INTERSPECIFIC ASSOCIATIONS BETWEEN EPIFAUNISTIC ARTHROPODS ON THE EASTERN CHIPMUNK, *TAMIAS STRIATUS,* AND AN OVERVIEW OF ARTHROPOD COEXISTENCE ON MAMMALS IN GENERAL

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ABSTRACT

Interspecific coexistence between arthropods epifaunistic on mammals is discussed, utilizing the community associated with the eastern chipmunk, *Tamius striatus,* in central Tennessee, for exemplary purposes. This community consists of 15 insect and mite species, the eight most abundant of which were subjected to statistical analyses. Significant positive associations were evidenced between the sucking louse, *Hoplopleura erratica,* and with three other species (the flea, *Ctenophthalmus pseudagyrtes,* the laelapid mite, *Androlaelaps casalis,* and the chigger mite, *Eutrombicula alfreddugesi*); the presence of any one of these three species resulted in statistically higher *H. erratica* densities when both were present on the same host individual. Comment is made on the occurrence of congeneric laelapid mites in the genera *Haemogamasus* and *Androlaelaps* on eastern chipmunks. Consideration is given to the difficulty of interpreting associations between epifaunistic arthropod species since some of these live permanently on the host while some are associated with it mainly during feeding; others normally utilize alternate microhabitats such as leaf litter or the host nest (some of these may be rapidly feeding or facultative hematophages) and some are phoretic. The situation is further complicated since many species colonize discrete areas of the host whether in the presence or absence of other species and furthermore, most epifaunistic species exhibit aggregated dispersion patterns with respect to densities on different host individuals. The nature of interspecific competition and coexistence between epifaunistic arthropods on mammals is discussed and because of the apparent significance of host grooming, circumstantial evidence is presented for the likelihood of the existence of some form of host-mediated competition.

INTRODUCTION

Epifaunistic arthropods associated with mammals are those forms exhibiting some degree of extended physical association with the host skin surface and its outgrowths (collectively termed the dermecos).

The exact nature of coexistence and any competition between epifaunistic arthropod species on mammals has long been a dilemma (Waage 1979; Marshall 1981). The principal conjecture lies with the determination of which factor(s) is (are) in short supply for potentially competing species. Although certain host individuals may carry large ectoparasite populations, blood/lymph/skin availability is not normally a limiting factor (Nelson et al. 1977; Marshall 1981; Kim 1985; Waage and Davies 1986). Competition for host space in its own right similarly does not seem to occur in the majority of situations since epifauna is often present at low densities on mammals (Kim 1985; Waage and Davies 1986) and most species are more concentrated on certain host sites than on others. Interference competition is plausible in some instances and many epifaunistic arthropods (certain beetles, triatomid bugs, sucking lice, cheyletid, erythraeid, parasitid and laelapid mites, pseudoscorpions, etc.) physically disturb or prey on the other dermecos inhabitants (Buxton 1939; Arthur 1976; Schofield 1982; Balashov 1984; Kim 1985) but data on interference competition are scant. Most previous studies have largely ignored the issue of possible current interspecific competition by explaining coexistence through evolutionary trends in the past acting to segregate interacting species by resource partitioning via niche contraction. Partitioning such as the utilization of different host sites (or host species), contrasting phenologies, different feeding modes and predictable size ratios have been noted (e.g., Jameson 1950; Jameson and Brennan 1957; Dubinina 1964, 1967; Nelson and Murray 1971; Parker and Holliman 1972; Nelson et al. 1975; Nilsson and Lundqvist 1979; Shepherd and Edmonds 1979; Day and Benton 1980; Nilsson 1981; Fritz 1983; Nelson et al. 1984) and are undoubtedly prevalent but offer little towards an understanding of the nature of any current competition between these species or what factors may have caused these patterns. A similar case can be presented for coevolution theory (Waage 1979, 1980). Also, there is currently much disagreement over the prevalence of interspecific competition in natural communities and on the significance of such interaction in molding community structure and size (Strong et al. 1984).

The present survey represents an attempt to analyze coexistence and to determine the importance of any interspecific competition between mammalian epifauna by exemplifying the arthropod community normally residing on the eastern chipmunk, *Tamias striatus,* in central Tennessee. Various authors have recorded the epifauna of this mammal (e.g., Hyland and Fain 1968, Fain and Hyland 1970; Amin 1976a,b; Whitaker et al. 1979; Payne and Jones 1982; Goddard et al. 1986) and Durden (1983a) has surveyed those species associated with eastern chipmunks in central Tennessee.

