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The importance of blood-sucking insects

Insects are the pre-eminent form of metazoan life on land. The class Insecta contains over three-quarters of a million described species. Estimates for the total number of extant species vary between 1 and 10 million, and it has been calculated that as many as 10^{19} individual insects are alive at any given instant (McGavin, 2001). That gives about 200 million for each man, woman and child on Earth! It is estimated that there are 14 000 species of insects from five orders that feed on blood (Adams, 1999) but, thankfully, only 300 to 400 species regularly attract our attention. These blood-sucking insects are of immense importance to humanity.

Humans evolved in a world already stocked with blood-sucking insects. From their earliest days insects would have annoyed them with their bites and sickened them with the parasites they transmitted. As humans evolved from hunters to herders, blood-sucking insects had a further impact on their wellbeing by lowering the productivity of their animals. It is reasonable to assume that, because of their annoyance value, humanity has been in battle with blood-sucking insects from the very beginning. In recent years this battle has intensified because of an increasing intolerance of the discomfort they cause, our fuller understanding of their role in disease transmission and the demand for greater agricultural productivity. But despite considerable advances in our knowledge of the insects and improvements in the weapons we have to use against them, there is still no sign of an eventual winner in this age-old battle.

Many keen observers of nature suspected that insects were in some way involved with many of the febrile illnesses of humans and their animals well before confirmatory scientific evidence was available. The explorer Alexander von Humboldt recorded such a belief amongst the tribes of the Orinoco region of South America. The great German bacteriologist Robert Koch reported the belief of the tribes of the Usambara Mountains of East Africa that the mosquitoes they encountered when they descended to the plains were the cause of malaria (Nuttal, 1899). Sir Richard Burton, in his travels in East Africa, recorded the similar belief of Somaliland tribes that mosquitoes were responsible for febrile illnesses (Burton, 1860). Many of the peoples living near the tsetse fly belts of East and West Africa associated tsetse flies with sleeping sickness of humans and nagana of animals. In our

Table 1.1 *An outline of the early investigations that laid the foundations of medical and veterinary entomology.*

Date	Source	Subject
1878	Manson	Development of *Wuchereria bancrofti* in a mosquito
1893	Smith and Kilbourne	*Babesia bigemina,* the causative agent of Texas cattle fever, transmitted by the tick, *Boophilus annulatus*
1895	Bruce	Transmission of nagana by tsetse fly
1897	Ross	Malaria parasites seen to develop in mosquitoes
1898	Ross	Transmission of avian malaria by mosquitoes
1898	Simond	Transmission of plague from rat to rat by fleas
1899	Grassi, Bignami and Bastianelli	*Anopheles* spp. are the vectors of human malaria
1900	Reed *et al.*	Transmission of yellow fever by the mosquito *Aedes aegypti*
1902	Graham	Transmission of dengue by mosquitoes
1903	Bruce and Nabarro	Sleeping sickness in humans transmitted by tsetse fly
1903	Marchoux and Salimbeni	Transmission of fowl spirochaetes, *Borrelia conserina,* by the tick *Argus persicus*
1907	Mackie	Spirochaete causing relapsing fever transmitted by lice
1909	Chagas	*Trypansoma cruzi,* causative agent of Chagas' disease, transmitted by reduviid bugs

own western tradition North American stock ranchers held the belief that Texas cattle fever was transmitted by ticks (in the class Arachnida, not Insecta) well before this was confirmed experimentally.

The fact that insects are vectors of disease was only confirmed scientifically at the end of the nineteenth century. The key discovery was made in 1877 (reported in 1878) by a Scottish doctor, Patrick Manson, working for the customs and excise service in China. He found that larval stages of the filarial worm, *Wuchereria bancrofti*, developed in the body of a mosquito, *Culex pipiens quinquefasciatus* (Manson, 1878). This was the start of an avalanche of investigations that laid the foundations of medical and veterinary entomology. Some of the key discoveries of this era are outlined in Table 1.1. The main insects involved in the transmission of all the most important vector-transmitted diseases (Table 1.2) are now well known. The list of diseases transmitted is an impressive one and includes the medical scourges malaria, sleeping sickness, leishmaniasis, river blindness, elephantiasis, yellow fever and dengue, and the veterinary diseases nagana, surra, souma, bluetongue, African horse sickness and Rift Valley fever

Table 1.2 *Rounded estimates for the prevalence of disease, the number at risk and the disability adjusted life years (DALYs) for major vector-borne diseases. Figures in millions (M). (DALYs were introduced in the World Bank Development report of 1990 as an estimate of the burden a disease causes to the health of the population. They are often used for comparative purposes and for use in prioritization.)*

