The evolution of insect/vertebrate associations

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The evolution of close vertebrate associations has occurred in seven orders of insects, resulting in a great diversity of interactions which range from commensalism to true parasitism. The evolution of each taxon of vertebrate associates is discussed in turn, some new ideas on the development of certain groups are presented and, on a broader scale, a general model for the evolution of ectoparasitic insects is proposed. It argues that all vertebrate associates have evolved along one of two macroevolutionary pathways which differ only in the sequencing of adaptations facilitating host association and host feeding. These pathways lead to parasite types which differ greatly in their life history and intimacy of host association.

Some microevolutionary processes influencing the diversification of ectoparasites are discussed, in particular the process of insect/vertebrate coevolution and the forms this may take. Host specificity, one consequence of coevolution, is recognised as an important factor influencing the structure of ectoparasite communities, and a hypothesis is presented that competition between ectoparasite species, mediated by host defensive responses, is also important in determining community structure.

KEY WORDS: insects – ectoparasites – evolution – coevolution.

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INTRODUCTION

Close associations between insects and vertebrates have arisen independently in seven insect orders; the Dermaptera, Phthiraptera, Hemiptera, Coleoptera,
Diptera, Siphonaptera and Lepidoptera. Many, but not all, insect/vertebrate relationships may be considered 'parasitic'. Some classical definitions of parasitism (e.g. Baer, 1951; Olsen, 1962) would require that the insect be nutritionally dependent on its vertebrate host, and that it reduce the host's fitness in some way. When we consider the diversity of insect/vertebrate associations, and particularly the evolutionary transition from free-living to haematophagous forms in many taxa, parasitism in the above sense becomes but one of a number of possible interactions. Alternatives include situations where an insect might feed on a host without being dependent upon it (facultative haematophagy), or where an insect might be dependent on a host without causing it injury (e.g. phoresy). To avoid confusion, the terms 'parasitism' and 'ectoparasite' in this article will be applied only to haematophagous forms (facultative or obligate), where a negative effect on host fitness is a reasonable but often undemonstrated assumption. This distinction made, there remain a large number of non-parasitic vertebrate associates which feed either on other host substances (dermal secretions, lachrymal secretions, skin) or not at all.

Because of the poor geological record for insects, there is virtually no direct evidence for the evolution of vertebrate associates from free-living taxa. Instead, inference must be made from taxonomic and ecological affinities between existing vertebrate associates and free-living forms. Unfortunately, some of the better known groups are highly evolved, parasitic forms such as the Culicidae and Siphonaptera, whose evolutionary origins are obscure. At the other extreme groups with clearer links to free-living ancestors, such as some commensal Coleoptera and Lepidoptera, have received little study. Thus there are gaps in our knowledge at both ends of the spectrum of insect/vertebrate associations, and many evolutionary reconstructions must be largely speculative.

The insects to be discussed are all associated with hosts as adults (though larval associations may also occur). Excluded here will be insects which are parasitic solely in the larval stages, such as the parasitic members of the dipteran families Neotiphilidae, Gasterophilidae, Calliphoridae, Cuterebridae and Oestridae. The evolution of larval parasitism in these groups has been discussed by several authors (Zumpt, 1965; James, 1969; Papavero, 1977).

This article reviews what is known or thought about the origin of the different insect groups associated with vertebrates. It then attempts to identify those macroevolutionary processes by which parasitic insects have evolved from free-living forms, and considers some of the microevolutionary processes which have influenced the diversification of these taxa and their coevolution with their hosts.

**DERMAPTERA**

The Dermaptera are presently classified into three suborders, the Forficulina, Arixeniina and Hemimerina. The latter two groups contain only a small number of species all of which are viviparous and exhibit close vertebrate associations (Giles, 1974; Nakata & Maa, 1974).

The Arixeniina are found in caves and hollow trees in the East Indies associated with molossid bats of the genus *Cheiromeles* and, less commonly *Tadarida*. Marshall (1977) has studied the association of *Arixenia esa* Jordan and *Cheiromeles torquatus* Horsfield in Malaysia. The insect feeds on the dead skin and
dermal secretions of its hosts, as well as on exudates from the mouth, nose, ears, anus and genital openings. The relationship therefore appears to be commensal, perhaps even mutualistic if a sanitary function can be ascribed to the earwig's feeding patterns, but it is worth noting that Arixenia may indirectly reduce host fitness by transporting the phoretic flea, Lagaropsylla turba Smit from the cave floor to the Cheiromeles roost.

A. esau spends most of its time off the host on the walls of the roost and has also been found on the floor of the cave where it will feed on bat guano, although this diet alone is not adequate for survival (Marshall, 1977). Individuals have also been collected on rare occasions from flying bats (Medway, 1958), suggesting a slight phoretic (dispersive) function to the relationship. A related genus of earwigs, Xenaria, exhibits a less intimate association with molossid bats, and may feed primarily on other insects in guano (Marshall 1977; Nakata & Maa, 1974), suggestive of a more primitive stage in vertebrate association.

The Hemimerina contains two genera. The genus Hemimerus is associated with the African rodent genus Cricetomys, and Araeomerus is associated with the rodent genus Beamys. In a study of the biology of Hemimerus talpoides Walker on C. gambianus Waterhouse, Ashford (1970) found insects feeding intermittently on dried skin and exudates from the eyes, mouth and ears of the hosts. Rehn & Rehn (1936) suggested that Hemimerus may feed on a fungus which produces bare patches in the host's fur, noting that Cricetomys which had no earwigs possessed more of these bare patches. While Hemimerus is thought to live continuously on the host, Araeomerus may exhibit a less advanced association. Specimens of this genus have been collected not only from Beamys fur but from food stores in their burrows, where they may feed on vegetable matter (Hanney, 1963).

Vertebrate associations in the Arixeniina and Hemimerina probably arose first through a close association with vertebrate dwellings (roosts and burrows, respectively) and, possibly, a dependence on materials produced or collected by the hosts (dung, food stores), followed by a shift to phoresy and feeding on the host. Among the diverse feeding habits of the living Forficulina (Popham, 1959), some casual vertebrate associations are found which resemble the first stage of the pathway just suggested. A few forficulines are common scavengers or predators in bird nests (Hicks, 1959; personal observations) and one cave dwelling species, Cheiloschises bimammatus Hebard, in West Malaysia has been collected from flying bats, (Marshall, 1977) suggesting an incipient phoretic association.

PHTHIRAPTERA (MALLOPHAGA AND ANOPLURA)

Members of the Mallophaga and Anoplura are strict vertebrate associates and pass their entire life cycles on the host. The Mallophaga possess chewing mouthparts while the more advanced Anoplura possess piercing mouthparts and are wholly haematophagous. There are no members of these orders which exhibit an intermediate state of vertebrate association indicating a transition from free-living forms, however it is generally thought that the living Psocoptera resemble closely the free-living ancestors of the Mallophaga.

The psocids are an ancient order which live in litter and detritus and feed on fungus, algae, pollen and other organic material. They are occasionally found in the nests of vertebrates and some species have been collected from the fur of
mammals (Pearman, 1960; Rothschild & Clay, 1952; Mockford, 1971) and the feathers of birds (Mockford, 1967). Most of these casual vertebrate associates belong to the family Liposcelidae and bear a resemblance to the Mallophaga in their lack of wings, dorso-ventral flattening and enlarged, flattened femurs. Mockford (1967) has suggested that occasional psocid/vertebrate associations may serve a phoretic function, noting the broad distribution of species collected from migratory birds, and also a nutritive function, involving some feeding by psocids on host epidermis.

In the early, nest-dwelling progenitors of the Mallophaga, feeding on shed integument in the nest may have gradually led to the adoption of the same diet while on the host and, subsequently, a continuous vertebrate association. The most primitive diet of Mallophaga is probably host epidermis. This diet is typical for the suborder Ischnocera where, for at least some species, host skin is all that is necessary for development and reproduction (Hopkins & Chamberlain, 1972). Besides skin, hair and feathers, some Mallophaga feed on secretions of sebaceous glands. Blood can occasionally be obtained from open wounds (Hopkins, 1949). Deliberate feeding on capillary blood is known in many Amblycera, particularly species which attack the base of feather quills (Wilson, 1983; Clay, 1957). This adoption of haematophagy in some Mallophaga appears to be correlated with the modification of the chewing mouthparts into organs which can break intact skin (Bouvier, 1945).

In the mallophagan suborder, Rhyncophthirina, the mouthparts are born on an elongate rostrum which appears to be a true piercing apparatus. This presumably haematophagous group appears to be intermediate between the Mallophaga and the Anoplura (Symons, 1952; Mukerji & Sen-Sarma, 1955). It is possible that the Anoplura, which are restricted to mammals, evolved their haematophagy via a similar modification of mouthparts. The evolutionary trend from feeding on epidermis to facultative and, finally, obligate blood-feeding has undoubtedly occurred through selection for the utilization of more nutritive food resources. The advantage to an insect of a switch to blood feeding might be expected to appear in the form of increased longevity and fecundity, and indeed values obtained for louse fecundity show somewhat higher rate of egg production in the Anoplura than in the Mallophaga (Murray, 1979).

A hypothesis for the evolution of the Mallophaga and Anoplura may be summarized in several steps: (1) a preadaptive nest association in early psocid-like forms leading to phoresis and casual feeding on host epidermis, (2) morphological and behavioural modifications permitting continued existence on the host, efficient feeding on skin and, in some cases, facultative haematophagy, and (3) further modification in physiology and mouthpart morphology permitting piercing of host tissue and a wholly haematophagous diet.

The first hosts of the early Mallophaga were probably nest-dwelling reptiles of the Triassic (Rothschild & Clay, 1952; Stenram, 1964). The recently established links between Archaeopteryx and some cursorial, ground-dwelling dinosaurs (Ostrom, 1975), suggests that the shift by Mallophaga from reptiles to birds was ecologically opportune and probably occurred early in the evolution of the Aves. The shift to mammalian hosts may have been secondary to this. The Anoplura probably evolved independently from a psocid-like stock along a similar pathway to the Mallophaga, attaining their wholly-haematophagous lifestyle by the Cretaceous (Kim & Ludwig, 1978).
Obligate ectoparasitic relationships are known from several hemipteran families, the Cimicidae, Polycytopidae, Reduviidae and, possibly, the Lygaeidae. Piercing of vertebrate tissues, in some cases involving blood uptake, has been frequently reported in other Hemiptera, and these instances shed light on the process of ectoparasite evolution in this order.