The interpretation of the term 'interspecific competition' is a necessary prerequisite to this work. Because of its applicability and wide acceptance, the definition used by Pontin (1982) as 'an interaction between two (or more) species which results in reduced population size of both (or all) competing species' will be used here. Conversely, two or more interacting species may show increased densities when they occur together (mutualism) or just one of the species might benefit from this association (commensalism). Density measurements for the various arthropod species both in the presence and absence of other species and the reciprocal situation should therefore reveal these relationships.

MATERIALS AND METHODS

The epifauna associated with the small population of eastern chipmunks live-trapped within a five ha area of deciduous woodland about 11 km southwest of Nashville, Davidson County, Tennessee, was continuously surveyed between October 1977 and November 1979 (so that chipmunks were also examined during their winter torpor by trapping those individuals that became active above-ground during mild spells). Captured chipmunks were anesthetized with ether and systematically searched for epifauna by carefully pushing fur aside with probes and fine forceps; a low-power binocular microscope aided this effort. Any epifauna located was removed, identified, recorded and, in most cases, returned alive onto the same host individual (voucher specimens are principally in the collections of the Smithsonian Institution, Washington, D.C. and those of the author). Host attachment sites were also recorded and converted to mean numbers of each species per square cm of surface area for each of the designated host sites (Figure 1). Chipmunks were dye-marked to facilitate recognition of individuals and released at their capture site as soon as full recovery from anesthesia was evident. To avoid data bias, records were not taken from any given animal more than once per month although most entered traps more frequently than this.

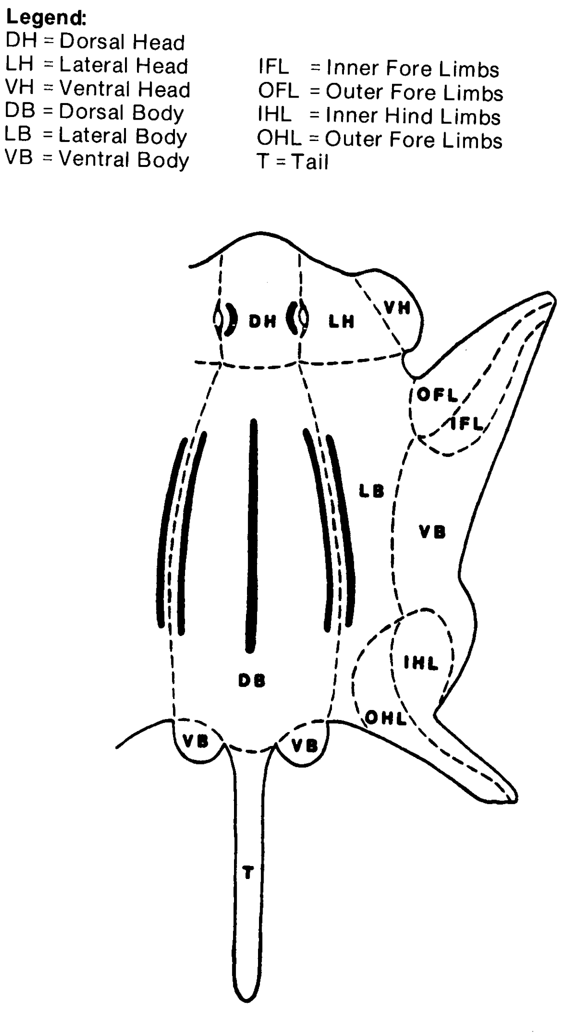
Tests for interspecific associations between the epifauna recorded were accomplished using Cole's (1949) coefficient by considering the presence or absence of each species in the presence of other species on the same host individual and by Mann-Whitney U tests applied to the numbers of each species ocurring in the presence versus absence of the other species.

Biologies of all epifaunistic arthropod species collected during this survey were studied in order that any other factors that might influence associations between them could be considered (Durden 1981, 1982, 1983a,b).

RESULTS

Records were taken from 381 chipmunk captures over the survey duration. The eleven most abundant arthropod species taken from chipmunks during this period are listed in Table 1 together with their principal infestation parameters. An additional four species were also collected (the hystrichopsyllid flea, *Epitedia wenmanni,* the lathridiid beetle, *Lathridius liratus,* larvae of the cuterebrid botfly, *Cuterebra emasculator,* and an undetermined species of cheyletid mite) but each of these was represented by a total of less than five specimens and will not be considered further.