Disease	Prevalence	At risk	DALYs	Major distribution	Major vectors
Malaria	273M	2100M	42M	Tropics and subtropics	Anopheline mosquitoes
Onchocerciasis (river blindness)	18M	120M	1M	Tropical Africa, Yemen, Latin America	Blackflies (*Simulium* spp.)
Lymphatic filariasis (elephantiasis)	120M	1100M	5.6M	Africa, Asia and South America	Various mosquitoes
African trypanosomiasis	0.5M	50M	2M	Sub-Saharan Africa	Tsetse flies
Chagas' disease	16–18M	120M	0.7M	Central and South America	Triatomine bugs
Leishmaniasis	12M	350M	2M	Africa, Asia and Latin America	Sandflies
Dengue	50M	3000M	0.5M	Asia, Africa and Americas	Various mosquitoes

Data largely from World Health Organization web pages as of 11 December 2002: http://www.who.int/tdr/media/image.html.

(the piroplasms being tick-borne). Gauging the extent of these diseases is much more problematical, even for human disease. One reason is that health statistics are a moving target, particularly for those diseases such as yellow fever that occur as epidemics. But the greatest problem is that the heartland of these vector-borne diseases is in the under-developed world where, for a variety of reasons, accurate statistical data are often difficult or impossible to gather. For this reason, figures given for the extent of a disease are often not based entirely on hard data, but are an estimate founded largely upon the experience of an expert. Table 1.2 gives an estimate of some of the major vector-transmitted diseases of humans, but obviously, as just indicated, care needs to be taken in the interpretation of the figures.

Blood-sucking insects cause very serious losses to agriculture (Table 1.3). One way this happens is through the transmission of parasites. The

Table 1.3 *Estimated losses in agricultural production caused by blood-sucking insects.*

Insect	Year	Animal mainly affected	Estimated losses (millions US$)	Geographical region
Haematobia irritans (horn fly)	1991	Cattle	800	USA
Stomoxys calcitrans (stable fly)	1965	Cattle	142	USA
Tabanids	1965	Cattle	40	USA
Mosquitoes	1965	Cattle	25	USA
Melophagus ovinus (sheep ked)	1965	Sheep	9.4	USA
Lice	1965	Cattle	47	USA
		Sheep	47	
		Swine	3	
		Goats	0.8	
Tsetse fly	1999	Cattle	4500	Sub-Saharan Africa
Insects, ticks, mites	1994		3000	USA

Information from: Budd, 1999; Geden and Hogsette, 1994; Kunz *et al.*, 1991; Steelman, 1976.

most celebrated case is trypanosomiasis, transmitted by tsetse flies across 9 million km^2 of Africa (Hursey, 2001), and estimated to cause agricultural losses of about US$4.5 billion a year (Budd, 1999). The counter argument has also been proposed that the tsetse has prevented desertification of large areas of land by overgrazing, and has been the saviour of Africa's game animals. The debate has been clearly outlined by Jordan (1986). Other examples of spectacular losses caused by insect-transmitted disease are the death in 1960 of 200 000 to 300 000 horses in Turkey, Cyprus and India caused by African horse sickness, transmitted by *Culicoides* spp. (Huq, 1961; Shahan and Giltner, 1945); and the estimated deaths in the USA, between 1930 and 1945, of up to 300 000 equines from Western and Eastern equine encephalitis transmitted by mosquitoes (Shahan and Giltner, 1945).

In the developed countries it is usually direct losses caused by insects themselves that are of greatest concern. In exceptional circumstances the insects may be present in such numbers that stock are killed; for example, 16 000 animals died in Romania in 1923 and 13 900 in Yugoslavia in 1934 because of outbreaks of the blackfly *Simulium colombaschense* (Baranov, 1935; Ciurea and Dinulescu, 1924). More usually losses are caused not by death but by distress to the animal. Good examples are the reductions in milk yields, weight gains or feed efficiencies that are commonly caused by the painful bites of the tabanids and biting flies. Estimated losses in the USA have been calculated (Steelman, 1976). More recent estimates suggest insects, ticks and mites cost the US livestock producer in excess of $3 billion annually (Geden and Hogsette, 1994). The horn fly is perhaps the major pest in the USA, with an estimated loss in excess of $800 million annually (Kunz *et al.*, 1991). Losses are caused by reduced feed conversion efficiency, reduced weight gains and decreased milk production and are the result of blood loss, annoyance, irritation and behavioural defensive responses on the part of the host.

