

Host dependency among haematophagous insects: A case study on flea-host association

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Abstract. Obligatory haematophagy is the end result of long standing interspecific associations. Present day specificities to host, blood meal and physiological stage of the host are all offshoots of the primitive interspecific associations. The cause/effect relationship of these dependencies and specificities are probably based on the route through which haematophagy evolved in different groups of insects.

In the present analysis, flea-host association is taken into consideration. It is possible to find an array of host relationships ranging from promiscuous and catholic host associations to strict ones. In general 3 categories may be recognized. In fleas like *Xenopsylla cheopis* a utilizable protein in an optimum concentration gives the necessary stimuli for maturation (Cheopis-type), while in a second group the stimuli is provided by certain circulating hormones of the host (Cuniculi-type) as seen in rabbit flea *Spilopsyllus cuniculi* and in a third group (Monositus-type) a priming period characterized by tissue fluid feeding and neosomy is necessary before whole blood diet can stimulate maturation as exemplified by *Tunga* spp.

It appears that vertebrate associations of Siphonaptera initiated as adaptations to the nest microhabitat and haematophagy and adaptations to physical/chemical factors of epidermal habitat being subsequent developments.

Keywords. Haematophagy; flea-host associations; nest microhabitat; epidermal habitat.

1. Introduction

Obligatory haematophagy is the end result of long standing interspecific associations. Such associations lead to metabolic dependency and/or dependency to physical and/or chemical environmental factors relating to the breeding place of the host and/or epidermal habitat offered by the vertebrate host.

According to Smyth (1962) metabolic dependency with regard to endoparasites may be evident in one or more of the following: (i) developmental stimuli; (ii) nutritional material; (iii) digestive enzymes and (iv) control of maturation. Blood feeding triggers not only the development of ovary in the adult but also influences moulting in exopterygote haematophages. This influence is negotiated through the hormones secreted as a result of either the mechanical stimuli from proprioceptors of gut/abdomen or chemical stimuli from diffusible substances or digestion products from blood meal. In all haematophagous insects blood meal supplies nutritional materials necessary for reproductive and house keeping metabolic functions. Nematoceran and brachyceran Diptera, however, supplement their blood meal with phytoexudates or nectar and the carbohydrates derived from this source are mainly used for flight and routine metabolic functions. Fritz (1983) mentioned that as dextrose was present in low concentration in blood, acquisition of the necessary sugars for haematophagous insects like streblids which feed only on blood, was by frequent blood feeding. This requires experimental verification. Clements (1963), Engelmann (1970), Nelson *et al* (1975), Prasad (1987) and others deal with nutrition

and reproduction of haematophagous insects. Ectoparasites are not dependent on the host for supply of digestive enzymes, because they are adequately equipped with the necessary enzymes to digest the blood meal. According to Waage (1979) evolution of many dipteran/vertebrate associations have come about through the advantage gained by those species which are able to digest their host's blood cell proteins and use it for longevity and reproduction. Depending on the route through which haematophagy evolved, the group may already possess the necessary protease (pre-adapted) or may evolve the digestive capacity more gradually (Waage 1979). But it is important to remember that some of the dietary proteins control the rate of midgut protease synthesis and the quantity secreted. Maturation is a host dependent feature of haematophagous exo- and endopterygotes. Except in a few cases of autogenous egg production, stimulation of ovaries from resting stage at emergence depends on blood intake by the insect. Similarly though not spermatogenesis (in certain ticks even spermatogenesis is under the control of blood feeding) mating competency in male is induced only after blood feed.

These points clearly indicate that haematophagous arthropods are metabolically dependent on the host for several functions. Waage (1979) suggested that the nature and intimacy of an ectoparasite/host relationship will depend on the sequence in which regular physical associations (habitat preference, host seeking behaviour and morphological adaptations promoting capacity to feed on the host, physiological capacity to digest host substances and behaviour associated with initiation and termination of feeding) occur.