Piercing, sucking mouthparts are a plesiotypic character in the Hemiptera. It is impossible to know the original diet of this order but Cobben (1978) suggests that it was predatory. Phytophagy and insectivory are widespread and, while there are some differences in mouthpart morphology between forms with these different diets (Miles, 1968; Cobben, 1978), a number of species (e.g. some Anthocoridae, Geocoridae) feed on both plant and insect tissue. Furthermore, both phytophagous and insectivorous Hemiptera have been reported ‘biting’ humans. Such incidents have been collected and examined by a number of authors (Myers, 1929; Usinger, 1934; Esaki, 1934; Judd, 1952). These attacks are often associated with unusual environmental conditions, such as strong lights at night (Usinger, 1934; Miller, 1971). Extreme hunger and chemical stimuli may also be involved (Bergevin, 1925).

While a variety of Hemiptera will feed on vertebrates accidentally, the frequency of such interaction is bound to be low, except in situations where insect and vertebrate live in close associations (e.g. nests and burrows). A number of species, for instance, are sometimes found in nests of small mammals and birds where they may overwinter, feeding on other insects or seeds collected by their ‘hosts’ (Kiritschenko, 1949; Hicks, 1959; Sklyar, 1971). Other species occur regularly in nests, suggesting a dependence on the nest microhabitat, or, possibly, on the host itself. The lygaeid genus, Harmosticana, for instances, is found in squirrel nests in Africa and India (Miller, 1957). The nest dwelling lygaeid genus, Clerada, are thought to be true blood-suckers (Lent, 1939).

Lyctocoris campestris (F.) is a frequent inhabitant of bird nests, where it feeds on other insects, primarily lepidopterous larvae (Woodroffe, 1953). This species has been reported on a number of occasions to pierce human skin (Woodward, 1951; Stys & Daniel, 1957) and will, in fact, take a blood meal (personal observation). While Nordberg (1936) has suggested that this insect feeds on birds in nests, this has not been verified. Lyctocoris is particularly interesting in that it is systematically intermediate between predatory ‘flower bugs’ (Anthocoridae) and haematophagous ‘bed bugs’ (Cimicidae) (Usinger, 1966). Apparently it is also ecologically intermediate between these two families and their respective diets. While many anthocorids exhibit a preference for more open habitats (flowers, leaves on trees), a few species, like Lyctocoris, inhabit straw piles and other dry, dark environments (Anderson, 1961). Such a habitat preference may have initially brought anthocorids into contact with animal nests, which may be especially attractive because of the higher prey densities associated with faeces-contaminated substrates. Haematophagy evolved as a secondary adaptation facilitated by frequent vertebrate contact. A similar evolutionary path may have been traversed by the predatory ancestors of the Cimicidae. A lyctocorine has been described from South America which bears a close morphological resemblance to cimicids (reduced wings, dorso-ventral flattening), suggesting additional parallels between lyctocorine and cimicid evolution (Carayon & Usinger, 1965).
According to Usinger (1966), the Cimicidae probably evolved on bats, as the most primitive forms are found on these hosts. They have subsequently radiated onto birds and man, possibly because of his early cave-dwelling habits (Busvine, 1976). Physical association with the host is restricted to brief feeding periods, and the rest of the time is spent resting in cracks in the host dwelling, not necessarily in the immediate vicinity of the host. Such a life style contrasts strongly with the related Polycidentidae. This order is also haematophagous and probably arose from a cimicid stock (Ferris & Usinger, 1939). Little is known of their biology except that they are restricted to bats, live continuously on the host and are viviparous.

In the Reduviidae, which are for the most part predatory, the bloodsucking Triatominae are exclusively parasitic on vertebrates, primarily birds and mammals (Usinger, 1944). Like the cimicids, most if not all triatomines rest in the vicinity of the host and associate with it physically only for brief feeding periods. An ancestral predatory origin for the triatomines is suggested by the tendency of some species to be cannibalistic (Wood, 1976).

Ectoparasitism appears to have evolved in the Hemiptera through (1) a primary preadaptation of mouthparts for piercing and sucking, (2) secondary evolution of an association with vertebrate dwellings and (3) facultative haematophagy followed by behavioural and physiological adaptations permitting more efficient blood-feeding. The independent evolution of this habit in the Cimicidae and Reduviidae represents a remarkable convergence in biology and behaviour. Both *Cimex* and *Triatoma*, for instance, have evolved the capacity to utilize thermal stimuli in host location (Rivnay, 1932; Wiesinger, 1956), a sensory modality which was of little use to their predatory ancestors. It is also interesting to note that the presumed ancestors of these haematophagous groups, the Anthocoridae and predatory Reduviidae, both use salivary venom to immobilize prey (Edwards, 1961; personal observations). Perhaps these secretions represent, in both groups, the progenitors of anesthetic secretions which permitted painless feeding on hosts in later-evolved haematophagous forms.

### COLEOPTERA

Close vertebrate associations have been discovered in five families of the Coleoptera; the Cryptophagidae, Staphylinidae, Leptinidae, Platypsyllidae and Scarabaeidae. Several reviews of beetle/vertebrate associations exist (Kolbe, 1911; Theodorides, 1950; Barrera & Machado-Allison, 1965) but more recent studies have greatly increased our knowledge of these relationships.

All cases of beetle/vertebrate association appear to have arisen from a dependence on a microhabitat created by the vertebrate host. One such habitat has been the nests of mammals and birds. The extensive studies of Medvedev and his colleagues on the Coleoptera of small mammal burrows in the U.S.S.R. (Medvedev & Vysotszkaya, 1969; Medvedev & Sosnina, 1973; Medvedev & Sklyar, 1974) have provided much interesting information. In one study (Medvedev & Vysotszkaya, 1969), 39 of the 245 species and races identified from nests were also collected from the fur of nest inhabitants. While most of these associations were probably accidental, repeated collection of certain species from mammal fur, including some Cryptophagidae, the catopid, *Nargus anisotomoides* (Spence)
(Anisotomidae) and the leptinid, *Leptinus testaceus* Müller (Leptinidae), suggested to the authors more regular and intimate host associations. Evidence from other studies supports this hypothesis. Jeannel (1936) reported the catopid, *Catopidius depressus* Murr., from the fur of rabbits, where it may feed on epidermis. Cryptophagidae are also abundant in bird nests (Hicks, 1959) and two Mexican species, *Loberopsyllus traubi* Barrera and *L. halffieri* Barrera, have been found to live as adults in the fur of the Volcano Mouse, *Neotomodon alstoni* (Barrera, 1969). *L. traubi* adults live on the rump and hindquarters of their hosts where they attach to host hairs with their mandibles and feed on dead skin, hair and other material collected by the scraping action of the mouthparts. The egg, larval and pupal stages are thought to be passed in the host's nest.

The family Leptinidae contains a number of species which occur as adults in the fur of rodents and insectivores (Park, 1929; Reid, 1942; Buckle, 1976). The most thorough study of their biology has been made by Ising (1969) on *Leptinus testaceus* in Germany. He found that the larvae live exclusively in the litter of rodent nests, feeding on shed hair, skin and host feces, while adults live intermittently in the fur, usually on the posterior end of the host, and in the nest. On the host, they scrape off pieces of hair and dead skin with their mouthparts. The host appears to serve both for phoresy (transportation to new nest sites) and as a source of nutrition.


The family Platypsyllidae possesses one species, *Platypsyllus castoris* Westw. which is restricted to *Castor*. The biology of this species has been studied by Wood (1964). Larvae and adults live on the hosts, while the egg and pupal stages are passed in the beaver den. The larvae feed on host epidermis and on the oily secretions of the dermal glands, this latter substance being the sole diet of the adult beetle, which possesses mandibles modified to serve a sucking function. Large numbers of beetles may produce sores on the host, and, thereby, obtain blood. The association of two distantly related beetle species with beavers is not particularly surprising when one considers the strong selective pressure for the adoption of phoresy which must have occurred during the evolution of the unusual nesting habit in the host. This phoretic behaviour permitted the colonization of a nest microhabitat isolated by water from other competing non-phoretic nest insects, and facilitated the secondary shift to a diet of host skin and secretions.

Staphylinids of the subfamily Amblyopini inhabit the fur of rodents and marsupials in South America and Tasmania (Seevers, 1955; Machado-Allison, 1968; Machado-Allison & Barrera, 1972). Adult beetles congregate near the tail of their hosts where they attach to, and feed upon, the skin. This activity is known to cause local irritation and possibly a flow of blood, small amounts of which have been found in the gut of *Amblyopinus tiptoni* Barrera (Barrera, 1966). The gradual modification in this subfamily of morphological features adapted for feeding on host tissues has been discussed by Barrera & Machado-Allison (1965).

Another microhabitat association in the Coleoptera which has led to vertebrate associations is coprophagy. A number of scarabaeids are known to associate with mammals whose dung they utilize for oviposition (Haltter &
Matthews, 1966). In Australia, some species of *Onthophagus* attack themselves by modified claws to the hindquarters of kangaroos (Matthews, 1972). During defecation by the host, these beetles attack the fresh dung as it appears and quickly prepare it for oviposition and burial. This phoretic habit has the clear advantage of permitting the rapid utilization of dung in habitats where rapid dessication renders it useless after short periods of exposure. The adult beetles may also feed on host secretions or exudates (Arndt, in Britton, 1970). Other species of *Onthophagus* and *Copris* inhabit the burrows of mammals (Halffter & Matthews, 1966).

In the Neotropics, scarabaeid beetles of the genera *Uroxys* and *Trichillum* live in the fur of tree sloths (Bradypodidae) (Arrow, 1933; Boucomont, 1928). The larval habits of most of these species is unknown, but a yet undescribed species of *Trichillum* from Brasil, which occurs in great numbers on *Bradypus*, develops as a larva in the dung of its host (Best et al., in prep). The occurrence of several species of phoretic scarabaeids (and moths, see below) on sloths may be related to the unusual defecation behaviour of these mammals. Tree sloths usually bury their dung at the base of trees on the rain forest floor at roughly weekly intervals (Montgomery & Sunquist, 1975). The infrequent deposition of dung, its relative lack of odour, and its burial and patchy distribution on the forest floor may have selected for more efficient means of dung location by coprophages, such as using the host as transportation to fresh dung deposits.

Dung beetles have also been observed associated with monkeys and tapirs (Halffter & Matthews, 1966). In some observed associations adult beetles may simply be responding to the odour of feces on mammals. Such attraction is also responsible for the incidence of rectal myiasis in mammals (Theodorides, 1950).

The first stage in the evolution of vertebrate associations in the Coleoptera appears to have been the establishment of a larval dependence on the habitat of vertebrate nests or dung. This may have facilitated the accidental association of adult beetles with mammals, and in many cases such phoresis may have carried a selective advantage with regard to locating new larval resources. The establishment of phoresis brought adults into prolonged contact with host integument and at this point feeding on the host may have begun. Subsequent modification of mouthparts, as in *Platypsyllus*, permitted some species to exploit additional, possibly more nutritious host resources.

