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Factors Involved in the Host-Specificity in Mallophaga Sens. Lat., (Phthiraptera: Insecta) Infesting Birds

The Mallophaga are parasitic both on mammals and birds with an intimate relationship between the host and the lice, since the host body itself forms the most immediate environment for these obligatory parasites. The high degree of the close host-parasite relationship has been well utilised by the phthirapterologists not only in the taxonomic studies, but also in evaluating the relationship of the host groups, their phylogeny, migratory routes, and even in the interpretation of ancient geographical connections (Kéllér, 1960; Lakshminarayana, 1972, 1975b and; Lakshminarayana and Satyarani, 1976). For an understanding of the development of host-specificity, the various factors associated with the parasites have to be taken into consideration and these are broadly arranged as follows.

THE IMMEDIATE ENVIRONMENT AND THE ORGANISATION OF THE PARASITE

These obligatory external parasites have limited viability outside the host body which is composed of the plumage (or pelage) and offers a very good shelter, food, and insulates the lice from the external environmental fluctuations to which the host is subjected. In a true sense the microclimate of the parasites is within the feather (or hair) cover. Different species normally require different temperatures for the completion of their life-history; the host body itself offers different ranges of temperature, for example, Ash (1960) reported that the skin temperature

differs from that of the feather cover.

The amblycerous lice may occur on any part of the body, but the areas of oviposition and probably feeding seem to be restricted, while the ischnocerous lice have definite areas of distribution. The more recent studies of Ash (1960) revealed that some species occur in one zone, but feed or oviposit in the other. A sort of niche specificity is met with amongst the lice, and often intra- and interspecific competition exists between them. Clay (1949, 1950) recognised two ecological niches for the bird-infesting species, namely, the head and neck niche, and of the abdomen and wing niche. These niches affect the form of the lice. Those inhabiting the head and neck niches have short and round bodies with circumfasciate head, while those of the abdomen and wing niches have elongate and flattened bodies. The primitive position of the male genital opening is believed to be ventral or ventro-terminal, and during copulation the end of the body is recurved so that the genitalia can be approximated with the ventrally placed female genital opening, as in the elongate forms. Since this phenomenon is difficult in the short-bodied forms, the opening lies on the dorsal surface. The head and neck niche forms though escape preening are subjected to other dangers like exposure to dry climate because of sparse feathers or where the host spends most of the time under water. The abdomen and wing niche forms escape preening by developing elongate and slender bodies. Clay (1949) states that invasion from one niche to the other is rare, and only possible if the niche is empty. She cited the two classic cases, namely, *Sturnidoecus* invading the head niche and *Columbicola* the wing and abdomen niche, each developing the characteristic features of the forms normally inhabiting these niches.

The bird-infesting Ischnocera are feather feeders, but the Amblycera ingest blood also. The food also influences the colours of the parasite in certain cases. The lice are specific to specific host groups and this is largely attributed to the feather condition. The feather structure affects the head structure. The asymmetry in *Struthiolipeurus* parasitic on rheas and ostrich is attributed chiefly to the peculiar feather structure (Lakshminarayana, 1973).

PATTERNS OF DISTRIBUTION AND SPECIATION

The classification of hosts into true hosts, pseudohost or non-hosts, originally proposed for aphids, and later extended to thrips (Lakshminarayana, 1968) is equally applicable to lice also (Lakshminarayana, 1972a).

Host-specificity is forced on lice during the course of evolution or speciation. Thus, the factors involved in speciation are the same as those involved in specificity. A purview of the present day distribution of bird lice suggests that certain genera and species are specific to certain host orders, genera and species. As a rule, same or closely related species of lice are found on closely related hosts, suggesting that the latter might have acquired them from the common ancestor. Since the feather (or hair) offers a more or less uniform temperature, shelter, and food to the parasite, the microclimatic fluctuations are much smaller for the parasite than for its host. Thus, while the host, reacting to its own environmental fluctuations, evolved at a rapid rate, the parasite evolved at a slower rate (normally referred to as having undergone a retarded evolution). Consequently, we find either the same species, or sub-species, on closely related hosts, even though the hosts appear to be unrelated at the first sight. Rapid evolution amongst the hosts has resulted in certain modifications of the host body which offered empty ecological niches to the ancestral parasites. This, however, created a tendency or stimulation in the latter for further speciation, at a faster rate. Thus two clear trends are noticeable in the speciation of lice, namely, a retarded evolution due to uniform conditions of shelter and food, and an accelerated evolution due to the availability of empty ecological niches and modifications of the feather structure consequent upon host evolution. Retarded evolution produced generic or specific groups or complexes amongst the lice, while accelerated speciation produced large number of genera and species. K  ler (1958) feels that accelerated evolution dominates retarded evolution in the speciation process. The latter is restricted to some special cases.

