AN ANALYSIS OF THE PHYSICAL AND ECOLOGICAL PARAMETERS SUSTAINING POPULATIONS OF FEATHER MITES (ACARINA: ANALGOIDEA)

by

Jeffrey A. Hodes

Submitted in Partial Fulfillment of the Requirements
for the Degree of
Master of Science
in the
Biology
Program

Paul C Peterson 6/2/77
Adviser Date

Leon Rand 6/6/77
Dean of the Graduate School Date

YOUNGSTOWN STATE UNIVERSITY

June, 1977

ABSTRACT

AN ANALYSIS OF THE PHYSICAL AND ECOLOGICAL PARAMETERS SUSTAINING POPULATIONS OF FEATHER MITES (ACARINA: ANALGOIDEA)

Jeffrey A. Hodes

Master of Science

Youngstown State University, 1977

It is the intent of this study to explore the niche and population structure of feather mites from four species of the family Icteridae: red-winged blackbird (*Agelaius phoeniceus*), common grackle (*Quiscalus quiscula*), brown-headed cowbird (*Molothrus ater*), Brewer's blackbird (*Euphagus cyanocephalus*), one species of the family Sturnidae (*Sturnus vulgaris*) and a single species from the family Picidae (*Cyanacitta cristata*). From each of the 44 birds examined the remiges and ventral primary coverts were removed and population counts were made of mites directly from individual feathers. Differences in feather morphology were described by selecting three primary remiges (Nos. 3,5,7) and three secondary remiges (Nos. 3,5,7) and measuring the barb widths from selected feather zones. Data were subjected to a factorial analysis of variance among feather types. Further analysis included the selection of an additional twenty-four characters from these feathers which were subjected to multivariate procedures. The procedures included character standardization, computation of similarity coefficients, cluster analysis, and ordination by principal component analysis and multidimensional scaling. From this data differences between birds and among feathers were noted. When the mite population is superimposed on the feather data evidence of host-partitioning was observed.

ACKNOWLEDGEMENTS

I wish to express my appreciation to Dr. Paul C. Peterson for providing materials, facilities, and encouragement needed to complete this study. Appreciation is also extended to Dr. Warren T. Atyeo, University of Georgia, who provided preserved mite material and a Model 20 Wild-Heerbrugg phase contrast microscope used for parts of this study. Appreciation is finally extended to Mr. William J. Kurey and Mr. Norman T. Vujevic for their assistance in the collecting of avian species and their expertise in demonstrating techniques of photomicroscopy. The support of the National Science Foundation (BM 575-03394), Dr. Warren T. Atyeo, principal investigator is also acknowledged.

TABLE OF CONTENTS

LIST OF FIGURES

FIGURE PAGE

LIST OF FIGURES (cont.)

LIST OF TABLES

INTRODUCTION

All species of the feather mite superfamily Analgoides (Acari) are obligate parasites which form host-parasites associations with all major avian taxa except the Sphenisciformes (penguins). Prior to 1963, there were approximately 100 analgoid mite genera which had been assigned to six heterogenous families recorded from a broad range of disparate avian hosts. Presently, 1400 or more described species and an equal or greater number of new species which are subdivided into 45 subfamilies, 240 named and 106 new genera (Peterson, 1975).

The species are most commonly found between adjacent barbs on the dorsal surface of primary and secondary flight feathers, however during heavy infestations the tail feathers may provide an additional site of infestation. Only a few variations in this pattern have been noted. In the analgoid complex (Peterson, 1975), all groups are exclusively associated with the downy feathers of the breast. Another known restricted habitat of another group is that of the inside of the quills of the flight feathers (Kethley and Johnson, 1975). A further example of host-partitioning has been described by Atyeo and Peterson (1976) in the genus Rectijanua; found in feathers of the neck region in ducks. Thus if feather mites can partition their host, efforts to ellucidate host-parasite associations must include a detailed analysis of the physical parameters of each feather type in an effort to identify the optimum conditions needed for the survival of feather mite population.

The vast majority of research on the ecological and physical parameters sustaining populations of feather mites has been conducted by the Russian parasitologist, V.B. Dubinin, from the years 1938 - 1958. During these 20 years of research, he observed and recorded correlations between the feather mite's morphology and behavior, and many of the interactions of individuals and of populations with their macro- and microenvironment.

The question of a typical microniche for a species of feather mite is extremely complex, because there are many factors which can influence this distribution. In the micro- and macroenvironments not only must each factor be isolated but the environmental interactions must be shown relating to each other. Taken separately an environmental factor can show its effect on the life of an individual specimen or on the entire population of feather mites. When these stresses are considered collectively they can operate as an integrated complex of factors which fixes some biological and/or ecological peculiarity of the parasite in relation to its host. Such influences do not always change in fixed succession for the benefit of the host-parasite relationship; in some cases they can take on catastrophic dimensions involving the sharp reduction or extinction of the feather mite population on its host, i.e. freezing. It is requisite therefore that an understanding of the physical and ecological parameters surrounding this population be delineated in detail prior to the consideration of host-parasite associations.

Aspects which affect the macroenvironment of the feather mite are, to some extent, weather related. However, a direct dependence of the changes in the life cycle of feather mites caused or influenced by weather conditions does not exist. Nevertheless, in the life cycle there are observed noticeable coincidences in feather mite behavior in relation to the behavior of the bird and the seasonal changes which occur in the host's environment (Dubinin, 1954).

Environmental stress of host,
i.e. seasonal physiological stress
↓
Change in host's activity (s)
↓
Change in host's environment
or physical being
↓
Change in ectoparasite's environment
↓
Change in parasite activity
↓
Change in parasite's physical placement
on host or parasites general life cycle

Dubinin has enumerated the effects of some weather related conditions and their subsequent effects on mite populations. Temperature, both the environmental temperature and the bird's body temperature, effects not only the specific localization of mites but also the vital activity of the enitre mite population (Dubinin, 1951). When the temperature is low, the mites tend to localize toward the base of the feather. Conversely, when the temperature is higher the mites tend to localize further from the quill. Apparently, temperature affects the entire population by lengthening (in cool periods) or shortening (in warm periods) the normal life cycle and thus changing the population size for a period of time in what would be the normal life cycle of the mite.

Humidity was shown to be a significant factor in relation to the feather mite population, in that the mite has an optimal humidity relative to its surroundings. The optimum humidity for each species probably varies but generally the mite requires a relatively low humidity (Dubinin, 1951).

Dubinin (1951) also showed the significance of sunlight in relation to the feather mite's localization on the flight wing feather. Feather mites, it was observed, avoid lighted places. When mites were observed on the plumage of birds, these mites exhibited a pronounced negative phototaxis. This can be further demonstrated by the fact that when feather mites can choose between lighter colored and darker colored feathers they are more often found on the darker plumage (Dubinin, 1948).

When one observes further the life cycle of feather mites, it shows remarkable similarities with seasonal changes which affect the host. In the annual life cycle of the host there are four very distinct periods; these periods include the times of nesting and fledgling, moulting, and migration or over-wintering of the bird. These periods are characterized by specific reactions of the feather mite. Changes of the normal physiological rhythm of the bird must be examined as an integral part of the entire state of the individual mite and of the population of mites as a whole to changes in the surrounding environment.

During the period of migration of birds, considerable changes in the sex and age composition of the population of feather mites occurs (Dubinin, 1950b, 1952). These changes are not found in direct dependence with the changes of the physiological state of the bird host. Similarly, these changes are not entirely caused by seasonal changes or climactic factors. However, it may be a combination of these factors which effects the state of the host's feather mite population during migration.

During the changes in the ecological conditions which precede the bird's migrations and throughout this migration, different species of feather mites exhibit a number of differences in their adaptations to their hosts. These individual adaptations characterize, to a certain extent, a stage of the feather mite's yearly physiological rhythm. The extent to which these changes occur can be compared among the mites found on those birds which do migrate great distances and those birds which do not migrate.

These yearly adaptations of feather mites to the migrations of birds occur in three ways (Dubinin, 1938, 1946). In the first area are the mites found on those birds which are settled, nomadic, and which migrate slowly with frequent stops along their route. Adult mite species from these groups of birds express rather weak adaptations to migration. The feather mites of these species only withdraw to the deeply lying layer of plumage of birds and accumulate in the downy parts of the feathers of the wing and sometimes of the body (<u>Gabucinia delibata</u>). The second group contains the great majority of mites which are adapted to living on migrating birds. This group of mites endure the migration of their hosts in the egg stage. The egg is deposited by the parasite before migration to the wing feathers and/or covert. Those adult mites which remain on the surface of the feathers of the bird lay eggs and die.

Finally, the third group of species is composed of mites which are adapted to their host migration by the withdrawal of the deuteronymphs of the mite to the subcutaneous cellular tissue, where they are preserved throughout the entire migration and over-wintering of the birds. A good example of this life cycle is that of Pterolichus ardeae. Dubinin's (1937, 1951) summary first assumes that the forms found under the skin are truly the deuteronymphs of P. ardeae because he could not culture them from the skin or observe them leave the host's skin after over-wintering. During the migration from wintering to summer grounds the night heron seems to carry only deuteronymphs. The adult form of Pterolichus therefore must either die in Africa or during the time of flight. Upon arrival, the deuteronymphs which were located under the skin, leave the host's body in the form of adults. At first the population changes very slowly, but in May and June the numbers increase simultaneously with the diminishing of the number of deuteronymphs under the skin. In July, the conversion ends and the intensity of infection of adult birds by Pterolichus ardeae greatly decreases again. The reason for this decrease is due to the mite's reestablishment on fledgelings, since at this time P. ardeae has been observed on fledglings.

In August and September there occurs another decrease in the percentage of infection by P. ardeae on the adult bird and an increased in fledglings and adults by deuteronymphs. Apparently, during this period the eggs laid earlier on the skin give rise to the first larva which then crawl under the skin, where they develop subcutaneously into deuteronumphs. This infestation occurs only in September with the infection reaching 95% before departure, at which time the cycle repeats itself (Dubinin, 1951).

During periods of moulting, feather mites can be found crawling over the entire body of the bird host abandoning their previous localization. It is interesting to note that the feather mite seems to know in advance as if by some "sense" that a given feather may soon fall out. The mite abandons the feather by crawling over to adjacent remiges or covert feathers. What may play a significant role in this detection by the mite is the change in the wing feather's normal position before moulting and its unnatural vibration during flight (Dubinin, 1951). The natural wear of a feather may also have some effect on the movement of feather mites, previous to the time of moulting, from one feather to another feather (Dubinin, 1949).

Besides these physical factors which occur before moulting there are also behavioral changes in the bird. Birds become sluggish, less mobile, and often the bird gives up flight, gathering at times in large flocks, e.g. ducks. This new temporary life disturbs the normal conditions of habitation of feather mites on the wing feathers (temperature, humidity, air flow, etc.) and the mites tend to abandon their former habitat and crawl randomly from feather to feather on the entire wing. Just before the complete loss of the feather, the mite population abandons the wing feathers and transfers to the wing coverts and even, in some cases, to the body of the bird (Dubinin, 1951).

During the time of moulting there is a general decrease in the size of the mite population not related with the loss of feather mites which occurs to some extent as feathers are moulted. This decline of part of the mite specimens is due to their movement onto parts of the host where conditions are unfavorable for the existence of the species (Dubinin, 1951).

In summary, the moulting of birds is a significant factor which has an influence not only on the movement of feather mites to a different location on the bird and the size of the population, but which signals the continuation of the life cycle of the organism. In this regard the bahavior of the feather mites at the time of moulting of the host, is an adaptive trait which has parallelled avian evolution (Dubinin, 1951). Ecological adaptations of feather mites to the migration of their hosts could be viewed as phylogenetically complicated interrelations of two organisms in their historical development (Dubinin, 1949).

The movement of feather mites from one host to another occurs in a number of ways (Dubinin, 1950b, 1951). During the nesting and fledgling period, some of the parent bird's feather mite population change their niche position from the parent to the young bird. Dubinin (1951) described this direct transfer of the feather mites from the parent bird to the fledgling during the nesting period. Infection depends on, first the degree of development of wing feathers as niches, second the degree of specialization of the feather mite to a definite position on the feather, third the impossibility of its settlement on other feathers, fourth the size of mite and its mobility, and finally the habitats of the young fledglings.

In addition there is a minimal length of the wing feather's vane to which mites can adapt. Consider the entire complex of biological changes which occur as the growth of the fledgling's feather continues, this entire growth pattern can determine the environment and characteristics of the mite. Taking only the growth rate of the vane as an index for the approximate time for mite transfer to its young host, this data permits the placing of feather mites into three groups. The first contains the species of the genus Trouessartia which are large and relatively sedentary forms. These mites transfer to fledglings only when the vanes of the wing feathers are 80 - 90% of their adult size and form. The second group is composed of more specialized species of the genera Megninia, Eustathia, Michaelichus, Pterodictes, Pteronyssus, and Proctophyllodes in which mites transfer to fledglings only when the vanes of the new host wing feathers are roughly 2/3 their adult size. The final group is represented by the small, agile species of the genera Pterolichus and Gabucinia which transfer and establish successful populations when the wing feathers are less than 30% of adult size (Dubinin, 1950). This order is observed clearly in those species of bird which are recolonized by several different species of mite which are assigned to different groups, i.e. the host fledgling is colonized by different mite groups as the length of the vane increases.

The migration of mobile feather mite stages to the fledgling explains the decrease of these mites on the adult birds. This decrease seems to be even more pronounced on female birds when they are the primary parent and tend to spend more time with the young. During the period of infection of different feather mite types there seems to be a point where in some birds there are almost no mobile mites seen on the parent bird (Dubinin, 1951).

In the studies pertaining to the morphology and function of the wing feathers of birds, micro-structure of wing feathers, and the aerodynamic data of these systems, it has been made possible to characterize the variations in the physical conditions of existence of feather mites on different groups of feathers or on different sections of one wing. In birds with only slight differentiation of the structure of their feathers, the parasitism of a species of mite may occur on many representatives of a single genus, a family of birds, or, less often, to another avian order (Dubinin, 1950e).

Within the feather mite's somewhat hostile environment, different species of mites do not colonize their hosts randomly but rather are adapted only to a certain microstructure of a feather. The distribution of feather mite species on the dorsal surface of the remiges depends on the number of wing feathers, their stiffness, structure, coloring, character of flight and a series of other physical and biological features. Depending on the feather mite's loci on a feather, the morphologic structure of different species of feather mites can be considered characteristic features which carry on the adaptive character of the feather mite (Dubinin, 1950a).

Dubinin (1947) established a basic direction in the change or coevolution of feather mite and host bird relationships. Dubinin's study of morphological and ecological aspects of the various forms of feather mites in their relationship to the distribution of different species or groups of species on the body of birds has made possible general observations concerning parasite types and their hosts from gross morphologic characters.

Dubinin (1947) postulates that the total size of the body of the mite in the most advanced and the most primitive of the feather mite representatives, is somewhat larger. The largest species of feather mites, i.e. Sulanyssus caputmedusae and Alloptes phaethonis (1 - 1.5mm) are found on the most primitive birds. On the other hand, the smallest species (.3 - .6 mm) are generally found on birds of more recent origin, i.e. Proctophyllodidae.

