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A STUDY OF THE HOST DISTRIBUTION AND SOME RELATIONSHIPS OF BITING LICE (MALLOPHAGA) PARASITIC ON BIRDS OF THE ORDER TINAMIFORMES[1]

PART II[2]

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CORRESPONDENCE BETWEEN SIZE OF HOST AND PARASITE

The effect of the environment upon the biota is often manifested by certain changes in the structure and size of the organism. In a genus of Mallophaga distributed over a group of birds, the size of the parasite is roughly related to that of the host (Harrison, 1915). Clay (1951) presents several instances of this correlation but the small number of her examples is insufficient to utilize statistical tests to check the validity of this idea.

The tinamous and their Mallophaga presented an opportune situation to investigate this phenomenon more inclusively. The wing length has been judged to be one of the best criteria to designate size in birds. An attempt was made to record the wing length of tinamous from the taxonomic literature. This proved unfeasible due to the various methods of measuring wings and also the tendency of some authors to cite just the range of the measurements. It was necessary to measure the 1500 tinamous in the Conover Collection of the Chicago Natural History Museum to have a set of reliable measurements. The wing of each individual was held flattened against a steel ruler and the length to the nearest millimeter was taken between the proximal end of the humerus and the apex of the longest primary. To arrive at a value which could be considered typical of the species or subspecies, a weighted mean was used which took into account differences in the number of males and females in the measured series.

The problem of picking structures to measure in the Mallophaga as indices of general size is more difficult. Abdomen and total length are some of the better criteria of size but are too variable within the small series of many species to be of use. The head length at the midline between the apex of the clypeal margin and the occipital margin usually proved to be one of the most constant within species yet showed consider-

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[2]Part I of this series appeared in the July, 1957, issue of these ANNALS (Volume 50, Number 4). Generic allocations of Mallophaga are those of Hopkins and Clay (1952), with the following exceptions: *Austrokelloggia* Carriker 1936 is not separable from *Kelloggia* Carriker 1903, *Heterogoniodes* Carriker 1936 is at most a well-defined species group of *Megapeostus* Carriker 1936, and *Heptapsus* Carriker 1936 is a synonym of *Pterocotes* Ewing 1929.

able range throughout the genus. The prothorax showed a more constant size but was usually the same length throughout a genus.

To ascertain if size of host and parasite show a mutual relationship, the correlation coefficient r was computed using the formula,

$$r = \frac{\Sigma xy - \bar{x}\Sigma y}{\sqrt{(\Sigma x^2 - \bar{x}\Sigma x) \quad (\Sigma y^2 - \bar{y}\Sigma y)}}.$$

Student's *t*-test was calculated from

$$t = \frac{r\sqrt{N-2}}{\sqrt{1-r^2}},$$

to determine whether the observed correlation coefficients differed significantly from zero.

Due to the small sample size of less than 100, the standard error of *r* cannot be used to check its significance. However, Fisher's *z*-transformation may be used in establishing fiducial limits to the value of the correlation coefficient in the population from which the sample *r* has been drawn (Snedecor, 1946: 150).

Table I illustrates the method of computing *r* for the females from the genus *Strongylocotes*. The correlation coefficients, the *t*-test results and their probabilities (*P*) along with the 95% fiducial limits are recorded in Table II. These limits are those in which 95 cases out of 100 may be expected to contain the true population parameter. Genera such as *Megaginus* and *Pseudophilopterus* are not included as an inadequate number of specimens was available from different hosts. The small number of species in such genera as *Lamprocorpus*, *Trichodopeostus*, *Nothocotus* and *Cuclotocephalus* prevent a computation of *r*.

It may be noted from Table II that all of the

TABLE I

METHOD OF COMPUTING *r* FOR THE RELATION BETWEEN THE HEAD LENGTH OF FEMALE MALLOPHAGA OF THE GENUS *Strongylocotes* AND THEIR HOSTS