Coefficients of association between those epifaunistic arthropod species recorded on more than 15 hosts are given in Table 2 and reveal a highly significant positive association between the sucking louse, *Hoplopleura erratica,* and the chigger mite, *Eutrombicula alfreddugesi.* Mann-Whitney U tests (Table 3) show significantly higher densities of *H. erratica* when any of three other species were present on the same host individual; these were, the flea, *Ctenophthalmus pseudagyrtes,* the laelapid mite, *Androlaelaps*



Legend:
DH = Dorsal Head
LH = Lateral Head
VH = Ventral Head
DB = Dorsal Body
LB = Lateral Body
VB = Ventral Body
IFL = Inner Fore Limbs
OFL = Outer Fore Limbs
IHL = Inner Hind Limbs
OHL = Outer Fore Limbs
T = Tail

Figure 1. Schematic representation of designated chipmunk body surface divisions used for host site preference analyses (areas not to scale). Initials refer to sites spelled out in Table 4.

Table 1. Infestation parameters for epifaunistic arthropods from 381 eastern chipmunks in central Tennessee for 1977-1979.

Epifauna	Phenology	% hosts inf.[1,2]	$\bar{X}$/host[1,2]
Lice:			
Hoplopleura erratica (Osborn)	Year-round	27.0	5.4
Fleas:			
Ctenophthalmus pseudagyrtes Baker	Spring & Autumn	16.4	0.2
Flies:			
Eutrichota finitima (Stein)	Apr.-Nov.	14.3	0.2
Mites:			
Balaustium sp.	Jun.-Jul.	8.6	0.2
Androlaelaps casalis (Berlese)	May-Nov.	28.3	1.3
Haemogamasus pontiger (Berlese)	Jul.-Aug.	7.7	0.1
Eulaelaps stabularis (Koch)	Oct.-May	20.9	0.6
Dermacarus hylandi Fain	Feb. & May	(2 chipmunks infested)	
Aplondontopus sciuricola Hyland & Fain[3]	—	—	—
Eutrombicula alfreddugesi (Oudemans)	Jun.-Oct.	19.8	8.0

[1] These numbers do not correspond to those in Table 4 because some specimens became detached from hosts during processing and could not be assigned to a host site.
[2] Infestation parameters are collective figures for those months in which the species listed was recorded.
[3] *A. sciuricola* was sampled only in October, 1979 when 33.3% of chipmunks yielded mites; detailed data were therefore not taken continuously.

Table 2. Coefficients of association (C) between epifaunistic species on eastern chipmunks in central Tennessee.[1]

Species[2]	N(chipmunks)	C-S.E.	x^2	P	Association
H. erratica/A. casalis	281	-0.04±0.16	0.15	0.5-0.8	Random
H. erratica/E. stabularis	18	+0.02±0.36	0.23	0.5-0.8	Random
H. erratica/E. alfreddugesi	143	+0.41±0.10	15.29	< 0.001	Positive
C. pseudagyrtes/H. erratica	184	+0.16±0.09	2.35	0.1-0.2	Random
C. pseudagyrtes/E. finitima	67	-0.07±0.55	0.30	0.5-0.8	Random
C. pseudagyrtes/A. casalis	135	+0.05±0.12	0.008	0.9-0.95	Random
C. pseudagyrtes/Haemogamasus sp. A	60	+0.26±0.14	1.91	0.1-0.2	Random
E. finitima/H. erratica	151	+0.16±0.10	1.74	0.1-0.2	Random
E. finitima/A. casalis	142	-0.11±0.27	0.42	0.5-0.8	Random
E. finitima/E. alfreddugesi	90	+0.27±0.20	1.01	0.2-0.5	Random
Haemogamasus sp. A/*H. erratica*	85	+0.12±0.13	0.22	0.5-0.8	Random
Haemogamasus sp. A/*E. finitima*	65	+0.32+0.15	2.49	0.1-0.2	Random
Haemogamasus sp. A/*A. casalis*	81	+0.44±0.24	2.10	0.1-0.2	Random
Haemogamasus sp. A/*E. alfreddugesi*	72	+0.27±0.19	0.82	0.2-0.5	Random
E. alfreddugesi/A. casalis	145	+0.14±0.11	1.20	0.2-0.5	Random

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[1] Data are taken only from those months in which both species listed were present.
[2] The species that infested fewer chipmunks is listed first.

