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A REASSESSMENT OF THE NUMERICAL DISTRIBUTION OF WATERMITES
(ARRENURUS spp.)
ON DRAGONFLIES IN RELATION TO PARASITISM AND DISPERSAL

by

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SYNOPSIS.

Analysis of published data on the attachments of watermites to dragonflies show highly “clumped” distributions suggesting adaptation for dispersal rather than parasitism. Variations in the degree of “clumping” with increasing mite loads suggest that searching is random but that host discovery is greatest when mite searching coincides with host emergence.

Analysis of the numerical distribution of mites phoretic on individual insect hosts suggested that the prevalence of species in which attachment frequency fitted a negative binomial distribution provided evidence for the aggregation of “phoretics” within the range of the host from which dispersal of mites could be assumed to take place on attachment to the host insect (Binns, 1975). The associations of the larvae of Arrenurus reflexus Marshall (Hydrachnellidae: Arrenuridae) with the dragonfly Leucorrhina intacta (Hagen) (Insecta: Odonata) and of the related A. fissicornis with its dragonfly host Libellula luctuosa Burm. (Mitchell, 1967) were omitted from this discussion since the relative importance of dispersal and parasitism in mites in which engorgement of the attached larva clearly took place (e.g. Mitchell, 1967, 1969; Treat, 1969), is difficult to assess. However, data previously analysed (Binns, 1975) did include some records for parasitic Hydrachnellids (Efford, 1963) and for others in which the degree of parasitism was less certain (e.g. Killington & Bathe, 1946). Here, MacNulty (1971) claimed that small numbers of attached mites themselves indicated phoresy rather than parasitism. However, Mitchell (1967) suggested that, since many species of Arrenurus from isolated habitats lack the parasitically-feeding larval stage, the main role of larval association with host insects, as in the majority of Arrenurus species, was dispersal between relatively short-lived, aquatic habitats. Re-examination of Mitchell’s (1967) data provides interesting confirmation of previous suggestions regarding mite attachment and dispersal (Binns, 1975) and a possible resolution of the problem of phoretic dispersal versus parasitism.
ATTACHMENT FREQUENCY IN *Arrenurus* spp.

Two theoretical patterns of mite-attachment were considered by MITCHELL (1964): (i) a uniform parasitism requiring an exact regulation of the number of parasites per host, such as CROFTON (1971 b) assumed would be common in parasites exerting lethal effects, thus preventing a general reduction of host vitality due to pathogenicity (e.g. ABDEL-MALEK, 1949; UCHIDA & MIYAZAKI, in Münchberg, 1954), and (ii) a "clumped" distribution where relatively few host individuals carry the majority of the parasites. A statistical examination of the frequency distribution of individual mite attachments was not attempted by MITCHELL (1967), though it was inferred that *A. fissicornis*, in which the incidence of parasitism was 98% of hosts (cf. MITCHELL, 1964), exhibited a "clumped" distribution and *A. reflexus*, a more uniform or random distribution.

Using data for mite numbers from samples of dragonflies, taken both sequentially and from different host emergence-zones (MITCHELL, 1967; Tables 1 & 2), estimates of variance ($s^2$) for twelve populations of each species of *Arrenurus* were obtained using the formula: variance ($s^2$) = (mean mite number $\times$ coefficient of variation)$^2$; both statistics obtained from MITCHELL (1967). The figures thus derived were then plotted against the mean number of attached mites ($m$) to give an estimate of the structure of mite distribution (Figs. 1 & 2, cf. TAYLOR, 1961). Each plot was then tested against a Poisson distribution in a $\chi^2$ test (Table 1) using the formula $\chi^2 = s^2 \times (N-1)$ (SOUTHWOOD, 1966).

<table>
<thead>
<tr>
<th>Libellula luctuosa</th>
<th>Leucorrhina intacta</th>
</tr>
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<tbody>
<tr>
<td><strong>$s$</strong></td>
<td><strong>Zones</strong></td>
</tr>
<tr>
<td>Times</td>
<td>3.3(8)</td>
</tr>
<tr>
<td>Times</td>
<td>2.4(5)</td>
</tr>
<tr>
<td>Times</td>
<td>16.4(14)</td>
</tr>
</tbody>
</table>

$\chi^2 \times 10^{-2}$. Bracketed figures = number of insects in sample.

In both *A. reflexus* and *A. fissicornis* the calculated values greatly exceeded the expected $\chi^2 (P < < 0.001)$ such that the index of dispersion ($\chi^2 \div (N-1)$) (SOUTHWOOD, 1966) exceeded unity in each of the twenty-four populations of *Arrenurus*. This suggested that, in the majority of populations, each species displayed a "clumped" (but otherwise undefined) distribution (cf. MITCHELL, 1967; 1969: cf. BINNS, 1975).