**Diptera**

Vertebrate associations have arisen in a large number of Dipteran families, and it is convenient to break down a discussion of dipteran associates into two sections, one dealing with the Nematocera and primitive Brachycera and one dealing with the 'higher' Diptera or Cyclorrhapha.

In the Nematocera and Brachycera Tabaniformia, bloodsucking associations with vertebrates have arisen in the female sex of the Psychodidae, Ceratopogonidae, Simuliidae, Culicidae, Tabanidae and Rhagionidae. The Diptera arose in the Permian from a Mecoptera-like stock (Tillyard, 1935), and these families probably had their origin in the late Permian or early Mesozoic. Beklemishev (1937) has suggested that the first Deptera evolved from entomophagous mecopteroid ancestors and were likewise predators on other insects. Downes (1958, 1970) has presented this argument in more detail, making
a comparison of the mouthparts and feeding biology of the living Mecoptera, Nematocera and primitive Brachycera. He concluded that piercing, mandibulate mouthparts and entomophagy were plesiotypic characters of the Diptera. The absence of piercing mouthparts in some lower flies would then represent a secondary loss from a mandibulate stock.

According to the theory of Beklemishev and Downes, haematophagy in lower flies evolved through a switch in adult feeding behaviour from a predatory habit to a blood-sucking one. The alternative hypothesis, that mandibulate predatory or bloodsucking groups arose independently several times from non-mandibulate stocks, has also been forwarded (Mayer, 1955; Mackerras, 1954). Specific alternate hypotheses include that of Mackerras (1954) who suggests that the bloodsucking Tabanidae arose from plant-sucking forms, and Mattingly (1965), who has suggested that the ancestors of the Culicidae, which possess a soft, flexible proboscis not typical of predatory flies, may have pierced the skins of soft fruit for nourishment. It is worth noting, however, that mosquitoes will feed on soft-bodied insects such as caterpillars, and are capable of developing eggs on such a diet (Harris et al., 1969).

Entomophagy in mosquitoes is one of several known instances of switching between haematophagy and entomophagy which tend to support the hypothesis of Beklemishev and Downes. Some members of the ceratopognid genus Forcipomyia feed ectoparasitically on insect haemolymph, while others feed on mammalian blood. In the same family, Culicoides anophelis Edwards feeds on blood-engorged mosquitoes, while a race of this species, C. a. flavescens Macfie, feeds on cattle (Mayer, 1955). Most members of the Rhagionidae are predacious on smaller insects, but a few North American representatives of the genus Symphoromyia feed on the blood of vertebrates.

Larval associations with vertebrates in these haematophagous families are virtually nonexistent. In most groups, the larval stage is completely independent of the adult host and is passed in aquatic or damp terrestrial habitats. A possible exception to this is to be found in the Phlebotomidae. Some larvae develop in caves on bat guano and the adults feed on the resident bats (Lewis & Lane, 1976: Williams, 1976). Larvae also occur in animal burrows, but in some cases these forms can develop in any situations where moist leaf material is present (Hanson, 1961) and in others adult flies do not appear to feed on the mammals infesting the burrows where their larvae develop (Harwood, 1965). Thus, even in the Phlebotomidae, larval dependence on host microhabitats is not clearly indicated.

A probable scenario for the evolution of ectoparasitism in the lower Diptera would involve adaptations leading to a radical switch in adult feeding behaviour from entomophagy to bloodsucking. No dependence of larvae on vertebrate microhabitats are indicated which would facilitate adult associations with vertebrates. It is possible that early predatory forms frequented damp, recessed habitats which served as prey breeding sites as well as shelters for small amphibians and reptiles. Potential hosts may have been encountered frequently in such habitats and accidental feeding may have occurred. Some predatory Diptera are occasionally attracted to vertebrates; the rhagionid, Symphoromyia crassicornis Panz., for instance, has been observed to feed on human sweat (Lindner, 1938), a behaviour possibly related to the habit of feeding on water droplets and aphid and plant exudates exhibited by other rhagionids.

Other predatory species may have encountered vertebrates while preying upon
dipterans which were already haematophagous. Feeding near mammals on engorged mosquitoes, for instance, has been observed in the Ceratopogonidae (Mayer, 1955; McCrae, 1969). By such behaviour, a predacious fly might not only encounter vertebrates but develop physiological adaptations for haematophagy as well.

The evolution of the Diptera Cyclorrhapha is thought to have begun in the late Mesozoic and to have involved two distinct changes in feeding ecology, a switch in larval habits from an aquatic or semiaquatic substrate to a terrestrial one, and the loss of mandibulate mouthparts in the adult, which were replaced by a soft labellum for 'sponging' liquids off surfaces (Oldroyd, 1964). Many vertebrate associations have arisen independently in these taxa.

Several species of the acalypterate family Chloropidae feed as adults on the sweat and lachrymal secretions of ungulates, man and other vertebrates. This relationship has probably arisen through a modification of adult feeding behaviour from an original diet of liquified, decaying animal and vegetable matter. This transition is suggested in the feeding habits of two species of Hippelates in Florida. *H. bishoppi* Sabrosky is attracted to decaying fish but not to skin secretions of vertebrates, while *H. pusio* Loew is attracted to both fish and vertebrate secretions (Jay, 1962). In both species, flies visiting the food baits were predominantly females.

The larvae of these chloropids develop in decaying vegetable matter and are not particularly associated with vertebrates in this stage, although they are sometimes more common in areas where the soil contains animal excrement (Hummaeli & DeFoliart, 1967). Besides lachrymation and sweat, adult *Hippelates* have been observed to feed on blood from wounds caused by feeding tabanids (Roberts, 1968).

A similar vertebrate association has been described in the ephydrid fly, *Chlorichaeta tuberculosa* in Guam (Bohart & Gressitt, 1951). Feeding on lachrymation and perspiration in this species is probably more casual than in some *Hippelates*, the primary adult diet being carrion and excrement. The larvae are aquatic.

The vertebrate associations found in two other acalypterate families, the Milichiidae and Mystacinoibiidae, by contrast, involved much closer larval and adult association with the host and its microhabitat. The milichiid fly, *Carnus hemapterus* Nitzsch., is commonly found in bird nests, where the larvae develop in nest detritus and the adults live on nestlings. Adult flies are physogastric and flightless (wings broken off at the base), and are usually found at the base of wing axillae or on areas of bare skin on the legs and wings (Lloyd & Philip, 1966). The proboscis of male and female *Carnus* is heavily sclerotized at the base and possesses a soft labellar tip, probably adapted for probing and feeding on quill gland secretions (Bequaert, 1942; Capelle & Whitworth, 1973). Flies are ovoviviparous and larvipositor in the nest, where the offspring overwinter as pupae (Bequaert, 1942). Larval associations with bird nests are common in a number of other milichiids not exhibiting adult associations (Hicks, 1959) and probably represent an incipient stage in the evolution of the close insect/bird relationship found in *Carnus*.

In New Zealand, a very unusual form of drosophilid fly, *Mystacinobia zelandica* Holloway, is found associated with the fruit-eating bat, *Mystacina tuberculata* Gray in its roosts in hollow trees (Holloway, 1976). Both the larvae and adults feed on
bat guano, which is rich in yeast and fungi, but the apterous, spider-like adults are also found commonly in the fur of the host. The adults have typical, sponging mouthparts and there is yet no evidence that they feed while on the bats. The vertebrate association appears instead to be a phoretic one by which flies are dispersed to new roosts. The importance of such phoresis to the insect is reflected in its absolute dependence on the microhabitat of an active roost, as larvae will not mature when temperatures fall below 25°C (which would occur when the roost is abandoned). Holloway (1976) suggests that this strange insect may have evolved from a drosophilid stock which originally developed in trees on fermenting sap or similar substances.

Another association with bats has arisen in the fly, Mormotomyia hirsuta Austen, which van Emden (1950) has placed between the Acalyptratae and the calyptrate family Scatophagidae. This species is known only from a bat-inhabited crevice in the Ukazi Hills of Kenya. The larvae apparently develop in bat guano, but the behaviour of the adults, which are apterous, hirsute and spider-like, is unknown. They possess soft, labellar mouthparts and van Someren (in van Emden, 1950) has suggested that they may feed on the dermal secretions of bats, observing that on human hands they preferred hairless areas, where they readily imbibed sweat from the skin. As with the Mystacinobiidae, a larval association with bat guano has probably been primary in the evolution of the yet poorly understood adult association with bats.

In the Calyptratae, the role of a larval dependence on a vertebrate-produced microhabitat is strongly suggested in the evolution of vertebrate associations in the superfamily Muscoidea. Oldroyd (1964) considers this group to have evolved from compost-feeding forms in the late Mesozoic, subsequently radiating into phytophages (many Anthomyiidae) and coprophages (many Muscidae). Coprophagous Muscidae are dependent on animal excrement for larval development and have evolved a number of adult associations with vertebrates, particularly ungulates.

Early casual associations with ungulates may have occurred in muscids owing to the proximity of the animals to the dung from which adult flies emerged. Besides the nutritional aspects of such associations, discussed below, association with ungulates conferred on female flies ready access to freshly-deposited dung for oviposition. Male flies, in turn, by associating with ungulates, would locate and mate with females most likely to find good oviposition sites. Therefore, selection for phoresy would be expected to occur simultaneously in both sexes.

The correlation of vertebrate association with the rapid and efficient location of oviposition sites may be observed in a number of species. The face fly, Musca autumnalis De Geer, for instance, rests on cattle during the day and is one of the first dipteran species to oviposit in fresh dung (Teskey, 1969). The rapid physical changes in dung and the intense competition with other Diptera make such early colonization highly advantageous. A more extreme case is found in Haematobia irritans Linn. which lives continuously on cattle as an adult, leaving only to oviposit. During defecation by the host, the flies cluster around the flanks and anus and fly off to oviposit in dung as soon as it is dropped. As a result, H. irritans is almost always the first in the succession of fly species to colonize dung pats, which it does, on average, about 15 seconds after their deposition (Mohr, 1943).

Most adult muscids possess soft labellae for imbibing surface liquids. Some species, such as Hydrotaea dentipes (Fabr.) feed only on the moist surfaces of dung
(Mahan'ko, 1973), while others, including species of Hydrotaea, Musca and Morellia, feed on both dung and surface liquids of ungulates such as saliva, lachrymation and perspiration. Hammer (1941) has extensively reviewed the diverse feeding interactions of coprophagous muscids and cattle. Blood may be occasionally acquired in some species by feeding at wounds or at punctures caused by biting flies (Patton & Craig, 1913a; Garcia & Radovsky, 1962).