Table 3. Comparison between numbers of epifaunistic species in the presence versus absence of other species (on the same chipmunk individual) by the Mann-Whitney U-test.

Species[1]		N(hosts)	$\bar{X}$	U	P[2]
H. erratica:	*C. pseudagyrtes* absent	27	10.6		
	C. pseudagyrtes present	10	82.1	4.53	< 0.01*
H. erratica:	*A. casalis* absent	46	14.0		
	A. casalis present	30	21.6	3.34	< 0.01*
H. erratica:	*E. alfreddugesi* absent	11	1.8		
	E. alfreddugesi present	14	22.4	1.65	< 0.05*
A. casalis:	*H. erratica* absent	55	6.4		
	H. erratica present	30	2.6	0.73	0.75 > 0.77
A. casalis:	*E. alfreddugesi* absent	26	8.9		
	E. alfreddugesi present	11	3.6	0.12	0.53 > 0.55
E. alfreddugesi:	*H. erratica* absent	12	28.9		
	H. erratica present	14	53.1	0.20	0.55 > 0.57
E. alfreddugesi:	*A. casalis* absent	18	60.8		
	A. casalis present	11	7.2	0.48	0.67 > 0.69

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[1] *Records are only from those months in which both species listed were taken.*
[2] *Probability values taken from Giri (1975).*
* *Designates significant interactions*

casalis, and the chigger, *E. alfreddugesi.* Although the densities of some species were lower in the presence of certain other species, none of these relationships were statistically significant.

Table 4 gives host site data for the three epifaunistic species exceeding 100 specimens and also occurring on more than 15 chipmunks. In addition to the species considered in Table 4 (all of which showed significantly contrasting predilection sites), some other arthropods showed obvious site preferences although data were less numerous. All *Haemogamasus* spp. mites were taken from the host tail, rump and outer hind limbs, *Aplodontopus sciuricola* mites (phoretic deutonymphs) were recorded only from the host tail hair follicles and most of the c. 3,200 *D. hylandi* deutonymphal mites were situated on the host rump and posterior flanks.

The fairly extensive dispersion data assessing the distributions of the arthropod species with respect to numbers infesting different host individuals are given by Durden (1981). These data (segregated by infestation periods or bimonthly for *H. erratica*) reveal aggregated dispersions for most species, exceptions being for *C. pseudagyrtes* (except for August-December 1978, when dispersion was aggregated), and the anthomyiid fly, *Eutrichota finitima,* both of which conformed to the Poisson series showing that infestation by these two species was essentially random. Also, *Haemogamasus* sp. A showed random infestations when scarce but aggregation when more abundant. *Hoplopleura erratica, A. casalis,* the mite *Eulaelaps stabularis* and *E. alfreddugesi* all showed aggregation except when any of these species was scarce when dispersion was random.

DISCUSSION

Coexistence in the epifaunistic community of eastern chipmunks.

In analyzing the constituent members of the epifaunistic arthropod community of *T. striatus* recorded in this survey, it is noteworthy that four species of confamilial (laelapid) mites were taken (belonging to the genera *Androlaelaps, Haemogamasus* and *Eulaelaps),* and also that two congeneric *(Haemogamasus* spp.) mites were recorded. According to some sources (see citations referenced in the Introduction), the occurrence of congeneric, or even confamilial, organisms (and taxonomically unrelated species occupying very similar niches) in the same habitat, normally occurs only if avoidance mechanisms are followed to reduce conflict for resources. Thus, Jameson (1950) and Jameson and Brennan (1957) elaborately showed that closely related epifaunistic species on their study mammals were segregated by host species, host sites, contrasting phenologies, feeding strategies/apparatus, or sizes (conforming to Dyar-Hutchinson ratios) or occurred on the same host species but in contrasting vegetational zones. This trend cannot be said to hold for the laelapid mite species taken in this study; all occurred on the same host species (although none are specific to *T. striatus)* in the same probably too low for significant interspecific competition. It seems possible, however, that some interspecific competition between the vegetation type and occupied very similar host sites. *Eulaelaps stabularis* is nevertheless separable through its contrasting phenology (one that has not previously been reported for this species) and its larger size. Although there is some difference between mouthpart morphologies for these species, there is some confusion regarding the exact food sources each of them utilizes (Evans et al. 1968; Krantz 1978). Neither *Haemogamasus* species was common, however, and their population densities were more frequent mites, *A. casalis* and *Haemogamasus* sp. A was occurring although data from Tables 2 and 3 do not readily support this view.