Host	Mallophaga: Mean Head Length in mm. (x)	No.	Birds: Mean Wing Length in mm. (y)	No.
Tinamus solitarius	1.071	2	262.8	4
T. major robustus	0.975	5	248.1	11
T. m. fuscipennis	0.975	2	243.4	15
T. m. peruvianus	0.954	3	240.3	22
T. osgoodi osgoodi	1.014	2	245.9	9
Nothocercus j. julius	0.972	5	197.3	8
N. bonapartei frantzii	0.888	6	224.2	5
Rhynchotus r. rufescens	0.976	13	203.1	27
R. r. maculicollis	1.020	9	214.1	10
Nothura boraquira	0.778	2	148.5	35
Crypturellus cinereus	0.643	3	172.1	30
C. soui meserythrus	0.822	2	133.7	25
C. s. modestus	0.683	4	133.9	22
C. s. harterti	0.763	2	131.0	29
C. s. nigriceps	0.739	2	129.2	8
C. s. inconspicuus	0.774	6	130.7	22
C. obsoletus obsoletus	0.792	3	165.9	20
C. o. punensis	0.744	2	161.6	9
C. o. griseiventris	0.782	2	165.9	7
C. brevirostris bartletti	0.743	3	140.6	13
C. undulatus undulatus	0.779	6	183.8	45
C. noctivagus garleppi	0.791	8	170.9	12
C. strigulosus	0.787	3	165.7	21
C. cinnamomeus goldmani	0.785	2	167.6	5
C. c. intermedius	0.771	2	165.5	10
C. c. vicinior	0.810	4	170.2	22
C. c. delattri	0.813	3	167.7	6
C. boucardi boucardi	0.782	9	172.4	22
C. parvirostris	0.645	2	117.1	43
C. tataupa tataupa	0.733	5	132.1	49

$\Sigma x = 24.804$
$N = 30$
$\Sigma x^2 = 20.890016$
$\bar{x} = 0.8268$
$\Sigma xy = 4506.0099$

$\Sigma y = 5305.3$
$N = 30$
$\Sigma y^2 = 987595.15$
$\bar{y} = 176.843333$

$$r = \frac{4506.0099 - 0.8268(5305.3)}{\sqrt{(20.890016 - 0.8268(24.804)) \; (987595.15 - 176.843333(5305.3))}}$$

$r = +0.8706$

correlation coefficients are strongly positive, and as indicated by the *t*-test, differ significantly from zero. The reliability of *r* is fairly good with the exception of the ***Heptapsogaster minor*** group. In this instance, *r* tends not to be very reliable as a consequence of the small sample size.

It seems reasonable to state that the data indicate a well-defined relationship between size of host and size of parasite. A probable causal agent in this instance might be one of limitation of territory. Small species of tinamous as *Crypturellus soui* harbor approximately the same number of species of Mallophaga as much larger birds like *C. boucardi.* Apparently the same number of niches are available on both these host species although the size of the *Lebensraum* varies greatly. Consequently, there may have been a selection for size in these Mallophaga in their environment. Food supply probably does not play a role as there is an abundance regardless of host size.

From the viewpoint of the ecosystem, the most significant finding is that the entire Mallophaga fauna react as a whole to their environment. For instance, one may examine all twelve species from *Crypturellus soui* and note that almost every species is smaller than its counterpart on *C. boucardi.*

RELATION BETWEEN NUMBERS OF BIRDS INFESTED AND MALLOPHAGA SPECIES PRESENT

In studying the distribution of plant and animal species in communities and their subdivisions, the characteristic of "over-dispersion" or "contagious distribution" has been shown to be of general occurrence. This subject has been the topic of recent investigations (Fisher, Corbett, and Williams, 1943; Cole, 1946; and Bliss and Fisher, 1953). The main thesis of these papers seems to be concerned not as to the actual presence of over-dispersion but what type of mathematical model best fits the situation.

Communities of ectoparasites are among the most favorable types to analyze by this technique. The ease of collecting an entire population of obligatory ectoparasites such as Mallophaga, Anoplura, and Acarina from a single bird or mammal plus the concept that each individual in the host species population is a small ecological community creates ideal conditions for a study of this sort.

