

THE BEHAVIORAL ECOLOGY OF VERMIN

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SYNOPSIS

Some topics in evolutionary biology might be of interest to medical entomologists, particularly those concerned with the dispersal of ectoparasites. These include:

Sexual selection—Male competition and female mate choice may influence the propensity to disperse, which hosts are chosen, and where parasites are located on an animal. Phoretic flies on beetles can serve as models for vertebrates and their vermin and illustrate some possible sexually selected patterns of distribution.

The maintenance of sex—There is a cost to sexuality best described as the cost of producing males. Plant, but not animal, ectoparasites commonly mitigate this cost through cyclic parthenogenesis. It is suggested that phenotypic variability produced by the immune system of vertebrates may select for genetically heterogeneous offspring, i.e. sexual reproduction.

The extended phenotype—The notion that "gene" activity may extend into the form and behavior of a symbiont suggests that symptoms of infection or infestation should be considered from the perspective of both the host and the parasite. Vertebrate pathogens may influence the movement of ectoparasitic vectors.

INTRODUCTION

I am not a medical entomologist and I do realize there is a certain presumption in writing on topics outside one's field of study. However, the perspective of an outsider can sometimes include features overlooked by the specialist. With this somewhat arrogant apology in mind, I will present some behavioral and evolutionary themes that might be of interest to medical entomologists. These topics are sexual selection, the maintenance of sex and the notion of the extended phenotype, particularly as they pertain to ectoparasitic insects and what seems to me to be a central problem in medical entomology, the dispersal of insects both between and over the surfaces of host animals.

SEXUAL SELECTION

Sexual selection results from the difference in male and female investment in offspring (Trivers 1972, Thornhill 1980). At its simplest, females invest in large gametes and their reproductive success is limited by their ability to make eggs and obtain the highest quality paternal genes for their offspring. Males make cheap gametes and their reproduction is limited by their access to females. Mate competition among low-investing males creates intrasexual pressures that commonly result in the evolution of fierce, fast, or sneaky males. Female choice of mates generates intersexual selection that

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can favor, among other things, male advertisement and greater female powers of discrimination.¹

Intra- and intersexual selection influence the movement of ectoparasites. As a simple example, it can behoove males but not necessarily females to go from host to host to find as many mates as possible.² Among ectoparasites this is reflected by the winged males but flightless females of the bat infesting fly *Ascodipteron* spp. (see Hackman 1964).

Things get more complicated. In *Carnus hemapterus*, an acaelypterate fly that feeds on the skin secretions of nestling birds, all females and two-thirds of the males shed their wings (Capelle and Whitworth 1973). Apparently among male *C. hemapterus* there are both searchers and stayers. Reasons for the difference are unknown but might include the probability of sharing the nest with females and how intimidating the local rivals are.

When the possibility of females foraging for the best possible mates is added, complexity is compounded. The tiny dung fly *Borborillus frugipennis* (Sphaeroceridae) is a kleptoparasite that lays its eggs in the dung stores of scarab beetles (Sivinski 1983). It bears a number of parallels to certain lice and fleas and the symbionts can serve as a kind of scale model of a vertebrate and its vermin. A fly often stays on a single host for 30% of its adult life, for it rides on beetles both underground and in the air, and important to any extrapolation, it mates upon the host. Like *Carnus*, *B. frugipennis* males are stayers or searchers. This is not obvious from wing polymorphisms but is seen in the way flies behave when they mount unoccupied scarabs. Some hop on and ride, others scurry over beetles, dismount and await another that they search in turn. However, in *B. frugipennis* female as well as male dispersion appears to be influenced by sexual motives.

The mean male/female sex ratio of beetle-back fly groups rises and then falls with the increasing size of the group. This pattern is actually due to a female's preference for sparsely and densely inhabited beetles (Sivinski, unpublished data). Females may like empty beetles because of the lower levels of competition their larvae are likely to face, and there is some evidence that females come to bigger groups in order to mate with the most competitive of a large sample of males (see Sivinski 1984). If so, these beetle-back aggregations are similar to what Richard Alexander calls resource based leks (Alexander 1975, Lloyd 1979). That is, females prefer certain resources not only because of their quality as food or oviposition sites, but also because of the sexual opportunities offered by associated males.