Other differences in body types and shapes have been shown in the anatid birds. On the wing feathers of these birds some of the feather mites parasitize that part of the vane where the expanded ventral edges of the barb form a flap-like structure which project ventro-laterally and contacts the tegmin from adjacent barbs and serves as an air corridor. This formation is extremely important to the life of a feather mite because this formation protects them from the external factors of the host, i.e. air currents, water washing the mite off the feather, and extremes in temperature. Mites which live on the feathers lacking these corridors often possess hypertrophied lateral appendages, membranes and setae which increase the width of the body so that it occupies the entire space between the barbs and thus fastens the body of the mite to the feather (Dubinin, 1950a, 1950e). Formation of these special structures of attachment is apparently directly related to the conditions of habitation of one mite species to a specific host.

Further specialization of feather mites appears in the structure of the legs. In many groups of feather mites there exists a distinct specialization of the legs or parts of the leg. The claws of the tarsi are subject to hypertrophy, some of the segments become fused, setae enlarge, and ambulacra become more developed.

One such example of this is a species of mite described by Dubinin (1949b), Dogielacarus uncitibia. The male of this species has a modification in the second pair of legs. These modifications enable the mite to clasp plumulaceous barbules of the wing feathers with a triangle formed by the opposing spines of the tibia and genua. A long ventral setae of the tarsus II presumably aids in the holding of the male in position by becoming entwined with the nearby barbules.

Adaptations of feather mites can also occur with the peculiarities of the conditions of habitation on the host. Mites on smaller birds (passerines) are found to be more mixed between primary and secondary feathers because the physiology and structure variations of primary and secondary wing feathers are not expressed sharply. However, short wingedness and the characteristic flight connected with these types of birds cause the differences in the character of these feather groups to become more similar.

Another adaptation is a tendency for the reduction in body and leg chaetotaxy. Most if not all of the species which live among the small secondary remiges of the host, where there is no extreme movement of air, possess a full set of setae. These setae (Dubinin, 1947) are necessary structures which seem to define the extent of a habitable zone in the area around the feather mite. The localization of the mite between the exposed barbs of the primary wing feathers are constantly exposed to air currents while the bird is in flight. This exposure would then exclude the possibility of the preservation of long setae on the dorsal side of the body due to wind pressure against these body parts which would tend to dislodge the mite from its host. When reduction of setae does occur, part of them disappear completely and others are preserved in the appearance of the smallest microsetae. Also subject to the process of reduction and possible disappearance are the ventral setae. These setae are well developed in mites which are found among the covert feathers of the body of the birds and are absent in those mite species which are from the wing feathers. Lateral and caudal setae, positioned horizontally to the plane of the feather remain large and part of them are expanded, therefore increasing the total area of contact thus favoring closer attachment of the parasite to the host (Dubinin, 1947).

The ecological parameters surrounding a feather mite population have enormous biological and adaptive significance for existence of any species of feather mite in its very distinctive natural conditions. Analysis of different places of habitation of different ages and species of mites in different geographic areas and seasons permits one to compare different localizations of mites in relation to different ages and species of mites in different seasons and geography.

On the basis of studies made by Dubinin of the structure of different sections of plumage of the wing, he ascertained that the more diverse the ecological and physical conditions of different sections of the feather integument, the more species of feather mites are found on them. For example, when the primary and secondary wing feathers differ sharply in structure and function (gulls, ducks, etc.) the number of mite species which parasitize is relatively high, 3 - 5 species. On the other hand, the more similar or less diverse the integument of the host, the less diverse the species' composition of parasites. For example, when the wing feathers do not sharply differ in structure and stiffness, usually only one, rarely two, species of mites are found (herons, owls, majority of passerines). Different sections of the bird's wings, due to different functions and stresses, have their own ecological characteristics and are settled by certain species of feather mites. Feather mite populations, which are adapted and normally found on the wing of birds which have little or no rotation of feathers (passerines), are scattered with seeming little precision related to the area in which it must inhabit. On birds which have a high degree of feather rotation, the mites are found 80 - 90% of the time on the third, fourth and fifth primary feathers compared to the latter which seemingly do not have the structure in their habitation patterns (Dubinin, 1951).

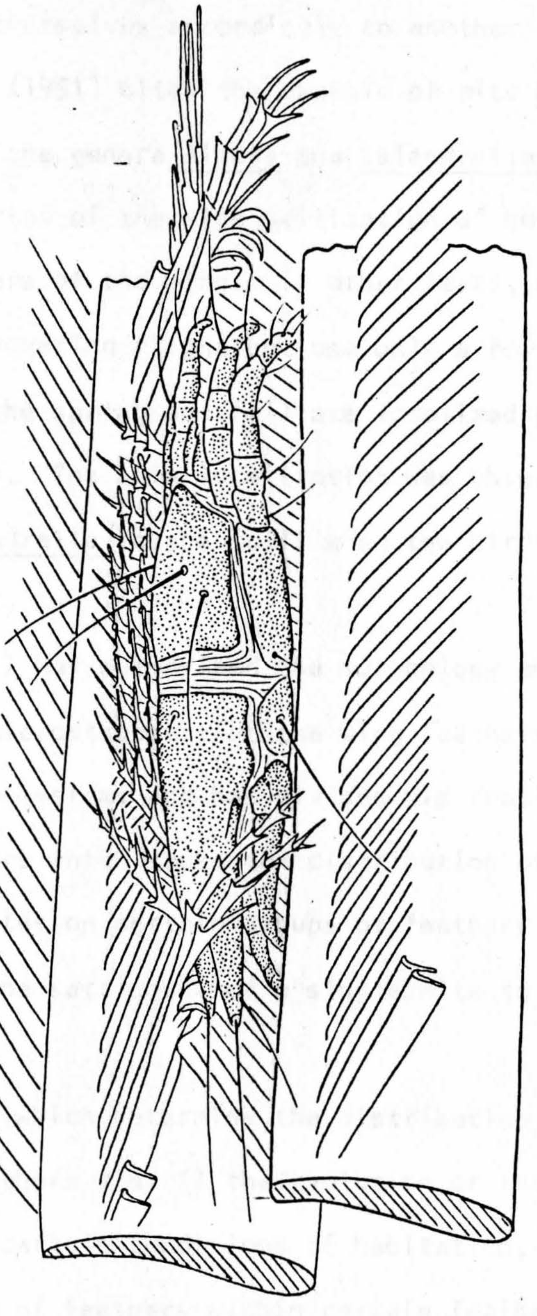
Corresponding to the character and places of localization, Dubinin (1951) has placed all feather mites into four different ecological and morphological groups: 1) feather mites of primary wing feathers, some examples being from the genera <u>Microspalax</u>, <u>Freyana</u>, <u>Pteronyssus</u>, Mesalges, Pterodectes, 2) feather mites of secondary wing feathers: from genera Alloptes, Proctophyllodes, Analges, Megninia, 3) a special group of mite species of the genera Trouessartia which are primarily from the secondary wing feathers but place themselves on the dorsal surface of the feather (Fig. 1), 4) feather mites which parasitize in the quills of the wing and covert feathers of different birds are represented by mites from the genera Syringobia, Dermglyphus and Thecarthra.

There are also evident differences in localization of different species of feather mites revealed when different developmental stages of mites are studied. Dubinin (1951) considers it a rule that the larval and nymphal phases of all feather mites are localized in different places on different feathers when compared to the adult forms of that same species.

The flight of birds is produced by means of their specialization in a certain direction in the process of adaptation to conditions of existence. This was determined by natural selection which began in the evolutionary development of a given bird. Important to the feather mite is that development which occurred in the peculiarities or differences of structure and function of the bird's wing. Flight, in combination with characteristics of the wing, from the point of view of the macro- and microscopic structure and aerodynamic data, was an important factor in the evolution of feather mites determining the physical parameters for the existence of these ectoparasites (Dubinin, 1950e).

Figure 1. *Trouessartia motacillae*, the normal location on (of female *T. motacillae*) on dorsal side of flight feather in barbules (after Dubinin, 1951).

Fig. 1



Dubinin (1951) has made further observations of bird flight and has divided these into different types: soaring, hovering, and rowing. Based on these variations in flight behavior, mites will frequently relocate themselves accordingly to another area of the wing or feather. Dubinin (1951) cites the example of mite Montesauria bilobata in larks of the genera Alauda and Calandrella in the springtime, i.e. in the period of the wide utilization of hovering, are settled on all feathers of the wing. In other larks, which do not possess a prolonged hovering flight but use only a rowing flight, the same species in the spring and fall are localized primarily on the primary wing feathers. The same localization was observed in the mites from Alauda and Calandrella in the fall, when the birds use a rowing flight more frequently.

Dubinin (1951) has summarized the morphology and function of the wings of birds, the microstructure of the wing feathers, and the aerodynamic data of these systems and has divided his conclusions into two areas, 1) those factors which cause the distribution of different species of feather mites on certain groups of feathers and 2) those factors which limit the settlement of a single mite to areas of a feather.

Those factors which determine the distribution of species on certain groups of feathers are: 1) the evolution or interadaptation of parasite and host to certain conditions of habitation, 2) the macro- and microscopic structure of feathers within certain feather groups and the difference between them and the feathers in neighboring groups, 3) the aerodynamic character of these above groups connected with the general configuration of the wing and with the character of flight (Dubinin, 1951).

Those factors which limit the settlement of mites on the area of each feather are: 1) the structure and inter-arrangement of tufts of the outer and inner vanes of the feather in its different parts, 2) the differences in the microscopic structure of the barbs of different sections of the vanes, 3) the presence on the vanes of zones of friction with their characteristic structure, and 4) aerodynamic peculiarities of different sections of a certain feather (Dubinin, 1951).

Limited precise data is presently available about the structure of feather mite populations since the studies by Dubinin relied heavily on museum skins. However, a review of Dubinin's work is important in that it defines many of the stresses on the feather mite's macro- and microenvironment.

Although usually host-specific, some mite species can occur on as many as a dozen hosts. Limited data are available on the distribution between bird types, the distribution among feather types, feeding habits and nutrition of the mites. It is believed that such information is requisite to a thorough understanding of host-parasite associations.

It is the intent of this study to explore the niche and population structure of the feather mite. To ellucidate this host-parasite relationship, a detailed analysis of the physical parameters of each bird type and feather type is needed to identify the optimum conditions for the survival of a feather mite population. With the analysis of the physical parameters of the host, the population structure of the parasite can then be described and detailed in relation to its niche.

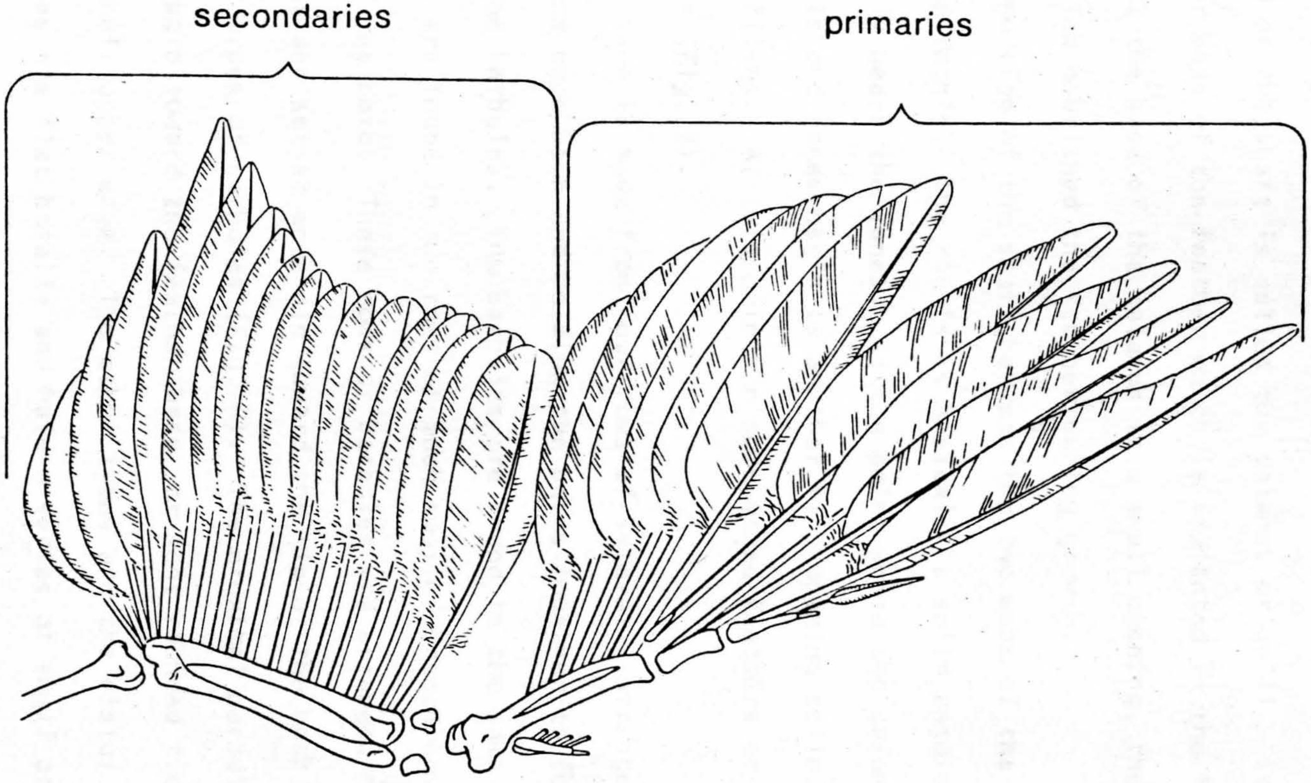
Microhabitat

Feathers are the most complex derivations of the integuments to be found in vertebrate animals. The feather displays an enormous variety of modifications, each of these morphological differences is the result of variable function within and among feather types. There are five commonly distinguished types of feathers: 1) large stiff feathers, remiges, of the wing and rectrices of the tail; 2) moderate-sized, partly firm feathers that cover the body (contour feathers); 3) small, fluffy down feathers of the breast; 4) hairlike filoplumes; and 5) the tiny bristles of the face. Once formed all mature feathers are noncellular structures composed of caratene. The feather receives nothing but physical support from the body of the bird.

Remiges of the wing and rectrices of the tail are the largest and most highly specialized of all feathers. Such specializations are adapted for flight and/or display. The remiges of primary importance are two types, primaries and secondaries. The primaries are the flight feathers attached to the hand, or manus (Fig. 2). Their number is very variable within and among avian groups. Most passerine birds have ten primaries, other taxa vary from 9 to 12. The outer most primary is reduced in size in many species, such that it is often difficult to recognize (Vantyne, 1959). The secondaries are those flight feathers attached to the forearm or ulna. The secondaries have a broader variance in number ranging from 6 to 32. The number of feathers in this group seems to be related to the length of the forearm.

Figure 2. A diagram of an outstretched wing illustrating gross morphological difference between primary and secondary feathers and illustrating feather numbers (after Lucas and Stettenheim, 1972).

Fig. 2



A typical vaned feather, whether it is a primary or secondary flight feather, a tail feather, or even a contour feather, is made up of a central shaft and vanes on either side of the shaft. The bare proximal end of the shaft is called the calamus or quill. It is the short tubular base of the feather which is implanted in the feather follicle. At the base of the calamus is a small opening, the inferior umbilicus which nourished the feather during growth.