If every bird were equally liable to be infested with different numbers of species of Mallophaga, the differences between various individuals would be purely random and the distribution would conform to the Poisson series (Bliss, 1953). As Bliss points out, a Poisson distribution may be recognized by its expected variance being equivalent to the mean. In cases where the variance is significantly greater than the mean, "over-dispersion" is present. The negative binomial has been shown by Bliss to be as useful as any of the other distributions, such as Fisher's logarithmic series and the Neyman contagious type A, in studies on ectoparasites. This present study has utilized the Poisson, negative binomial, and logarithmic series distributions in an analysis of the Ischnoceran populations. The methods of fitting these distributions have been discussed in the papers of Fisher, Corbett, and Williams (1943) and Bliss and Fisher (1953). The estimate for the negative binomial has the exponent ***k*** computed by the method of maximum likelihood, which tends to give a more efficient fit than one based either upon the first and second moments or upon the ratio of the total number of units in the sample to the number of units without organisms. The observed distributions of

TABLE II

CORRELATION COEFFICIENTS BETWEEN SIZE OF HOST AND SIZE OF PARASITE

MALLOPHAGAN GENUS	STRUCTURE MEASURED	SEX	NO. (*N*) OF HOST AND PARASITE POPULATIONS	*r*	*t*	*P*	95% FIDUCIAL LIMITS Lower	95% FIDUCIAL LIMITS Upper
Pseudolipeurus	Head length[a]	♂♂	16	+.8138	5.2396	<.001	+.533	+.933
" "	" "	♀♀	17	+.8214	5.5777	<.001	+.567	+.934
Strongylocotes	Head length[b]	♂♂	23	+.8388	7.0603	<.001	+.628	+.935
" "	" "	♀♀	30	+.8706	9.3636	<.001	+.744	+.937
Kelloggia (s.l.),	Prothorax	♂♂	47	+.7482	7.5649	<.001	+.586	+.852
including *Austrokellogia*	with	♀♀	39	+.8161	8.5899	<.001	+.674	+.902
Physconella	Head length[b]	♂♂	17	+.8284	5.7278	<.001	+.578	+.936
" "	" "	♀♀	17	+.8078	5.3076	<.001	+.535	+.928
Megapeostus	Head length[b]	♂♂	26	+.9223	11.6910	<.001	+.832	+.965
" "	" "	♀♀	25	+.8874	9.2249	<.001	+.760	+.950
Pectenosoma	Thorax length	♂♂	19	+.8529	6.7357	<.001	+.651	+.942
" "	" "	♀♀	18	+.8680	6.9921	<.001	+.674	+.950
Heptapsogaster	Head length[b]	♂♂	8	+.8163	3.4616	.01	+.263	+.965
minor group	" "	♀♀	9	+.7425	2.9328	.02	+.155	+.942

[a]Measured at midline between anterior edge of dorsal anterior plate and occipital margin.
[b]Measured at midline between anterior clypeal margin and occipital margin.

Mallophaga species per bird skin and the expected frequencies computed from the previous mentioned distributions are shown in Table III.

Table IV lists the Chi square (X^2) values, degrees of freedom (n) and probability (P) for each type of distribution fitting the observed frequencies. Although P is below the usual .05 level of significance for any one of the distributions for *Crypturellus* and *Tinamus*, the Chi square values for the negative binomial are the lowest of the three distributions. This lack of agreement may be attributed to the small value of n.

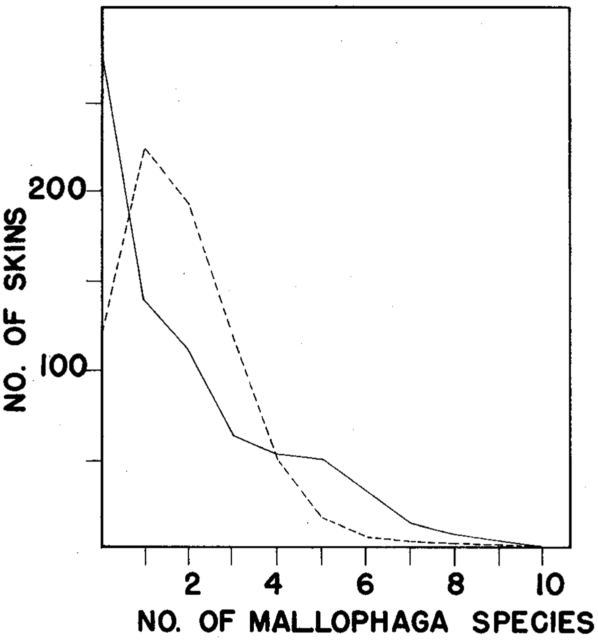

FIG. 1.—Graph showing observed and expected (Poisson) number of different species of Mallophaga encountered on skins of the host genus *Crypturellus*. The observed distribution is represented by a solid line while the calculated Poisson is indicated by a hyphenated line. As an example, three species of lice were found on 64 skins while if they had been randomly distributed (Poisson), three species would have occurred on 116 skins.

