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LOCAL DISTRIBUTION OF PSOCOPTERA IN THE MATO GROSSO, CENTRAL BRAZIL

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ABSTRACT

The Psocoptera collected on different vegetation types and in leaf litter in central Brazil from September 1968 to May 1969 are enumerated, and their distributions discussed in relation to habitat variations. As in temperate regions, some species are very limited in a habitat and others more widely distributed on a range of vegetation types. The effects of food, dispersal, and seasonal climatic factors on psocid distributions in Brazil are discussed.

INTRODUCTION

The ecology of Psocoptera in the tropics has received very little attention, and there are no published accounts which deal primarily with natural communities of tropical psocids. In many tropical areas these insects have been little collected and, consequently, their taxonomy as well as their biology is inadequately known. Identification of immature stages, and their association with adults has hampered study of Psocoptera in some temperate regions, as well as in the tropics. In South America, a very large proportion of the species in any survey of Psocoptera is likely to be undescribed, and taxonomic work is a necessary prerequisite to biological studies.

This paper is an account of the ecology of Psocopteran communities of different vegetation types in the Mato Grosso, and is based on work undertaken with the Xavantina/Cachimbo Expedition from September 1968 to May 1969.

Psocoptera may form a significant fraction of the insect biomass on trees in temperate regions (Reichle & Crossley, 1967), and in this habitat they feed by grazing on epiphytic microflora and casual debris on bark and foliage surfaces (Broadhead, 1958; New, 1970a). Work on British species, in particular, has shown that many are more limited in their habitat range; thus, particular arboreal species may be found predominantly on bark or on foliage (Broadhead, 1958; New, 1969a, 1970a, 1971a; Pearman, 1928), or may be limited to either conifers or broadleaved trees (New, 1968, 1970a). Further, some species are predominantly subcortical (Broadhead, 1947) and others are rare on trees and occur mainly on grasses or low ve-

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getation, in leaf litter, or are 'domestic' species associated with stored products or human habitation. Although some species of Psocoptera show little habitat 'preference', data from work in temperate regions are sufficient to show that much habitat limitation occurs, and that this is in part due to food preferences, the effect of particular foods on fecundity and/or the opportunity for dispersal. The work to be described here was undertaken partially to discover whether tropical Psocoptera may show a comparable degree of habitat specificity to that demonstrated in some temperate species. The more pronounced seasonal climatic differences in temperate regions result in particular psocid habitats (such as deciduous foliage) being available for only part of the year, and influence the continuity of populations in a given area.

This expedition provided the opportunity for studying the psocid fauna of a remote area, containing a wide range of possible habitats, over a period adequate to at least indicate seasonal or phenological changes in faunal composition.

Adults of 137 species of Psocoptera were collected during this survey; about 90 of them new to science. In all, nearly 30,000 specimens were collected. The taxonomy of the collection has been partially worked out (New 1971b, c, 1972a,b,c, in press a,b,c, Badonnel, in prep.) and all the material separated into species: those species still undescribed are here given an ordinal for reference, and will be fully characterised before long. These papers, and other recent taxonomic work on South American Psocoptera (Badonnel 1962, 1963, 1967; New 1972d, in press d, e) are sufficient to emphasise the difficulty of undertaking biological work on S. American Psocoptera without previous detailed taxonomic work. Nymphs of about 50 American species have been associated with adults by direct rearing, and it is possible to identify most unassociated nymphs to family- and, in many cases, to genus (New, unpublished).

THE STUDY AREA

The major part of this survey was conducted in the 20×20 Km square centred on the Expedition's Base Camp (12°49'S, 51°46'W.), but data resulting from short trips to various outlying areas (Table 1) are also included.

The area around the Base Camp (B.C.) (Fig. 1) which is about 260 Km north of Xavantina, has been the subject of intensive studies by natural scientists of various disciplines but, at the time of this work the area had been little disturbed by human habitation. Most parts of the 'square' were easily accessible, as paths had been cut through the vegetation. The B.C. was at an altitude of c. 400 m, and on a substrate of Devonian- Carboniferous age (Askew & al., 1970). The climate of the area permits a somewhat arbitrary division into 'wet' and 'dry' seasons from the B.C. data (Daultrey, 1970), October to March have amounts of rain from about 100 to 300 mm each month, April about 80 mm, and other months very little rain. During the 'dry' season, mean daily minimum temperatures are considerably lower than in the wet season (Fig. 2), but the mean daily maximum temperatures differ comparatively little (annual range c. 30-35°C.). Fig. 2 indicates that this survey extended from the end of the dry season, to the end of the following wet season. In general, the climate of the area is, according to Eidt (1968), the savanna subregion of the Tropical Rain Climate, near its northern boundary, with the monsoon subtype.