Among the more vagile ectoparasites, such as Hippoboscidae and Streblidae, perhaps further study will add sexual partners already on an animal to the list of qualities such as hair size, molting pattern, health, grooming, and body temperature that influence the suitability of hosts. If so, this will probably not be a universal criterion for host choice. Some species may typically occur in such large numbers that the differences among animal borne populations will be trivial. That is, if the sample of males on each host is very large then the between-host variance in male quality is apt to be low and animals will present a similar set of sexual partners. For example, such lack of between-site variance might explain the failure of yellow dung fly, *Scatophaga stercoraria*, females to choose dung pat oviposition sites on the basis of resident males (see the results of Borgia 1979).

The distribution on an animal's surface, as well as dispersal among

animals, can be sexually selected. A *B. frigidipennis* perched on a beetle's horn is usually a male. Horns may be good lookouts from which to search for females. Among ectoparasites there are patterns of distribution where adults are separated by sex, or less widely dispersed than their immatures. Some of these may be reflections of mating strategies (see Table 1). For instance the biting louse of cattle (*Haematopinus eurysternus*) has an intriguing distribution. Females are broken up into adult and nymphal clusters. Adults in groups of up to 60 oviposit together on the back of the neck. Males occur on the sides of the neck, or are associated singly or in small groups with nymphal clusters (Craufurd-Benson 1941). There may be a complex sexual environment on backs of cattle where some males obtain mates by waiting for the immatures they guard to grow up, while others condense on mating grounds that are near but not in breeding sites, either to intercept migrating females or to form leks where females shop for the most attractive mates.³

THE MAINTENANCE OF SEX

While considering sex, it is worth noting its surprising ubiquity among very intimate insect ectoparasites, particularly lice. There is a cost to sexuality best described as the cost of producing males; generally, a lineage would increase twice as fast if it consisted of parthenogenetic females. Therefore, there must be a greater than 2-fold reproductive advantage in producing genetically variable offspring for sex to resist replacement by asexual mutants (see Bell 1982 for a lengthy discussion). Most conjectural

TABLE 1. EXAMPLES OF ECTOPARASITE DISTRIBUTIONS THAT MAY REFLECT MATING SYSTEMS.

| Order Insect | Comments and References |
|---|--|
| Dermaptera <i>Hemimerius talpoides</i> | Adults more anterior on backs of rats (Ashford 1970). |
| Hemiptera Cimicidae | Aggregations of cimicids off hosts—bug trains (e.g., Lee 1955, Overal and Wingate 1976, Cheng 1973). |
| Phthiraptera <i>Haematopinus eurysternus</i> and <i>Damalinea bovis</i> | Adult and nymphal clusters on cattle (Craufurd-Benson 1941). |
| Diptera <i>Melophagus</i> spp. | Males congregate on hind parts of sheep (Graham and Taylor 1941). |
| <i>Mystacinobia zelandica</i> | Communal oviposition and adult clusters off bat-hosts (Holloway 1976). |
| <i>Joblingia schmidtii</i> and <i>Trichobius yunkerii</i> | Swarm in bat caves (Wenzel et al. 1966). |
| Siphonaptera <i>Echidnophaga gallinacea</i> | Males on body, females on heads of chickens (Suter 1964). |

advantages to sex suppose environmental heterogeneity selects against genetically homogeneous clones, and one of the most important sources of environmental heterogeneity is biotic, the unpredictable amalgam of predators, competitors, and symbionts (e.g., Hamilton et al. 1981). Relationships with hosts are certainly intense and it is easy to see why colonizing ectoparasites might be sexual products. But it is less clear why sex should continue once a compatible, relatively unutilized animal has been reached. It would seem that cattle backs should be more biotically homogeneous than the pasture in which they stand. There are very few records of predation on lice by animals other than the host, and little opportunity for, or direct evidence of competition (see however, Wenzel and Tipton 1966, and Hopkins 1949). Actually a few species of biting lice do what is expected of them; males become progressively more rare after an animal is colonized (all are Ischnocera, see citations in Marshall 1981). This type of reproduction is much more common, however, among the ectoparasites of plants such as aphids and scales (see Price 1980 for a discussion of parthenogenic parasites).