MITCHELL (1969) considered host discovery as the matching of mite and host habitats within the "mite-host intersect". Where this was "narrow", i.e. the degree of coincidence of the mite and host habitats was limited, host insects could be expected to carry many fewer or many more mites than the mean. This qualitative description accords with a "clumped" distribution (see, e.g. WATERS, 1959) and is consistent with the occurrence of parasites which CROFTON (1971 a) characterised by their negative binomial distributions (e.g. EFFORD, 1963). These were expected to arise by several mechanisms, one of which (CROFTON, 1971 a; No. 2) was the non-random distribution of infective stages (cf. MITCHELL, 1969).

CROFTON (1971 b) suggested that, where a parasite is greatly "over dispersed", i.e., has a highly clumped distribution (see SOUTHWOOD, 1966), such that $k < 1$ ($k$ being the exponent...
of the negative binomial equation), pathogenic effects of the parasite are rarely significant in determining the equilibrium between a host and parasite population since the parasite population rarely reaches a sufficient size due to the interplay of ecological factors other than parasitism (when such a parasite may be considered as "harmless"). This supports Mitchell's (1969) suggestion that Arrenurus populations are limited by factors operating prior to host exploitation. These ultimately govern the interplay of the host-parasite populations, both up to and during the process of host selection, when non-random distribution of infective stages reflects the extent of population constraints limiting the time and places where larvae are active in host finding. Uneven host discovery could then further reflect at least two other factors (Mitchell, 1969); larval searching behaviour (which may itself be restricted by habitat), and their readiness to attach to hosts already carrying mites (Crofton, 1971 a).

Attachment frequency and site of attachment.

The mode of attachment of both species of Arrenurus as examined by Mitchell (1967) — asymmetrical groupings of mite larvae on the host abdomen — apparently allowed an unrestricted distribution of attachments leaving ample membrane surface for further attachments (cf. Crofton, 1971 a). However, in some mites the attachment site does appear to be restricted; e.g. to lateral ranks (Efford, 1963; Binns, 1972), sutures (Mitchell, 1959) or scattered points on the body surface (Soarec, 1942). It has been assumed that these defined, symmetrical arrangements, which are characteristic of host-specific or "stenoxenic" associations (Treat, 1969), limit interference with host locomotion (Efford, 1963). While Efford demonstrated interspecific competition for attachment sites between parasites on Mayfly nymphs, the distribution of attachments for a given species of mite was unaffected by increasing load. However, restriction of attachment sites clearly provides an upper limit or point of truncation of attachment frequency which would be significant in limiting parasite loads, absolutely, thereby preventing lethal effects on the host (see above) or, as in Arctoseius cetratus, a phoretic which is a predator of the eggs and larvae (Binns, 1972; cf. Treat, 1973), restricting the level of predation on the progeny of the host. In such cases, neither must attachments limit host fecundity by interference with copulation.

In the cases so far examined (Binns, 1975 and in the present paper), loading constraints disruptive of negative binomial or other "clumped" frequency distributions have not been found. However, in Digamasellus fallax, a nematophagous phoretic of Lycoriella auripila (Diptera: Sciaridae) more "excessive clumping" of populations than would be expected have occurred (Binns, 1973) which indicates a tendency towards more uniform loads \( \frac{s^2}{m} < 1 \). Similarly, in apparently stenoxenic mites (Binns, 1975; Fig. 1) a direct relation between \( k \) and increasing mite frequency was noted (cf. Taylor, 1961). Each species of Arrenurus (Fig. 1 & 2) appeared to show greater variance \( (s^2) \) when average loads were maximum (cf. Mitchell, 1967; 1969), suggesting that clumped distributions occurred even at relatively high frequencies (cf. Binns, 1975). However, in A. reflexus, which has a stenoxenic association with L. intacta (Mitchell, 1967), mite samples from both sexes appeared to show a decreasing degree of "clumping" with increased loads with successive samples in time (Fig. 1; circles) as was also, but less clearly, the case in A. fiscicornis (Fig. 2). Further, previous observations suggested that stenoxenic associations appear to favour the female (Binns, 1972;
FIG. 1: *Arrenurus reflexus* on *Leucoorrhina intacta*. Distribution of attachment frequency in two species of *Arrenurus* from samples of male and female dragonflies taken at different times and host-emergence zones. (Redrawn from Mitchell, 1967).

cf. 1973; TREAT, 1969; 1973). In *A. fissicornis*, which is most numerous on *L. luctuosa* but which regularly occurs on three other hosts (MITCHELL, 1967), mites were more numerous but appeared to be less "clumped" on male hosts (Fig. 2).