The classification of South American vegetation types is not clearcut, and much of the non-forested region is often categorised under the broad heading of 'cerrado' (see discussions in Eiten, 1963, 1972; Goodland, 1971). Goodland (1971) has pointed out that such terms as 'campo' and 'grassland' are also inappropriate to describe such vegetation, which has most often been loosely termed a 'savannah'.

Five basic vegetation types were recognised around the B.C. (Fig. 3):

1. Campo, a term here used to imply areas of open country, with few or no trees and only local patches of shrubs. Although such areas superficially appear to be dominated by various grasses



FIG. 1. Sketch map of main study area, a 20 x 20 Km square around the Base Camp. The area shown represents a small area in the centre of the square shown in the inset map of South America. Diagonally dotted area is predominantly cerradão; southern area predominantly cerrado with gallery forest along streams.



Fig. 2. Records of rainfall (mm) — histogram, and mean daily minimum temperatures (°C, dots) at the Base Camp, October 1967 - May 1969, with period of present survey indicated.



Fig. 3. Schematic section across stream (centre) to show relationships of different vegetation types; A, gallery forest; B, cerrado; C, campo; D, dry forest or valley forest; E, cerradão (partly after Askew *et al.*, 1970, vertical slope scale exaggerated).

and (in wetter areas) sedges, a large number of herbs are also found. No attempt is made here to delimit the various 'sub-divisions' of campo mentioned in the literature, and the term is used to embrace all types of treeless areas dominated by grasses and herbs, and having little vegetation more than 1.5-2 m high.

Strips of campo were found between gallery forest and true cerrado (Fig. 3). These were generally 50-200 m wide and their boundaries abrupt. Some larger areas also occurred, mainly in broad valleys, in which they gradually gave way to the sedge/*Mauritia* community at the head of gallery forests and were bounded by cerrado on their higher regions.

2. Cerrado, which is the typical savannah vegetation of much of central Brazil, has been estimated to occupy about 1.5×10^6 Km² (Goodland, 1971). The term is used here to embrace Goodland's (1971) categories of 'campo cerrado' and 'cerrado sensu stricto'. It is primarily a woody type of vegetation and often has a sparse orchard-like appearance. The ground layer is well developed, and trees are rarely more than 6-8 m tall. This general type of vegetation extends south from the latitude of the B.C. to Brasília, and shows considerable morphological variation.

3. Cerradão is intermediate in appearance between cerrado and forest: Eiten (1963) has succinctly described it as 'a closed woodland of cerrado vegetation', although forest species are present in situations in which cerradão forms a transitional zone between cerrado and forest. Trees reach about 12-15 m in height, but their density and species diversity appear to be similar in cerradão and cerrado (data in Goodland, 1971).

Although ungrazed by domestic animals during most of this survey, all the cerrado and much of the cerradão, around the B.C. showed signs of having been burnt at some stage. Many of the trees possessed marked pyrophytic adaptations.

4. 'Dry forest'. At about the latitude of the B.C., the 'cerrado' type of vegetation gives way abruptly to forest which then continues unbroken to the north, and grades into the Amazonian rain forests. This type of forest, which is not especially associated with water courses is here termed 'dry forest'. It is a low forest (15-18 m) with a closed canopy and very little undergrowth: a few emergent trees rise to 25-30 m.

5. Gallery forest. The area around the B.C. is traversed by numerous small streams, which form part of the headwaters the of Rio Baracaju, a tributary of the Rio das Mortes (see Green, 1970). For most their length, these streams are bordered by a strip of tall (35-40 m) gallery forest up to 0.5 Km wide. Many of the trees are buttressed, and include large species of *Qualea* and *Sloanea*.