Over much of its geographic range, *T. striatus* is infested by the laelapid mite, *Androlaelaps fahrenholzi* (see Whitaker and Wilson 1974), but in this survey, its congener, *A. casalis,* was recorded. Competitive exclusion between these two species may have occurred in the evolutionary past with contrasting outcomes in different regions ('the ghost of competition past' (Connell 1980)). Other explanations including random distributions or historical accident are also feasible however. The situation is further complicated since *A. fahrenholzi* may actually represent a complex of species (Goff 1980).

The exact nature of the positive associations of *H. erratica* with *C. pseudagyrtes, A. casalis* and *E. alfreddugesi* in this survey was not resolved. There could be some advantage gained by one species utilizing feeding holes made by another, or certain chipmunk individuals (such as inefficient self-groomers) might provide more favorable habitats for more than one species; numerous other

Table 4. Density of epifaunistic arthropod species on different host sites of eastern chipmunks.

		***Androlaelaps casalis*[1]** (30 hosts, 132 mites)		***Eutrombicula alfreddugesi*[1]** (30 hosts, 1439 chiggers)		***Hoplopleura erratica*[1]** (61 hosts, 1648 lice)	
		% of mites	**Density[2]**	**% of chiggers**	**Density[2]**	**% of lice**	**Density[2]**
Head:	Dorsal	3.8	0.07	1.3	0.27	7.0	0.85
	Lateral	3.0	0.05	0.1	0.01	5.9	0.70
	Ventral	0	0	0	0	3.3	0.70
Dorsal Body:	Ant.	0	0	0	0	30.3	1.16
	Med.	5.3	0.10	0.9	0.18		
	Post.	17.4	0.33	12.0	2.45		
Lateral Body:	Ant.	0	0	0.2	0.02	25.1	0.54
	Med.	0	0	1.1	0.13		
	Post.	3.8	0.04	1.5	0.26		
Ventral Body:	Ant.	0	0	0	0	7.1	0.28
	Med.	0	0	1.5	0.31		
	Post.	2.3	0.04	12.6	2.71		
Fore Limbs:	Inner	0.8	0.02	7.9	2.19	4.4	0.34
	Outer	0	0	0	0		
Hind Limbs:	Inner	0.8	0.01	52.8	8.37	16.6	0.74
	Outer	29.6	0.43	7.2	1.13		
Tail		33.3	0.58	1.0	0.20	0.3	0.03

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[1] Using x^2 tests, all three epifaunistic species showed host site preferences significant at the 99% level.

[2] Density values given represent calculations of the mean number of each species per square cm of host surface area for infested chipmunks.

perturbations are feasible. It is interesting that the presence of *H. erratica* did not reciprocally increase densities of any of the three species that positively influenced its own numbers, so that these associations may not be truly mutualistic but instead reflect commensalism in favor of *H. erratica.* Also notable, is the fact that no significantly negative (potentially competitive) interactions were recorded between epifaunistic species in this study.

There was some segregation of phenologies between the arthropod species recorded in this survey. *Hoplopleura erratica* was the only species taken from chipmunks throughout the year although there was a substantial winter (December-March) population decline. In fact, all species except *E. stabularis* declined or disappeared at this time. *Eulaelaps stabularis* conversely was most abundant during this period possibly reflecting either a phenological displacement (in response to interspecific competition?) or successful adaptation to winter feeding (if *E. stabularis* is an obligate hematophage this could be significant since most chipmunks are torpid with restricted peripheral blood flow at this time although arousal of the host to activity can be frequent). *Ctenophthalmus pseudagyrtes* was taken in distinct spring and autumn broods which is interesting since this flea may be principally parasitic on voles, shrews and moles. Most of the other species exhibited phenologies concentrated over the summer months (April-November) and were not readily separable.

Other investigations into associations between mammalian epifauna.