From such facultive haematophagy, a gradual sophistication of blood-sucking habits and structures has occurred, culminating in the obligate haematophagy and piercing mouthparts of genera like Haematobia and Lyperosia. The modification of mouthparts for bloodsucking has involved the enlargement of the pre-stomal teeth, situated between the labellae, into rasping and cutting organs, and the sclerotization of the labium. Musca sorbens Wied., for instance, by virtue of its pre-stomal teeth, can abrade scabs over wounds, thereby gaining access to pus and blood (Bohart & Gressit, 1951). Enlargement of these teeth has permitted some species, such as Musca lineata Brunetti and M. planiceps Wied. to open wound scars and start blood flow, while still other species, such as M. gurneyi Patton & Craig and M. insignis (Austen), are capable of causing wounds in undamaged skin (Patton & Craig, 1913b). Patton (1938) has reviewed this morphological modification of feeding apparatus in Musca, and Mahan'ko (1973) has studied the similar transition in the genus Hydrotaea and compared generally the oral teeth of different Muscidae.

The haematophagous muscid genus Stomoxys, which possesses a highly modified piercing proboscis, may have arisen by a pathway similar to that just described for other Muscidae, although the larval associations of Stomoxys do not appear as restricted to host dung as in other muscids.

The phylogenetic relationships of the remaining ectoparasitic Cyclorrhapha the Glossinidae, Hippoboscidae, Streblidae and Nycteribiidae, have been much disputed. Whether these families are monophyletic or polyphyletic (the usual associations made are Glossinidae-Hippoboscidae and Streblidae-Nycteribiidae) is unclear, but for the present discussion, Griffiths' (1972) monophyletic classification will be assumed, implying an origin of all families from a common muscoid stock.

All members of these groups are pupiparous, feed only on blood and possess highly specialized, piercing mouthparts. The absence of intermediate forms linking these groups with non-bloodsucking stocks makes discussion of their evolution difficult. Furthermore, the importance of larval habitats in this evolution cannot be evaluated because this stage is not free-living. Thus, little more than speculation is possible.

The association of the Glossinidae with large mammals suggests that they may have evolved from dung-feeding forms and subsequently lost this pre-adaptive larval dependence. The swarming of males around hosts in Glossina is reminiscent of the stages suggested above for the evolution of male/host associations in dung-feeding forms. The Hippoboscidae are parasitic on a variety of birds and mammals. Bequaert (1954) has suggested that they evolved from species which developed as larvae in bird nests, but Theodor (1957) believes there is no strong evidence to favour birds over mammals as the original hosts. Both the Glossinidae and Hippoboscidae deposite their puparia on the ground in a variety of habitats, though some Hippoboscidae do place them in the nests of their hosts. While the Glossinidae feed for brief periods, the Hippoboscidae spend most of their adult lives on the host. Most hippoboscids are winged and
movement from host to host can be frequent (Corbet, 1956). Flightless species are found associating with swifts and swallows, which return to the same nest sites year after year. The deer ked, Lipoptena cervi Linn. sheds its wings after settling on a host, and the sheep ked, Melophagus ovinus Linn. is apterous and attaches its puparia to the hairs of its host.

The Streblidae and Nycteribiidae are associated exclusively with bats. Prepupae are deposited on the walls of the bat roots and adults live more or less continuously on hosts. The Streblidae assume a variety of morphological forms, some winged, while the Nycteribiidae are wingless and spider-like. Jobling (1949) believes these groups to have evolved from non-bloodsucking flies which lived in caves and developed on bat guano. Oldroyd (1964) has proposed an 'opposite' evolutionary pathway, arguing that the batflies evolved from glossinid-like flies which shifted to chiropteran hosts and subsequently became adapted to the cave environments. Without more information on the ancestors of these groups, it is impossible to select between these hypotheses.

The evolution of vertebrate associations in the Diptera reveals a great variation in adaptative 'pathways'. This is particularly apparent in the evolution of haematophagy. The Nematocera and Brachycera Tabaniformia, for instance, appear to have evolved from a stock preadapted as adults for bloodsucking by their piercing mouthparts and predatory behaviour, with regular host associations being a subsequent evolutionary step, while in most 'higher' flies, larval dependence on nests or dung promoted phoretic associations of adults with the host and preadapted flies for the subsequent evolution of piercing mouthparts and bloodsucking behaviour. Considering these very differing origins for haematophagy, the convergence observed between these groups in such aspects as the stimuli used in host-finding (Gatehouse & Lewis, 1973) and feeding regulation (Friend & Smith, 1972; Galun, 1976) is striking.

An interesting difference between 'lower' and 'higher' bloodsucking flies is the restriction of haematophagy to females in the former but not in the latter. This difference is probably related to the ecological context in which vertebrate associations evolved in both groups. In the early Muscidae, as suggested previously, vertebrate association was advantageous to males because the host provided a site for the aggregation of phoretic females. Both sexes, through host association, were exposed to the advantages of host-feeding from the onset of such behaviour. In the 'lower flies', I have suggested that initial bloodfeeding events followed accidental encounters of flies with hosts. In such a situation, selection for host association might have been more intense in females, where blood meals would be particularly beneficial to egg nutrition and development. Were genes for such a behaviour to become linked to those involved in egg development and nutrition, haematophagy might evolve only in the female sex, where it conferred a considerable selective advantage. In a few cases male Nematocera are known to associate with vertebrate hosts, possibly for the purpose of mating (Mattingly, 1970; Jones et al., 1977), but these probably represent secondary modifications from the standard male mating swarms which are not at all associated with vertebrates.

**Siphonaptera**

The Siphonaptera are a highly specialized, wholly haematophagous order with no clear links to a living non-parasitic stock. A mecopteroid origin for this group
has been argued on morphological grounds (Tillyard, 1935; Hinton, 1958; Rothschild, 1975a; Schlein, 1979). Fleas are a relatively ancient group, the first fossils are known from the Cretaceous (Riek, 1970), and an analysis of specimens from Eocene amber has led Peus (1968) to conclude that the order as we know it was fully developed by this period. The Siphonaptera probably first evolved vertebrate associations with mammals, switching later to birds when a common nest habitat afforded access to both sorts of host (Rothschild & Clay, 1952; Holland, 1964). Hopkins (1957) suggests that this shift has occurred 16 times in the evolution of the order.

The eggs of fleas are usually laid in the nests of their hosts and the larvae feed there on detritus, other insects and on the blood-rich faeces of the adult fleas. This latter component may be important in development but is not always necessary for successful larval growth (Sharif, 1948). Adult fleas feed exclusively on blood.

Rothschild (1975b, and personal communication) has identified two broad trends in the lifestyle of fleas. A more primitive association with the nest microhabitat is preserved in many groups of the superfamily Ceratophyloidea. This lifestyle is characterized by infrequent and brief associations with the host, and often considerable adult movement between hosts and nests. A contrasting lifestyle is exhibited by many members of the Pulicoidea, which show prolonged adult associations with the host, some forms (e.g. *Tunga*) living buried in the host epidermis throughout the entire adult stage. Certain changes in the structure of mouthparts and grasping organs have accompanied the development of this prolonged host association (N.C. Rothschild, 1916). Larval associations may also occur in these groups (Freeman & Madsen, 1949). An exceptional case of larval association with the host is found in the family Pygiopsyllidae, where the species *Uropsylla tasmanica* Rothsch. attaches its eggs to host hairs, and the larvae burrow into the host skin (Dunnet, 1970).

If analogies with living Mecoptera are valid, the mecopteroid ancestors of fleas were probably associated with detritus and fed as larvae and adults on plant material or live arthropods (Hepburn, 1969; Byers, 1971). The mecopteran family Boreidae resemble fleas in being aperous and capable of leaping. They live in moss, feeding on detritus and/or insects. If ancestral Siphonaptera were of similar habit, it is easy to see how their populations might have become aggregated in nest microhabitats rich in organic detritus and arthropod prey. If these early forms possessed piercing mouthparts for entomophagy (as in some living Mecoptera), a direct switch to haematophagy may have been possible. The invasion of a nest microhabitat by predatory ancestors, followed by a switch to haematophagy and the evolution of increasingly intimate host association is a possible scenario for the evolution of the Siphonaptera. Without more information on these early forms, however, this remains but one of several possible pathways by which parasitism may have evolved in this order.

**LEPIDOPTERA**

Vertebrate associations have arisen in a number of lepidopteran families and, as with the Diptera, two general types of relationships may be distinguished; those involving prolonged adult association with the host and larval
dependence on the host's microhabitat, and those involving only brief adult feeding associations and no larval dependance.

The former group is represented primarily by about five species of Neotropical pyralid moths which live in the fur of tree sloths. Although it was long thought that these insects were truly parasitic and passed all life stages on the host, some recent studies (Waage & Montgomery, 1976; Best & Waage, in preparation) have revealed a very different life history. The larvae of sloth moths develop in the dung of their hosts, which is usually buried on the forest floor. Adult moths emerge from pupation in the dung and fly to the forest canopy where they locate and settle on a sloth. Species of the genus Cryptoses live on or near the surface of the fur, while Bradypodicola hahneli Spuler appears to live deep in the fur near the surface of the skin. In this latter species, both sexes lose much or all of their wings through abrasion after settling in the sloth's fur and are therefore flightless while on the host.

The continuous, phoretic association of female moths with sloth facilitates the location of fresh dung piles for oviposition. In Cryptoses choloepti Dyar in Panama, males are three to four times as common sloths as females, although the primary sex ratio is about one to one (Waage & Montgomery, 1976). Perhaps this reflects the tendency of males to remain and accumulate on sloths in order to compete for newly-arriving females, in contrast to a regular loss of females from the host population at each defecation by the host.

Another close vertebrate association may be found in a yet-unidentified lepidopteran which has been collected in numbers from the fur of the heteromyid rodents Liomys and Heteromys in Costa Rica (T. Fleming, personal communication). Some tineids (Ceratophaga sp.) live as larvae in the shed (and, rarely, the unshed) horns of African antelope, where they presumably feed on keratin (Gozmany & Vari, 1973). Associations with vertebrate nests and dung, which might resemble incipient stages in the evolution of phoretic behaviour, are known in a number of Lepidoptera. The tineid, Amydria effrentella Clemens lives in the nest of the rodent, Aplodontia, where it feeds on vegetable material in the larval stage (Johnson & Martin, 1969), while A. arizonella Dietz lives in caves and develops on bat guano (Davis, 1972). A tineid has been found in the dung of tree sloths which, unlike its pyralid competitors, is not phoretic (Best & Waage, in preparation). Tineidae and Oecophoridae are also common in bird nests (Hicks, 1959). Zagulaev (1971, 1972) has discussed the evolution of the nest association in the Tineidae and the ecological adaptations it has involved.