The relations between these five vegetation types are shown in Fig. 3, in which schemes of sequence for a symmetrical and an asymmetrical valley are shown (partially after Askew & al. 1970, who also give a vegetation map for the area). In many instances, boundaries between vegetation types were sharp, enabling discrete samples to be taken from several vegetation types within 100-300 m. This applied especially to the gallery - forest - campo - cerrado sequence in symmetrical valleys: in asymmetrical valleys, boundaries were often not as well-defined. Askew & al. (1970) recognised a type of 'valley forest' found between gallery forest and cerradão in asymmetrical valleys, but pointed out that its limits are difficult to show: it is here included in the category of 'dry forest', which it most resembles.

The other areas visited (Table 1) were away from the 'transition zone' between cerrado and dry forest, and samples of psocids from them may be more truly representative of the particular vegetation type examined.

SAMPLING METHODS

Samples of Psocoptera were collected weekly from the five vegetation types around the B.C. by beating (cerrado, cerradão, forests) or sweeping (campo, forest undergrowth). At least five separate areas of each vegetation type were examined each week but, other than for Palmaceae (New, 1971b), psocids from different tree species were not separated in samples. The difficulties of recognising different tree species, together with the high floristic diversity and low density of any species, and the low psocid densities encountered, rendered such separation impracticable. Each sample at a particular site was taken along a transect of c. 100 m, and all trees and other vegetation in an approximately 1 m wide strip were beaten to a height of 2 m, or swept.

In addition, several of these 'transect' samples were taken each month across profiles such as those shown in Fig. 3, with the aim of comparing the occurrence of psocids on different adjacent vegetation types. Together, these samples gave a gross comparison of the incidence of Psocoptera in different vegetation types. Each of these contains a number of different psocid habitats, which were also sampled separately in each:

1. Living and dead foliage were beaten separately, the number of samples taken depending on the availability of the latter. To indicate colonisation patterns onto dead foliage at different times throughout the survey, branches of various trees were partially broken at about monthly intervals, so that the foliage died but remained on the trees. Living branches on the opposite side of the same trees and the 'Killed' branches were sampled weekly.

2. Bark was sampled, in many cases from the trees used for the 'foliage' samples, by removing areas approximately 30×10 cm, and breaking and sifting it in a tray. In the absence of more efficient extraction apparatus or accurate covers, the edge effects (Safranyik & Graham, 1971) and live recovery efficiency will be influenced by the bark type (smooth, rough, laminate, or deeply furrowed). Such bark types were sampled in comparable numbers in different areas. Many superficially burned forest and cerrado trees had loosened bark. This was particularly evident in a stretch of dry forest some 30 Km north of the B.C. and in such situations subcortical insects were sampled by removing areas of bark (c. 30×10 cm) and retaining all specimens found. 3. Litter was sampled by sifting all leaves on $1/4 \ge 1/4 =$ areas of ground on a tray. Although this method is not as satisfactory as using more efficient extraction methods (New, 1969b), the samples taken are mutually comparable and taken in a standard manner.

Palm trees provide an unusual series of habitats for Psocoptera (New, 1971b), and were sampled independently of other kinds of vegetation. Numbers of living and dead fronds, and sheathing leaf bases were examined weekly in cerrado and cerradão (New, 1971b), and larger bulk samples taken irregularly from other areas.

This sampling programme provided for a comparison of Psocoptera between the five vegetation types on two levels; firstly, a gross comparison of total Psocoptera in different areas and, secondly, a comparison of Psocoptera in more limited habitats within and between vegetation types. No account is taken here of psocids found on vegetation used for building construction: these, and the wide range of domestic species collected in buildings will be discussed in a later paper. The colonial web-building Archipsocidae are likewise not enumerated or considered in detail in this account, other than for one species found in campos. Several colonies examined contained several hundred individuals, and the presence of such large aggregates is misleading when considering overall faunal composition.

Most psocids from the above samples were killed and stored in alcohol. Others, and psocids from additional uncontrolled samples, were kept alive for breeding purposes, association of nymphs and adults, examination for parasites, and tests for survival on different substrates. No detailed examination of food material and gut contents was possible in Brazil, but series of leaves and bark samples were coated with acetate films, which were then later examined microscopically after mounting in lactophenol containing aniline blue (Broadhead, 1958). In the laboratory, psocids were kept in glass tubes, under conditions that were uncontrolled other than for the maintenance of a high humidity. Detailed life-history data for a range of species will be published elsewhere.