The sheer annoyance that blood-sucking insects cause to us can easily be overshadowed by their importance in medical and veterinary medicine. In some parts of the world, at certain times of the year, there may be so many blood-sucking insects that any activity outside is difficult or impossible without protective clothing. For example, the biting activity of the midge *Culicoides impunctatus* is thought to cause a 20 per cent loss in working hours in the forestry industry in Scotland during the summer months (Hendry and Godwin, 1988). Such disruption is common during the summer blooms of insects at many of the higher latitudes, and also in many of the wetter areas of the tropics. These levels of annoyance are still rare for most people, and for this reason the concept of nuisance insects is much more difficult to grasp than that of a vector or an agricultural pest causing economic damage. Perhaps the best way to view annoyance caused by insects is as a tolerance threshold. It can then be viewed as a variable with widely separated upper and lower limits; a handful of mosquitoes may be a minor inconvenience to the beggar in the street but intolerable to the prince in the palace.

I suggest that, in the developed world at least, we are increasingly intolerant of nuisance insects. There are several underlying reasons: the increased awareness in the general population of the importance of insects in the spread of disease (sometimes over-exaggerated); the growing stress placed on hygiene and cleanliness; and increasing urbanization, so that for many people blood-sucking insects are not the familiar, everyday things that they were once to our grandparents working in a rural economy. This reduction in our tolerance of nuisance insects causes problems. The extended leisure time and mobility of many people in the developed world means that they spend more time in increasingly distant places. The countries involved are often anxious to promote and develop their tourist industries, and this has led to pressure to control nuisance insects. This can be seen in places such as the Camargue in southern France, the Scottish

Highlands (Blackwell, 2000), the Bahamas, New Zealand (Blackwell and Page, 2003), Florida and many parts of the Caribbean (Linley and Davies, 1971). In addition, population growth has put increased pressure on marginal land which in the past may have been left alone because of nuisance insect problems. Development of this land for leisure, commerce or housing with no insect control input can be disastrous for the developer, user or purchaser.

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The evolution of the blood-sucking habit

It is believed that haematophagy arose independently at least six times among the arthropods of the Jurassic and Cretaceous periods (145–65 million years ago) (Balashov, 1984; Ribeiro, 1995). The very patchy nature of the insect fossil record means that discussion of the evolution of the blood-sucking habit has until now relied heavily on detective work, with the major clues lying in the diversity of forms and lifestyles seen in modern-day insects, and in some cases in the details of their relationships with vertebrates. From careful interpretation of this evidence quite credible accounts of the likely evolution of the blood-sucking habit can be made. From this starting point it has been convincingly argued that the evolution of the blood-sucking habit in insects has occurred on several occasions, in each case along one of two main routes (Waage, 1979), and these are discussed below. Insect molecular systematics is beginning to emerge from its 'Tower of Babel' stage (Caterino *et al.*, 2000) and it will make a major contribution in defining the detail of the evolutionary routes taken by haematophagous insects (Esseghir *et al.*, 1997; Hafner *et al.*, 1994; Lanzaro *et al.*, 1998; Mans *et al.*, 2002; Sallum *et al.*, 2002). The proposed population bottleneck suffered by phlebotomines in the late Pleistocene and the subsequent radiation of the species out from the eastern Mediterranean sub-region is a good example of what we can expect (Esseghir *et al.*, 1997).

2.1 Prolonged close association with vertebrates

In the first route it is suggested that haematophagous forms may have developed subsequent to a prolonged association between vertebrates and insects that had no specializations immediately suiting them to the blood-sucking way of life. The most common association of this type is likely to have centred around the attraction of insects to the nest or burrow of the vertebrate host. Insects may have been attracted to the nest for several reasons. The humid, warm environment would have been very favourable to a great many insects. In some circumstances, such as the location of the nest in a semi-arid or arid area, the protected habitat offered by the nest may have been essential to the insects' survival. For many insects the nest would also have proved attractive for the abundant supply of food to be found there. Certainly many current day insects such as the psocids are attracted to the high concentrations of organic matter to be found in nests. Indeed, psocids may become so intimately associated with this habitat that they develop a phoretic association with birds and mammals, climbing into fur and feathers, to be translocated from one nest site to another (Mockford, 1967; Mockford, 1971; Pearman, 1960).

Initially feeding on dung, fungus or other organic debris, the insects attracted to the nest would also have encountered considerable quantities of sloughed skin, hair or feathers. The regular, accidental ingestion of this sloughed body covering probably led to the selection of individuals possessing physiological systems capable of the efficient use of this material. Behavioural adaptations may then have permitted occasional feeding direct from the host itself. It is easy to see how this may have gone hand in hand with the adoption of a phoretic habit. Morphological and further behavioural adaptations would have allowed the insect to remain with the host for longer periods with increasingly efficient feeding on skin and feathers.