The extreme specificity amongst obligatory parasites has helped parasitologists to make certain deductions. Eichler (1949) has discussed these cases in detail. These deductions are usually referred to as Fahrenholz's Rule, Szidat's Rule, Eichler's

Divergence Rule (Eichler, op. cit.), Harrison's Law (1915), Hopkins' Principle (1942, 1949, Lakshminarayana, 1970 a, b) and Clay's Hypothesis (1951). Fahrenholz's Rule states that the ancestors of extant parasites must have been parasites of the ancestors of extant hosts; Szidat's Rule states that primitive hosts are parasitised by primitive parasites and advanced hosts by specialised parasites, a phenomenon, exhibited in the *Laemobothrion* complex (Lakshminarayana, 1970 a, b); Eichler's Divergence Rule (named after the proposer by Hopkins) enunciates that while an isolated group of hosts does not harbour many kinds of parasites, comparable groups of hosts with many species or groups which show near affinities to other groups, not only many parasite species (each with its own distinct species), but also many genera can be met with; Harrison's Law postulates that in a parasitic genus distributed over a number of closely related hosts, the size of the parasitic species is more or less proportional to the size of the host, i.e., the larger the host, the larger the size of the parasite, with the sole exception of parasites that infest ostrich and rheas, namely, *Struthiolipeurus* spp. Lakshminarayana (1973) clarified that because of a secondary infestation by this group of parasites (*Struthiolipeurus*), the size is not proportional to that of the host; Clay (1951) tried to explain the correlation between the size of the parasite and the size of the host with the help of Wetmore's view that larger birds have lower body temperature, and Bergman's law that colder climates have larger forms of species. Lakshminarayana (1970 a) named it Clay's hypothesis; Hopkins' Principle named after the proposer (Lakshminarayana, 1970b), suggests that a single correspondence of louse species between two hosts with hypothetical relationship with one another, means very little, two such resemblances established a probability, and three resemblances makes it a certainty. In case of wild hosts, the study of the parasite life-cycle to establish in the laboratory whether a particular parasite is a natural parasite or a specific one or not, is extremely difficult. Lakshminarayana (1972 a) suggested that if a louse species occurs on a host (other than its natural one), and is consistently reported at different intervals, and in all stages, one may safely conclude that the host may be a true one (or established secondary host). The case was well illustrated by *Saemundssonina sterna* Linn., a natural parasite

of *Sterna h. hirundo* Linn., found on *Gelochelidon n. nilotica* Gmelin, from several parts of the world, and also of the other subspecies of *G. nilotica*. It may also be safely concluded that if a parasite species (or a genus) is more widely distributed on a number of host genera and species, than another closely related species, then it is probable that the former is phylogenetically older to the latter. Another interesting factor in specificity is that primitive host groups like Phasianida, tinamou, etc., harbour a number of parasite genera and species, thereby indicating that divergent groups of parasites have speciated on these hosts during the course of evolution:

Isolation plays a dominant role in the development of specificity as well as speciation. Some aspects of this role are summarised below:

(a) *Physical isolation*: Clay (1949) pointed that the host body acts as a biological island, comparable to a geographical island, and has the same effect on the distribution of its parasite fauna. Just as geographical islands have water barriers, two host species (except in case of prey and predator, and foster parents) do not come in close contact with each other and often avoid each other's territory. Therefore, parasites of one host species are physically isolated from those of the other, which has a definite effect in developing host-specificity. The same is the case with parasites on populations of the host species. Allopatric speciation occurs in much the same way as in other communities in the lice also, and where two populations of hosts have chance mixing, the lice of the combined populations develop sexual incompatibility like asymmetry in the genitalia as in *Goniocotes mayuri* Lakshminarayana and Emerson, and *G. parviceps* Piaget, parasitic on the peafowls, *Pavo cristatus* Linn., and *P. muticus* Linn. (Lakshminarayana and Emerson, 1972).