This suggests that larval searching is random and that host discovery is greatest when the mite is most numerous (cf. BINNS, 1975). Thus, the peak of larval searching coincides with the end of the emergence period of *L. intacta* (cf. MITCHELL, 1967) and with the emergence of males of *L. luctuosa*.

**DISPERSAL AND PARASITISM.**

Random distributions of parasite loads \(\frac{s^2}{m} = 1\), requiring precise regulation of numbers and reflecting a common range of mite-host habitats (MITCHELL, 1967; 1969), have apparently yet to be demonstrated. Such conditions would, however, remove both the necessity and the possibility for dispersal (BINNS, 1975). The apparent absence of "parasitism" of this type among externally attached mites therefore suggests that at least the initial adaptive role of host attachment is phoretic dispersal, the characteristic, "clumped" frequency distribution of which
Fig. 2: *Arrenurus fssicornis* on *Libellula luctuosa*. Distribution of attachment frequency in two species of *Arrenurus* from samples of male and female dragonflies taken at different times and host-emergence zones. (Redrawn from Mitchell, 1967).

is maintained, even though the attached mite imbibes the fluids of the host and is "parasitic". Thus, in both species of *Arrenurus*, the relationship between mite and host habitats appears to produce a distribution of mites adapted for dispersal, i.e. movement of phoretically attached individuals away from areas of aggregation within the range of the host (Binns, 1975). Thus, "If the survivorship of mites is relatively high on the periphery (of the "mite-host intersect") the mites tend to broaden the intersect" (Mitchell, 1969) and achieve a redistribution within the range of the host; i.e. a "dispersal" (see Southwood, 1966) away from areas of aggregation. This appears to be characteristic of purely phoretic mites (Binns, 1975) and of those which may be (secondarily) parasitic.

While dragonflies appear to return to water with their loads largely intact (Mitchell, 1967), Davies (1969) found that loads of *Sperchon* on blackflies, a day or more old and netted away from streams, were much smaller than on newly emerged flies. The preponderance of *A. fssicornis* on the males of *L. luctuosa* has survival value in that these spend a greater amount of time over water (Mitchell, 1967). In this species (Mitchell, 1964; 1967) detachment begins with mites falling from their hosts so that there is variation in the persistence of attachment within species (cf. Treat, 1973). However, attached mites may outlive the hosts (Greenberg, 1961) and such variations in mite loads with time must be considered in assessments of host age based declining mite counts (Mitchell, 1967; cf. Corbet, Longfield & Moore, 1960).
Mites with non-parasitic larvae are perforce localised owing to ineffective dispersal (Mitchell, 1964) and are therefore unable to colonise temporary habitats available to dispersing forms. However, adaptation for dispersal, beginning with phoresy, and tending to parasitism, would clearly be expected, the initial distribution of mites between habitats again being non-random. In fact, Mitchell (1957) suggested that the primitive watermite life-cycle involved a dispersing larval stage, the loss of which is a secondary feature. However, "pupal parasitism" (Grenier, 1943) suggests an alternative derivation of associations with insects, beginning with a non-dispersing larva and leading to phoresy and parasitism.

Summary.

Estimates of the distribution of the larvae of two species of watermite (Arrenurus spp.) based on values of variance ($s^2$) derived from published accounts of their attachment to their dragonfly hosts, showed that assumed a non-random, "clumped" distribution. The aggregation of infective stages within the range of the host, which is thus reflected, is considered as indicating that the association with the host is primarily dispersive, as in phoresy, rather than parasitic. The requirements and mechanisms for limiting attachment frequency are discussed. Variations in the degree of "clumping" with increasing mite load suggest that searching is random but that host discovery is greatest when the mite is most numerous.

SOMMAIRE.

Des estimations de la courbe de répartition des larves de deux espèces de l'acarien (Arrenurus spp.), basées sur des valeurs de la variance, $s^2$, citées dans des publications sur l'attachement de ces acariens à leurs hôtes (les libellules) ont montré que, dans les deux cas, ces courbes ont une forme non-aléatoire, avec des points de haute concentration. On considère que l'aggrégation, aux endroits fréquentés par l'hôte, des acariens au stade de développement infective, qui est montré par la forme de ces distributions, indique que l'association de l'hôte avec les acariens est de nature dispersive comme dans la phorésie, plutôt que parasitaire.

On aminé les conditions nécessaires, et les mécanismes, pour limiter la fréquence de l'attachement des acariens à leur hôte. Le fait que le degré auquel les courbes de répartition ont des points de haute concentration se modifie, à mesure que le nombre des acariens est plus grand, suggère que la recherche des hôtes serait aléatoire, que leur découverte, cependant serait la plus fréquente, lorsque le nombre des acariens est le plus grand.

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