It is reasonable to ask how trees and cows differ as sexual substrates? Could the genetic scrambling of animal ectoparasites be an attempt to keep up with changes in host phenotype, a pace of change that is not matched in long-lived plants? This is not to say that plants do not respond to their parasites, but that animals defend themselves in ways that plants do not, such as by learning and employing a sophisticated immune system (see Smith 1983 for an example of plant response). It is well known that animals differ in susceptibility to infestation. For example, the body louse, *Pediculus humanus*, has been known to do well on one person, while refusing to feed on his brother (Riley and Johannsen 1938). The head louse, *Pediculus capitis*, while specific to humans, prefers women to men and European strains do not survive on blacks (citations in Marshall 1981). My impression is that the causes of such variances are not always well understood (e.g., Nelson et al. 1977). Certain individuals may carry compounds in their blood that are toxic to endosymbionts or, as in the case of the generally undrinkable blood of guinea pigs, have haemoglobins that crystalize and rupture the gut (see Krynski et al. 1952, Nelson et al. 1975); or perhaps they carry psychoactive compounds like a turn of the century French sailor whose blood caused body lice to fight each other with "apparently vicious intent" (Foot [1920] in Riley and Johannson [1938]; note that *Polybia* wasps will not sting a hand covered with underarm perspiration, suggesting "secondary chemicals" that protect humans against insects other than ectoparasites; see Young 1978). Some forms of defense are known to be acquired. A rise and then a fall in the number of lice, mites, and keds on an animal is a fairly common pattern (e.g., Nelson et al. 1977). For example, local vasoconstriction that leaves insects unable to feed is a major form of such an acquired resistance. This and other less understood reactions are apparently regulated by the immune system.

It is tempting to think that a louse never bites the same animal twice; that the defensive physiology of the host is sufficiently labile to force migration/sexual recombination or to select for genetic shuffling in the parasites that stay.

THE EXTENDED PHENOTYPE

A third area of evolutionary thought with implications for medical entomology is the notion of the extended phenotype recently formalized by Richard Dawkins (1982). Its basic concept is that the expression of a genetic program commonly extends beyond the body walls, the traditional limits of gene activity. Few would argue that caddisfly cases and termite mounds have evolved through the differential reproduction of genes the constructions themselves do not contain, but these are only the most obvious extrusions of gene activity through an animals "skin". Dawkins (1982) has emphasized the possibility that animals have evolved means to physically or psychologically control each other and that nature may be a tangle of manipulative forces stretched among incompletely autonomous genomes. An outcome of extended phenotype thinking is heightened doubts about whose genes are controlling whose body in cases of parasitism. That is, do "symptoms" benefit the infector or the infected.⁴

Consider the dispersal of animal diseases. Only a few microbes seem to take a direct hand in their own contagion. For instance certain bacterial pathogens of arthropods luminesce and probably attract new victims or vectors to themselves (see Harvey 1952, also Sivinski 1981, 1982). But usually microbes would be best served by subverting their larger and more complex hosts into spreading them around (Holmes and Bethel 1972, Ewald 1980, Dawkins 1982).

Such manipulation does not have to entail prodigious intellectual or physical feats. One need only reflect on who benefits from sneezes associated with cold virus or the biting of rabid dogs.⁵ An example closer to our theme is that of tse-tse flies, which when infected with *Trypanosoma brucei*, feed more often and more voraciously (Jenni et al. 1980). The trypanosomes are associated with mechanoreceptors in the labrum that function in a feedback loop to restrict probing. Probing is essential for transmission of the trypanosome. A "gene" that changes the site of infection in a vector thus can be better dispersed by undermining a fly's ability to determine how much biting is enough.

Does anything like this influence the movement of ectoparasites? The only case I know of is where a nematode that infects the flea *Spilopsyllus cuniculi*, apparently causing its victim to remain and mate on doe rabbits rather than moving onto their litters (Rothchild 1969). The purpose, if any, is obscure. But one can imagine obviously functional changes in the behavior of ectoparasitic vectors that might be worth searching for. As an example, it has been noted many times that some fleas and lice leave sick or disturbed hosts (see citations Marshall 1981). A pathogen that causes mild disease and could lower thresholds to cues ectoparasites use to monitor host health (e.g., body temperature), would be able to hijack a flea out of an environment eroded by antibodies. I know of no evidence for such hijacking, but it is worth noting that sucking lice that might be vectors sometimes appear to leave sick hosts more rapidly than certain biting lice that cannot be vectors (again see citations Marshall 1981). Be that as it may, as a general principle, it should be useful to keep in mind the options open to the protagonists in diseases.