Preferences and adaptations to microenvironment of the epidermal habitat is an important component of host specificity. The type of integument of the host (feather vs hair), the temperature conditions of the epidermal habitat, thickness and texture of skin, the extensiveness of the peripheral circulation etc can be very decisive factors in host preferences. Among many insect species non-nutritional chemicals play primary role in determining host selection and suitability (Slansky and Scriber 1985). Subsequent to Hosoi's (1958) discovery of the importance of adenine nucleotides as phagostimulants for the mosquitoes *Culex pipiens* several studies have shown that many unrelated groups of haematophagous insects show adaptation to same phagostimulatory chemicals (convergent evolutionary trend) as well as marked diversity in mechanism of blood recognition (Galun 1986). Galun and Rice (1971) found that the source of adenine nucleotide at least for *Aedes aegypti* and *Glossina austeni* is blood platelets. They suggested that quantitative variations of platelet ATP of different mammals could contribute to differences in host preferences of haematophagous insects. The diversity which Galun (1986) speaks about relates to those which recognize blood through the properties of plasma, yet others through some cellular fractions and a third group somewhat intermediate between these.

Having thus outlined some generalities regarding host-haematophagous arthropod associations, a more specific case of flea-host association and specificities may be examined.

2. Flea-host association

The maximum flea representatives parasitize rodents and insectivores (table 1). Undoubtedly the lifestyle of the host (foraging, breeding and nest/burrow

Table 1. Distribution of flea families on mammals and birds.

Host record	Flea families	Host record	Flea families
Monotremata	Pulicidae, Stephanocircidae	Rodentia	Ceratophyllidae,
Marsupialia	Hystrichopsyllidae,		Coptopsyllidae,
	Pygiopsyllidae		Hypsophthalmidae,
Insectivora	Ceratophyllidae,		Hystrichopsyllidae,
	Chimaeropsyllidae,		Leptopsyllidae,
	Hystrichopsyllidae,		Macropsyllidae,
	Leptopsyllidae,		Pulicidae,
	Pulicidae		Pygiopsyllidae,
Chiroptera	Ischnopsyllidae		Rhopalopsyllidae,
Edentata	Malacopsyllidae,		Stephanocircidae,
	Tungidae		Tungidae
Lagomorpha	Hystrichopsyllidae,	Carnivora	Ancistropsyllidae,
	Leptopsyllidae,		Ceratophyllidae,
	Pulicidae		Malacopsyllidae,
			Pulicidae
			Vermipsyllidae
		Ungulata	
		Perissodactyla	Vermipsyllidae
		Artiodactyla	Ancistropsyllidae,
			Pulicidae,
			Vermipsyllidae
		Aves	Pulicidae,
			Rhopalopsyllidae,
			Tungidae

construction behaviours) influences considerably this differential rate of parasitization. Both these groups of hosts live in some sort of nests made in crevices or burrows. Even among bird fleas, most of these are found associated with species of birds which breed on ground and in banks or use mud freely in the construction of their nests (Rothschild and Clay 1952). Those which live on hosts without regular nesting sites have hypertrophied anchoring devices and would be highly promiscuous (Hopkins 1957; Traub 1980). Speaking of host association of fleas Holland (1964) stated that some species of fleas will breed on only a single species or genus of animal (as all *Amphalius*, *Geusibia* and *Ctenophyllus* spp. on *Ochotona* spp.) others may live on a more-or-less related group of hosts (as *Chaetopsylla setosa* Rothschild on many large carnivora); others again apparently breed indiscriminately on hosts sharing a common habitat (as *Ctenophthalmus pseudagyrtus* Baker) on shrews, moles and microtine and cricetine rodents or *Dasypsyllus gallinulae perpinnatus* Baker on many species of Passeriformes and other birds. Based on the degree of closeness of fleas to their hosts, they may be broadly classified into nest ectoparasites (nest-burrow blood suckers) and host ectoparasites. While the former are found most of the time off the host (certain species of *Coptopsylla* and *Ceratophyllus*) the latter either remain attached to the body of the host for the whole life time (slow feeding intradermal parasites) such as *Tunga* and *Echidnophaga* or spend more time on the host in a free state moving about among the fur like *Ceratophyllus*, *Leptopsyllus*, *Xenopsylla* and others which are also fast (rapid) feeders taking several blood meals (Balashov 1984; Nelson *et al* 1977). The distribution and