The mouthparts developed for this lifestyle, in which the insect feeds primarily on skin and feathers, were almost certainly of the chewing type, such as those seen in the present-day Mallophaga. While these mouthparts are not primarily designed to pierce skin some mallophagans do feed on blood. *Menacanthus stramineus*, a present-day mallophagan, feeds at the base of feathers or on the skin of the chicken. The insect often breaks through to the dermis, giving it access to blood on which it will feed (Emmerson *et al.*, 1973). Blood has a higher nutritional value than skin and is far easier to digest. This is reflected in the increased fecundity of blood-feeding Anoplura compared to skin-feeding Mallophaga (Marshall, 1981). Once blood was regularly encountered by insects, it is likely that its high nutritional value favoured the development of a group of insects that regularly exploited blood as a resource. This would have developed progressively, through physiological, behavioural and morphological adaptations, first to facultative haematophagy and eventually, in some insects, to obligate haematophagy. One way in which the progression from skin feeding to blood feeding may have occurred is seen in members of the mallophagan suborder the Rhynchophthirina, such as the elephant louse, *Haematomyzus elephantis*. This insect possesses typical mallophagan biting-type mouthparts (Ferris, 1931; Mukerji and Sen-Sarma, 1955) which are not primarily adapted for obtaining blood. By holding the mouthparts at the end of an extended rostrum (Fig. 2.1) the insect manages to use them to penetrate the thick epidermal skin layers of the host to get to the blood in the dermis.

It is thought that haematophagous lice developed from an original nest-dwelling, free-living ancestor (Kim, 1985) along the pathway described above. We do not know when the change occurred from free-living nest

Figure 2.1 Despite having the chewing mouthparts typical of mallophagans, *Haematomyzus hopkinsi* is unusual in feeding on blood. The chewing mouthparts are held on the end of an unusual, elongated rostrum, which may well be an adaptation helping the insect reach the blood-containing dermis through the thick skin of its wart-hog host. (Courtesy of Vince Smith)

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dweller to parasite, but it may well go right back to the appearance of nesting or communal living in land-dwelling vertebrates, which is thought to have happened during the Mesozoic (225–65 million years ago). So lice may have predated the emergence of mammals and birds and been parasitic on their reptilian ancestors (Hopkins, 1949; Rothschild and Clay, 1952). It is highly likely that ancestral forms were parasitic on primordial mammals and that from there they radiated along the lines of mammalian evolution. Helping drive this rapid speciation of the permanent ectoparasites was the reproductive isolation they suffered from being confined on specific vertebrate hosts, which may well have enhanced the effects of classical geographic reproductive isolation. Co-evolution of the host and permanent (and to a lesser extent temporary) ectoparasites probably led to rapid speciation in lice and other ectoparasitic forms. The evidence for co-speciation in lice is strong. Sequence analysis of mitochondrial cytochrome oxidase I genes suggests co-speciation in the pocket gophers *Orthogeomys, Geomys* and *Thomomys* and their chewing lice (Fig. 2.2) (Hafner *et al.*, 1994). Co-speciation also predicts temporal congruence between chewing lice and gopher speciation. This is borne out by analysis of the molecular data, in which the synonymous substitution rate is approximately an order of magnitude greater in the lice compared to the gophers. This roughly parallels the differences in generation times of the two groups, suggesting equal rates of mutation per generation. While the case for pocket gophers and their chewing lice is strong, the extent to which co-speciation is generally the case is unclear. Classical taxonomy, which has tended to group species with origins on the same host, may be misleading. Molecular studies are showing this is a dangerous practice and that not all species have stuck to the co-evolutionary model mentioned above (Johnson *et al.*, 2002a; Johnson *et al.*, 2002b).

Some beetles also appear to be developing along the evolutionary highway described above. Several hundred species have been reported from nests and burrows (Barrera and Machado-Allison, 1965; Medvedev and Skylar, 1974). Most of these are probably free-living, feeding on the high levels of organic debris to be found at these sites. Some of these beetles have developed a phoretic association with the mammal which allows them to transfer efficiently between nest sites. Many of these phoretic forms also feed on the host by scraping skin and hair, and some have progressed to the stage when they will occasionally take blood (Barrera, 1966; Wood, 1964).

The prolonged association of the insect with the vertebrate, which is the cornerstone of this first route for the evolution of the blood-feeding habit, may not always have relied on encounters in the nest habitat. Free-living ancestral forms with few, if any, clear adaptations for the blood-sucking way of life may have also developed prolonged associations with