The portion of the shaft between the two webs of the vane is called the rachis. The rachis is basically a solid angular shaft which actually bears the vanes. At the point where the calamus ends and the rachis and vanes begin is another tiny opening called the superior umbilicus. At this point in some vaned feathers arises the after feather (Fig. 3).

Each vane is made from four rows of laterally arranged barbs. Branching from each barb and holding the barbs together to form the vanes, are the barbules. The barbules are found in the same plane as the barb but are found in two rows of much smaller branchings, one on each side of the barb. These rows of barbules are arranged parallel to each other and set at an angle toward the tip of the barb. There are two distinct types of barbules (Fig. 4). The proximal barbules, on the side of the barb toward the feather base, present rounded ridges or flanges on their upper edge. The other types are the distal barbules. These barbules are flat basally and have a series of small projections (barbicels). These small projections along the middle and end portions of the barbule bear hook-like structures on the underside. These hook-bearing barbules on one barb overlap at right angles the smooth proximal

Figure 3. A typical flight feather illustrating details of vane and barbs (after Welty, 1968).

Fig.3

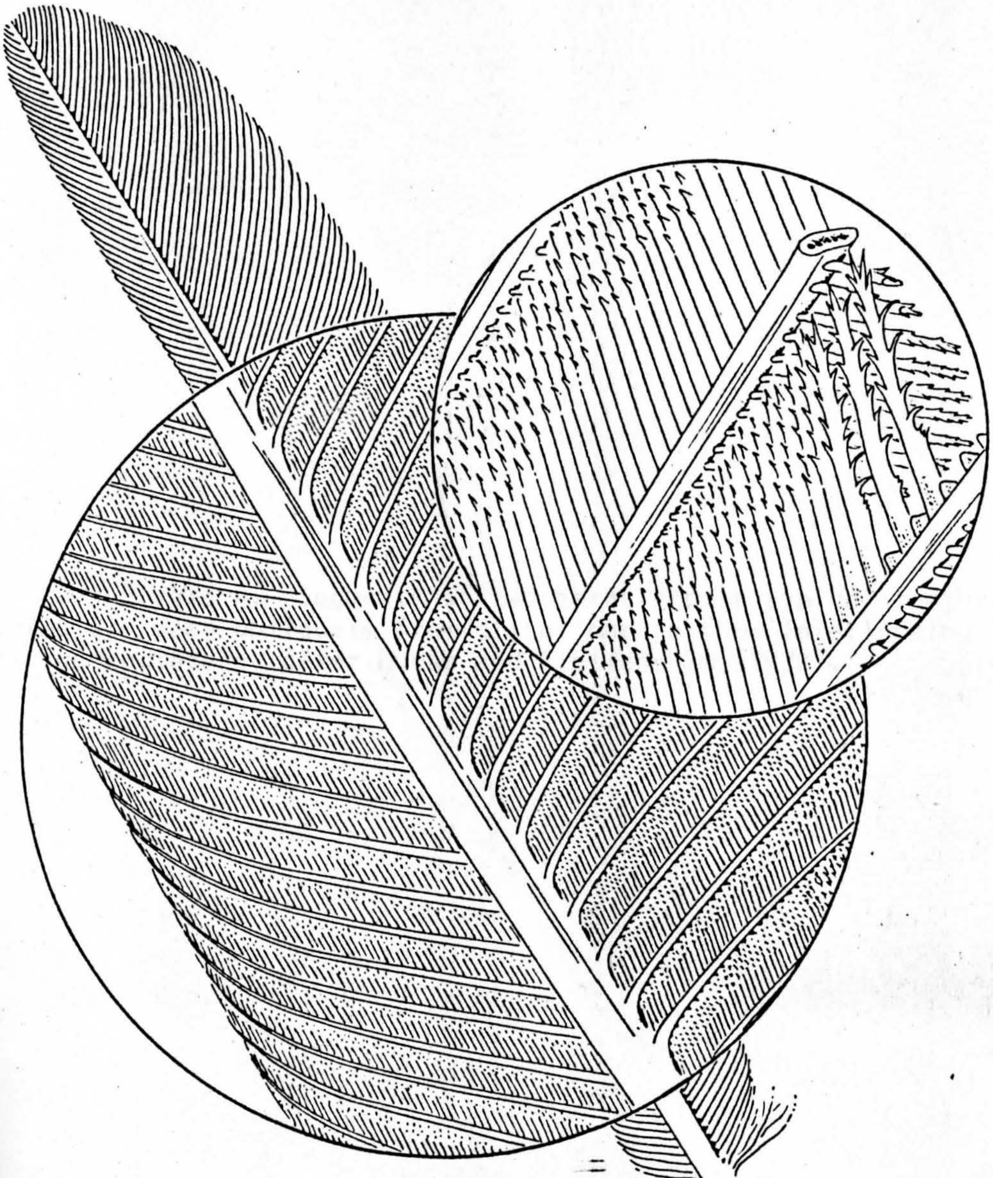


Figure 4. Segments of two barbs from a typical feather. The barbs are seen obliquely from distal end to show interlocking of parts and nomenclature (after Lucas and Stettenehim, 1972).

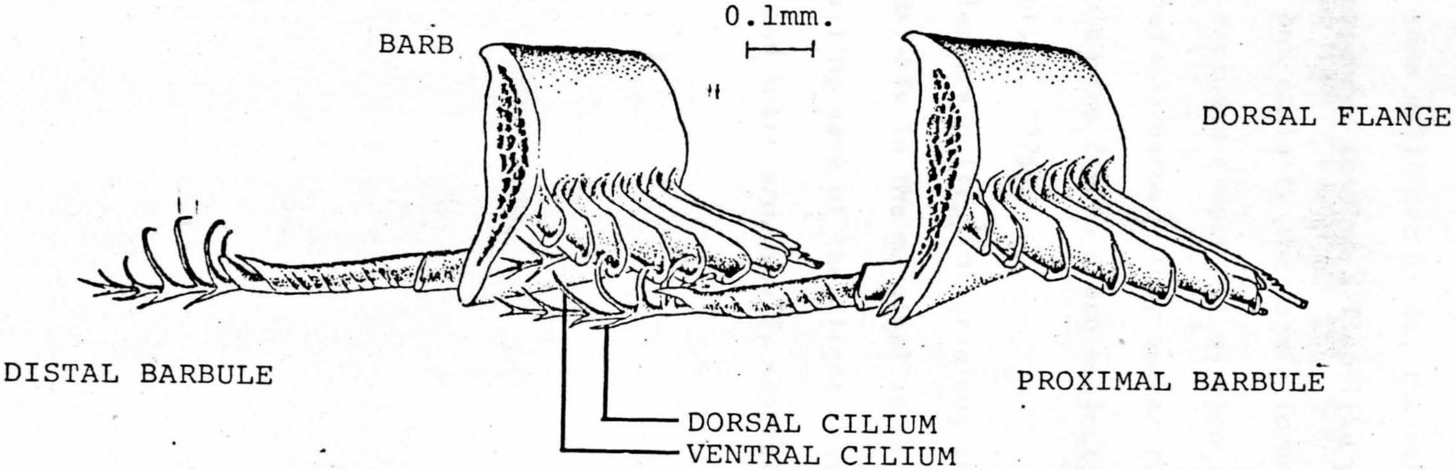

BARB
0.1mm.
DORSAL FLANGE
DISTAL BARBULE
PROXIMAL BARBULE
DORSAL CILIUM
VENTRAL CILIUM

Fig.4

barbules of an adjoining barb providing a vane with tremendous rigidity and extraordinary lightness. In some bird groups such as the ducks, geese, hawks, eagles and some galliform birds, the ventral portion of the barb is narrowly expanded to form a flap-like structure which projects ventrolaterally and contacts the tegmin form adjacent barbs and form "corridors". These expanded ridges act as flap valves and prevent air from passing upward between barbs. They appear to be adaptations for modes of flight in which the feathers are subjected to strong air pressure from below (Peterson, 1975).

The distal barbules are quite similar along the basal portion of a barb, but differ considerably in the marginal zones of the terminal portions. Toward the trailing edge of the flight feather the base is much longer and narrower and there are usually several large recurved ventral barbicels.

MATERIALS AND METHODS

Birds used for this study were all field collected at various sites in Northeastern Ohio. Immediately after the birds were collected, the remiges of the wing and rectrices of the tail were sprayed with Cryokwik (freon) to immobilize the feather mites, thus allowing no further movement to distrub the present population structure. The birds were then returned to the laboratory and placed in a freezer for subsequent study.

All flight feathers and the ventral coverts were removed on each bird representative to examine the feather mite population as it existed on each bird and feather studied. From these feathers the third, fifth, and seventh primaries and the third, fifth, and seventh secondaries were taken as representative feathers for further examination. These feathers were first divided into three areas roughly corresponding to the angle between the barbs and the shaft (Fig. 5). The angle is acute at the basal portion of the feather and increases toward the tip of the feather. Each area was further divided into three zones (Fig. 6 and 7). These zones include (A) zone of unmodified barbules next to the quill, (B) zone of long friction barbules located midlength along the barb, and (C) zone of short friction barbules located distally at the trailing edge of the feather. In each of these zones, barb width measurements were taken and subjected to a factorial analysis of variance within and among feather zones.

Figure 5. An isolated feather showing areas roughly corresponding to the angle between the barbs and the shaft (after Dubinin, 1951).

Figure 6. An isolated primary flight feather showing zones of modified and unmodified barbules and zones of friction between feathers (after Dubinin, 1951).

Figure 7. An isolated secondary flight feather showing zones of modified and unmodified barbules, and zones of friction between feathers (after Dubinin, 1951).

Fig. 5

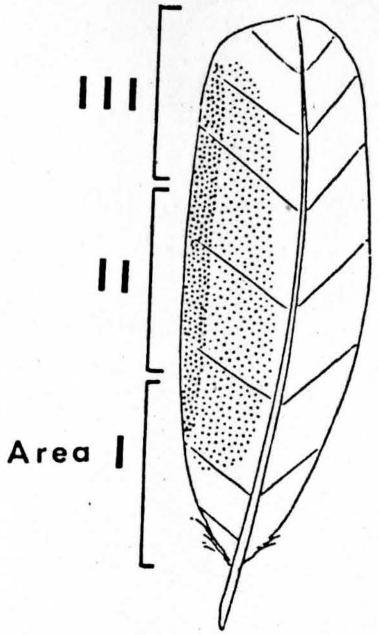


Fig.6

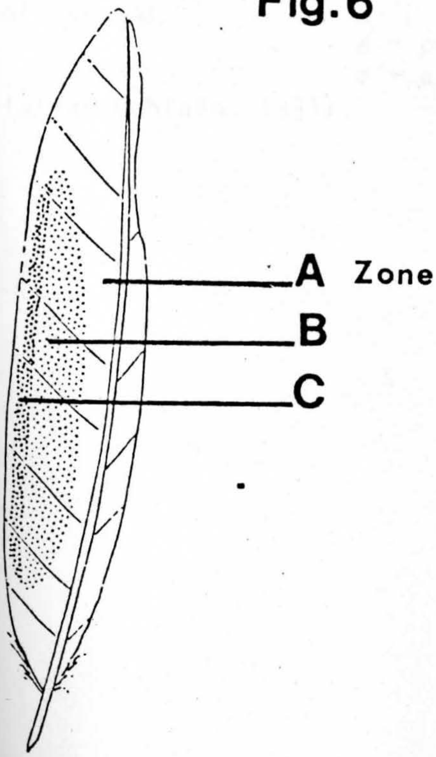


Fig.7

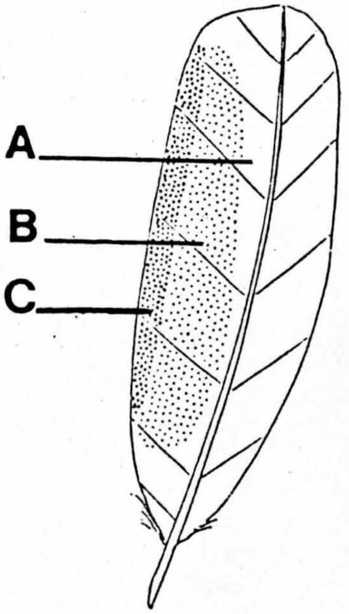


Figure 8. Flight feathers in relaxed position showing zones of overlap;

a - protected area
b - unprotected area

Figure 9. Flight feathers in flight position showing zones of overlap;

a - protected area
b - exposed area

(after Dubinin, 1951).

Fig. 8

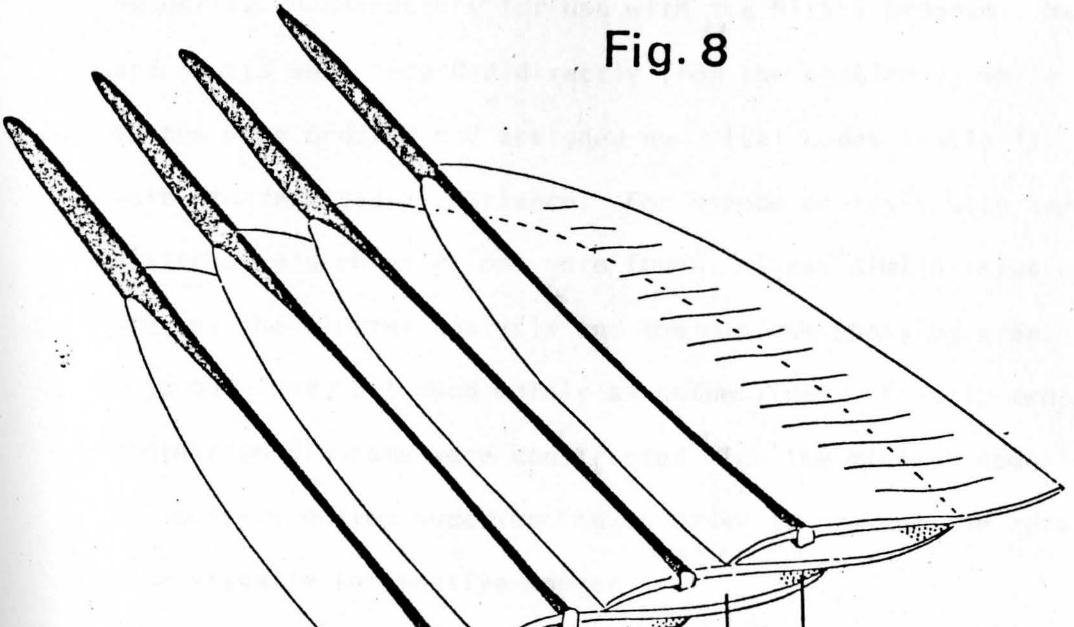
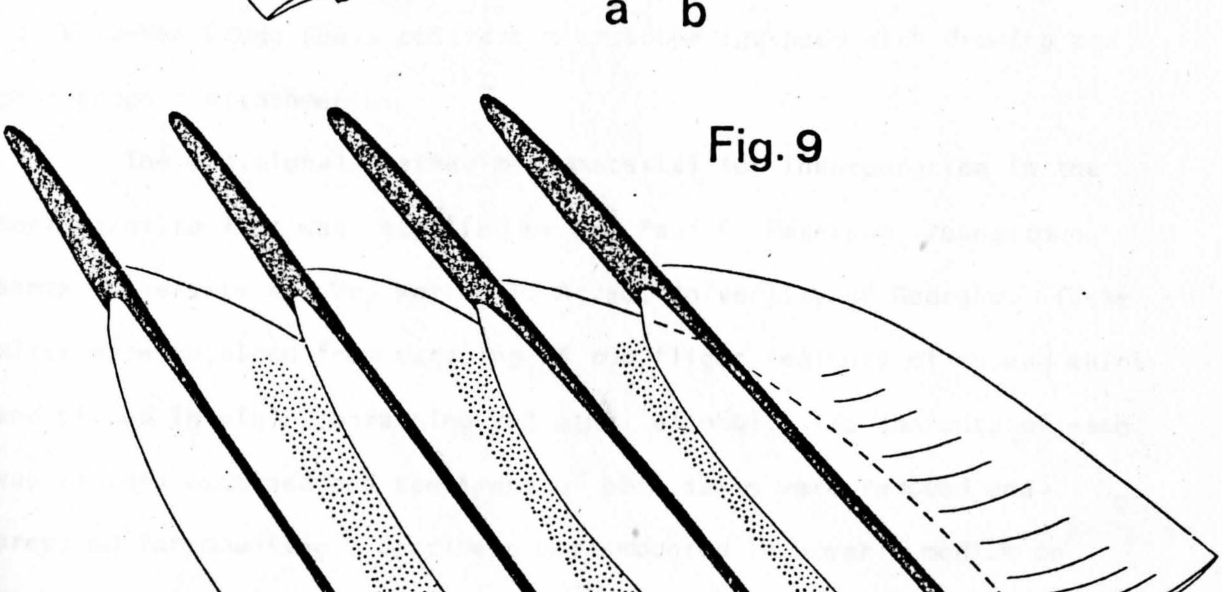


Fig. 9



More precise data on feather morphology was obtained by selecting 24 characters for use with the NT-SYS program. Measurements and counts were recorded directly from the specimens, while qualitative shapes were ordered and assigned numerical codes (Table 1). Characters were standardized by variance. For Q-mode analysis both taxonomic distances and correlations were found. These similarities were structured by the cluster analysis and the minimum spanning tree. Phenograms were obtained, but used mainly as guide lines. Finally two-dimensional ordination diagrams were constructed with the minimum spanning tree and subsets option superimposed in order to present the results in a more visually informative manner.