host specificities of the nest fleas are controlled by the microenvironmental conditions prevailing in the nest of the host animal. To a certain extent this would be true of the other groups also. Hopkins (1957) qualified fleas as nest specific rather than host specific, because the larvae are free-living and are considerably influenced by the nesting conditions of the host. There are several instances to show that nesting conditions of hosts influence the distribution and host preference/specificity of fleas. Sharif's (1948) studies in the Deccan Plateau showed that rat fleas *Xenopsylla cheopis* and *X. brasiliensis* were predominantly associated with domestic rats, whereas *X. astia* with field rats like *Bandicota* and *Tatera*. He suggested larval nutrition to be the most important factor in this pattern of distribution. According to him the larvae of *X. astia* were dependent on the presence of vitamin B in the diet whereas the other two species could grow even in its absence. In nature the profuse growth of fungi in the burrows of *Bandicota* and *Tatera* provide the necessary B-vitamins whereas the comparatively dry nests of domestic rats do not encourage fungal growth and so are not suitable for *X. astia*. While Sharif's nutritional hypothesis helps to give possible explanation for the preponderance of *X. astia* on semi domestic and wild rodents like *B. malabarica* (= *B. indica*) and *T. indica* in the places of his study, it does not explain the comparative absence or rarity of *X. cheopis* from the nests of these hosts. In spite of the actual interchange of fleas between semi domestic and domestic rats (Annual Reports of the Haffkine Institute; Prasad 1966) burrow faunistic studies of field rodents show the absence or rarity of *X. cheopis* (Joshee 1961; Kamath 1961). It would be unwise to say that *X. cheopis* cannot breed in a nest which contains nutritionally rich litter. It could be that the excess of ground moisture is injurious to *X. cheopis* larvae. *X. cheopis* is known to have a predilection for comparatively dry situations (Pollitzer 1954). Another interesting instance is the distribution of *X. nubica* which is specific in northern Uganda to Gerbillinae of two genera. The preferred species of Gerbil is common in southern Uganda but here the flea is absent presumably because the gerbil burrows here are too damp. Burrow conditions similarly appear to control the distribution of *X. cheopis* which in East Africa is restricted to *Rattus rattus* in the southern areas, but occurs freely on a wide variety of field rats in the northern areas possibly because the burrows of field rats in northern area offer a similar drier condition as those of *R. rattus* in the southern areas. Moisture conditions of the nesting sites seem to affect the distribution of bird fleas also. The hen flea *Ceratophyllus gallinae* is found more frequently than any other fleas in the nest of sparrows, starlings, sparrow-hawks, swallows etc where comparatively dry atmosphere prevail. The moorhen flea *Dasypsyllus gallinulae* prefer nests with damp conditions such as those of robin, warblers, finches, blackbirds etc. The duckflea *C. garei* on the other hand can survive in wet swampy situations which prove fatal to the other two species of fleas and this is the only flea found in the nest of ducks, geese and certain waders and sea birds. That the distribution and host preferences are not guided by the nesting conditions alone (at least in some cases) is interestingly illustrated by the distribution of these 3 bird fleas in the nests of pheasants and partridges. Nesting habits of these birds are similar and they often use each others nest. Yet *C. gallinae*, *D. gallinulae* and *C. garei* are found in the nest of pheasant, but *C. garei* is the only flea in partridge nest.

There is very little information on the role of host odour influencing host association of fleas. The existing information are varied. The studies of Benton *et al* (1959) indicate preference of *Sylvilagus floridanus*, the natural host, by the flea

Cediopsylla simplex over an opossum *Didelphis marsupialis* in twin host choice experiments. Bates (1962) negated the possibility of olfaction as an important factor in host finding by bird fleas. Shulov and Noar (1964) found the rat fleas *X. cheopis* making a clear distinction between hosts, preferring white rat to 3 other species of murids *Meriones tristrami*, *Acomys dimidiatus* and *Microtus guentheri*. Humphries (1968) found olfaction playing no role in host location by the hen flea *Ceratophyllus gallinae* while Vaughan and Mead Briggs (1970) found that rabbit flea *Spilopsyllus cuniculi* was strongly attracted to the urine of the host, but showed no host specificity. Benton *et al* (1959) found *Ctenophthalmus pseudogyrtis* unable to recognise its natural host the chipmunk *Tamias striatus* from distances exceeding two inches. A static air olfactometer showed that the rat fleas *X. cheopis* and *X. astia* are neither able to distinguish the presence of a host nor are they able to discriminate between *R. rattus*, *R. norvegicus* and *Mus musculus* even at short distances of 6 cm (K Jaya and R S Prasad, unpublished results). In these cases the host choice take effect after reaching it as shown by Sgonina (1939, cited by Humphries 1968) for certain mammal fleas. This is strengthened by the fact that there is an interruption of regular feeding and breeding if the antennae of the female fleas are blocked before releasing them on live host. Though a small percentage of female *X. astia* whose antennae were painted with nail polish and the maxillary palps ablated before releasing on the host, were blood fed, none laid eggs (R S Prasad, unpublished results). Whether some host-borne chemical signal is involved or not is not known. It is significant to remember that flea transfer between unrelated hosts such as prey to predator, dog/cat flea to human beings etc (Hunter *et al* 1979) are probably indications of want of ability to distinguish interspecific differences in host-borne cues. However, an air-borne kairomone emanating from the new born young rabbit which is also present in the urine is involved in boosting copulation and egg production in *S. cuniculi* (Rothschild and Ford 1969, 1973).