In contrast to these relationships, a number of moths exhibit much less continuous, but just as tightly coevolved associations with vertebrates. These include some species of tropical and subtropical Noctuidae, Pyralidae and Geometridae which feed nocturnally on the lachrymal secretions of large mammals. This host association is limited to relatively brief feeding periods at the host's eyes; during the day the moths rest on forest foliage and the larval stages feed on green plants (Büttiker, 1967). The intimacy of this association is variable, ranging from species which feed only occasionally on eye secretions and more commonly on perspiration and liquids from dung and urine (oligolachryphages), through species which feed regularly at the eyes but also on these other substances (hemilachryphages), to species which feed exclusively at the eyes, often for longer periods than the above groups (eulachryphages) (Bänziger, 1972).
This classification suggests that the eye-frequenting habit evolved through the gradual modification of a diet of animal wastes to include secretions of living animals, followed by a specialization to this habit and, finally, obligate lachryphagy. This initial feeding on dung, urine and carrion is found in many Lepidoptera (Norris, 1986; Downes, 1975), and these substances may share with animal secretions certain nutrients or attractants which facilitated the shift to feeding on vertebrates, such as salt (Shannon, 1928), which is known to arrest butterflies feeding at mud puddles (Arms et al., 1974), amino acids or fatty acids. The importance of water availability in the evolution of lachryphagy should also be stressed. The distribution of eye-frequenting moths, for instance, conforms to seasonally dry habitats, often deficient in nectar resources, suggesting that eye-feeding may have evolved under selective pressure to exploit novel sources of water (Bänziger, 1972; Böttiker, 1973). Facultative lachryphagy, in fact, can be elicited from the sphingid moth, Manduca sexta Johannsen, in the laboratory when denied a water source for a day or two (personal observations). Sphingids also occasionally feed on vertebrate secretions in the field (Shannon, 1928).

The mouthparts of most moths are clearly preadapted for feeding on tears and other free liquids, but are incapable of piercing skin and taking blood, although some lachryphages will take blood exposed in the surface of hosts (Böttiker, 1959, Bänziger, 1972). True blood-sucking behaviour, however, has evolved in the noctuid, Calpe eustrigata Hmps., which feeds nocturnally on large mammals in the Malaysian region (Bänziger, 1971, 1975). This species belongs to a group of moths which as adults suck the juices of fruits after piercing the rinds with highly modified, sharp-tipped proboscis (Bänziger, 1970; Cochereau, 1974). These feeding modifications clearly preadapted members of this group for a shift to piercing vertebrate tissues, and Bänziger (1970) has demonstrated the similarity between the fruit-piercing action of Calpe thalictr Bkh. and the skin-piercing action of its congener, C. eustrigata, which will also pierce fruit under laboratory conditions.

The evolution of eye-frequenting and blood-sucking moths poses some interesting questions regarding the relative benefit of parasitism to the different sexes. In C. eustrigata, for instance, only males are known to attack vertebrates. Females make up the majority (75%) of eye-frequenting individuals in the eulachryphage, Lobocraspis griseifusa Hmps., in Thailand (Böttiker, 1967) and in some other, but not all, eye-frequenting moths. Collenette (1984) found that noctuids attracted to sweat-impregnated clothing in the Amazon were either represented nearly entirely by males (13 species) or entirely by females (7 species). Finally, moths and butterflies attracted to puddles and animal wastes are almost always males. A better knowledge of the ecology and nutrition of lepidoptera associated with vertebrates and their products is necessary before these differences between the behaviour of the different sexes can be understood.

**OTHER ASSOCIATIONS**

Regular vertebrate associations in the Hymenoptera are known in the bee families Halictidae and Meliponidae. The former group, often called sweat bees, feed on the perspiration of vertebrates, while the Meliponidae are known to imibbe perspiration, lachrymal and nasal secretions and fluids from vertebrate sores (Schwartz, 1948). In the Meliponidae, this association has probably evolved
from initial diets of animal products (dung, urine, carcasses) upon which these bees also feed. The larval stages, of course, are completely independent of vertebrates. Phipps (1974) has described an exceptional case of haematophagy by a vespid wasp.

The sucking mouthparts of the Thysanoptera preadapt their order to piercing vertebrate tissues. Accidental attacks on vertebrates have been reported on occasion (Bailey, 1986; Arnaud, 1970).

THE EVOLUTION OF INSECT/VERTEBRATE ASSOCIATIONS: 

Macroevolutionary considerations

Certainly the most striking aspect of insect/vertebrate associations is their great diversity. Besides differences in the extent and nature of feeding on the host, vertebrate associates exhibit considerable variability in their life histories and intimacy of host association. At one extreme exist taxa like the Anoplura, which live continuously on their hosts, while at the other extreme are groups like the Culicidae, which associate with hosts only for brief feeding periods. These differences have been emphasized in several classifications or ectoparasite types. Tatchell (1969), for instance, classifies ectoparasites as either fast feeding (those which associate with the host for brief feeding periods) or slow feeding (those which remain attached to the host for prolonged periods). Nelson et al. (1975) add life history characteristics to a similar classification and recognize three types of ectoparasites; field parasites (brief feeding periods, free living most of life cycle), nest parasites (brief feeding periods, live in dwellings of hosts), and host parasites (live continuously on hosts). Marshall (1976) relates the intimacy of the host relationship (and the consequent host specificity of the ectoparasite group) to the mobility of the insects involved. He classifies ectoparasites into four types; (1) wingless forms, confined continuously to hosts, (2) winged or wingless forms largely confined to hosts, at least as adults, (3) wingless forms confined to host dwellings, and (4) highly mobile, winged or wingless forms.

Why has the evolution of insect/vertebrate associations produced such different life history types? Perhaps this diversity of life histories reflects a comparable diversity in the macroevolutionary pathways by which vertebrate associations have evolved.

For the great majority of insects, vertebrate associations are accidental and of neutral or negative value to the insect’s fitness. The transition from this sort of relationship to a positive commensal or ectoparasitic relationship has required, in every case, a number of morphological, behavioural and physiological adaptations. These adaptations may be classified into two general groups:

(1) Adaptations promoting regular physical association with the host. These include habitat preference, host-finding behaviour and morphological adaptations to living on the host.

(2) Adaptations promoting the capacity to feed on the host. These include mouthpart structure, the physiological capacity to digest host substances and the behaviour associated with the initiation and termination of feeding. Both sorts of adaptations are necessary for the evolution of feeding associations with vertebrates. I suggest that the nature and intimacy of an ectoparasite/host relationship will depend on the sequence in which these two sorts of adaptations occur.
Table 1. Characteristics of different taxa of vertebrate associates and the alternate evolutionary pathways they suggest. See text for explanation and more detailed discussion of each group.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Probable habits of parent stock</th>
<th>Intimacy of association</th>
<th>Secondary adaptations</th>
<th>Sex of associates</th>
<th>Suggested pathway</th>
</tr>
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<tbody>
<tr>
<td>DERMAPTERA</td>
<td></td>
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<td></td>
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<tr>
<td>ARIXENIINA</td>
<td>bat roost associates (type 1)</td>
<td>relatively brief feeding periods</td>
<td></td>
<td>M, F</td>
<td>I (?)</td>
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<tr>
<td>HEMIMERINDA</td>
<td>nest associates (type 1)</td>
<td>continuously on host</td>
<td>piercing mouthparts Anoplura (type 2)</td>
<td>M, F</td>
<td>I</td>
</tr>
<tr>
<td>PHTHIRAPTERA</td>
<td>nest associates (type 1)</td>
<td>continuously on host</td>
<td></td>
<td>M, F</td>
<td>I</td>
</tr>
<tr>
<td>HEMIPTERA</td>
<td>terrestial predators (type 2)</td>
<td>brief feeding periods</td>
<td>nest associations, continuous associations (Polyct.) (type 1)</td>
<td>M, F</td>
<td>II</td>
</tr>
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<td>CICICOIDES</td>
<td>terrestial predators (type 2)</td>
<td>brief feeding periods</td>
<td>nest associations (type 1)</td>
<td>M, F</td>
<td>II</td>
</tr>
<tr>
<td>REDUVIOIDEA</td>
<td>terrestial predators (type 2)</td>
<td>brief feeding periods</td>
<td>nest associations (type 1)</td>
<td>M, F</td>
<td>II</td>
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<td>prolonged in adult stage</td>
<td></td>
<td>M, F</td>
<td>I</td>
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<td>CRYPTOPhAGIDAE</td>
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<td>prolonged in adult stage</td>
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<td>M, F</td>
<td>I</td>
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<td>M, F</td>
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<td>dung associates (type 1)</td>
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<td>II</td>
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<td>F</td>
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<td></td>
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(rarely M)
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<th>Family</th>
<th>Nest Associates (Type 1)</th>
<th>Prolonged in Adult Stage</th>
<th>Sucking Mouthparts (Type 2)</th>
<th>Male, Female</th>
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<td>I</td>
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<td>I</td>
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<td>Bat roost associates (Type 1)</td>
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<td>Piercing Mouthparts (Type 2)</td>
<td>M, F</td>
<td>I</td>
</tr>
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<td>Glossinidae</td>
<td>Dung associates (? , Type 1)</td>
<td>Brief Feeding Periods (But Male Swarms)</td>
<td>Piercing Mouthparts (Assuming Muscidae Origin) (Type 2)</td>
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<td>I</td>
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<td>I</td>
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</tr>
<tr>
<td>Pyralidae (Sloth Moths)</td>
<td>Nectar Sucking, Other Liquids (Type 2)</td>
<td>Brief Feeding Periods</td>
<td>More Intimate Associations (Eulachryphages) (Type 1)</td>
<td>M, F (F Often Dominates)</td>
<td>II</td>
</tr>
<tr>
<td>Noctuidae</td>
<td>Fruit Piercing (Type 2)</td>
<td>Brief Feeding Periods</td>
<td></td>
<td>M</td>
<td>II</td>
</tr>
</tbody>
</table>
Vertebrate dwelling ectoparasitic females might have advantages gained by promoting feeding behaviour and mouthpart morphology, permitting ingestion of more nutritious host tissues, such as blood (type 2 adaptation), would lead to an ectoparasitic lifestyle. Alternatively, a free-living insect stock might be preadapted to feed on nutritive vertebrate tissues, such as blood, by virtue of mouthparts and behaviour adapted for other diets (type 2 adaptation). For instance, mouthparts adapted for piercing and sucking of plant or arthropod tissues may also be effective in obtaining blood from vertebrates. Nutritional advantages gained by occasional contact with, and attempted feeding on, vertebrates might select for host-finding behaviour or habitat preferences leading to more regular vertebrate associations (type 1 adaptations) and an ectoparasitic lifestyle.