APPENDIX

¹—While the major concern here is the sexual selection of parasite behavior, parasites themselves might provide opportunities for sexual selection to occur in their hosts. Hamilton and Zuk (1982) have argued that displays of male vigor and ability to grow and maintain extravaganzas of feathers or fur could be advertisements of resistance to parasites. Such a scheme is an improvement over traditional “good gene” models since coevolution of parasite and host might generate genetic variance that intersexual selection could not exhaust.

²—A related problem among the more vagile bloodsucking “micropredators” of veterinary importance is whether males should search for females on or near hosts. It seems curious for instance that one can be surrounded by large numbers of sanguinary female mosquitoes, but that no male mosquitoes are overhead taking advantage of the concentration. There are at least two determinants of male search strategy: 1) where are females most likely to be concentrated, i.e. encountered (see Sivinski and Stowe 1980), and 2) the value of females in the different locales they inhabit—in a monogamous species that normally mates upon emergence, subsequent concentrations on hosts are sexually useless to searching males. Parenthetically, where females mate more than once and the last ejaculate fertilizes most of the eggs, copulations just before oviposition are most valuable, and females aggregated around a host may not be attractive if the host is widely separated from oviposition sites (see Thornhill and Alcock 1983).

There are some data from the Diptera with which to test the later of these determinants; i.e., the principle of changing female value over space and time. Mosquitoes have distinct feeding and oviposition sites, and females generally copulate only once (Gillett 1972). Male mosquitoes would be predicted to concentrate their mating efforts at emergence sites, and as expected, males are only rarely found in the vicinity of hosts. However, I have found 13 species where males are located near hosts (the bizarre kleptoparasite of ants *Malaya leei*, Miyagi 1981; *Mansonia* sp., McIver et al. 1980; *Eretmapodites chrysogaster*, Gillett 1972; *Aedes aegypti*, Hartberg 1971; *A. albopictus*, Basio et al. 1976; *A. dominici*, Bates 1949; *A. furcifer*, Jupp 1978; *A. pseudoscutellaris*, Horsfall 1955; *A. scutellaris*, Forbes and Horsfall 1946; *A. triseriatus*, Loor and DeFoliart 1970; *A. varipalpus*, Lee 1971; *A. vittatus*, Reeves 1951; *A. diantaeus*, Horsfall 1955). These exceptions are of interest because 11 out of the 12 haematophagous species develop in small containers, principally rot holes (compared to only 59% of 409 species of *Aedes* in Horsfall 1955). Such small, ephemeral, widely dispersed development sites may make it difficult for males to search for emerging mates. If so, they are “forced” to locate older females, ones less likely to be receptive, in the vicinity of hosts (note that several *Aedes* species are found both near animals and in the vicinity of their own emergence site, suggesting a dual sexual strategy).

A similar case occurs in horn fly, *Haematobia irritans*. Females mate once, both sexes are on cattle, and larvae develop in the ephemeral and dispersed medium of cattle dung (see Bruce 1964). In a close relative, the moose fly, *Lyperosiops alcis*, copulatory frequency is unknown but males are associated with hosts, and females have been found ovipositing on feces several inches up the rectum of freshly killed moose (Snow 1891).

A possibly contrary system to the proposal that males prefer to patrol emergence sites in female monogamous species and oviposition sites in polyandrous ones, is the multiple mating and male host occupancy of certain psychodids whose females feed on reptile blood (notably *Phlebotomus vexator*; see Chaniotis 1967). Larval substrates are undetermined but may consist of host feces. If so, the difficulty is mitigated since valuable last

matings before oviposition could be obtained by males stationed on the female. Males of ceratopogonid *Culicoides utahensis* wait in the ears of rabbits for feeding females (Downes 1969). Again, it is possible that larvae develop in the litter of the host's burrow. Likewise, in "bobos" (*Paraleucopis mexicana*) a chamaemyiid that laps fluids from the eyes of birds and reptiles, both sexes are found about hosts and larvae are thought to develop in the litter of birds' nests (Smith 1981).

