins. Their usual vectors are mosquitoes that are active at night. But in the Southern Pacific and Asia, where vectors are diurnal, the filaria cycle is reversed, and microfilariae are found during the day, in the peripheric blood system. If a host travels across several time-zones, changing his periods of activity and rest, the circàdian cycle of his parasites also changes. Furthermore, microfilariae tends to concentrate in those regions of the body of the host which are most susceptible to mosquito bites.

7.4 Morphology

Morphological co-adaptations that facilitate or impair the access to diasporae by vectors have been described by many observers. From the first remarks made during the 18th century to Darwin' studies of orchid reproduction and plant pollination, the complex interactions between plants and vectors raised a number of unanswered questions. The theory of natural selection, as first proposed by Darwin, had difficulty in explaining what possible advantages the first small rudimentary variations might have, before they could be really useful. Precise co-adaption between insects and plants posed a problem, if the occurrence of small aleatory, random, modifications was to be accepted. In Ospovat and in Desmond & Morris we find a good historical account of the long arguments that took place in the later decades of the 19th century and that ended in the present neodarwinian theory of evolution.

7.5 Differences

There are several differences between the relationships of zoochores/pollinators with pants, and those between vectors and hosts of parasites, a we shall see.

With few exceptions, birds and mammals are important as zoochores and hosts, but not as vectors(s. s.) of parasites, with the exception of the Chiroptera. Arthropods and insects in particular, are the main zoochores and vectors.

Holems recognized that apparently, two of the general adaptations of plants to seed dispersed by animals elucidated by Levin and Lester or Pijl(synchrony, both annual and diel, and site-coordination) are also well developed in vector-borne parasites. The host already provides a nutritional reward and attractants for the vector, so those adaptations might be considered superfluous in the parasites. The basic adaptive strategies of vector-borne parasites and animal dispersed plants seem remarkably similar.

In this particular case, the similarity is only apparent. As pointed out in the item describing trophic relations, pollinizers and zoochores guarantee the survival of the host plants and their own diasporae, to the contrary of what happens with vectors and parasites. As stated at the beginning, this problem reminds us of that of mimicry. Where Muellerian convergence is involved, different species, all of them equally protected against predators, profit from the common appearance of form or color, achieved through a process of convergent selection. In the case of batesian or true mimicry, the selective pressures are divergent: in the model selection tends to make it recognizable as inedible, but in the mimic, selective forces operate to make it resemble the model. So, similar results evolve from different mechanisms and selective pressures.

In both instances, involving vectors and mimics, the quantitative degree of risk will determine the direction of the selective process; preserving or eliminating the organisms concerned.

As to feeding behavior, Holmes described, among other types of strategies, to mimic the normal food of the intermediate host, such as some hymenolepidid eggs which mimic diatoms normally eaten by the ostracod host etc. or the egg packets of other hymenolepidids, which mimic the filamentous algae eaten by the amphipod host.

8 Concluding remarks

Knowledge of the ecology and the true nature of vector activities is paramount for their successful control.

As we have seen, it is a common fact among vectors(s.l.) that males and females of the same species occupy distinct ecological niches. In flies and mosquitoes, the male is phytophagous, while females are hematophagous. In many cases, specially among flies, animals of both sexes have one plant meal before females start feeding on blood. This fact is important in terms of population studies, collecting techniques, and vector control. The fact that we know very little about males of certain vectors of human and animal diseases, which have no direct parasitological importance, impair our knowledge of the ecology of the species. Furthermore, the presence, frequency, and abundance of males influences the behavior of females. Very often, females are attracted by the males and not by the chance of a blood-meal. It is only through the understanding of community structure and functioning that we can plan rational and effective lasting control of vectors.

In 1929, the malarial vector Anopheles gambiae was accidentally introduced in Northeastern Brazil, from Africa. Aggressive, biting in broad daylight, capable of reproducing in road ditches and potholes, these mosquitoes dispersed along the coast. In 1938, 1939 and 1940 an epidemy of malaria killed around 20000 people. A successful campaign eradicated this mosquito in three years, at a cost of over two million dollars. The success of this campaign, which is described in many texs on the ecology of invasions, was due to the following factors: the species was not native of that region; its dispersion was limited; human and financial resources were sufficient, and had been mobilized in a short span of time. But most of all, as Elton wrote: It is quite certain that the campaign could never have succeeded without the intense ecological surveys and study that lay behind the inspection and control methods.

Malaria provided yet another text-book example of the importance of the ecological knowledge from the control of vectors and parasites.

In 1898, Adolfo Lutz was commissioned to investigate an outbreak of jungle malaria among workers of a branch of the Sao Paulo Railway under construction in the slopes of the Serra do Cubatao, Southeastern Brazil. In 1903, Lutz published a remarkable paper, where he described the ecology of a new species of mosquito that breeds in the little pools of the rain water that accumulates among the leaves of bromeliad plants. Many years later, endemic malaria threatened a population of one and one-half million people living in an area of roughly 33000 square kilometers, in the State of Santa Catarina, along the same mountain range. In that region, three species of Anopheles (Kerteszia) are responsible for the transmission of the three malaria parasites. In this case, control was directed at the elimination of the bromeliads. Klein described the situation and concluded that to eliminate the risk of malaria it was necessary to destroy the forest vegetation in and around towns and cities. Some 30 million square meters of forest were thus destroyed. As this extreme action did not results in the elimination of malaria, a center for ecological studies was installed in the malarial region. This project ended in 1953, and a great body of ecological knowledge was amassed. Klein eventually concluded that it is necessary that man dominates nature, not by the forces of destruction, but rather by the judicious use of the means offered by technical knowledge obtained through extense scientific research.

An example of a well succeeded program of vector ecological control is also well publicized case of the rabbits introduced in Australia during the 18th century, that became a pest. The Brazilian parasitologist H. Beaurepaire Aragao suggested the use the Myxoma virus which does not infect man, to reduce the rabbit populations. In Europe, the vectors are fleas, but in Australia, are mosquitoes(Fenner, 1954; 1965). After a number of tries, the situation changed to an equilibrium between rabbits and viruses, rabbit populations having been reduced to tolerable levels. For its implementation, scientists of four continents collaborated and success must be credited to the large body of ecological knowledge that was obtained and used.

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