All measurements and mite observations were made with a Model 20, Wild-Heerbrugg phase contrast microscope equipped with drawing and photographic attachments.

The additional feather mite material for incorporation in the host-parasite list was supplied by Dr. Paul C. Peterson, Youngstown State University and Dr. Warren T. Atyeo, University of Georgia. These mites were obtained from scraping of the flight feathers of museum skins and placed in vials containing 70% ethyl alcohol. The contents of each was closely examined and specimens of both sexes were removed and prepared for mounting. Specimens were mounted in Hoyer's medium on glass slides with cover slips and then dried in an oven for three days at 50° C.

Data processing was carried out at the Computer Center of Youngstown State University (IBM 360/50). Two programs were used; the NT-SYS (Vers. 3., Mod. Level 1), developed by Rohlf, Kishpaugh, and

TABLE 1

LIST OF CHARACTERS AND CHARACTER STATES

1. Barb width: Area I, Zone A
2. Barb width; Area I, Zone B
3. Barb width: Area I, Zone C
4. Barb width: Area II, Zone A
5. Barb Width: Area II, Zone B
6. Barb width: Area II, Zone C
7. Barb width: Area III, Zone A
8. Barb width: Area III, Zone B
9. Barb width: Area III, Zone C
10. Number of barbs at quill per 5 mm in Area I
11. Number of barbs at quill per 5 mm in Area II
12. Number of barbs at quill per 5 mm in Area III
13. Depth of groove at loci I A
14. Depth of groove at loci II A
15. Depth of groove at loci III A
16. Length of feather measured from inferior umbilicus
17. Width of leading edge of feather measured from the quill at half length
18. Width of trailing edge measured from quill at half length
19. Type of feather: primary (0), secondary (1)
20. Feather number: 3 (0), 5 (1), 7 (2)
21. Notched: yes (0), no (1)
22. Number of interlocking barbules per 1 mm at loci I A
23. Number of interlocking barbules per 1 mm at loci II A
24. Number of interlocking barbules per 1 mm at loci III A

Kirk (1972), the other program was an analysis of variance performed for a factorial design and was developed for IBM by H.O. Hartley.

TABLE 2

HOST-PARASITE LIST

Icteridae

- *Molothrus alter a.* (Cowbird)
    - *Proctophyllodes egglestoni*
    - *Pterodectes* sp.
- *Quiscalus quiscula* (Common Grackle)
    - *Proctophyllodes egglestoni*
    - *Proctophyllodes mexicanus*
    - *Trouessartia rosterae*
    - *Proterothrix* sp.
- *Euphagus cyanocephalsa* (Brewers Blackbird)
    - *Proctophyllodes egglestoni*
- *Agelaius phoeniceus* (Red-winged Blackbird)
    - *Proctophyllodes egglestoni*
    - *Mesalges* sp.
    - *Pterodectes* sp.

Sturnidae

- *Sturnus vulgaris* (Starling)
    - *Proctophyllodes egglestoni*
    - *Trouessartia rosterae*
    - *Pteronyssoides* sp.

RESULTS: POPULATION COUNTS

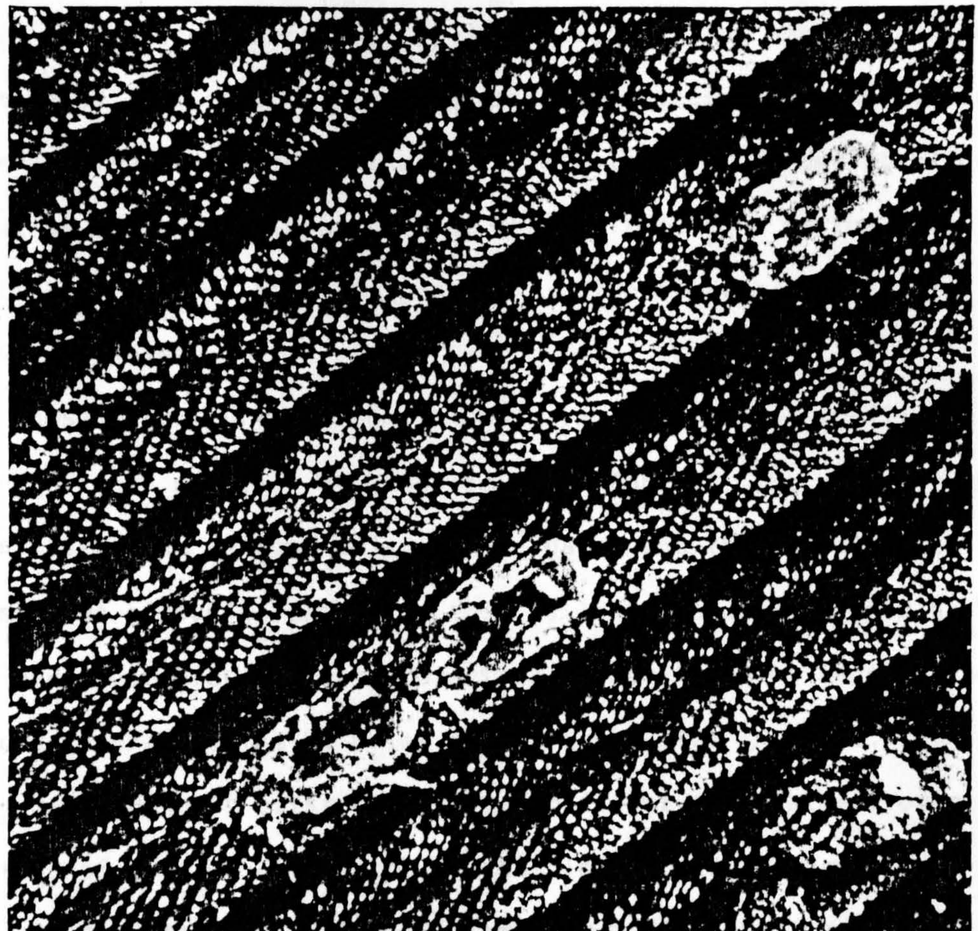
The feather mite, Proctophyllodes egglestoni, was found to be a common parasite of the bird species investigated. Other mite species have been recorded but P. egglestoni is the only one common to all seven birds. In starlings, this species is a new world parasite. Presumably this secondary invasion can be explained by the similarities of physical parameters which hosts have in common, i.e. similarities in feather types and stresses, nesting and migratory habits (Atyeo and Braasch, 1966).

The species P. egglestoni is localized primarily on the dorsal surface of the flight feather on the trailing edge. However some individuals can be found on the leading edge when the population is large. Those mites found on the leading edge are usually females. In general the feather mite attaches itself to the proximal barb within 2 mm of the quill unless the population is large. In such cases as many as eight (8) mites were observed between two barbs 5 mm from the quill. The mite's anterior is toward the quill in all cases except during copulation at which time it is usually the nymph whose anterior portion is toward the quill.

When the mites are found in zone A (Fig. 6), they are always affixed to the proximal barb parallel to the barb. Observations seen to point to the fact that the mite closest the quill wedges itself into the space between quill and barb for protection. It is also expected that this mite and those further along the groove formed by the two

Figure 10. Feather mites in Zone B on Red-winged Blackbird 5 secondary remige (50x).

Fig. 10



barbs get their legs affixed in between the barbules for further protection from being swept away by air currents. The ambulacrum and/or the tactile setae must entwine the proximal barbules to further affix the mite and thus keep the feather mite from falling off during flight. This must be especially important for those mites found on the first four primaries i.e. primary remiges 5 - 9. These mites are almost exclusively females.

Those mites further from the barb in Zone B (Fig. 10-11) are not found in the same position as those found in Zone A. The mites in this area are positioned perpendicular to the barbs and thus parallel to the barbules. The probable reason for this is that the depth of the barb is shallow and would provide less protection. Therefore the legs of the mite would intertwine the barbules and hold the mite in place.

When a wing is outstretched during flight the feathers overlap. These areas of overlap divide the feather into protected areas and exposed areas (Peterson, 1975). Differently modified ectoparasites are found in two of the major feather zones (A and B). Zone C would appear to be too exposed during flight to support a mite population (Fig. 8-9).

There were no mites found in Zone C, which leads to the conclusion that the area of overlap of feathers plays a very important part in the protection of mites from the elements of flight. Zone A and portions of Zone B are overlapped by the ventral part of the preceeding feather. Zone C and the remainder of Zone B are not afforded this overlap and are thus exposed to air currents during flight.

Another protected area is that area covered by the primary coverts. This additional area of overlap is significant because it is

TABLE 3

POPULATION COUNTS OF PROCTOPHYLLODES EGGLESTONI

	Red-Winged Blackbird				Red-Winged Blackbird			
Feather Number	Females	Males	Nymphs	Others	Females	Males	Nymphs	Others
9	34	-	-	-	23	1	1	-
8	17	1	-	-	6	-	2	-
7	20	5	2	0	8	-	-	-
6	14	1	-	-	-	-	-	-
5	7	4	1	-	1	-	-	-
4	5	4	2	2x	2	-	-	-
3	4	4	1	-	-	-	-	-
2	10	9	3	-	-	-	-	-
1'	1	3	2	-	-	-	-	-
1''	3	3	5	-	-	-	-	-
2	1	6	2	-	-	-	-	-
3	1	2	1	-	-	2	1	4 (e)
4	3	8	10	1x	1	4	3	-
5	3	15	8	6x	-	6	1	2 (e)
6	-	1-	4	-	-	8	2	-
7	1	8	4	4x	1	7	4	1x
8	-	10	6	4x	1	15	8	6x
9	-	4	6	3x	1	26	18	14x

*x = copulating adult male with female tritonymph

(e) = egg

TABLE 3 con't.

POPULATION COUNTS OF PROCTOPHYLLODES EGGLESTONI

	Red-Winged Blackbird				Red-Winged Blackbird			
Feather Number	Females	Males	Nymphs	Others	Females	Males	Nymphs	Others
9	39	3	-	-	16	1	-	-
8	22	-	-	-	23	4	1	-
7	11	4	2	-	18	2	-	-
6	12	3	1	-	12	-	-	-
5	5	2	0	-	9	-	-	-
4	8	-	-	-	6	3	2	-
3	2	6	2	-	3	-	-	1(e)
2	1	8	4	-	-	6	2	10(e)
1'	-	9	3	-	1	3	4	6(e)
1''	1	17	16	-	-	13	1	4(e)
2	-	13	11	-	4	12	3	1(e) 1x
3	-	21	26	1	-	4	6	3(e)
4	1	8	6	1x	-	8	4	-
5	-	10	9	4x	-	11	7	3x
6	2	28	7	6x	2	17	18	11x
7	1	13	4	2x	1	9	10	6x
8	4	21	11	9x	-	17	13	11x
9	-	17	16	12x	-	11	9	6x

*x = copulating adult male with female tritonymph

(e) = egg

TABLE 3 con't.

POPULATION COUNTS OF PROCTOPHYLLODES EGGLESTONI

Red-Winged Blackbird

Feather Number	Females	Males	Nymphs	Others
9	47	-	-	-
8	35	4	-	-
7	39	1	-	-
6	19	-	2	-
5	12	2	-	-
4	4	1	-	-
3	-	1	4	-
2	4	1	-	-
1'	3	3	3	6 (e)
1''	1	1	1	1 (e)
2	-	4	6	2 (e)
3	2	3	12	1x
4	1	8	11	4x
5	-	14	18	10x
6	1	11	18	9x
7	-	16	24	19x
8	4	22	16	13x
9	1	18	19	10x

*x = copulating adult male with female tritonymph

(e) = egg

TABLE 3 con't

POPULATION COUNTS OF PROCTOPHYLLODES EGGLESTONI

Feather Number	Starling				Starling			
	Females	Males	Nymphs	Others	Females	Males	Nymphs	Others
9	10	-	-	-	18	-	-	-
8	7	-	-	-	9	-	-	-
7	3	-	-	-	5	2	-	-
6	8	-	-	-	3	-	-	-
5	2	-	-	-	4	-	-	-
4	1	-	-	-	2	-	2	-
3	7	1	-	-	1	2	-	-
2	1	-	-	-	3	-	1	2 (e)
1'	1	-	-	-	1	1	-	-
1''	-	-	1	-	4	-	2	-
2	-	-	-	-	-	4	-	-
3	-	1	-	-	-	-	3	-
4	-	1	4	-	-	1	4	1x
5	1	2	1	-	2	-	3	-
6	2	3	1	1x	1	2	3	1x
7	-	1	2	-	-	12	6	3x
8	-	3	4	1x	-	11	5	4x
9	1	6	4	1x	-	7	3	2x

*x = copulating adult male with female tritonymph

(e) = egg

TABLE 4

POPULATION COUNTS OF PROCTOPHYLLODES EGGLESTONI ON THE RED-WINGED BLACKBIRD (AGELAIUS PHOENICUS) AND THE STARLING (STURNUS VULGARIS)

	Red-Winged Blackbird Totals				Starling Totals			
Feather Number	Females	Males	Nymphs	Others	Females	Males	Nymphs	Others
9	159	5	1	-	28	-	-	-
8	52	4	3	-	16	-	-	-
7	106	15	7	-	8	2	-	-
6	57	4	3	-	11	-	-	-
5	34	8	1	-	6	-	-	-
4	23	8	4	2x	3	-	2	-
3	9	11	6	2 (e)	8	3	-	-
2	13	24	9	10 (e)	4	-	1	2 (e)
1'	5	16	12	6 (e)	2	1	-	-
1''	5	34	22	7 (e)	4	-	3	-
2	5	35	22	3 (e)	-	4	-	-
3	3	32	46	3 (e) 2x	-	1	3	-
4	6	36	34	6x	-	2	8	1x
5	3	56	39	25x	3	2	4	-
6	5	74	49	26x	3	5	4	2x
7	4	53	46	32x	-	13	8	3x
8	9	85	56	43x	-	14	9	5x
9	2	76	68	45x	1	13	7	3x
Totals	589	581	426	19 (e) 180x	69	60	49	20 (e) 14x

TABLE 4

POPULATION COUNTS OF *PROCTOPHYLLODES EGGLESTONI* ON THE RED-WINGED BLACKBIRD (*AGELAIUS PHOENICUS*) AND THE STARLING (*STURNUS VULGARIS*)

	Totals			
Feather Number	Females	Males	Nymphs	Others
9	187	5	1	-
8	68	4	3	-
7	114	17	7	-
6	18	4	3	-
5	40	8	1	-
4	26	8	6	2x
3	17	14	6	2 (e)
2	17	24	10	12 (e)
1'	7	17	12	6 (e)
1''	9	34	25	7 (e)
2	5	39	22	3 (e)
3	3	33	49	3 (e) 2x
4	6	38	42	7x
5	6	58	43	25x
6	8	79	53	28x
7	4	66	54	35x
8	9	99	63	48x
9	2	89	75	48x
Totals	658	641	475	21 (e) 194x

additional protection for Area I (Fig. 5). This area has been shown to be significant in the protection of feather mite eggs and nymphs from air currents since large numbers of individuals of these types were observed in this area.