At least in the case of rat fleas it has been shown that defensive behaviour of the host influences not only the establishment of flea ectoparasites on the host but also their breeding potentials (Lila Chandy and Prasad 1987). For example mortality of adult fleas was high and fecundity rate low on white mouse, *M. musculus* albino, whose grooming activities are more intense than white rat *R. norvegicus*. Variations in grooming activities associated with age and sex of the host appeared to be important in intraspecific differences noticed in mortality (higher on adult and female rats compared to young and male rats respectively) and fecundity rates (higher on young and male rats compared to adult and female rats respectively).

Since all the species of adult fleas have only blood as their food, these have to derive the nutrients necessary for meeting day to day metabolism as well as reproductive functions from blood itself. Frequent feeding is a characteristic of fleas except those such as *Tunga* spp. which are slow and continuous feeders. The question as to how far do variations in the blood components affect host suitability and specificity is difficult to answer as there is very little information on the nutritional compatibility of the blood from different hosts. From early 1900 there are indications of interspecific variations in host suitability. Bacot (1914) noticed that only when fed twice would *X. cheopis* lay eggs on human beings, even then the fecundity was very poor. Strickland (1914) found *Ceratophyllus* (= *Nosopsyllus*) *fasciatus* fed on mouse, rabbit or man did not lay eggs, but if the same lot was allowed to feed on rat, egg laying resulted shortly

after feeding. Haas (1965) studied the comparative suitability of 4 murine rodents to fleas *X. cheopis* and *X. vexabilis* and showed that wild *M. musculus* figured as the most unsuitable host for both the species of *Xenopsylla* whereas *R. exulans* appeared to be the best host for *X. vexabilis* and *R. norvegicus* for *X. cheopis*. Prasad (1969) based on comparative fecundity studies of *X. cheopis* concluded that even though flea mortality was high on *R. rattus* and *M. musculus* (albino) and was low on *Bandicota bengalensis*, the former two hosts proved most suitable for *X. cheopis*. Samarina *et al* (1968) showed that fertility value of *Ceratophyllus consimilis* was highest when fed on hamster than on rat or mouse. This was found to be true for *C. (=N.) fasciatus* and *X. cheopis*. Bibikova (1965) found that feeding on unspecific host usually takes much longer and blood of usual host digests faster. The results of direct feeding of fleas need not necessarily reflect nutritional influences because there would be several non-nutritional parameters interfering feeding and quantity of blood ingested. The pupal production of human strain of *Pulex irritans* fed directly on man or artificially on citrated human blood was much higher than when fed on dog/citrated dog blood. Fox strain of *P. irritans* on the contrary did not reproduce when fed either directly on man or artificially on citrated human blood. The pupal production of the same strain was high when fed directly on dog, but did not reproduce when fed artificially on citrated blood of dog (Hudson and Prince 1958). Experiments involving artificial feeding of rat fleas *X. cheopis* and *X. astia* on heparinised blood of frog, chick, white rat, house rat, white mouse and man through the skin of a young white rat (the usual host for laboratory rearing of these fleas) showed that all the blood samples could induce yolk deposition, but a significantly higher percentage of *X. astia* fed on *R. rattus* blood showed yolk deposition while a significantly lower percentage of *X. cheopis* showed yolk deposition with chick blood. Similar experiments to assess egg laying potential when fed on heparinised blood of frog, hen, white rat, house rat, gerbil and man showed no significant difference in egg production attributable to the interspecific variations in blood sources, whereas with regard to *X. cheopis* no definite conclusions could be drawn due to poor gorging and erratic egg laying. However, egg laying started on the 9th day on blood of house rat whereas on blood from other sources egg laying started only around 13–16 days after the first blood meal. No such marked difference could be noticed with *X. astia* where egg laying started at the earliest by the 4th day and latest by the 7th day. These blood samples were offered through the skin of a young white rat, a host with which these fleas are familiar in the laboratory as white rat is used as host for laboratory rearing of these fleas (Kamala Bai and Prasad 1976, 1981). Feeding these fleas artificially on blood fractions of white rat showed that blood cell fraction triggered yolk deposition but plasma alone did not. The factor associated with this nutritional inadequacy of blood plasma was shown to be the protein concentration because when plasma was fortified with rabbit albumin, yolk deposition was initiated (Kamala Bai and Prasad 1976). Subsequent studies on artificial diet showed that both quality (fleas were not able to utilize bovine albumin in place of bovine haemoglobin for yolk synthesis) and quantity (twice fed fleas laid more eggs than those fed once artificially) of protein are important and that a diet balanced with salts, sugars, cholesterol and B-vitamins in addition to protein and a phagostimulant (ATP) was necessary for vitellogenesis. However, B-vitamins appear to be dispensable for *X. astia* (Kamala Bai and Prasad 1979, 1981). It then follows that the amino acid composition of blood proteins is an important attribute in