Bliss (1953) believes that better agreement can often be achieved by testing the agreement of the observed with the expected second and third moments of the negative binomial. *Nothocercus* shows a significant fit ($P = .40$) to the logarithmic series. The value of N (the number of skins observed) was fairly small in this instance in contrast to the much larger series of *Crypturellus* and *Tinamus*. It should be mentioned that when the zero class is disregarded, the negative binomial converges to the logarithmic series. The balance of the genera, particularly *Rhynchotus* and *Nothura*, show agreement with the negative binomial and even closer conformity to the Poisson series. These last four genera have a maximum of two to five species of Mallophaga occurring on a single skin while *Crypturellus*, *Tinamus* and *Nothocercus* may harbor up to eight or nine species simultaneously. Bliss (1953) states, "This phenomenon of substantial agreement with the Poisson at low densities and with the negative binomial at higher densities has been observed with both plant and animal populations".

A portion of the data from Table III has been graphed in figures 1 and 2. At the level of four species per skin for *Crypturellus* and three species per skin for *Tinamus*, there is a crossing of the curves for the observed and Poisson values. For the number of species above this point, a greater number are encountered on an individual host than could be expected by chance. An interspecific aggregation is present which appears to make the bird more favorable for multiple infestation once a minimal number of species are present. There is evidently a conditioning of the environment by the presence of several species with possible diversified feeding habits which allow additional species to occur.

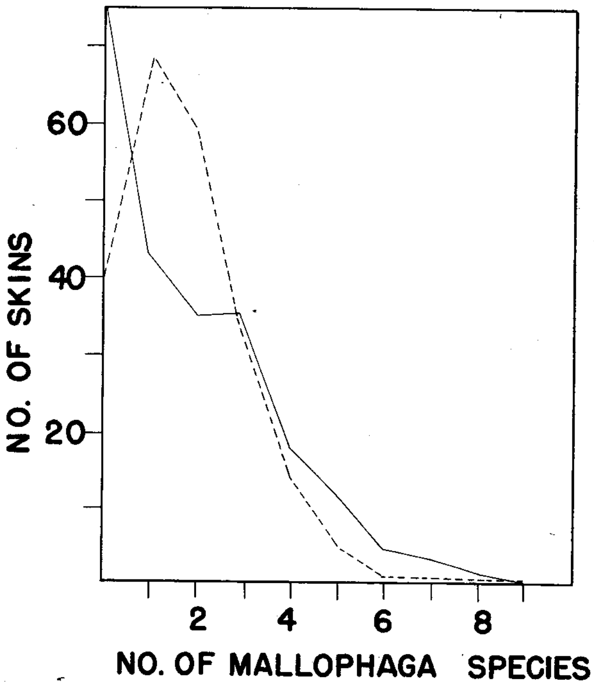

FIG. 2.—Graph showing observed and expected (Poisson) number of different species of Mallophaga encountered on skins of the host genus *Tinamus*. The observed distribution is represented by a solid line while the calculated Poisson is indicated by a hyphenated line.

ASSOCIATION OF MALLOPHAGA SPECIES ON HOSTS OF THE GENUS *Tinamus*

A paper by Cole (1949) provides a method of measuring the amount of interspecific association between pairs of species. By use of his coefficient, it is possible to express the positive or negative association of two species beyond that which