Multiple inseminations and near-host male aggregations also occur in tse-tse (*Glossina* spp: Muscidae) (citations in Mulligan 1970, Tobe and Langley 1978). Peculiarities of tse-tse reproduction remove any difficulty. Unlike most Diptera, *Glossina* spp. are viviparous, so that zygote formation occurs long before deposition of offspring.

Male host occupancy occasionally occurs in other vertebrate-associated fly taxa. Lack of information on mating behavior and/or oviposition sites precludes analysis in these species: *Culicoides nebeculosus* (Ceratopogonidae) (Downes 1955); *C. variipennis* (Jones et al. 1977); *Lutzomyia vexatrix* (Psychodidae) (Chaniotis 1967); *Tabanus auro-puntatus*, *Haemoptopota sewelli*, *H. pluvialis* (Tabanidae) (Bailey 1948); and *Wilhelmia equina* (Simuliidae) (Wenk and Schlorer 1963).

³The idea of lekking is particularly appealing when thinking about ectoparasites on large animals. Like lake-breeding mosquitoes or highly polyphagous tephritids, many ectoparasite populations look like they can be widely distributed over an extensive and fairly uniform "resource surface" (see Burk 1981 and Sullivan 1981 for discussions of the relationship between resource concentration and mating systems). An effect of uniformity can be unpredictability in locating sexual partners, and the result of this can be the evolution of true or nonresource-based leks where males aggregate and signal from an arena devoid of any special resources other than the males themselves (see Bradbury 1981 for recent consideration of lek evolution).

⁴As an illustration with some preliminary data, consider galls, "subcutaneous" parasites of plants. Galls are formed around a number of organisms including cynipid wasps and cecidomyid flies. One of their striking qualities is the breadth of their structural complexity and color. They range from green warts to objects that rival flowers. If color is treated as a symptom of infestation the extended phenotype question is: in whose interest, the plant or the insect, is the color produced?

To expand the metaphor of the flower, could these colors attract Hymenoptera, parasitic ones as opposed to pollinators? Up to 70% of galls are commonly parasitized (Russo 1979). Color and shape could be a flag that a plant raises over an infection to attract the macroscopic equivalent of an antibody. Gall formers of course would try to strike the colors down. Are some colors attractive to parasites? Yes. Catches of parasitoids are higher on gall-sized yellow balls (Tack-Traps® covered and hung in trees) than green or red ones (green 29 parasitoids, 9% of catch; red 21 parasites 7.6% of catch; yellow 67 parasites, 14.75% of catch; yellow > red, green $p < 0.05$) (Sivinski, unpublished data).

Is yellow a common color on galls? Yes, of 525 oak-leaf galls, 20% are yellow or have yellowish tints at some point in their development. (This and following color data collected from the keys and descriptions of Felt 1918 and Russo 1979.)

Is there any reason to think that the presence of yellow is a signal? Perhaps. If we compare oak-root galls hidden underground to those visible on twigs and branches, a higher proportion of those that can be seen have the purported signal color (18% of 165 branch galls vs. 7% of 14 root galls).

Is color more common in situations where selection for parasite removal is strongest? Perhaps. Many gall-forming insects are weak fliers and poor dispersers, so perennial plants run the risk of reinfection by the offspring

of the previous seasons' parasites. Annuals however are less likely to survive their gall formers and in the absence of younger relatives to protect, should invest less in disinfecting. Yellow seems more common on perennial galls of compositoid plants (0 of 13 annuals and 12 of 107 perennials).

On the other hand, gall formers could benefit from gaudy houses. Many galls have defensive attributes such as spines or tannic acid levels of up to 65% that could be advertised by bright warning colors. It is interesting that galls formed by bacteria, fungi and mites, and presumably immune at least to parasitoids, are sometimes brightly colored.

Both or neither of these explanations may be correct, but they should illustrate the possibility that the appearance or behavior of an animal may not be the work of its own genes and that "symptoms" deserve being considered from both perspectives.

⁵The ability of a sick host to defend itself against vectors is considerably curtailed. Mosquitoes given a choice of feeding on a healthy or malarious mouse almost always suck from the infected animal (Day et al. 1983). It might be interesting to look for any differences in the ability of animals to discourage vermin when ill with diseases transmitted by and without vectors. Would the former be more listless, less able to brush away a fly?

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