Previous surveys have also revealed interspecific associations between arthropods on mammals. Evans and Freeman (1950) noted a strong negative association between the fleas, *Ctenophthalmus agyrtes nobilis* and *Malaraeus penicilliger,* on field mice, *Apodemus sylvaticus,* but a moderately positive one between these species on bank voles, *Clethrionomys glareolus,* in England, a phenomenon which they attributed to contrasting properties of the dermecos of the two host species. Reisen et al. (1976) noted both positive and negative significant associations between various arthropod species on hibernating *Myotis velifer* bats in Oklahoma. Nilsson and Lundqvist (1979) similarly found significantly positive and negative associations between species infesting small mammals in Sweden and Iceland with most relationships showing some degree of negative association. Faulkenberry and Robbins (1980) reported positive associations between flea species on gray-tailed voles, *Microtus canicaudus,* in Oregon. All these surveys, except the present one, have considered only the presence or absence of each epifaunistic species on the same host individual without consideration of population densities. Strictly then, for cases of negative association, these should probably more accurately be considered as measures of avoidance, competitive exclusion, or some other structuring influence. Stable interspecific competition allowing coexistence of both (or all) species in the same habitat (without competitive exclusion) is however, a viable situation (Pontin 1982; Strong et al. 1984; Kim 1985). In most cases, stable coexistence would appear to be a necessity for the occurrence of numerous arthropod species on the same host individual over reasonably long durations although this may be influenced by other factors such as the grooming activities of the host.

Host site usage by epifauna.

Considerable host site segregation is characteristic of the epifauna inhabiting the dermecos of *T. striatus;* tail hair follicle occupation by *A. sciuricola* on this mammal has been reported previously by Hyland and Fain (1968). Such resource utilization patterns are widespread for arthropods on mammals (see references cited in the Introduction) and often are of a non-interactive nature (Brooks 1980), i.e., they are evident in the presence or absence of other species. This probably reflects, as has been suggested in the literature, the consequences of interspecific competition in the past acting to segregate species on the dermecos via niche contraction. Other plausible explanations exist, however, such as random colonization of hosts on which saturation levels of the constituent species are not reached (Price 1977, 1980) or some selective advantage gained by aggregating species that accordingly maximizes their reproductive rate (Rhode 1979). A small, constant predilection site would also facilitate location of conspecifics for scarce arthropods, aiding mate encounters (Nilsson 1981; Kim 1985) which is especially useful if the arthropod has not evolved aggregation phenomomes. Another mechanism by which host site aggregation could be strongly influenced is via the grooming activities of the host. Murray (1961, 1965), Bell et al. (1962) and Weisbroth et al. (1974) have demonstrated large-scale differences between the infestation levels and bodily distributions of ectoparasites on grooming restrained versus control laboratory rodents (this involved restricted oral grooming in Murray's investigation but restricted limb grooming in the other experiments).

Although host site predilections are usually non-interactive, it is interesting that many are not and that under favorable conditions, other adjacent sites may be invaded. As mentioned above, prevention of host grooming allows ectoparasite populations to disperse from their usual sites (on the head for laboratory rodents) to other areas. Shepherd and Edmonds (1979) and Nilsson (1981) have similarly noted rapid (within days) radiative dispersal from the usual site when some factor(s) allow(s) an increase in abundance of certain arthropod species. In the former example, the authors suggested that this resulted from the flea species involved having a short-term (c. 100 years) association with its lagomorph host since it evolved on marsupials (i.e., insufficient time to adapt significantly to the predilection site on the new host). Nilsson and Lundqvist (1979) present data illustrating a shift in host site use by the laelapid mite, *Laelaps agilis,* when the confamilial species *Hirstionyssus latiscutatus,* is also present in the epifaunistic community. An interesting situation exists for five species of *Listrophorus* fur mites infesting muskrats, *Ondatra zibethicus,* in Indiana (Bauer and Whitaker 1981) whereby each species has its greatest density within a certain focus on the host but also occurs on the adjacently surrounding fur at slightly lower densities (together with other species at various densities) gradually diminishing in prevalence with increasing distance from its focal predilection site. Different *Listrophorus* species therefore have different predilection sites but also share these with congeners at lower densities, a consequence of each species tracking certain properties of the dermecos that gradually intergrade, according to the authors. The degree of adherence to a predilection site appears to be related to the evolutionary time scale that the host/arthropod species association has persisted. Long-term relationships, where predilection sites would most likely have been reinforced, seem to be characterized by non-interactive distributions, whereas short-term relationships are characterized by radiative dispersal from this site when the opportunity arises. Both strategies have advantages but evolution would normally tend to produce the former (Balashov 1984). This is well illustrated by larvae of the tick, *Ixodes ricinus,* where a small area on the head (usually the ears) on the field mouse *(A. sylvaticus)* host is located rapidly independent of any host interference (Nilsson and Lundqvist 1978). The

Listrophorus/muskrat situation is perhaps a special case since Bauer and Whitaker (1981) suggested that the various listrophorid species evolved independently (with independent predilection sites) on muskrats in adjacent geographic regions and have relatively recently invaded the Indiana host populations (and retained their predilection sites).