conferring nutritional adequacy of the blood meal. However, attempts to feed these fleas on artificial diets in which protein is replaced with amino acids failed.

Synchronization of breeding activities of the host and its flea ectoparasite has been demonstrated in the case of rabbit fleas *S. cuniculi*. Before the breeding season commenced female rabbits carried an extra load of fleas (Allan 1956). Following the observation of Allan (1956), Rothschild and Ford (1964a) discovered that the rabbit flea's ovaries can mature only on a doe rabbit during the last 10 days of its pregnancy or on a new born baby rabbit during the first 5 or 6 days of life. Their further work revealed that maturation was probably initiated and maintained only when corticosteroids circulating in the blood reached a relatively high level. Ovarian maturation induced as a result of direct spraying of hydrocortisone or corticosterone on the flea revealed a direct action of these hormones on the flea (Rothschild and Ford 1964b). Lutinizng hormone and progestins were found to induce ovarian regression. Growth hormone secreted by anterior pituitary constituted one of the major copulation factors (Rothschild and Ford 1966) which accounted for the fact that copulation of rabbit fleas took place only on nestling rabbits. Maturation of male rabbit flea *S. cuniculi* (defined as the stage of development at which sperm can be successfully transferred to the female spermatheca) is also under the influence of host's hormones (Rothschild *et al* 1970). Rothschild and Ford (1969, 1973) showed that in addition to the hormones described above there are certain pheromone-like nestling factor (kairomone) from the new-born young rabbits which speed up maturation and copulation and enhance sperm transfer. The rabbit flea *S. cuniculi* is not an isolated case of hormonal dependency. Rothschild and Ford (1972) showed that the breeding of the rabbit flea *Cediopsylla simplex* is similarly synchronized with the breeding cycle of the host. According to Rothschild (1965) *Ischnopsyllus*, the bat flea, could be another case where an ectoparasite respond to the sexual cycle of the host. These fleas crowd on female bats before they leave their winter quarters for their summer breeding roosts.

One of the most fascinating flea-host association is that of the so-called sticktight and chigoe fleas. The former is exemplified by the notorious pest of poultry *Echidnophaga gallinacea* while the latter by *Tunga* spp. In both the cases the females are permanent parasites on the body of their respective hosts. Continuous feeding, mating and egg laying are accomplished while firmly anchored on the body of the host. However, there are some major differences in feeding of these fleas. *Echidnophaga* feeds on whole blood soon after attachment whereas the work of Lavoipierre *et al* (1979a) show that *T. monositus* pass through 3 phases of feeding after attachment. In the first phase the major diet is tissue fluid exudate and neutrophil (exudate-neutrophil feeders) which lasts for about 10 days after attachment. Probably between the 10th and 14th day the flea passes through the 2nd phase in which the gut contents show mostly fibroblasts and collagenous materials (connective tissue feeders). The 3rd phase (14 days after attachment) is marked by feeding on whole blood. As in the case of rabbit flea *S. cuniculi* there appears to be an interesting correlation and synchronization of the reproductive activities of the flea and the feeding phases. Tissue feeding (phases 1 and 2) is associated with neosomy (change involving the hypertrophy of the abdomen especially the 2nd and 3rd abdominal segments) while the haematophagous phase initiates reproductive activities of the flea such as mating, ovarian development and egg laying. It is during the 2nd phase (connective tissue feeding phase) that the midgut epithelium