A key characteristic of these two hypothetical pathways is the presence of pre-adaptations towards ectoparasitism prior to selection for adaptations directly promoting this lifestyle. Characters preadaptive for one pathway are evolved secondarily in the other. A crucial role for preadaptation is general to the evolution of parasitic relationships (Cameron, 1956; Croll, 1966).

The evolutionary pathways proposed above represent theoretical extremes of the adaptive sequence. Hypothetical as they are, they make interesting predictions as to the life histories and phylogenetic affinities which might be expected in different taxa of vertebrate associates. Associates evolving through the first pathway, with type 1 adaptations preceding type 2 adaptations, should display the following characteristics:

1. Phylogenetic affinities with free-living insects exhibiting an association with nests, dung, etc.
2. Prolonged association with the host or its immediate environment, perhaps through several life stages.
3. Evidence of secondary acquisition of behaviour and mouthparts leading to haematophagy or a similar diet.

Vertebrate associates evolving along the 'reverse' pathway would, by contrast, exhibit:

1. Phylogenetic affinities with free-living insects exhibiting no vertebrate associations but possessing preadaptive feeding structures or behaviour.
2. Brief host associations, primarily for feeding and usually limited to the adult stage of the life cycle.
3. Evidence of gradual, secondary acquisition of close associations with the host or its microhabitat.

These simple predictions are compared in Table 1 with characteristics of the insect taxa reviewed above. Most groups fall clearly into one pathway or the other. Pathway 1 (type 1 adaptations followed by type 2 adaptations) is the more common (Mallophaga, Coleoptera, some Dermaptera, Diptera and Lepidoptera), although the secondary evolution of haematophagy has occurred.
in only a few groups. Phoresy is implied in the evolution of almost all Pathway I groups, especially where resources are extremely short-lived or difficult to locate, e.g. highly dispersed, buried dung (sloth moths and beetles), dung in arid habitats (kangaroo beetles), nests isolated by water barriers (beaver beetles).

Pathway II is indicated for groups preadapted for skin-piercing (Hemiptera, some Diptera and Lepidoptera) and eye-feeding (some Diptera and Lepidoptera). Interestingly, Pathway II groups exhibit great variability in the sexes associated with vertebrates, ranging from all males (Cepheus eustigmata) to all females (lower flies). Without the phoretic component of Pathway I, beneficial to both sexes (see p. 197) the evolution of vertebrate associations in these groups may have been influenced solely by the relative value of host tissues to each sex.

A few groups are difficult to place in one or the other pathway. The Dermaptera, for instance, exhibit both short and continuous host associations, while the highly specialized Siphonaptera offer no clues to the preadaptations of their ancestors.

The benefits of parasitism

Implicit in this discussion has been the assumption of a selective advantage to the evolution of vertebrate associations. The advantage of phoresis in the above cases is relatively straightforward. The nutritional advantage of feeding on host tissues, ultimately blood, is presumably associated with the acquisition of nitrogen to promote longevity and egg production. The amount and form of nitrogen in a variety of potential insect diets is presented in Table 2. Clearly, blood is richest in nitrogen, but much of this is locked in haemoglobin (Hb) and other proteins which may be inaccessible to evolving vertebrate associates. Insects switching from entomophagy to haematophagy (Pathway II) might be expected to possess some of the necessary proteases, in other forms this digestive capacity may evolve more gradually. The eulachryphagous moth, Lobocraspis griseifusa, for instance, is advanced relative to other eye-frequenting moths in having evolved gut proteases, presumably to metabolize epithelial cells imbibed

<table>
<thead>
<tr>
<th>Material</th>
<th>Total nitrogen (%)</th>
<th>Non-protein (%) nitrogen</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blood</td>
<td>19.2</td>
<td>0.05</td>
</tr>
<tr>
<td>Blood (without Hb)</td>
<td>4.73</td>
<td></td>
</tr>
<tr>
<td>Sweat</td>
<td>0.03</td>
<td>0.03</td>
</tr>
<tr>
<td>Tears</td>
<td>0.16</td>
<td>0.05</td>
</tr>
<tr>
<td>Skin</td>
<td>4.00</td>
<td>0.75</td>
</tr>
<tr>
<td>Insect haemolymphs A</td>
<td>1.20</td>
<td>0.40</td>
</tr>
<tr>
<td>B</td>
<td>0.57</td>
<td>0.35</td>
</tr>
</tbody>
</table>
with lachrymation (Bänziger, 1972). Another problem with blood as a resource is its deficiency in B vitamins. Wholly haematophagous species have overcome this problem by evolving symbiotic associations with microorganisms which provide these nutrients (Wigglesworth, 1952; Bequaert, 1952).

Access to blood and other host substances has permitted some ectoparasites to shift food-gathering more towards the adult stage and its highly dependable, nutritive resource, often with the loss of the egg and early larval stages. In the flea, Tunga monositus Barnes and Radovsky, complete nourishment for larval development is provided in the egg, and thus indirectly, by the blood meals of the mother (Barnes & Radovsky, 1969). Vivaparity is known in the dermapteran Arixeniinae and Hemimerina, in the hemipteran Polycenidae (Jordan, 1913) and in the dipteran Carnidae (Bequaert, 1942). Pupipary is exhibited by the dipteran families Glossinidae, Hippoboscidae, Streblidae and Nycteribiidae. Such maternal control over susceptible early stages increases the survivorship of offspring while reducing fecundity, and in this way resembles a shift in reproductive strategies towards the K-end of a theoretical r–K continuum (Southwood, 1976).

In considering the advantages of vertebrate association, it is also important to bear in mind the costs. A number of the risks insects run in associating with vertebrates will be discussed in the following section.

Microevolutionary considerations: coevolution

To this point, a broad, macroevolutionary perspective has been taken towards the evolution of insect/vertebrate associations. Two major steps, the development of host associations and of host feeding, are identified for the establishment of ectoparasite/host associations. In an analogous manner, Southwood (1973) has identified several macroevolutionary 'hurdles' in the establishment of insect/plant associations. To examine the subsequent diversification of ectoparasite groups, a more microevolutionary perspective is useful, concentrating on adaptations within specific host/parasite systems. Coevolution, a pattern of reciprocal adaptations between species which directly influence each other's fitness, is a process common to many host/parasite systems (Price, 1977, 1979). While the coevolution of plants and their insect parasites has received considerable attention (Ehrlich & Raven, 1965; Gilbert & Raven, 1975), the coevolution of vertebrates and their insect parasites has remained relatively ignored.

Of the insect associations discussed above, only the true parasitic ones generate the negative effect on host fitness that is the necessary 'spark' to the coevolutionary process (the possible mutualistic 'cleaning' associations between some Dermaptera and Coleoptera and vertebrates might also, of course, involve coevolution). Ectoparasites may reduce host fitness in two major ways, through injury and the loss of blood, and through infection and the transmission of disease. The importance of the first effect depends on the ability of the host to deter parasites and on its size, as smaller hosts will suffer more from a given amount of blood loss than larger ones. Wood (1974), for example, has obtained data suggesting that larger rats (Rattus, Neotoma) suffer lower mortality when exposed to large numbers of Triatoma than smaller individuals. Large hosts, such as sheep, have also been known to suffer severe anaemia and die as a result of
heavy ectoparasite infestations (Nelson et al., 1977). Even where host death is not likely, other measures of fitness may be influenced by ectoparasite feeding, such as the reduction in weight and milk production observed in livestock heavily attacked by ectoparasites (Steelman, 1976). Aside from direct blood loss, the irritation caused by ectoparasites may exhaust or distract hosts, making them more susceptible to disease, accident or predation, and reducing their overall feeding rate.

Reduction of host fitness as a result of disease transmission has been the subject of numerous studies in medical entomology, and may again involve mortality or some less drastic effect on fitness, depending on the virulence of the pathogen. Vector-borne diseases can be expected to result in more intense, but probably more local, selection pressure for parasite deterrence compared to the pressure exerted by blood loss and irritation alone.

Host defence and parasite response

Hosts have evolved a number of active and passive defenses against ectoparasitic insects. One of the most important active defenses is grooming. This takes a wide variety of forms, ranging from shaking of the body in order to dislodge parasites to painstaking removal of insects from the integument. The importance of grooming in reducing the intensity of parasite attack has been shown for a variety of vertebrates. Rapid growth of mallophagan populations on hosts artificially prevented from grooming occurs in mice (Murray, 1961; Bell et al., 1962) and birds (Nelson & Murray, 1971), and similar results have been obtained with tick populations on cattle (Bennet, 1969). Edman and his coworkers (Edman & Kale, 1971; Edman et al., 1974) have shown that grooming responses of some birds and small mammals to mosquito attack reduce the number of individuals taking blood meals and the size of blood meals taken. Kangwagye (1977) observed that the grooming responses of ungulates to tabanids, muscids and glossinids tend to shorten the feeding times of these parasites. In addition to self-grooming, allogrooming, the grooming of one individual by another, occurs in many vertebrates and is effective in reducing ectoparasite numbers (Bell & Clifford, 1964).

Another form of active defence against ectoparasitism is emigration from sites of intense parasite attack. In Greenland, reindeer avoid mosquitoes during their peak biting season by moving to higher ground (Longstaff, 1932). Tinley (1964) has observed that hippopotami take to the water in response to attacks by specific tabanids on land. Shifts of nesting site by birds from one breeding period to the next prevents the build up of nest-associated ectoparasites; birds which return to the same site every season must deal with very high ectoparasite populations in the nest (Rothschild & Clay, 1952). Teskey (1969) has described an interesting spatial response of cattle to the face fly, Musca autumnalis. At high fly densities, cattle often aggregate. While this can result in higher overall fly numbers, the majority of flies are distributed on the peripheral individuals of the herd. Aggregation is advantageous to that majority of individuals within the herd, away from the periphery (cf. the 'selfish herd strategy' of Hamilton, 1971). Horses may avoid tabanid attack by local migration to special "resting areas" and by aggregation, which reduces the number of fly attacks per individual (Duncan & Cowtan, in press; Duncan & Vigne, in press). Freeland (1976, 1977)
has suggested that aggregation in primates might also serve this function of reducing the number of attacks per individual.

Passive defences are also important in ectoparasite avoidance and repulsion. Evidence of physiological resistance to arthropod attack has been reviewed by Nelson et al. (1977). These authors observed that physiological host reactions which result in reduced ectoparasite feeding success occur more commonly against insects associated with hosts for long feeding period (keds, lice) than against parasites exhibiting brief associations (mosquitoes, fleas).