The examination of the population structure of the feather mite P. egglestoni on the Red-winged Blackbird can be described as a spacial arrangement. The primary loci of P. egglestoni females is on the primary remiges 4 - 9. Eighty six percent of the females of a given population are found in this area. The remaining 14% were found on primary remiges 1 - 3 and secondary remiges 1 - 9. In mite populations with less then 100 individuals this spacial arrangement was not as pronounced. Nevertheless, in smaller populations a higher percentage of females were still found located on primaries 9 - 4 (Table 3).

The male population exhibits a very similar population structure. The males were found to be primarily restricted to the secondary remiges and to a lesser extent on primaries one and two. Sixty one percent of the males were located on secondaries 5 - 9. When the remaining secondaries and primaries 1 - 2 are included, 90% of the male mites are located in this area.

The loci for the nymphal stages of P. egglestoni is more diverse than either the male or female populations. They do however show some tendency for site specialization. Copulating nymphs with adult male mites are primarily located in the same area as the males. However, the nymphs seem more restricted to the secondary remiges 7 - 9. The nymphs not copulating were found to occur with regularity on the secondary remiges 1 - 4 and to a somewhat lesser extent on primaries 1 - 2.

These areas appear to have a greater amount of protection for the developing mite. The overlap between feathers is greatest in this area and the primary coverts also afford extra protection for the developing mite.

The eggs of P. egglestoni are located on the remiges and primary coverts in the area from the second primary to the third feather of the secondary remige and the primary coverts which overlap this area. This area is protected from some of the stress brought about by flight by this feather overlap thus protecting the egg.

Two other feather mite populations were observed on certain red-winged blackbirds. These included a single species of Pterodectes and a species of Megninia. The Pterodectes sp. was located primarily on the primary feathers (1 - 5) with a few on the secondaries. This mite is relatively small and easily lodged between the barbs (Fig. 10). There was no noted specific loci for males and females. These mites seemed interspersed among themselves throughout their range.

The Megninia sp. are large mites with long setae. These mites are usually found in the plumage. When found on the flight feathers, they are located primarily on the secondaries. Roughly ninety percent were located on the secondaries 3 - 9. The remaining were located on primaries 1 - 2 and secondaries 1 - 2. This loci provides adequate protection for these mites during flight from the overlap of coverts and flight feathers. These mites were found exclusively in Zone A, that area nearest the quill, usually near the base of the feather.

On secondary feathers where *P. egglestoni* and *Megninia* sp. were found to coexist there was an apparant spacial difference in site preference. In such cases, the *Megninia* sp. was closest to the base of the feather while those of *P. egglestoni* were further toward the tip of the feather.

Life Cycle

During the development of *Proctophyllodes egglestoni* there are five basic life stages; egg, hexapod larva, protonymph, tritonymph, and adult. Usually only a single egg begins development in a given female, however one female of *Proctophyllodes mexicanus* from the common grackle (*Quiscalus quiscala*) has been observed with two equal sized eggs (Fig. 11-12). The female deposits the egg on the feather where development is completed.

P. egglestoni eggs are positioned on specific feathers for development; other related species are ovoviparous. In *P. egglestoni* two major sites of egg deposition from red-winged blackbirds were noted; on the remiges and the ventral primary coverts. On the flight feathers the eggs appear to be centrally located on secondaries 1 - 3 and primaries 1 - 3. All were deposited in Zone A (Fig. 6 - 7), along the proximal barbules in Area I where overlap between flight feathers and the ventral primary coverts occurs. Eggs were deposited in rows along the barb with no more than four between any two barbs on any flight feather observed (Fig. 13).

P. egglestoni eggs were also found on the primary coverts. These feathers overlap the primaries and secondaries at their basal region. On the coverts the eggs were differently positioned according

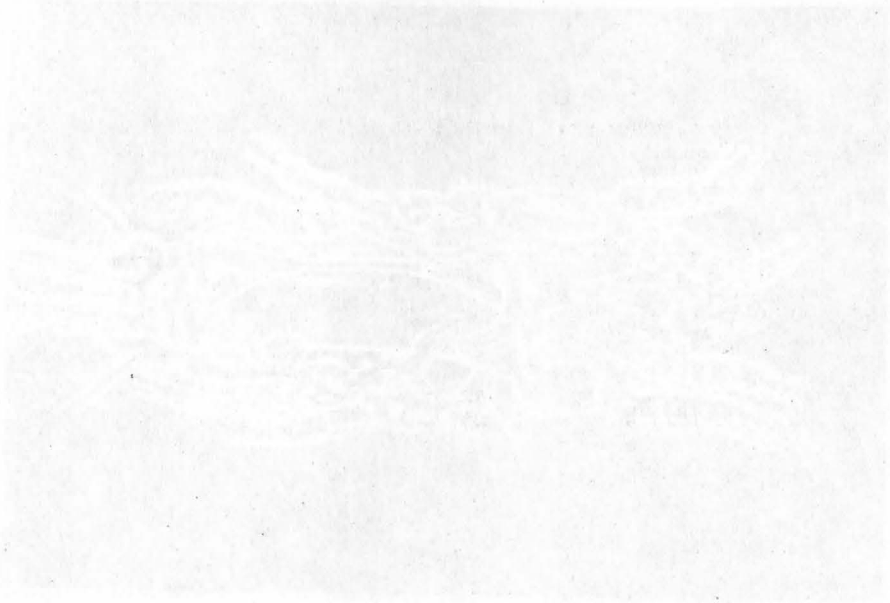
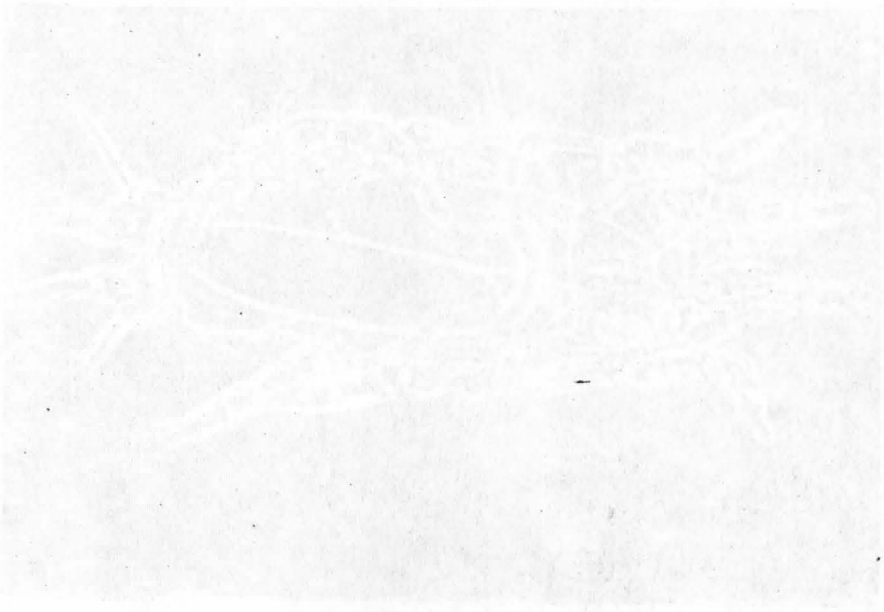


Figure 11. *Proctophyllodes egglestoni* with one egg (100X).

Figure 12. *Proctophyllodes mexicanus* with two eggs (100X).



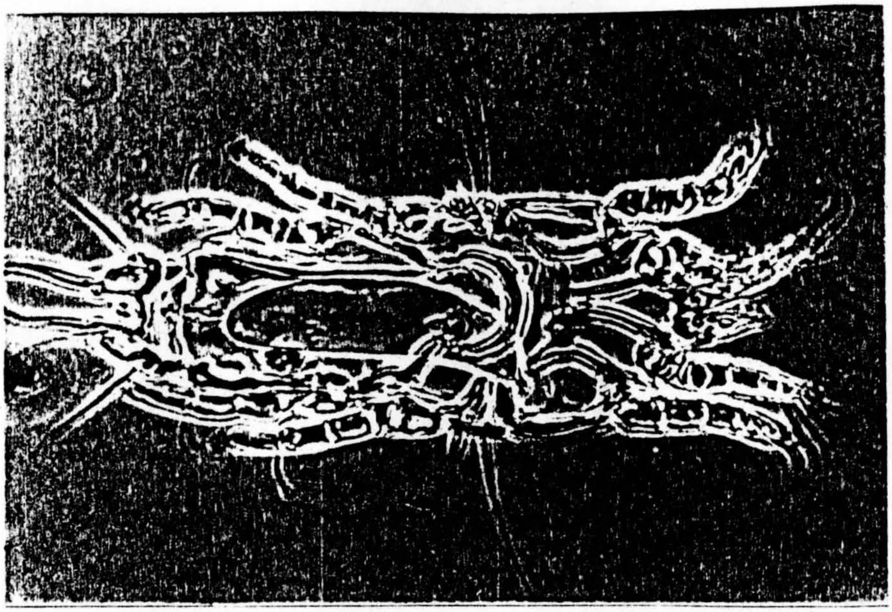


Fig. 11

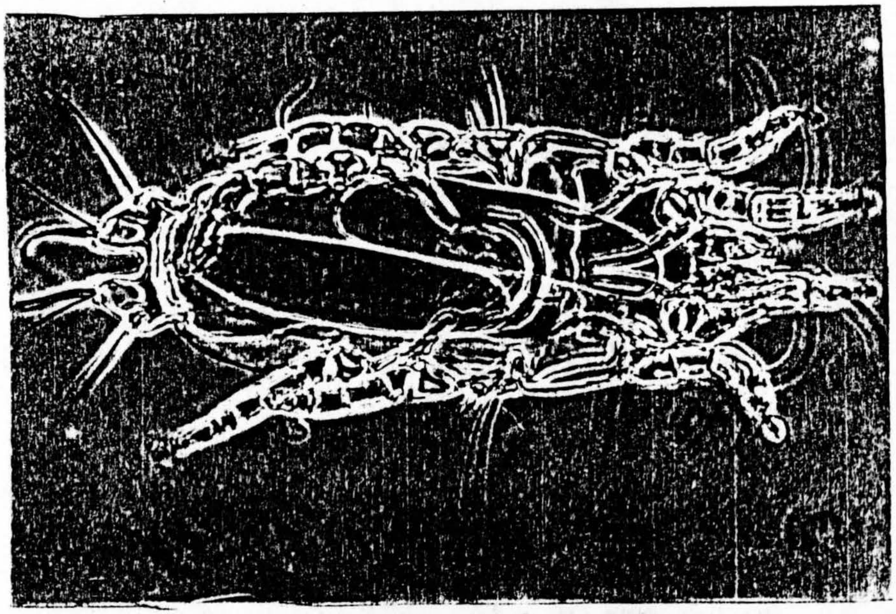


Fig. 12

Figure 13. Proctophyllodes egglestoni eggs on 2nd secondary remige (50x).

Fig.13

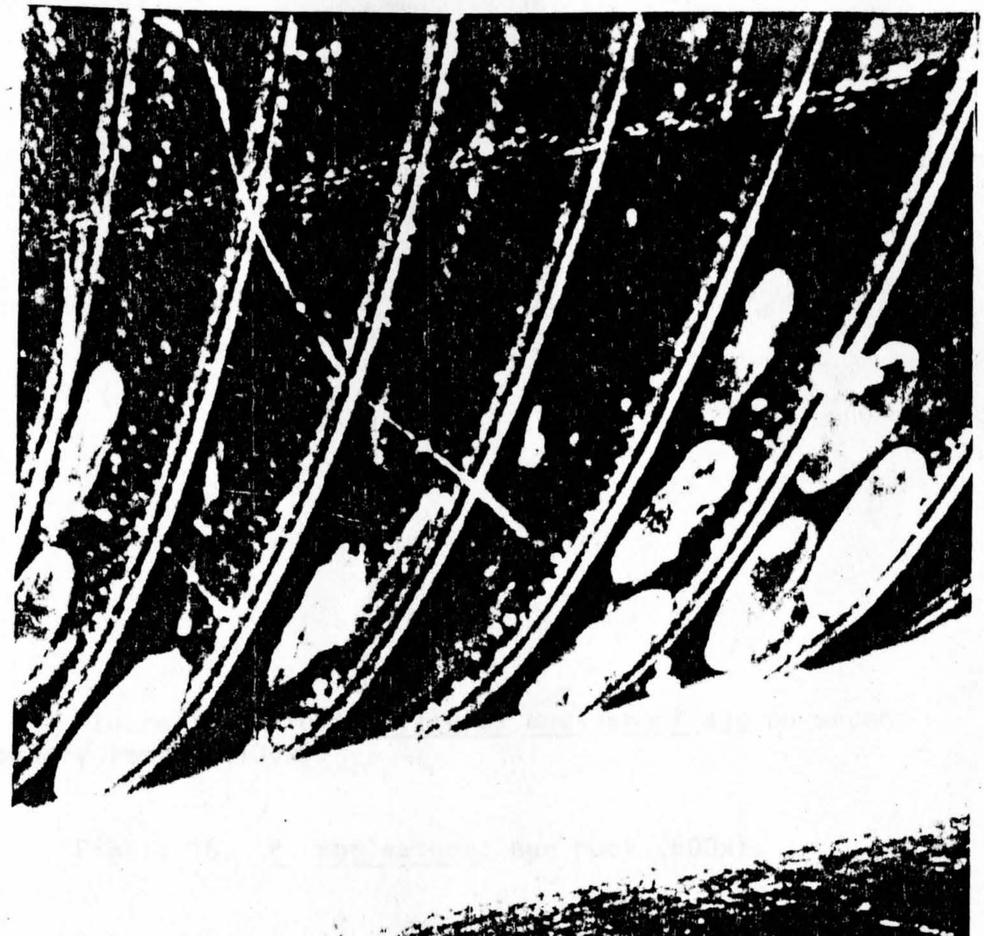
to the number of eggs present. When the number of eggs on a feather was high, eggs were located both on the proximal and distal barbule between barbs. The eggs were located at the base of the feather. Nearly all eggs were located no more than two cm from the superior umbilicus on the dorsal side of the ventral primary covert (Fig. 14).