hypertrophies with greater secretory activities, the condition resembling that seen in rabbit flea *S. cuniculi* (Mead-Briggs 1964). This increased secretory activity is probably for efficient utilization of the blood meal for ovarian maturation and egg production. According to Lavoipierre *et al* (1979a) there appears to be a remarkable integration between host inflammatory and repair responses and feeding behaviour, growth and reproduction of the flea and this interaction between the parasite and the host certainly does not appear to be fortuitous. It is replicative and predictable and is never anarchic. These authors also found the dorsal surface of the pinna of the ear to be the specific site for attachment of *T. monositus* and attachment elsewhere results in premature death of the flea. A comparative study showed that feeding behaviour of *T. monositus* is similar whether the host offered *M. musculus* albino or *Peromyscus maniculatus* (the natural host of this flea). However, the intake of neutrophils on the latter host was more during the cellular exudate feeding phase and haematophagy commenced earlier when on *Peromyscus* compared to *Mus*. There is an increase in the rate of neosomy also on *Peromyscus* (Lavoipierre *et al* 1979b).

3. Conclusions

One of the most prominent features that may be noticed in flea-host association is that fleas mostly parasitize hosts which dwell in burrows/nests. This being the case the climatological and/or nutritional requirements of the free living larval stages become important factors in host preference of adult fleas. This prompted many workers to suggest that fleas are nest specific rather than host specific. Rothschild (1966) recognized mainly two life styles of fleas. The closer association with the nest microhabitat (primitive, if it is accepted that the progenitors of fleas were scavengers in the nest of vertebrates) and closer association with the microhabitat of the epidermis of the host, sometimes extending to very prolonged and intimate associations as seen in *Echidnophaga* and *Tunga*.

But with regard to host association of adult fleas for which adaptation to epidermal habitat is also important, three categories may be recognized. The first is exemplified by a type like the rat fleas *X. cheopis*/*X. astia* (Cheopis-type). These are not nest fleas as they spend more time of their adult lives on the host compared to certain species of *Coptopsylla* or *Ceratophyllus*. The former is found on the body of the host for hardly 3 h in its life time and during this period it ingests about 50–100% of its own body weight of blood (Balashov 1984). In contrast to this *X. cheopis*/*X. astia* remain on the body of the host for longer periods, feed very frequently, ingesting each time only very small quantity of blood (usually less than their own body weight). This limited capacity is probably genetical and there is considerable restraint in the extensibility of the abdomen which restricts the quantum of blood it is capable of ingesting. This coupled with the comparatively large sized eggs into which fairly large quantities of yolk material are to be packed and the low protein storage capacity of haemolymph (K G Narayana Pillai and R S Prasad, unpublished results) makes it obligatory on the part of these insects to remain in close contact with the host which would facilitate frequent feeding (Prasad 1986).

The second category is the hormone bound fleas (Cuniculi-type) examples of which are the rabbit fleas and probably the bat fleas. There is no information on the mechanisms involved in the case of bat fleas. In rabbit fleas parasitism has advanced