Dispersion of epifauna within the host population.

Dispersion patterns of ectoparasites on mammals are usually aggregated with respect to numbers on different host individuals (e.g., Reisen et al. 1976; Durden 1980; Gyorkos and Hilton 1982; Langley and Fairley 1982) often conforming to certain mathematical distributions such as the negative binomial series (Nilsson and Lundqvist 1978, 1979). My data show that similar aggregation is also inherent in the distributions of some other epifaunistic species. In many cases, I consider this to reflect low exchange rates between chipmunk individuals for these species so that those hosts originally supporting small (versus absent) populations of a species early in the season eventually develop larger populations through reproduction and low dispersal rates of the arthropod. My data for those species showing random distributions at low density but aggregation at higher densities, support this view. Hazards and infrequent opportunities associated with dispersal may often promote confinement to one host individual (or its burrow/nest) for many arthropods. Also, when host exchanges do occur, those arthropods transferring to new host individuals are frequently lost soon afterwards (Durden 1983b) possibly due to resistance mechanisms (immune responses, tough integument or higher grooming efficiencies) against epifauna by certain host individuals. Janion (1975) has, however, recorded dispersal of fleas to other host individuals when a certain peak flea index on the original host was reached. Other theories addressing host/parasite heterogeneities (a complex series of random infestations, non-random distribution of infective stages and the presence of one parasite influencing the probability of additional infestations) should also be considered as affecting arthropod distribution patterns in many cases however (Esch et al. 1977).

Host grooming, competition and coexistence in epifaunistic communities.

What is the nature of interspecific coexistence between epifaunistic arthropods on mammals? The foregoing discussion has illustrated that the special ecological characteristics of many of these species do not appear to involve the usual interspecific competitive associations (with the probable exception of interference competition since aggressive and predatory epifauna obviously displace or consume other species in some cases). Exploitative competition between species involves competition for limited resources (food, space, etc.) but, as previously noted, such commodities do not normally appear to be limiting for epifaunistic arthropods. A clue towards an understanding of the nature of interspecific competition in this context may be gleaned from the experiments demonstrating increased ectoparasite densities on mammals restrained from grooming. Host grooming may have a profound influence on the density (and bodily distribution) of epifauna (with larger, sedentary species often being restricted to regions receiving less grooming attention). Exceptions predictably seem to occur for the agile species that can usually escape the attentions of the host animal. In addition to the above-mentioned well documented studies, other surveys have strongly indicated that the major source of ectoparasite mortality is often by host predation or grooming. Cattle restrained from grooming have significantly larger experimental populations of *Boophilus microplus* ticks (Bennett 1969) and captive field mice and voles are capable of ridding themselves of experimental flea infestations (Nikitina and Nikolaeva 1979). Overal (1980) noted more frequent grooming by the Panamanian bat, *Arbiteus jamaicensis,* when ectoparasitic *Megistopoda aranea* streblid fly infestations were larger; he considered this grooming to account for most of the fly mortality. Sheep keds, *Melophagus ovinus,* are removed from the fleece by being devoured by their hosts or by insectivorous birds (Evans 1950). The preening activities of some birds are of definite value in removing their chewing life. Foster (1969) has noted that orange-crowned warblers, *Vermivora celata,* are highly efficient at removing their lice and Nelson and Murray (1971) have recorded enormous increases in four louse species associated with domestic pigeons following beak clipping to prevent preening; this resulted in drastic weight and health deterioration of these birds including one fatality. Other studies implicating the significance of host grooming for epifauna removal include those by Corbet (1956) for hippiboscid louse flies, Snowball (1956) for ticks on cattle, Timm (1983) for chewing lice on gophers and Kethley and Johnson (1975), Nelson et al. (1975, 1977), Arthur (1976), Nilsson and Lundqvist (1979), Marshall (1981), Nilsson (1981), Balashov (1984) and Kim (1985) for epifauna in general. The principal requirements for a self-grooming mechanism to result in significant epifauna removal and subsequent non-interactive host site distributions (see later) are essentially those outlined by Murray (1961) for the removal of sucking lice from laboratory mice, i.e., that the technique is efficient, that sufficient time is spent grooming, that an adequate area of the body is groomed and that epifauna move into accessible areas. From other studies it therefore seems possible that an indirect interspecific competition, mediated through the grooming activities of the host is prevalent for epifaunistic arthropods. Waage (1979) made similar speculation and proposed the term 'host-mediated competition.'