The egg appears to have an unique structure for attachment which has never been reported. On the narrow tapered end is a hook-like projection which attaches to individual barbules (Fig. 15 - 16). This hook is either entwined between barbules or caught on each barbule thus fastening the egg in place. The remaining portions of the egg are free from attachment. There are apparently three factors which favor the deposition of this egg on specific sites of individual feathers; 1) the egg hook which attaches to the barbule, 2) the protected area between barbules, 3) the area of protection afforded by the overlap between the remiges and primary coverts (Fig. 8 - 9).

The emerging hexapod larva is generally unsclerotized except for a small propodosomal shield. In the protonymph, legs IV, additional setae and one pair of genital discs are found. A full complement of setae, weak sclerotization and a second pair of genital discs characterize the tritonymph. In the adult the genital apparatus, sclerotizations, and chaetotaxy are completely developed.

Figure 14. Proctophyllodes egglestoni eggs on primary ventral coverts (50x).

Fig. 14



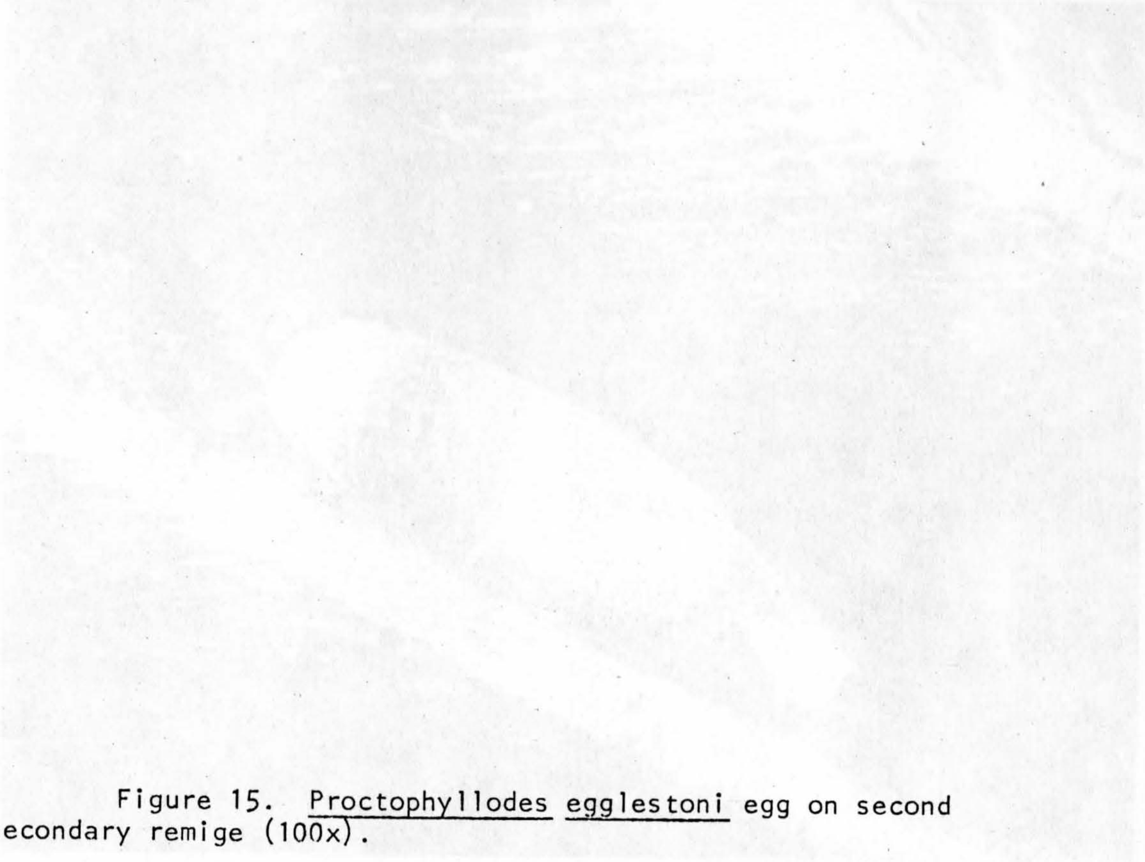
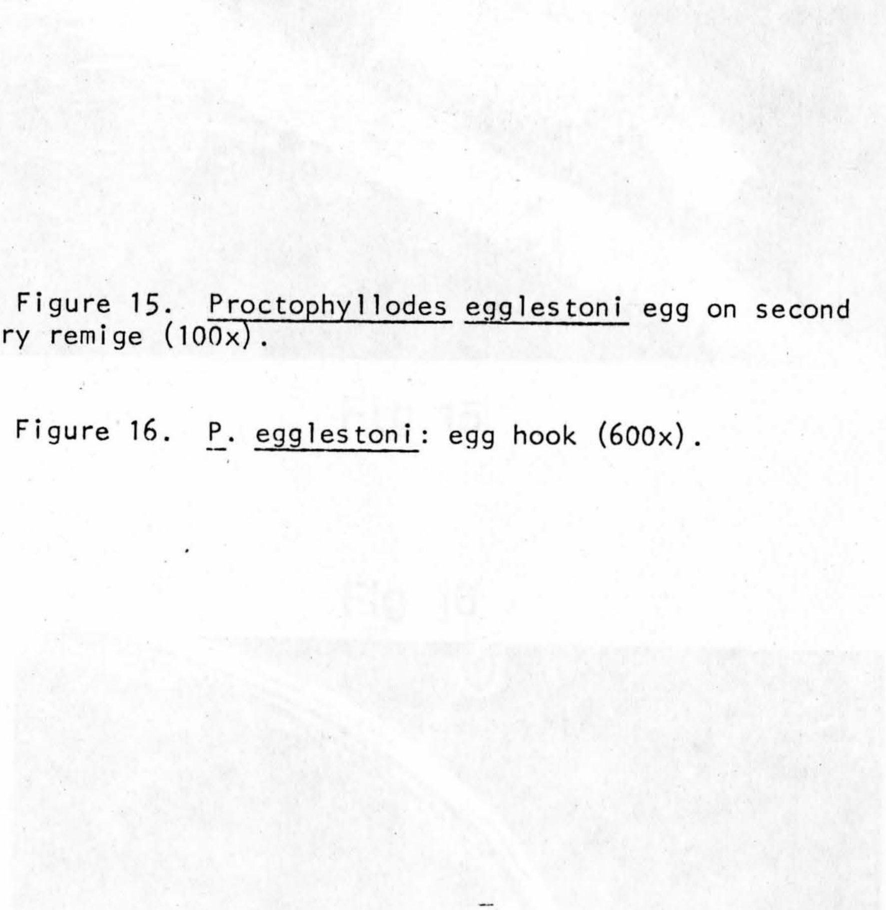


Figure 15. Proctophyllodes eggleston i egg on second secondary remige (100x).

Figure 16. P. egglestoni: egg hook (600x).



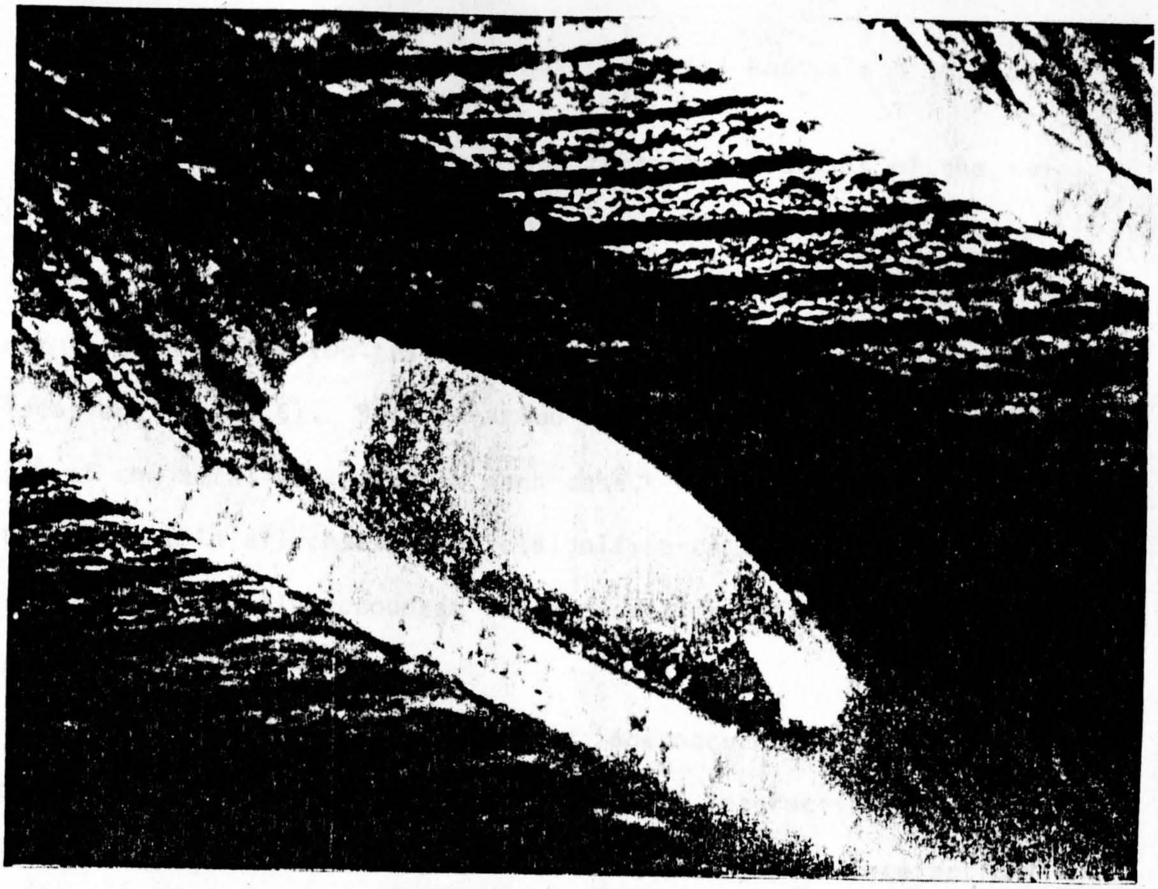
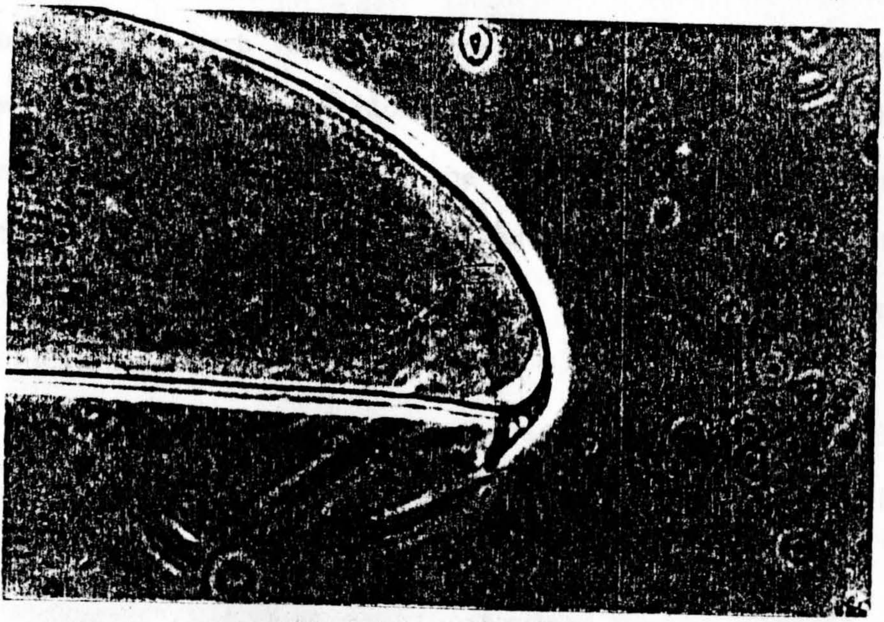


Fig.15

Fig. 16



RESULTS: Four-way Factorial Analysis

The results of the four-way factorial analysis of the two bird species in this study are shown in Tables 5 - 6. Of the four factors considered, three were shown as being significantly different in each of the two tests, namely feather zone (factor B), and barb location (factor C). Barb location can account for approximately 75% of the total variation in each case. Feather type (factor A) was significant in all cases. Where significance in the R factor exists it can be partially accounted for by additional factors of age and sex of the bird.

The most significant interactions occur in these tests between feather type and barb location (B-C interaction), and among feather type, feather zone, and barb location (A-B-C interaction). There were other significant interactions which occurred between areas but occurred in only one or two of the tests. Since similarities are being examined between hosts of a common parasite, it is these similarities which are of importance. Because the key to these interactions appears to be barb location, some understanding here is requisite. From the first barb location (Zone I) the distance between barbs increases rapidly to midlength of the feather then tapers off toward the distal end of the feather i.e. the distance between barbs is narrowest at the trailing edge, widest in the center, and at some intermediate location toward the quill.

The data obtained from direct observation of mite population counts of P. egglestoni seems to bear out some of the interactions.

Feather type, feather zone, and barb location are extremely important for the habitat (niche) produced by each of these factors combined shows a different population in one case or another depending on the amount of protection required by an individual. Feather number seems unimportant to mite populations as they vary little from feather to feather only over larger numbers of feathers does a population change occur.