Hair and feather covers also act as passive defences against many ectoparasites (although they provide a haven for host-restricted species). Hammer (1941) found that a variety of factors influenced the numbers of Haematobia irritans on cattle, including hair and skin thickness, odour and colour. An interesting passive mechanism for parasite avoidance might exist in the striping pattern of zebras. While zebra stripes have traditionally been associated with the avoidance of vertebrate predators (see MacClintock, 1976, for a discussion of these hypotheses), recent studies of the predators implicated (Kruuk, 1972; Schaller, 1972) cast doubt on this function. I suggest that the colouration of zebras might interfere with visual host orientation in the tsetse fly, Glossina, and thereby protect these mammals from tsetse-borne diseases. Laboratory studies of Glossina behaviour have shown taking off from a perch to be elicited by a moving black stripe (Brady, 1972). Below a certain stripe width this response is not elicited. Field studies of tsetse landing on boards carried across fields indicate that black boards are especially attractive but lose attractiveness as they are bisected by white stripes (Barrass, 1960). Perhaps the striping of zebras breaks up the image of a solid dark form which is an important visual stimulus for host-finding in tsetse. It is interesting to note that blood meal studies indicate that Glossina does not feed on zebras, although it does feed readily on the non-striped congener of zebras, the domestic horse (Ford, 1971). However, the recent demonstration of the importance of olfactory cues in host finding by tsetse (Vale, 1977a) complicates this hypothesis.

The defences raised by hosts against their ectoparasites have been countered by a number of adaptations, the most obvious of which are morphological adaptations to grooming pressure. In insects which remain on hosts for long periods, ctenidia and similar structures may aid escape movements through the host's pelage or resistance to removal by hosts (N. C. Rothschild, 1916; Baer, 1931; Marshall, 1979). Grasping organs for attachment to hosts have also become highly modified to the parasite's particular substrate and to the form of grooming directly against it. In general body form, a number of strategies appear to have been developed, including extreme dorso-ventral flattening (some lice, keds), extreme lateral flattening (fleas) and a spider-like form (nycteribiids, mormotomyids, mystacinobiids). In the Streblidae, all three forms are represented (Theodor, 1957).

Certain sites on the body may be less accessible to grooming activities than others, and ectoparasites may aggregate preferentially in these regions. In bird lice, such well-protected areas are utilized for oviposition, where there is minimal risk of eggs being dislodged (Rothschild & Clay, 1952).

Adaptations against grooming in ectoparasites with brief host associations include anaesthetic salivary secretions and rapid feeding times, both of which ensure that blood meals are completed without host disturbance. Gillett (1967)
found that **Aedes aegypti** (L.) mosquitoes from a three year old laboratory culture exhibited longer feeding times than wild caught individuals of **A. africanus**. Theobald and associated in this to the relaxation of selection pressure for rapid feeding in laboratory populations, where prolonged feeding does not incur the risk of host interference and, possibly, death. Many ectoparasites with brief host associations avoid host defences by feeding during periods when the host is at rest or sleeping.

**The diversification and structure of ectoparasite communities**

Extreme host specificity is one of the possible consequences of parasite/host coevolution and is widespread in ectoparasitic insects. Because of this intense specialization, particularly in ectoparasites closely associated with their hosts, the structure and diversity of some local ectoparasite communities can be largely predicted from the diversity of the local vertebrate fauna.

Much diversification within ectoparasite taxa has apparently resulted from the evolutionary divergence of host stock. In many groups, relatedness between parasites closely matches patterns of relatedness in host phylogeny, so much so that ‘rules’ have been created (Fahrenholtz’s Rule, Szidat’s Rule, Eichler’s Rule) for the relationship of host and parasite phylogenies (Eichler, 1948). Even some ectoparasites which do not associate closely with their hosts show patterns of diversification which match host patterns, for example the geographical association of the tabanid genus **Haematopota** with the ungulate family **Bovidae** (Oldroyd, 1964).

Modes of speciation in ectoparasitic insects cannot be simply described by the classical allopatric/sympatric terminology as differences in host association can be as important for reproductive isolation as geographical differences. To solve this problem, Eichler (1966) has proposed the terms allohospitalic, for speciation on different, related hosts, and synhospitalic, for speciation on the same host species. Thus reproductive isolation can be quickly achieved in ectoparasites which breed on their hosts by isolation of populations on different host species in the same habitat (allohospitalic, sympatric) or isolation on separated populations of the same host species (synhospitalic, allopatric). Clay (1949) has made a thorough study of host distributions in the Mallophaga Ischnocera and the modes of speciation they imply. She concludes that most speciation events have probably involved geographical isolation of parasite populations either on isolated host populations or as a result of discontinuities in the distribution of a parasite population across the range of a host (synhospitalic, allopatric). However, a number of cases of speciation involving shift of parasites to new host species (allohospitalic, sympatric) were also suggested. Evidence of synhospitalic, sympatric speciation is rare, presumably because it is difficult for two reproductively isolated populations to form on the same host population, but a possible example of an early stage of such speciation is the divergence of the body louse of man, **Pediculus humanus corporis** from the head louse, **P. h. capitis**. Busvine (1976) suggests that the adoption of clothing created a new niche for invasion by **P. h. capitis**, and that these populations have undergone subspeciation owing to this spatial isolation both on and, more importantly, between hosts, as head and body lice tend to occur on individuals belonging to different sections of the human population.

Speciation in ectoparasites which do not breed on their hosts has been
influenced much less by host specificity and more by microhabitat isolation. Sibling species complexes in mosquitoes combine remarkable morphological similarity with distinct differences in such characters as larval salinity tolerance, mating behaviour, and adult habitat preference and host preference, which may all contribute to reproductive isolation (Coluzzi, 1970).

To the extent that the presence of a host vertebrate will indicate the presence of a specific parasite, the local diversity of an ectoparasite community will be related to the diversity of vertebrate hosts. This relationship will of course hold better for host specific taxa than for generalists.

Another factor which will affect the local diversity of parasites is how many different parasite species a particular host species can accommodate. Are there limits on species packing by parasites on hosts, and if so, what determines them? A reasonable hypothesis is that interspecific competition between parasites may set limits on coexistence, but does such competition exist? Ectoparasite populations on hosts rarely if ever attain such densities that direct competition for feeding sites occurs, and blood is certainly not a limiting resource. Ectoparasite populations, as mentioned earlier, are directly affected by the host and its defensive responses, but there is no evidence that they are directly affected by populations of other parasite species.

Nonetheless, the spatial and temporal distribution of ectoparasite species attacking a particular host often assume patterns suggestive of classical niche partitioning (MacArthur, 1972) such as might result from interspecific competition. Prominent among such patterns are the non-overlapping spatial regions into which some related parasites divide the surface of their hosts. A much quoted example is provided by Dubinin (cited in Dogiel, 1964) for the glossy ibis, Plegadis falcinellus, which possesses four species of Mallophaga; one restricted to the head and neck, one to the wings and tail, one to the back and one to the belly and flanks. The occupation of more or less distinct host regions by the human head, body and pubic lice (Anoplura) may provide a more easily appreciated example of non-overlapping ectoparasite niches. Some quantitative examples of spatial partitioning between species of the same taxon are presented for other hosts, and for other ectoparasite groups, in Table 3. To these might be added several other studies which indicate, albeit in a more qualitative manner, spatial partitioning by Mallophaga on Turdus merula (Baum, 1968), Tabanidae on cattle (Olsufiev, 1935), Glossinidae on man (Nash, 1948), Streblidae on bats (Ross, 1961; Wenzel et al., 1966) and Siphonaptera on rabbits (Haas & Dicke, 1959). Spatial partitioning of hosts by parasites belonging to unrelated groups is probably uncommon, but the interesting observations of Breev (1950) on Diptera attacking reindeer deserve mention in this context. During the first year of his study, differences in feeding sites between Culicidae and Simuliidae were slight, but in the second year he found most Culicidae (70%) feeding on the horns and upper body of the host, and most Simuliidae (86%) feeding on the belly and legs, although both groups could feed with equal ease on all these regions.

Host resources may be partitioned along dimensions other than feeding site, an example of which is the diversity of feeding height and feeding time in some tropical forest mosquito communities, which in at least some cases results in very little overlap between different species attacking the same host (Gillett, 1971).

These patterns of species packing suggest both an upper limit on species diversity per host for any particular taxon, and some associated form of
Table 3. Some distributions of ectoparasite taxa on specific hosts, given as percentages of species found on different parts of the body

<table>
<thead>
<tr>
<th>Author</th>
<th>Host</th>
<th>Ectoparasite group</th>
<th>Species</th>
<th>Distribution on host: per cent collected from each region</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eveleigh &amp; Threlfall (1976)</td>
<td>Common Murre (Uria aalge)</td>
<td>Mallophaga—Ischnocera</td>
<td>Saemundssonia calva</td>
<td>head and neck: 87 4 6 0  body above wings: 5 44 45 8 wings and tail: 28 53 19 0</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Cumminggiella o. obliqua</td>
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<td></td>
<td></td>
<td></td>
<td>Austromegopon uriae</td>
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<td></td>
<td></td>
<td></td>
<td>Columbicola columbae</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td>Colpocephalm turbinateum</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Hoheristella lata</td>
<td></td>
</tr>
<tr>
<td>Nielsen (1971)</td>
<td>Cow (Bos taurus)</td>
<td>Diptera—Ceratoponidae</td>
<td>Culexodes absulutes</td>
<td>head and neck: 4 93 3  body above wings: 31 67 0 wings and tail: 0 6 94</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Culexodes punctatus</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td>Culexodes chioptrus</td>
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<td></td>
<td></td>
<td></td>
<td>Culexodes subfuscipennis</td>
<td></td>
</tr>
<tr>
<td>Wenk &amp; Schlörer (1966)</td>
<td>Horse (Equus caballus)</td>
<td>Diptera—Simuliidae</td>
<td>Wilhelmina equina</td>
<td>head and neck: 100 0  body above wings: 100 0 wings and tail: 0 100</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Wilhelmina salpingiensi</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Boophilus erythraophila</td>
<td></td>
</tr>
<tr>
<td>Kangwagye (1977)</td>
<td>Bullock (Bos taurus)</td>
<td>Diptera—Tabanidae</td>
<td>Haematopota brucri</td>
<td>head and neck: 2 2 0 0 96  body above wings: 2 10 4 3 81 wings and tail: 40 17 24 19 0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Haematopota patelesor</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td>Haematopota brumecenia</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Tabanus tarsioidea</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Tabanus thoraxinus</td>
<td></td>
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</tbody>
</table>

* Amblycera and Ischnocera behave somewhat differently on the host and appear not to partition the host relative to each other.