TABLE III

OBSERVED AND CALCULATED NUMBERS OF SPECIES OF LICE PER SKIN

No. of Species of Mallophaga per Skin (x)	No. of Bird Skins Observed (f)	Expected Number of Skins		
		Negative Binomial	Logarithmic Series	Poisson
	Genus *Crypturellus*			
0	275	260.04	——	124.48
1	140	171.47	212.00	221.02
2	113	110.43	88.78	196.21
3	64	70.55	49.57	116.13
4	53	44.89	31.14	51.55
5	50	28.50	20.86	18.30
6	12	18.06	14.56	5.42
7	15	11.43	10.45	1.37
8	9	7.23	7.66	0.30
9	4	4.57	5.70	0.06
10+	0	7.83	19.28	0.16
	$735=N$			
	Genus *Tinamus*			
0	75	66.83	——	39.61
1	43	58.65	72.08	68.61
2	35	40.20	29.34	59.42
3	36	24.99	15.93	34.31
4	18	14.73	9.73	14.86
5	12	8.40	6.33	5.15
6	4	4.68	4.30	1.49
7	3	2.57	3.00	0.37
8	1	1.39	2.14	0.07
9+	0	1.56	6.15	0.11
	$224=N$			
	Genus *Nothocercus*			
0	4	7.65	——	3.43
1	19	10.45	20.89	9.19
2	8	9.69	8.82	12.31
3	4	7.68	4.96	11.00
4	5	5.45	3.14	7.37
5	2	3.62	2.12	3.95
6	2	2.31	1.49	1.76
7	3	1.42	1.08	0.68
8	3	0.85	0.80	0.23
9+	0	0.88	2.70	0.08
	$50=N$			
	Genus *Rhynchotus*			
0	10	7.34		7.17
1	7	14.19		14.21
2	17	13.89		14.07
3	11	9.17		9.26
4	6	4.60		4.60
5	1	1.87		1.82
6+	0	0.94		0.87
	$52=N$			

TABLE III (*Continued*)

No. of Species of Mallophaga per Skin (x)	No. of Bird Skins Observed (f)	Expected Number of Skins		
		Negative Binomial	Logarithmic Series	Poisson
	Genus *Nothoprocta*			
0	66	61.87		61.10
1	43	58.14		58.81
2	42	28.01		28.30
3	9	9.21		9.08
4+	0	2.77		2.71
	160 = N			
	Genus *Nothura*			
0	144	144.53		144.54
1	64	60.05		60.06
2	8	12.48		12.48
3	1	1.73		1.73
4	2	0.18		0.18
5+	0	0.03		0.01
	219 = N			
	Genus *Eudromia*			
0	20	20.73		20.72
1	14	14.15		14.15
2	7	4.83		5.07
3+	0	1.29		1.06
	41 = N			

would occur if the species were randomly distributed. Cole's coefficient has the advantage of covering the range of +1 to −1, with the former indicating perfect association, the latter negative association and zero signifying random association. Species of Mallophaga occurring on the genus *Tinamus* were utilized for this special study. Each host specimen was considered as a single sample. The three species groups of *Heptapsogaster* (*minuta*, *grandis* and *parvula*) were not used as the nymphal stages of each could not be distinguished with sufficient certainty under the dissecting microscope. For the balance of the species, their presence could be determined accurately just by the presence of nymphs.

For computing Cole's coefficient, the data were set up in 2 X 2 tables as follows, with species A being the "least frequent of the two species under consideration."

		Species B		
		present	absent	
Species A	No. of times present	a	b	$a+b$
	No. of times absent	c	d	$c+d$
		$a+c$	$b+d$	$a+b+c+d=n$

The coefficient of association, with its standard error; when $ad \geqq bc$, is,

$$C \pm \sigma_C = \frac{ad-bc}{(a+b)\ (b+d)} \pm \sqrt{\frac{(a+c)\ (c+d)}{n(a+b)\ (b+d)}}\ .$$

When $ad < bc$, two other formulae cited by Cole (1949) are used.

The results are listed in Table V. With the exception of the coefficient of association between *Pseudolipeurus* and *Rhopaloceras*, all combinations of species achieve a positive association between 16% and 70% of the possible time.

The Ischnoceran fauna of a bird may be divided into a number of morphological types which occupy different ecological niches on the same bird (Clay, 1950). On the head and neck is found a round-bodied type with a large head to accomodate the enlarged mandibles and musculature. The wing niche is occupied by an elongate type with a narrow head and much smaller mandibles. Other morphological types are intermediate between these two and are presumed to inhabit the back and other niches. Of the Mallophaga occurring on *Tinamus*, *Pseudolipeurus* is found on the wings, *Rhopaloceras* on the head and the others such as *Pterocotes*, *Strongylocotes*, *Ornicholax* and *Kelloggia* on the dorsum. The coefficients of association showed the concurrence of several species on the same