(b) *Sexual isolation*: The morphological (and probably genetic also) changes in the shape of the abdomen, position of **genital opening**, structure of male genitalia, etc., produce strong sexual isolation amongst the parasite species and prevent interbreeding and therefore even if a louse species is transferred on to a new host accidentally, it cannot get established (presuming the feather structure or food is identical) unless both sexes or at least a fertilised female is transferred.

(c) *Literal host-specificity* : Literal host-specificity is a major factor in isolation. The transference of lice from one individual to the other is possible during coitus, breeding or roosting, between prey and predator, and between the nestling and the foster parents. The non establishment of lice of the foster parents on young cuckoos is suggestive of an inherent phenomenon of the host-specificity. Similar is the case of parasites from prey to the predator. It is possible for secondary infestation to occur during common dust baths, but in the long history of the subject there are negligible records of such infestation. Transference by phoresy or straggling (Hopkins, 1939) is also possible, but the parasites do not establish unless the host is a natural one or closely related to the natural host. The extreme case of host-specificity may be pointed by a simple example. *Rallicola mystax* Giebel, a parasite of *Porzana* spp., has not so far been reported on *Amaurornis*, a genus which is very close to *Porzana*. In fact the species are often placed one amongst the others because of close similarity (Lakshminarayana, 1972 c). The same is the case of certain species of parasites on the pheasants.

FACTORS AGAINST HOST-SPECIFICITY

The distribution of present day bird lice shows some discontinuities, which speaks against the theory of specificity. Discontinuous distribution may be due to (1) the present host orders, genera and species might have acquired the parasite species in the bygone ages, from a common ancestor, and diverged to such an extent that their original relationships are obscured, (2) parasite genera and species might have developed on parallel lines, due to identical feather conditions, (3) they may at one time have been widespread on many related orders or genera or species, but might subsequently have disappeared on the intervening populations, or link species, genera, or orders, (4) they might have achieved secondary establishment on hosts with identical feather conditions, (5) straggling (Hopkins, 1939) and (6) usage of common dust baths (Hopkins, 1949).

The lack of specificity in primitive species and genera is primarily responsible for the spread of closely related genera and species on a wide range of host orders, genera, and species, but the development of specificity in their descendents probably prevented back transfer, thereby resulting in the formation of several new species, complexes, and genera. This specificity might have been attained primarily by the physical isolation of the host, its feather structure, mechanism and physiology of feeding of the parasites, altered morphology, physiology, and breeding behaviour. The genetics of lice is not well understood.

ACKNOWLEDGEMENTS

The author is grateful to Professor M.S. Mani, Emeritus Professor, School of Entomology, St. John's College, Agra, and the Director of the Zoological Survey of India, for encouragement and facilities during the course of these studies. He is specially grateful to Dr. S. Khera, Deputy Director-in-charge for permitting him to present this paper at the Symposium and to his senior colleagues, Drs. S.K. Bhattacharyya, K.K. Tiwari and B. Biswas for several courtesies. He is also grateful to several of the workers quoted in the paper for information and inspiration.

SUMMARY

Analyses of intrinsic and extrinsic factors responsible for the host-specificity in Mallophaga have shown that the early evolved genera and species parasitising the early evolved host orders are less host-specific, than the later evolved genera, species and host groups. Further, the degree of infestation by Mallophaga on primitive host orders is correspondingly greater than the highly evolved groups showing greater tolerance and compatibility.

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Reprinted from

T. N. Ananthakrishnan (ed.): *Insects and Host-Specificity*, pp. 101-109
The Macmillan Company of India Ltd., 1977.