TABLE 5

FOUR-WAY FACTORIAL ANOVA OF BARB WIDTH IN REMIGES OF THE RED-WINGED BLACKBIRD

Source	df	SS	MS	F
Feather Type A	1	5079	5079	8.78***
Feather Number D	2	1060	530	1.0 ns
Feather Zone B	2	46692	23346	40.27***
Barb Location C	2	2597597	1298798	2239.20***
Birds R	10	9830	983	1.0 ns
AB	2	733	367	1.0 ns
AC	2	11855	5928	10.26***
BC	4	36984	9246	15.95***
ABC	4	3678	919	1.0 ns
AD	2	10406	5203	8.97***
BD	4	8634	2158	3.74*
ABD	4	3441	860	1.0 ns
CD	4	6183	1545	2.66 ns
ACD	4	16249	4062	7.00***
BCD	8	1957	244	1.0 ns
ABCD	8	6153	769	1.0 ns
Error	530	306788	579(2)	
Total	593	3,069,222		

*** (P 0.01)

* (P 0.05)

TABLE 6

FOUR-WAY FACTORIAL ANOVA OF BARB WIDTH IN REMIGES OF THE COWBIRD

Source	df	SS	MS	F
Feather Type A	a	17015	17016	80.26***
Feather Number D	2	1040	520	1.0 ns
Feather Zone B	2	4714	2357	11.11***
Barb Location C	2	1068441	534221	2519.90***
Birds R	5	4695	939	4.43
AB	2	1509	754	3.5*
AC	2	14098	7049	33.25***
BC	4	33599	8399	39.61***
ABC	4	22696	5674	26.76***
AD	2	1252	626	1.0 ns
BD	4	2016	504	1.0 ns
ABD	4	1176	294	1.0 ns
CD	4	753	188	1.0 ns
ACD	4	1431	357	1.0 ns
BCD	8	572	71	1.0 ns
ABCD	8	652	81	1.0 ns
Error	265	56192	212	
Total	323	1,231,845.00		

***(P 0.01)

* (P 0.05)

RESULTS: OTU Study

Feathers exhibit considerable diversity in size, shape and function. As a result of this diversity and the knowledge that numerous feather parasites are associated with blackbirds, it is requisite that details of the microniche be further defined. The physical differences in feathers among birds was interpreted by submitting data to a variety of subroutines in the NT-SYS system. The characters used, were chosen carefully to delineate differences and/or similarities among and between feathers. The multivariate subroutines used included character standardization, computation of similarity coefficients cluster analysis, ordination by principle component analysis and multidimensional scaling.

Although major bird species were obvious in this study, there was uncertainty as to the details of inter- and intra-group relationships which were not solved by the analysis of variance. Thus it was decided to apply a numerical taxonomic analysis in an attempt to clarify these relationships. This analysis did cluster bird types and feathers into similar groups that were previously obvious. Some relationships, however, did emerge that had not previously been detected.

For the purpose of relating these groups both phenograms and two-dimensional ordination diagrams were constructed. Phenograms were used mainly as rough guides because of their inherent distortions (Rohlf et al., 1972). In general, the ordination diagrams produced by multidimensional scaling show relationships generally comparable to those indicated in the phenograms. However the addition of the minimum spanning tree and subsets subroutines aided considerably in settling uncertainties as to closest relationships. Only factors I and II were plotted in these diagrams because 81% of the variation occurred between these two areas. It was therefore decided that this was enough variation to accurately display relationships within and among feather types and relationships between bird species.

The study of relationships began with the identification of 66 OTU's (Operation Taxonomic Units) identified as feather types. These feathers were from the blue jay, starling, and red-winged blackbird. Twenty four characters (Table 1) were then chosen from each bird's feather type. From the initial data matrix it was noted that the feathers from the blue jay were clustered in a distinct area and that the red-wing and starling clustered together. Also of interest was the phenogram which grouped all primary feathers of both starling and red-winged blackbird, and all secondary remiges of these two bird types together (Figure 18).

To examine the data obrained from the study of 66 OTU's more carefully, this data was subdivided into 18 and 24 OTU sets. With this data, grouping obtained more precisely delineated the differences and similarities which were difficult to ascertain from the 66 OTU data set (Table 7).

Included in the 18 OTU set were six feathers (primaries 3,5,7, secondaries 3,5,7) from each of three birds (blue jay, starling, red-winged blackbird). From this data an ordination diagram (Figure 19) and a distince phenogram (Figure 18) were constructed. These figures show similarities and differences between bird species and their

TABLE 7

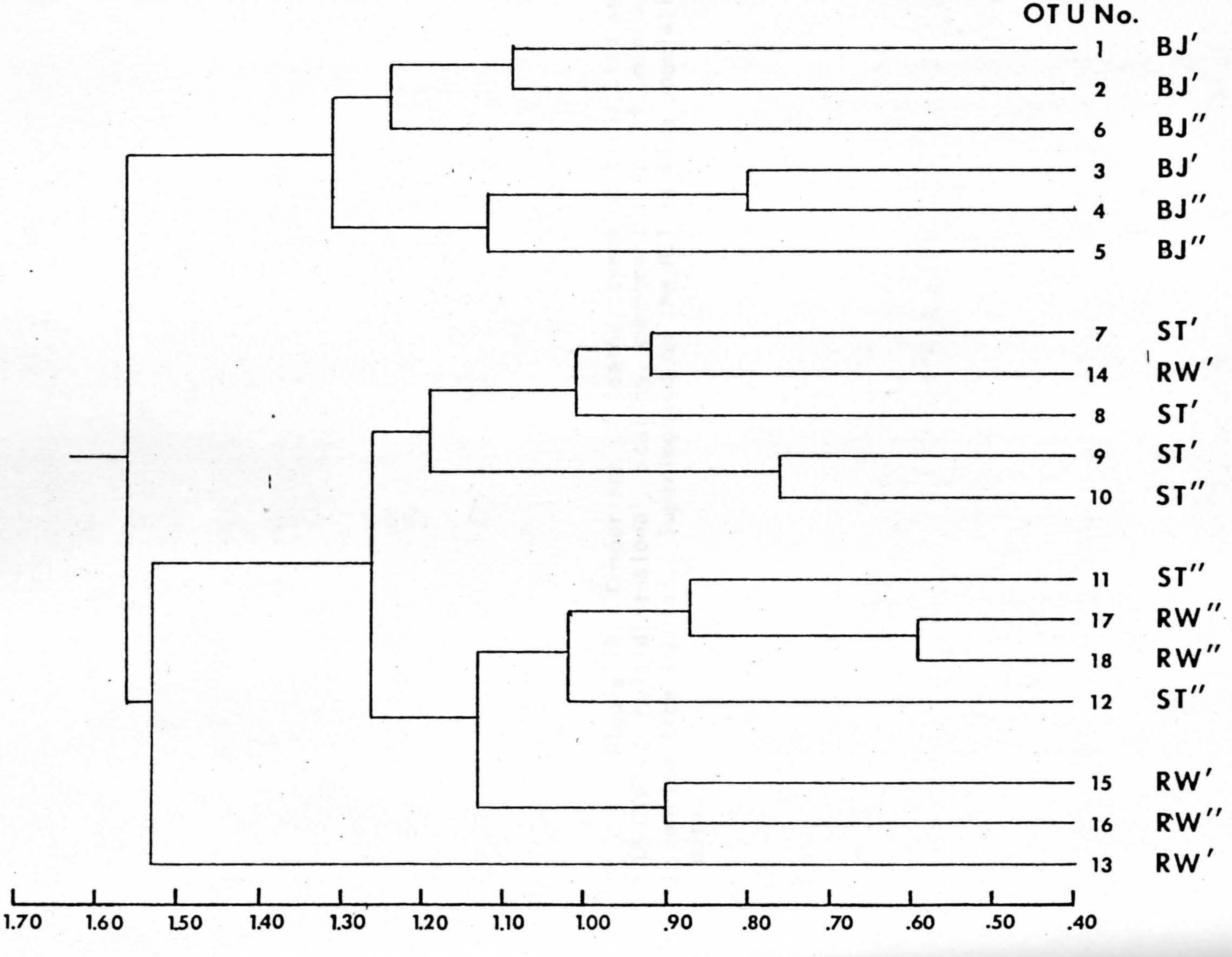
OTU Nos. for Figures and

OTU No.	Bird Type	Feather Type
1	Blue Jay	Primary (7)
2	Blue Jay	Primary (5)
3	Blue Jay	Primary (3)
4	Blue Jay	Secondary (3)
5	Blue Jay	Secondary (5)
6	Blue Jay	Secondary (7)
7	Starling	Primary (7)
8	Starling	Primary (5)
9	Starling	Primary (3)
10	Starling	Secondary (3)
11	Starling	Secondary (5)
12	Starling	Secondary (7)
13	Red-winged Blackbird	Primary (7)
14	Red-winged Blackbird	Primary (5)
15	Red-winged Blackbird	Primary (3)
16	Red-winged Blackbird	Secondary (3)
17	Red-winged Blackbird	Secondary (5)
18	Red-winged Blackbird	Secondary (7)
19	Red-winged Blackbird	Primary (7)
20	Red-winged Blackbird	Primary (5)
21	Red-winged Blackbird	Primary (3)
22	Red-winged Blackbird	Secondary (3)
23	Red-winged Blackbird	Secondary (5)
24	Red-winged Blackbird	Secondary (7)

Figure 17. Comparison of feather types of three bird species, 18 OTU study. Phenogram based on taxonomic distances between OTU's matrix correlation = 0.742.

BJ' - Blue Jay Primary Remige
BJ'' - Blue Jay Secondary Remige
ST' - Starling Primary Remige
ST'' - Starling Secondary Remige
RW' - Red-wing Primary Remige
RW'' - Red-wing Secondary Remige

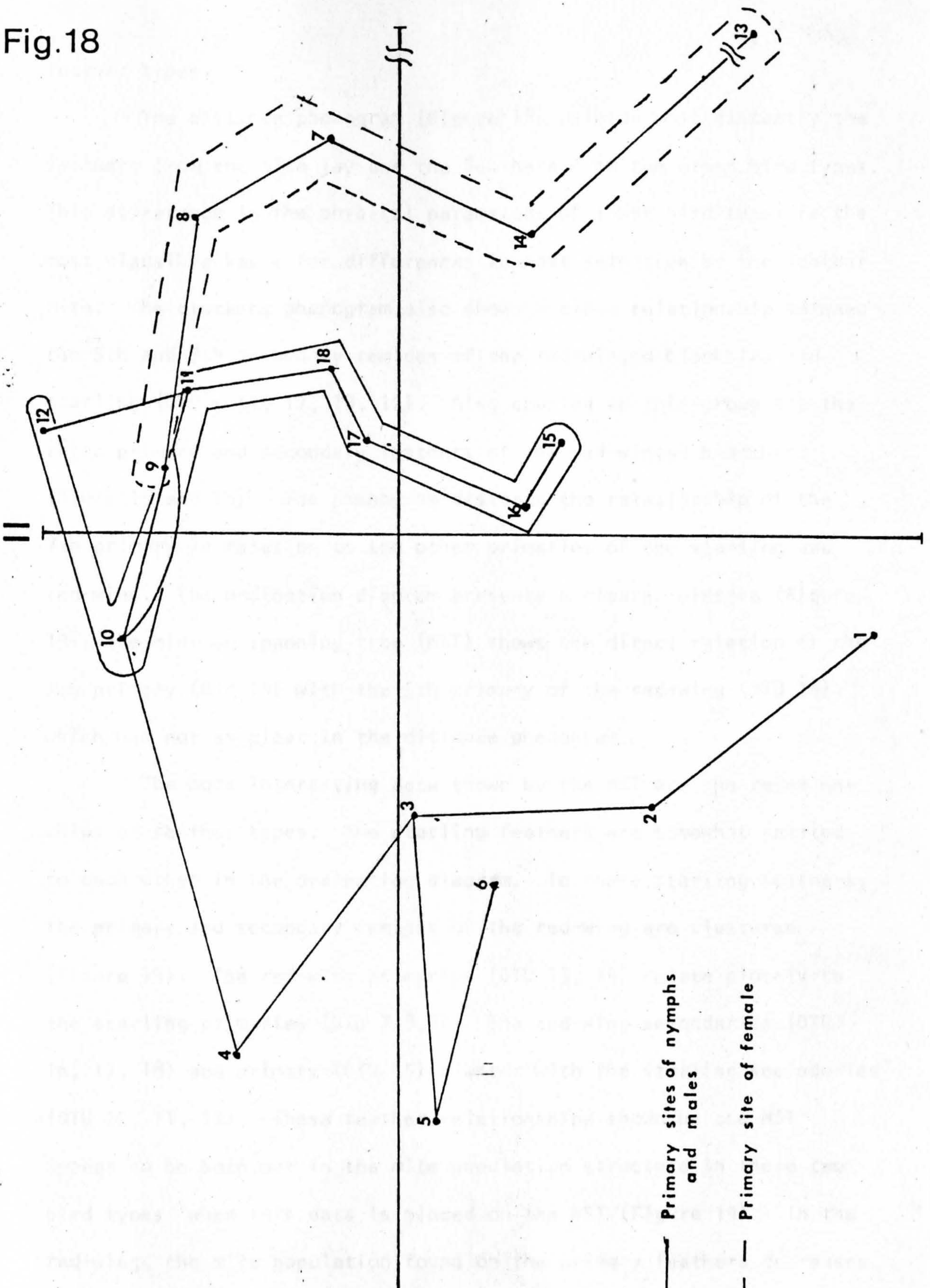
Fig. 17



OT U No.
1 BJ′
2 BJ′
6 BJ″
3 BJ′
4 BJ″
5 BJ″
7 ST′
14 RW′
8 ST′
9 ST′
10 ST″
11 ST″
17 RW″
18 RW″
12 ST″
15 RW′
16 RW″
13 RW′
1.70
1.60
1.50
1.40
1.30
1.20
1.10
1.00
.90
.80
.70
.60
.50
.40

Figure 18. Comparison of feather types of three bird species, 18 OTU's. Multidimensional scaling, component I vs. II, minimum spanning tree imposed. Superimposed on the MST is mite population data.

Fig.18


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
I
II
III
Primary sites of nymphs and males
Primary site of female

feather types.

The distance phenogram (Figure 18) relates most distantly the feathers from the blue jay and the feathers from the other bird types. This difference in the physical parameters of these bird types is the most plausible basis for differences in host selection by the feather mite. The distance phenogram also shows a close relationship between the 5th and 7th secondary remiges of the red-winged blackbird and starling (OTU's 11, 17, 18, 12). Also coupled to this group are the third primary and secondary feathers of the red-winged blackbird (OTU's 15 and 16). The phenogram distorts the relationship of the 7th primary in relation to the other primaries of the starling and red-wing. The ordination diagram presents a clearer picture (Figure 19), the minimum spanning tree (MST) shows the direct relation of the 7th primary (OTU 13) with the 5th primary of the red-wing (OTU 14) which was not as clear in the distance phenogram.

The more interesting data shown by the MST are the relationships of feather types. The starling feathers are somewhat related to each other in the ordination diagram. To these starling feathers, the primary and secondary remiges of the red-wing are clustered (Figure 19). The red-wing primaries (OTU 13, 14) relate closely to the starling primaries (OTU 7,8,9). The red-wing secondaries (OTU 16, 17, 18) and primary (OTU 15) cluster with the starling secondaries (OTU 10, 11, 12). These feather relationships shown by the MST appear to be born out in the mite population structure in these two bird types when this data is placed on the MST (Figure 19). In the red-wing, the mite population found on the primary feathers decreases sharply in the area of the 4th primary (Table 4) and other populations

Figure 19. Comparison of feather types of four birds, 24 OTU study. Phenogram based on taxonomic distances OTU's. Matrix correlation = 0.796.