The validity of quantitative comparison between samples containing many species relies heavily on the particular sampling method used. 'Beating' may be regarded as a reliable technique in that psocids living on foliage or bark of slender branches are, apart from colonial species living under webs, of reasonably uniform catchability. However, although similar transect lengths were used for each beaten sample, the number of psocids caught reflects their abundance over a ground area of that vegetation type rather than their abundance in relation to a known area of foliage or bark substrate: the numbers of individual plants beaten in transects over different vegetation types differ greatly, and different areas of the same vegetation type differ somewhat in density and floristic composition. Each transect sample is assumed to contain a representative collection of psocids from a range of plant species together representative of that vegetation type, and it is assumed that all psocids present on the parts of the plants beaten or swept were captured. By bulking the five samples taken from each vegetation type each week, a bulk sample representative of that vegetation type at that time is acquired. Such a sampling method is relatively unbiased when compared with, for examples, lighttrapping or soil arthropod extraction (see discussion in Bullock, 1971), but no attempt was made to balance the numbers of samples taken from rare and common tree species, so that more samples were taken from common species than from rare ones.

PSOCOPTERA ON DIFFERENT VEGETATION TYPES

Campo

This type of vegetation contained a smaller range of potential psocid habitats than those vegetation types containing numerous trees and, in most campos, Psocoptera were scarce. They were particularly scarce in the lower, wetter, campos which contained very little emergent vegetation, but the higher, dryer areas often contained elements of the cerrado fauna. The occasional emergent vegetation in dry campo, predominantly *Paepalanthus* spp. (Erio-caulaceae) and various Malvaceae, also supported cerrado psocids. Psocids collected in campo samples are enumerated in Table 2; there was little variation between different campo areas, and few species were common.

The most abundant psocids were a small complex of *Caecilius* species: two very similar species occurred together and in similar numbers, and a few specimens appear to represent a third species. The two more common species were continuously brooded throughout this study: the numbers of adults captured are shown in Fig. 4, and nymphs were taken throughout this period. These undescribed species are referable to the 'Division II, H-1 Group' of Mockford (1965) which is apparently restricted to South America. They were found on older standing grasses, and occasionally in the matted litter, but not on fresh growth which supports very



Fig. 4. Numbers of adult *Caecilius* A - C captured on campo grass and on cerrado palm trees in the Base Camp area of Central Brazil, September 1968 - April 1969.

little psocid food. Small nymphs were found on pubescent grass leaves, and appear to be able to feed from this substrate without difficulty. This contrasts with the nymphs of some temperate arboreal *Caecilius* species which are hindered in feeding by grass foliage pubescence, which also prevents their feeding on grasses during the litter phase (New, 1969b).

Breeding populations of these *Caecilius* were restricted to grasses (and, more rarely, sedges), but adults were sometimes found on broadleaved herbs. A distinct dispersal peak occurred in Jannuary and February. During this period, adult *Caecilius* were captured on cerrado palm trees (mainly *Syagrus* spp.) bordering campo areas. No eggs or nymphs were found on these trees, and it is inferred that establishment does not usually occur.

This dispersal peak occurred at a time when many of the lower campo areas were waterlogged, and it is possible that it is a regular annual occurrence in response to campo flooding, and that such dispersal could result in interchange between the, often isolated, campo areas and/ or in the recolonisation of campos burned during the previous dry season.

Several *Caecilius* species associated with palm trees in other regions are apparently more closely related to grass-frequenting forms than to other arboreal species (Mockford, 1965). The lack of the 'H-1 Group' species on most arboreal vegetation in Brazil, together with their casual occurrence on palm trees, infers that they are very specific to grasses and, probably, do not breed elsewhere. Acetate peels showed that food material on grasses was sparse, but corresponded well with that found in the psocid midguts, and, as the *Caecilius* did not exploit the litter to any large extent, the comparatively low density of these species may be partially explained by food shortage.