** these species specialize on ears.
interspecific competition. If, as suggested above, direct competition for feeding sites is unlikely, what other processes might generate these patterns? I present here a hypothesis that host grooming behaviour may effect a form of indirect competition sufficient to produce niche partitioning among ectoparasites.

Several studies indicate that at least some parasites elicit more intense and frequent grooming in hosts as their density increases (Owen, 1966; Edman & Kale, 1971; Webber & Edman, 1972). This, in turn, can reduce the feeding success or survivorship of ectoparasites, such that the probability of an individual feeding successfully decreases with increasing parasite density. Such a negative relationship between feeding success and parasite density has been shown for mosquitoes (Dow et al., 1957; Fujito et al., 1971; Edman et al., 1972) and tsetse flies (Vale, 1977b).

This density dependence may be applicable as well to communities of more than one species if grooming responses are similar for the different ectoparasites. Thus, in regions where a particular species overlaps with another, it is likely to encounter grooming pressure in excess of that elicited by its local density alone. In such regions each species suffers an intensity of grooming pressure elicited by the summed attacks of all species combined. Therefore where species overlap along a continuum of host resources, they experience a reduction in survivorship greater than in unshared regions with similar densities of each species, and this imbalance in fitness may lead with time to selection for reduced overlap and the formation of discrete niches along the continuum. Such a trend

Figure 1. Schematic diagram of possible interactions of ectoparasite species over a continuum of host resource (e.g. time of feeding, feeding site). A. Competitive exclusion—grooming in response to total parasite load will lead to the eventual exclusion of the slower-reproducing species (x) by the more rapidly reproducing one (y) when their niches overlap completely. (1) Densities before a bout of grooming (M=minimum population density necessary for reproduction of either species); (2) total parasite load; random grooming occurs above the threshold density, G, reducing populations to that value; (3) densities following the grooming bout, species x is now below its reproductive threshold (M). B. Competitive displacement—here x and y overlap in only part of their niche space. Random grooming at densities above G leads to gradual divergence of populations along the continuum, as indicated by the means of distribution (arrows) before and after the grooming bout.
is shown in a simplified schematic style in Fig. 1. This process of grooming-mediated competition might generate, with time, a pattern of more or less discrete feeding niches among parasites attacking a host, similar to the patterns of ectoparasite distribution described above and in Table 3. Haddow et al. (1968) anticipated this hypothesis in their explanation of the regular succession of biting periods found among seven sympatric species of Ugandan forest mosquito, “if all major crepuscular species were to reach their peak biting activity simultaneously, the pressure of biting would disturb the sleep of the hosts, to the detriment of blood-feeding and so of egg-production.”

The hypothesis of grooming-mediated competition must predict as well that if two species occupy precisely the same position on the continuum of host resources the species with the higher reproductive capacity or escape efficiency will eventually displace the other (Fig. 1). Thus we might also expect to see in ectoparasite communities the exclusion of one species by another of very similar ecology over the range of a host. As the interactions of ectoparasite species is a virtually unexplored subject, there is very little data to examine in this regard. However, interspecific exclusion has been suggested as the force responsible for certain species distributions in the Streblidae (Wenzel et al., 1966), Siphonaptera (Barnes, 1965) and Mallophaga (Hopkins, 1949). Exclusion between taxa is also suggested in some instances, for instance the virtual absence of Streblidae and Nycteribiidae from mollosid bats infested by Polyctenidae (Wenzel & Tipton, 1966), the relative absence of Mallophaga from some mammals infested by Anoplura and vice versa (Hopkins, 1949), and the exclusion of fleas by lice on rats (Hopkins, 1949) and peccaries (Samuel & Lowe, 1970). While grooming pressure may be responsible for these cases of exclusion, one cannot rule out the possibility of direct interference between ectoparasite species.

For some of the parasite communities mentioned above, species often exhibit morphological modifications which make them better adapted to the regions they occupy than to other areas occupied by other species. Whether such morphological adaptations initially predisposed different colonizing species to different regions or whether they appeared following isolation is unknown, but their existence does not contradict the hypothesis that grooming-mediated competition has acted over evolutionary time to create and maintain the present niche specificity. Morphological specialization to different host areas is particularly noticeable in bird lice (Clay, 1949), though even here species are known, in the absence of grooming pressure, to extend their activity beyond their usual feeding regions (Clay, 1949, Nelson & Murray, 1971).

The extent of niche overlap permitted under grooming-mediated competition is, of course, a function of the population dynamics and behaviour of the parasites and the form of the density-dependent grooming response. Niche overlap is therefore likely to vary considerably with changes in these different parameters (Waage, in prep). One factor which will strongly influence overlap is the susceptibility of different species to the same form of grooming. Coexistence at a particular feeding site or time may be promoted by behavioural and morphological differences in ectoparasites which force the host to adopt very different grooming behaviour for different species. Perhaps some of the diversification in ectoparasite body form mentioned above (e.g. louse-like, flea-like and spider-like shapes) reflects selection on parasites for escape from specific grooming responses effective against other species.
Price (1977) has noted that in parasite/host systems there may be a positive relationship between host size and the number of species of parasites attacking a host. In ectoparasitic insects, this relationship might be caused by an increase in the size and the number of host niches (grooming regions) for occupation. Ward (1957) has shown, however, that size increases between species of tinamou did not increase the number of associated Mallophaga, instead the size of the mallophagan species increased. If feeding niches decrease in size with body size, there may, however, be a minimal point at which resources are too limited and grooming too efficient in the niche to permit the existence of a breeding parasite population. The disappearance of specialized wing lice on smaller members of some bird taxa may be attributable to this (Clay, 1957).

A positive relationship between the diversity of insect parasites attacking a host and the geographical range of that host has been demonstrated in a number of instances for insects parasitic on plants (Strong, 1979). Dritschilo et al. (1975) have found a similar species/area relationship for mites associated with cricetid rodents in North America, which may be caused by (1) increased opportunities for species colonization and reduced extinction rates on widely distributed hosts, and (2) occupation of more diverse microhabitats by such hosts, each perhaps characterized by a somewhat different ectoparasite community. This relationship for mites and mice has been criticized on the basis of the poor host records available for such broad comparisons (Kuris & Blaustein, 1977; but see O’Connor et al., 1977). The similar paucity of good host records for most taxa of ectoparasitic insects greatly restricts our ability at present to examine the species/area effect and other interesting biogeographic relationships which may influence the diversity of insect communities associated with vertebrates.

**CONCLUSIONS**

This article has dealt with the appearance of insect/vertebrate associations and their subsequent diversification. I have suggested that the different ectoparasite lifestyles discussed are the product of two general evolutionary pathways. In one of these, preadaptive non-parasitic association with vertebrates leads gradually to the evolution of a capacity to feed on host blood (Pathway I). In the other, ectoparasitism arises through a preadaptation for feeding on vertebrates, a subsequent switch to this diet and the gradual development of host associations (Pathway II). These hypothetical pathways involve similar adaptations, but they occur in different sequences and lead, I suggest, to very different life history types.

It might also be true that these pathways appeared at different times during the evolution of insects. Pathway I probably appeared first in the Mesozoic, following the establishment of regular terrestrial dwellings by reptiles, birds and mammals, and the development of an insect fauna associated with nests and vertebrates therein. The appearance of homeothermy and parental care in birds and mammals (and dinosaurs?) further promoted associations with insects by providing (1) high nest temperatures and more favourable microclimate for commensals, (2) hair and feathers as both a source of food and shelter for phoresis and (3) higher densities of hosts over longer periods in nests (i.e., during breeding seasons). By contrast, Pathway II ectoparasites arose from forms with no such nest dependence and may have appeared much earlier on vertebrates. In
this regard it is interesting to note that in the hemipteran Triatominae and the
dipteran Culicidae, both Pathway II taxa, species are known which feed on
semiaquatic vertebrates with no terrestrial dwellings, such as amphibians and fish
(Usinger, 1944; Downes, 1970).

The diversification of ectoparasites has been closely linked to the evolution of
their hosts. Vertebrate extinction has been considerable (about 20% of all bird
families and 50% of all mammal families which have ever existed (data from
Romer, 1945)), and has undoubtedly involved the extinction of many parasite
species as well. Entire taxa may have appeared and disappeared in the past.
Ponomarenko (1976) for instance has described an unusual Cretaceous insect,
Saurophythus longipes, which he thinks belonged to a taxon ectoparasitic on
pterodactyls. It is important to remember therefore, that this review may cover
but a fraction of the insect-vertebrate relationships which have appeared over
geological time. The discovery of new relationships, either in the fossil record,
which seems unlikely, or among poorly studied living species (e.g., the mouse
moths of Costa Rica), may provide material for qualitative testing of the
hypotheses I have presented.

Among living ectoparasites, the process of evolution continues in the form of
coevolutionary interactions between parasite and host. Relatively little study has
been made of these interactions since the elegant invitation to the subject, Fleas,
Flukes and Cuckoos, written by Rothschild and Clay over 25 years ago. Much
information is needed on the precise effect of ectoparasites on host fitness in
order to determine the intensity of selection for defense against parasitism.
Evidence has been presented indicating that elaborate grooming behaviour,
movement between habitats and, perhaps, even colouration in vertebrates are
possible evolutionary responses to ectoparasite attack. On the ectoparasite side,
the unusual, often convergent body forms of different ectoparasites has long
been attributed to the avoidance of grooming, but the actual behaviour of
parasites on the host, and the effect of grooming on parasite survival and fitness
remains little studied.

The structure of ectoparasite communities are of interest both from an
evolutionary and a practical perspective. Host specificity and patterns of
distribution in time and space will influence which ectoparasites in a community
can act as disease vectors and which hosts as reservoirs. Competition between
parasite species, mediated by host defensive responses, may have played a role in
the evolution of community structure and, in particular, in the patterns of niche
partitioning. Important consequences of partitioning include the isolation of
disease cycles in certain regions of a habitat, e.g. the canopy vs. the ground cycle
of yellow fever with its different vectors. Grooming-mediated competition could
have a more immediate effect on disease transmission. Edman et al. (1974) have
suggested that host defences, particularly at high parasite densities, may prevent
mosquitoes from feeding on regular hosts and force them onto alternate species,
thereby possibly introducing diseases to other host-parasite cycles. Considerably
more research is needed on the interaction between parasite and host, and
between parasite and parasite, before the importance of grooming-mediated
competition in disease transmission can be evaluated. An evolutionary approach
to problems in ectoparasite biology may contribute both to the testing and
development of theory and to the understanding of these more practical aspects
of vector biology.
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