so much that the fleas are able to breed only if fed on a pregnant host. As it is with all narrow adaptations, it would have its own advantages and disadvantages. It would be interesting to know if these fleas would respond to hormonal changes associated with breeding of vertebrates other than their natural hosts. This association grades into a third and more intimate relationship which may be qualified as Monositus-type, seen in fleas belonging to the genera *Echidnophaga* and *Tunga*. There is no known hormonal involvement as in the previous instance and Lavoipierre *et al* (1979a) state that survival of *T. monositus* is dependent on the host inflammatory and repair responses with which there appear to be remarkable integration of feeding behaviour, growth and reproduction. As was already explained neosomy is dependent on tissue fluid feeding and reproduction on haematophagy. What are the precise physiological mechanisms guiding these two phases? The situation finds some parallel with the condition in ticks. In these cases also species variations in the host do influence blood feeding, rate of blood digestion etc. Are the reproductive functions of the first and the third groups influenced by common factors? Are these dependencies simply for dietary proteins? or are there any specificities for blood proteins or their constituent amino acids?. Milk fed *X. cheopis* and *X. astia* did not develop oocytes indicating that they are not able to utilize casein for ovarian maturation. Among blood proteins, bovine albumin in place of bovine haemoglobin did not trigger maturation (Kamala Bai and Prasad 1976, 1979). Does it mean that these fleas have evolved certain specificities in amino acid requirements? So far there are no experimental results which unequivocally declare that blood from certain species of hosts are nutritionally inferior or certain others superior.

There are indications of preferences to certain sites on the epidermal habitat. For example rat fleas *X. cheopis* seem to prefer the posterior half of the body of white rat especially the base of the tail, while *X. astia* prefer anterior half mainly the neck region. The areas preferred by *X. astia* are warmer than those preferred by *X. cheopis*. If there is any other factor influencing this preference is not clear (Prasad 1972). Rabbit fleas *S. cuniculi* choose the rabbit's muzzle and cheeks during the early stages after emergence and later move on to the ears where they become well anchored. *Nosopsyllus fasciatus* preferred the hind quarters of the host while *Leptopsylla segnis* the fore quarters. *T. monositus* show very strict preference for the dorsal part of the pinna of the ear.

From the present analysis it would become clear that nutritional status of the blood is only one of the many factors deciding suitability of a particular vertebrate as a host. Perfect adaptation to a host thus would depend on a proper coordination of factors influencing larval and adult environments. There are still wide lacunae in our understanding of host association of this group of insects.

Are haematophagy and vertebrate host association (specificities) the effect of primary adaptation to the nesting conditions of the host (cause) or vice versa? If the assumption that progenitors of Siphonaptera [probably a boreus-like Mecopteran (Hinton 1958; Rothschild 1975; Schlein 1980)] were primarily associated with the lair or nest of vertebrates (James and Harwood 1969) it might then follow that development of haematophagy and the associated factors like adaptation to host-borne chemical emanations and epidermal habitat were subsequent developments. As mentioned by Waage (1979) the invasion of a nest microhabitat by predator ancestor and the evolution of increasingly intimate host association is a probable scenario for the evolution of Siphonaptera. A nest/burrow habitat would offer 3

major food sources: (i) the detritous (for scavengers); (ii) the arthropod body fluid (prey-predator relationship) and (iii) the vertebrate blood (host-parasite relationship). Fleas have exploited the first and third sources of food offered by the nest/burrow habitat thereby optimizing on the available nutrient source and increasing fitness in the habitat. If this exploitation was directed by the cues correlated with the energy content of the food (theories of optimal diet/optimal foraging) is not known. Except for social insects, the fitness of an insect will be a function of individual survivorship and fecundity (Mitchell 1981). As it is evident from the foregoing account, survivorship of fleas is not influenced by nutrition alone. At least 3 factors in a nest/burrow habitat control survivorship: moisture content affecting mostly the larval stages; nutrient content of the nest/burrow detritus affecting the larval stages and behavioural resistance of host affecting the adult fleas. Fecundity on the other hand is controlled by nutrition. Proteinaceous meal is a must for ovarian maturation and egg production. About 16 (chicken)–23% (human) of protein content, vertebrate blood is nutritionally superior to either arthropod haemolymph [insect haemolymph has about 1–10% of protein (Wyatt 1975)] or plant sap which has practically no proteins. Vertebrate blood diet would thus offer definite advantage in reproductive functions to those which switched over to this diet and a selection at this level would be to the advantage of the organism. Such switching over could be possible under situations of indiscriminate feeding by the insect concerned. According to Emlen (1968) predators will tend to specialize in their diet (not necessarily on usually superior food) when food is abundant and to feed more and more indiscriminately as food becomes scarce. The feed back between the food's use and its value leads towards increased specialization. Change over from predation on arthropods to parasitism on vertebrates has other advantages also. For example, a vertebrate being larger, a single animal can support a large population of the parasite.

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