These were the only Psocoptera found during this work which were apparently restricted to grasses. Other psocids found on grasses were clearly casual, and were usually found to be more closely associated with herbs or arboreal vegetation in nearby areas. It is clear that casual invasion from nearby cerrado and gallery forests occurred frequently, and this was most clearly demonstrated in campos by examination of the emergent *Paepalanthus* spp.

These plants comprise a single vertical stem, up to about 2 m high, bearing successive whorls of short sheathing leaves from a basal rosette up to a terminal inflorescence 'head'. From September to December, dead persistent plants were present, with all foliage remaining attached. Rapid growth of young plants occurred in late November and early December and, by January, these were 30-40 cm tall and bore 30-50 leaves, the oldest of which were already dying. Near the inflorescence, leaves were short and widely spaced; near the base they were longer and more concentrated. These, and older dead plants, were examined for psocids: the head, and successive 30 cm lengths of stem were cut and examined for psocids and psocid eggs.

Very young plants and green foliage yielded no psocids, but several species became common on older plants, especially in the ramose heads: none of these were found on standing vegetation elsewhere in campos. They included colonies of *Archipsocop*- sis inornata New (in press c), and a common species of Lachesilla (A). A few individuals of a Pachytroctes and a Liposcelis found more commonly in old campo litter also occurred. A. inornata occurred almost invariably in the head of the plant, and Lachesilla predominantly in the heads and upper 60 cm of stem. This species of Lachesilla occurred also in cerrado (below), where it was much more seasonal in appearance due to food substrate availability, and it is possible that the persistent Paepalanthus stems in campos provide a small breeding reservoir for this species, from which dispersal to other vegetation types may occur. Numbers of Lachesilla A captured in different areas are shown in Table 3, and indicate that this species is widely distributed, though often occurring in low numbers.

Cerrado

Most species of Psocoptera were scarce on cerrado vegetation, and total numbers captured were low: in several initial 2 Km transect samples taken in September, only 5-18 psocids were captured on vegetation other than palms. Palm trees harboured a rich psocid fauna, and adults of 24 species of Psocoptera were taken from them. Three species of *Lachesilla* were very closely associated with palm trees (New 1971b), but other species were found also on other cerrado vegetation or in forests (Table 4). However, more intensive examination showed that, although psocids frequenting living foliage were generally scarce on other cerrado vegetation, many of those predominantly found on dead foliage or on bark were relatively numerous (Table 6). Beating did not adequately reflect the true numbers of bark-frequenting psocids on many of



Fig. 5. Numbers of Amphigerontia spp. (adults and nymphs) captured on cerrado vegetation in the Base Camp area of Central Brazil, September 1968 - April 1969.

the cerrado trees with deeply furrowed bark, and many of these were collected by direct searching.

Of the more common species (Table 5), most appeared to be continuously brooded, but two Psocidae (*Amphigerontia forcepata* New and A. obscura New, 1972b), both of which were found on many kinds of low shrubs, appeared to undergo discrete generations. Adults were found in September (Fig. 5), when no nymphs were present. Many of these were senescent, the females having laid most of their eggs. Small *Amphigerontia* nymphs were first taken in samples during February, and adults in March: none were found during the intervening months, and eggs laid by adults captured in September had not hatched by March, although they still appeared healthy. These may prove to be species associated with the dry season, and to undergo an egg diapause during the wet season.

Seasonal growth of particular components of the cerrado vegetation appears to markedly affect the seasonal abundance of some psocid species. For example, two species of *Lachesilla* (including that found in campos (above) were common on the dead foliage of an annual Rubiaceous herb, *Borreria* sp., which was common in cerrado and more open cerradão. They were numerous in September and October, when the dead, foliage-bearing stems of *Borreria* were present. In November much fresh growth occurred, the dead plants were overgrown and the foliage fell. The *Lachesilla* declined rapidly in numbers about this time (Fig. 6) although unhatched eggs were found on the old stems. A few *Liposcelis* later colonised the dead stems from the litter.