Host-mediated competition should ideally be linked with density dependent grooming by the host so that as epifauna increases in abundance, a threshold density is reached and intensive grooming ensues (although self-grooming is implicated here, mutual host interactions can be of definite value (Bell and Clifford 1964; Ledmell et al. 1970) Weisbroth et al. 1974; Nelson et al. 1984)) until the arthropod density is reduced to acceptable levels. Rust (1974) studied the population dynamics of the chewing louse, *Geomydoecus oregonus,* on the pocket gopher, *Thomomys bottae,* in California, and considered the existence of such a density dependent population regulation mechanism for these lice to be likely. This hypothesis could also explain the development of non-interactive predilection sites by acting to prevent arthropod species from radiating from infestation sites as their numbers increase. Any radiative dispersal would be checked by the host grooming response and diminished to a focus within the original infestation site. With recurrence of these reactions, what originally may have represented casual site preferences for the arthropod species, become reinforced over time through evolutionary adaptation to the specific attributes of the host site (length and density of fur, predominant hair type, epidermal thickness and hardness, skin secretions, body temperature, availability and type of blood capillaries, etc.). Similarly, if two (or more) epifaunistic species orginally colonized adjacent host sites then any area of infestation overlap between them would surpass the threshold density (collectively) for initiation of grooming so that arthropods in the overlap zone would be eliminated first, again reinforcing niche partitioning (Waage 1979). Nelson and Murray (1971) provided strong evidence that the contrasting host sites utilized by four species of chewing lice on pigeons are caused by the preening activities of the host since louse populations on birds prevented from grooming colonized abnormal sites by radiating out from their normally occupied sites. If the predilection sites or other requirements for two (or more) epifaunistic species are extremely similar then competitive exclusion could occur as may be the case for *A. casalis* and *A. fahrenholzi* on eastern chipmunks. Establishment of additional species into an epifaunistic community should depend on the similarity between niches for the potential colonizing species and those already established. Successful host invasion for a colonizer with requirements overlapping those of established species should be more difficult if host grooming is increased by its additional presence (Waage and Davies 1986) and its competitive exclusion will be more likely if it is sensitive to grooming. For epifaunistic species showing positive associations, as for some species on *T. striatus,* host mediated competition may not be significant or the disadvantages presented by it are outweighed by the mutualistic benefits gained; alternatively, host individuals supporting multi-species infestations may simply be inefficient groomers.

How do aggregated dispersion patterns (with respect to numbers on different host individuals) of epifaunistic arthropods correlate with host-mediated competition (since on many potential host individuals, epifauna is absent or scarce while on others it is abundant)? This aggregation, initiated by factors outlined previously, could facilitate this phenomenon and consequent niche partitioning, on those few (usually, although epifaunal aggregation is sometimes less distinct) host individuals supporting large numbers of arthropods so that it should act more strongly under these circumstances. When exchange of epifauna between hosts occurred in the evolutionary past then those arthropods migrating to 'cleaner' hosts would have exhibited their, already partially acquired, new non-interactive host site distributions.

A problem with interpretation and experimental manipulation of interspecific competition and coexistence between epifaunistic arthropods is that many species are not confined to the host dermecos. In fact, many are equally or more prevalent in burrow/nest debris than on mammals. Others (most fleas, reduviid bugs, hematophagous Diptera, etc.) are associated with the host only in certain stages (larvae and adults often occupy very different niches) or during feeding. Obviouly, host-mediated competition would act most strongly on those species permanently associated with the host dermecos and least so on those species at the other end of the spectrum. Although this generally appears to hold true, there does appear to be good spatial and temporal segregation of many hematophagous Diptera (Nematocera and Tabanidae) on mammals possibly because too many bites in close proximity or in rapid succession initiate defensive or evasive host behaviors.

It is anticipated that exceptions to this general scheme of host-mediated competition will surface and, at present, the major deviation appears to be for large grazing mammals whose ectoparasite densities and site usages may be more heavily influenced by seasonal meteorological factors (e.g., Murray 1965; Nelson et al. 1975); the epifauna of these animals may also be removed mainly by insectivorous birds. Nevertheless, Waage and Davies (1986) have presented field data strongly indicative of host-mediated competition between bloodsucking insect species on a mammal. These authors similarly note that host-mediated competition theory is similar to 'enemy-free space' models for insects on plants (Jeffries and Lawton 1984) except that, in the former situation, the 'enemy' is the host itself.

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