TABLE IV

CHI SQUARE VALUES FOR EACH TYPE OF DISTRIBUTION AND THEIR PROBABILITIES

HOST GENUS	POISSON			NEGATIVE BINOMIAL			LOGARITHMIC SERIES		
	X^2	*n*	*P*	X^2	*n*	*P*	X^2	*n*	*P*
Crypturellus	466.0260	5	.0005	28.3387	7	.0005	113.7655	8	.0005
Tinamus	74.7845	4	.0005	13.4414	4	.005	57.3921	4	.0005
Nothocercus	16.8886	3	.0005	11.7644	3	.005	1.6218	2	.40
Rhynchotus	5.7118	3	.10	5.7700	2	.05			
Nothura	1.0633	1	.20	2.4491	1	.10			
Nothoprocta	11.9356	2	.001	14.0236	2	.0005			
Eudromia	0.1501	1	.60	0.1681	0	——			

host is a normal situation and is to be expected with reasonable certainty in this group of ectoparasites. This persistence of an interspecies population may be interpreted as signifying a lack of competition between the Mallophaga on the back and also the possible cooperative interaction previously mentioned. This lack of competition is attributed to several density-dependent factors inherent to this particular host-parasite relationship. The preening activity of the host is an important method of regulating population size of the lice. Populations of lice increase tremendously in instances where a bird's bill is deformed to the point where it cannot preen itself (Worth, 1940, and Kartman, 1949). The common occurrence of taking dust baths in certain groups of birds, including the tinamous, is considered by some workers to be of significance in affecting population size. A final factor, possibly the most important, is the diversity of niches which permits a relatively large number of species to coexist in a rather limited micro-geographic area. Chandler (1916) has pointed out that the tinamous are the only group of birds with plumules in the feather tracts themselves but not in the intervening apteria. This lack of plumules between the separate feather tracts may thus produce a greater diversity of habitat for Mallophaga than is found in other groups of birds.

TABLE V

COEFFICIENT OF ASSOCIATION BETWEEN MEMBERS OF SOME OF THE GENERA OF MALLOPHAGA PARASITIZING *Tinamus*

PAIRS OF MALLOPHAGA	*C* ± σ
Kelloggia and *Pterocotes*	+0.473±.112
Kelloggia and *Strongylocotes*	±0.696±.118
Kelloggia and *Ornicholax*	+0.545±.125
Kelloggia and *Pseudolipeurus*	+0.343±.175
Pterocotes and *Strongylocotes*	+0.261±.187
Pterocotes and *Ornicholax*	+0.288±.125
Pterocotes and *Pseudolipeurus*	+0.290±.104
Strongylocotes and *Ornicholax*	+0.305±.067
Strongylocotes and *Pseudolipeurus*	+0.307±.099
Ornicholax and *Pseudolipeurus*	+0.158±.100
Rhopaloceras and *Kelloggia*	+0.171±.187
Rhopaloceras and *Pterocotes*	+0.370±.104
Rhopaloceras and *Strongylocotes*	+0.328±.106
Rhopaloceras and *Ornicholax*	+0.328±.107
Rhopaloceras and *Pseudolipeurus*	+0.016±.072

The possible effect of diversity of the habitat has been shown to be important in the distribution of certain fleas (Evans and Freeman, 1950). In studying the association of *Ctenophthalamus agyrtes nobilis* (Rothschild) and *Malaraeus penicilliger* (Grube) on *Apodemus s. sylvaticus* (Linné) and *Clethrionomys glareolus brittanicus* (Miller), they found Cole's coefficient of interspecific association to be −0.808±.175 for the former host and +0.537±.109 for the latter one. They attribute this difference of interacting behavior to the fur characteristics of *Clethrionomys*—somewhat longer and coarser than that of *Apodemus*. Evans and Freeman conclude that this may allow *C. agyrtes* and *M. penicilliger* to exist side by side on that host in contrast to the direct competition which may exist on *Apodemus*.

SUMMARY

1. A well-defined relationship exists between the size of host and parasite. This was demonstrated by use of the product-moment correlation coefficient, *r*, which was computed for seven Mallophaga genera and their hosts. Small host species harbor approximately the same number of parasite species as large-sized hosts but possess a fauna containing much smaller species.

2. A study of the relation between the numbers of birds infested and the number of different species of Mallophaga present has indicated that a greater number of species occur on a given host than would be expected by chance. An interspecific association is present which is favorable for the occurrence of mixed species populations.

3. A positive association between pairs of Mallophaga species on the genus *Tinamus* was demonstrated by use of Cole's coefficient of association. This positive association has been in part attributed to a possible cooperative interaction between species and a diversity of the habitat which permits several species to coexist in a limited microgeographic area.

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