BJ' - Blue Jay Primary Remige
BJ'' - Blue Jay Secondary Remige
ST' - Starling Primary Remige
ST'' - Starling Secondary Remige
RW' - Red-wing Primary Remige
RW'' - Red-wing Secondary Remige

Fig. 19

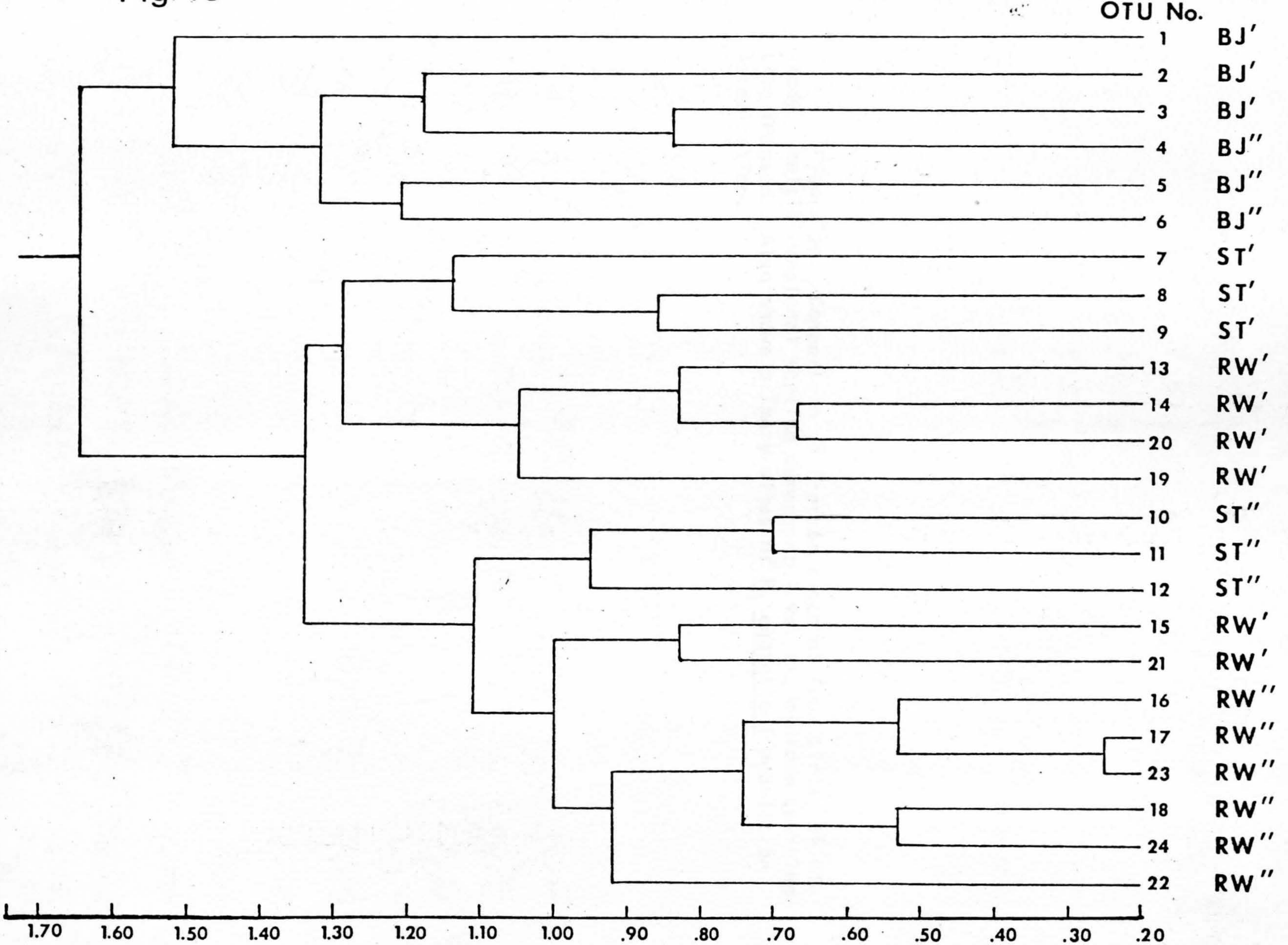
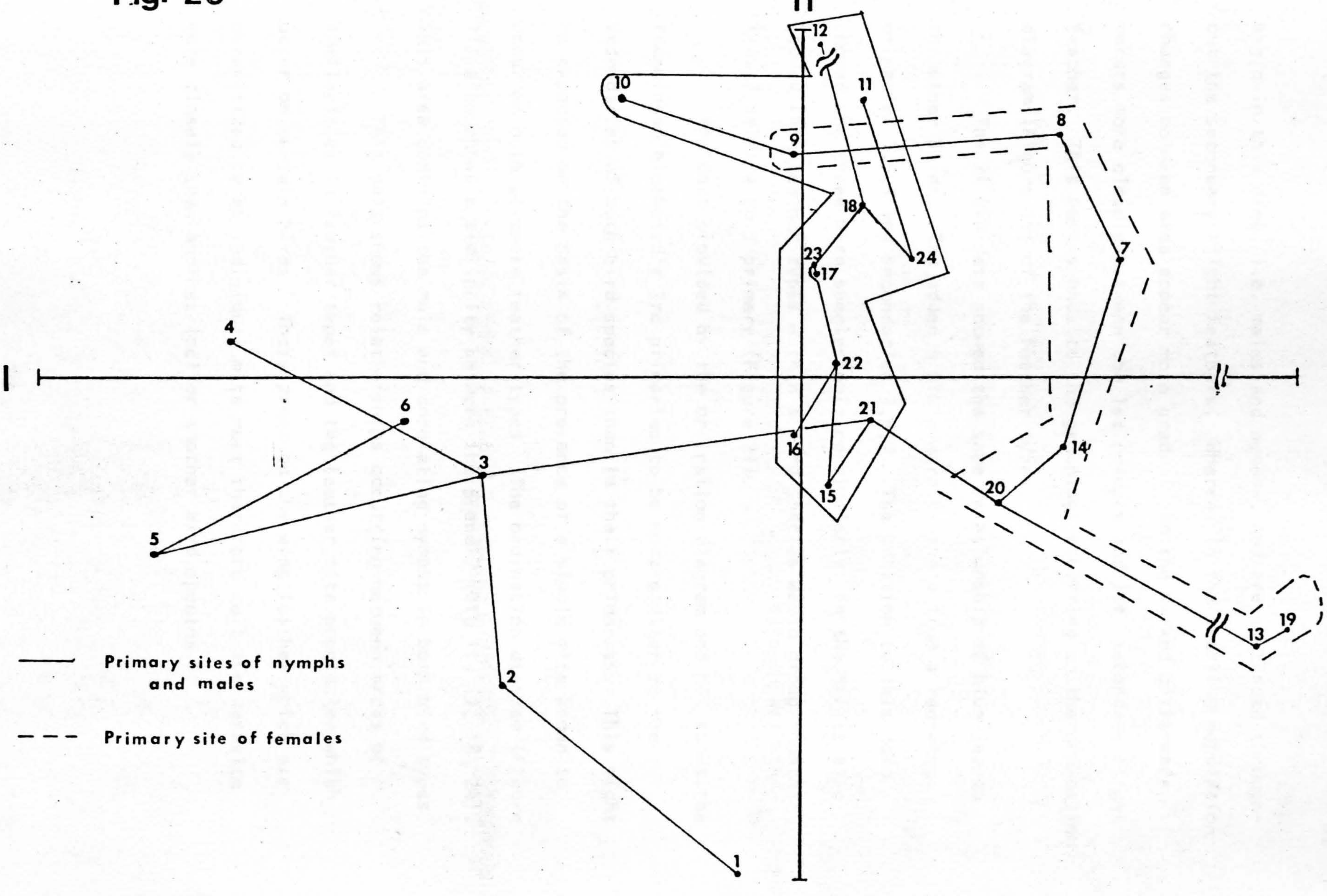

OTU No.
1 BJ′
2 BJ′
3 BJ′
4 BJ″
5 BJ″
6 BJ″
7 ST′
8 ST′
9 ST′
13 RW′
14 RW′
20 RW′
19 RW′
10 ST″
11 ST″
12 ST″
15 RW′
21 RW′
16 RW″
17 RW″
23 RW″
18 RW″
24 RW″
22 RW″
1.70
1.60
1.50
1.40
1.30
1.20
1.10
1.00
.90
.80
.70
.60
.50
.40
.30
.20

Figure 20. Comparison of feather types of four birds, 24 OTU study. Multidimensional scaling component I vs. II, minimum spanning tree imposed. Also shows primary sites of P. egglestoni population localization.

Fig. 20


II
I
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
—— Primary sites of nymphs and males
– – – Primary site of females

begin in this area, i.e. males and nymphs, and are continued throughout the secondary flight feathers. Whereas in the starling population changes between area appear more gradual and the marked difference occurs more closely between the 1st primary and 1st secondary flight feather. This corresponds to the groupings occurring on the ordination diagram (Figure 19) of the feather types.

The 24 OTU data showed the same relationship of blue jay to the other birds. The added 6 OTU's were feathers from a red-wing, primaries 3,5,7 and secondaries 3,5,7. The addition to this data showed the three bird species pairing similarly in the MST it also showed that feather types within a bird species would group together, i.e. 7 primary to 7 primary (Figure 21).

The data provided by the ordination diagram and MST shows the red-winged blackbird's 3rd primaries to be more similar to the secondaries of both bird species than to their primaries. This might be expected on the basis of the presence of a single mite known to occur on both of these feather types. The ordination diagram (Figure 21) also shows a similarity between the 5 and 7 (OTU 11, 12, 18, 24). This area contains the male and copulating nymphs in both bird types.

This data shows relationships occurring between areas of similarities in feather types and the feather mite population which occur on certain birds. These areas on the wing feather which are parasitized by an individual mite must therefore suit the parasite more closely than another loci or another bird species.

CONCLUSIONS

Dubinin's original concept of exposed versus unexposed areas of the flight feather supporting different mite populations can be expanded to different feather mite individuals (sexes and/or developmental stages) seeking different loci within and among birds. Within a mite species individuals appear to partition the host into acceptable and unacceptable loci for that individual's physical requirements.

The feather mite's micro- and macroenvironment have been shown to be quite diverse between and among birds, and between and among feather types. Yet within the niche are areas of similarity. It is this similarity which allows a particular mite species to inhabit a specific area on different birds. This can also be the case with different mite sexes and developmental stages within these different birds.

Within a particular mite species, in this study _Proctophyllodes egglestoni_, different sexes or developmental stages are capable of adapting to different feather sites on a particular bird species. The means of this adaptation can be differences in setae length, body length, specialized legs or a variety of other differences. Furthermore, these adaptions can involve combinations of individual differences.

Because the feather mite is adapted to specific physical host characteristincs, between hosts the mites' specific loci can vary. In some cases this loci can be wider or narrower on one bird compared to another. However the physical and biological parameters which characterize this loci, need to be roughly the same in order to support a population or individuals of a specific feather mite. It has been shown that the host need not always be of the same species, genera, or family to suit the spacial needs of a feather mite.

From this study it appears that when data on individual parasite loads are coupled with quantitative estimates of ecological and physical parameters among and within feather types and bird species, new insights can be gained in feather mite host-parasite associations.

LITERATURE CITED

Atyeo, W.T., and N.L. Braasch. 1966. The feather mite genus Proctophyllodes (Sarcoptiformes: Proctophyllodidae). Univ. Nebraska St. Mus. 5:1-354.

________, and J. Gaud. 1971. Feather mites (Analgoidea: Pterolichidae) of the hoatzin (Aves: Galliformes). Amer. Midland Nat. 86:152-159.

________, and P.C. Peterson. 1976. The species of the feather mite family Rectijaunidae (Acarina: Analgoidea). J. Georgia Entomol. Soc. 11(4):349-366.

Dubinin, V.B. 1938. Changes in the parasitic fauna of the glossy ibis (Plegadis, Falcinellus), produced by the age and migration of the host. Trudy Askrakhanskogo Gos. Zapovednika, 2:114-212. (In Russian).

________. 1947. Feather mites (Introduction to their study). Tezisy dokt. diss., Izd. Akad. Nauk. SSSR, Leningrad, 8 p. (In Russian).

________. 1948. Investigation of the adaptations of ectoparasites II. Ecological adaptations of feather mites and bird lice. Akad. Nauk. SSSR., Zool. Inst., Parazitol. Sborn., 9:191-222. (In Russian).

________. 1949a. Features of structure and biology of feather mites which inhabit the quills of feathers of terns. Akad. Nauk, SSSR., Zool. Ah., 28(5):421-430. (In Russian).

________. 1949b. New feather mites which parasitize in the downy part of wing feathers of birds. Akad. Nauk. SSSR., Doklady, N.S., 66(4):777-780. (In Russian).

________. 1950a. Feather mites of Gallinaceous birds of Kazakhstan. Izvestiia Akad. Nauk. Kazakhskou SSSR., No. 75, seriia parazit. (8):62-79. (In Russian).

________. 1950b. About routes of resettlement of feather mites of birds. Bull. Soc. Moskovskogo explorateurs nature. 55(2):29-42. (In Russian).

________. 1950c. Feather mites of wintering birds of the Lenkar anskian lowlands. Akad. Nauk. SSSR Baki Inst. Zool. Trudy 14:58-75. (In Russian).

Dubinin, V.B. 1950*d*. Systematic analysis of species of feather mites (Sarcoptiformes, Analgesoidea), parasites of Anatids. Magasin Parasitol. de L'Inst. Zool. Acad. D. Sc. URSS, 12:17-72. (In Russian).

________. 1950*e*. About the specificity of mites in connection with the evolution of their hosts. Advances in Contemporary Biology. 29(3):442-457. (In Russian).

________. 1951. *Feather Mites (Analgesoidea) Part 1. Introduction to their Study*. Fauna SSSR. Paukoobraznva, 6(5):1-363. (In Russian).

________. 1952. Adaptations of feather mites to the migration of birds and conditions of wintering. Acad. Sci. Tadshikistan SSSR. Issue 2:35-39. (In Russian).

________ and I. Vassilev. 1955. Ecologicofaunistic particulars of individuals of certain populations of feather mites (Acariformes, Analgespids) inhabitants of birds in different geological zones. Zool. Inst. Acad. Sci. Bulgaria, 5:91-114. (In Russian with English summary).

Dubinina, M.N. 1937. The parasitic fauna of the night heron (*Nycticorax nycticorax*) and their changes in connection with migratory hosts. Akad. Nauk. SSSR., Zool. Zh., 16(3):547-573. (In Russian).

Johnston, D.E. and J.B. Kethley. 1973. A numerical phenetic study of the quill mites of the family Syringophilidae. J. Parasitol. 59:520-530.

Kethley, J.B. and D.E. Johnston. 1975. Resource tracking patterns in bird and mammal ectoparasites. Misc. Publ. Entomol. Soc. Am., 9(5):231-236.

Lucas, A.M. and P.R. Stettehneim. 1972. *Avian Anatomy*, Part I. Agriculture Handbook 362. U.S. Government Printing Office, Washington, D.C., p 1-340.

Moss, W.W., P.C. Peterson, and W.T. Atyeo. A multivariate assessment of phenetic relationships within the feather mite family Eustathiidae (Acari). – In prep.

Peterson, P.C. 1975. An analysis of host-parasite associations among feather mites (Acari: Analgoidea). Misc. Publ. Entomol. Soc. Am., 9(5):237-242.

Rohlf, F.J., J. Kishpaugh, and D. Kirk. 1972. NT-SYS. Numerical Taxonomy System of Multivariate Statistical Programs. State Univ. New York, Stony Brook.

Van Tyne, Hosselyn and Andrew J. Berger. 1961. Fundamentals of Ornithology. John Wiley and Sons, Inc., New York, pp 1-624.

Welty, J.C. 1968. The Life of Birds. W.B. Saunders Co., Philadelphia. pp. 546.