Such seasonal predominance of particular species of psocids, linked with the availability of suitable feeding substrates or habitats, was indicated also in some other cerrado psocids. On palm



Fig. 6. Numbers of *Lachesilla* A and *Liposcelis* spp. taken in sweep samples from *Borreria* sp. in cerrado in the Base Camp area of Central Brazil, September 1968 - April 1969.

trees, on which living and dead foliage are present together throughout the year, such numerical peaks did not occur in the numerically dominant *Lachesilla* species, and the overall psocid populations remained fairly constant throughout the survey period. However, if the *Lachesilla* and campo *Caecilius* invaders are omitted from the palm tree samples, there appeared to be a marked increase in psocid numbers on dead foliage in March (Fig. 7). Numbers on living foliage remained low, but the dead foliage fauna was composed of several species, with none clearly dominant. Amongst the more common were *Pachytroctes A*, *Neurostigma dispositum* Roesler and species of *Echmepteryx*. These were all found also in other habitats (Table 4). Although few species appeared specific to palm trees, several other psocids were found in greatest numbers on them — for example, *N. dispositium*, which bred on dead palm fronds.



Fig. 7. Numbers of Psocoptera, excluding associated Lachesilla species and Caecilius A - C, taken in collections from living and dead palm tree fronds in cerrado and cerradão in the Base Camp area of Central Brazil, October 1968 - April 1969. (Numbers adjusted to 20 each of living and dead fronds on each sampling occasion).

Most of the cerrado examined had been burned at some stage, and the bark of trees and shrubs was charred to varying extents; consequently, much bark bore very little algae or lichens. The scarcity of psocids on exposed bark may be partially due to the lack of food, but the marked lack of subcortical communities on trees with loosened bark in comparison with forests (p. 129) suggests that other factors may also be involved.

Many of the cerrado trees have xerophytic foliage, bearing little microflora when alive, and much of this exposed to sun throughout the day. Such exposed foliage does not usually support many psocids. In contrast, dead persistent foliage — in which the leaves are frequently convoluted and bear a better defined fungal microflora — supported more psocids, but still relatively few when compared with damper, less exposed forest foliage (Table 6). Most cerrado trees appeared to be continuously rather than seasonally deciduous, and there was little evidence of seasonal increases in psocid populations related to the presence of aging foliage. In general cerrado psocid populations on trees were high only in less exposed situations in which adequate food resources were available.

Cerradão

Psocoptera were considerably more numerous in cerradão than in cerrado (Table 6), the difference largely reflecting the increased numbers and diversity of suitable arboreal habitats. As cerradão canopy is often closed, much of the lower foliage is comparatively sheltered. As in cerrado, most trees and shrubs showed signs of superficial burning. No psocids peculiar to cerradão were found, and the fauna more resembled that of forest regions, being generally richer than cerrado and more impoverished than forests.

Forests

Although the dry forests and gallery forests are floristically distinct, the overall psocid fauna and the diversity of psocid habitats are similar in each: they are here considered together. Many more psocid species were found in forests than in other vegetation types, but they included many rare species (some being represented by single specimens in collection), and comparatively few were common.

Foliage-frequenting psocids were broadly similar in forest and cerrado; a few species of *Caecilius* and *Polypsocus* occurred on living arboreal foliage, and a wider range of psocids frequented dead foliage. Several of the latter species were common in both forest and cerrado, and it seemed that their distribution was restricted only by that of persistent dead foliage.

This is particularly so for some Pachytroctidae. Fig. 8 shows the numbers of Pachytroctidae beaten from living and dead foliage, following cutting and breaking of some branches to produce persistent dead foliage. Fig. 8 indicates that rapid colonisation of dying foliage occurred at various times from November to February, whereas living foliage on the same trees remained psocid-free. It is inferred that these Pachytroctidae may be capable of such 'opportunistic colonisation' throughout the year. Lachesillidae colonised the cut branches only after 3-4 weeks, but again were present in all four series of trees: they appear to constitute a rather later 'successional stage' than the Pachytroctidae, and exploit dead foliage rather than both dying and dead foliage. In temperate regions, *Lachesilla pedicularia* (L.) is well known as an opportunistic coloniser of dead foliage, but it occurs also in hay stacks and other, similar, habitats. The Brazilian species was not found on dead grasses or palm thatching, and may be more specific in its habitat requirements. No Ectopsocidae were found on dead foliage, although several species widely distributed in other parts of the world exploit dead foliage. Most other species were taken in numbers too small to infer that they are foliage-frequenters, but some of these were not captured in other habitats (Table 6).

Bark-frequenting psocids were considerably more abundant and diverse than in cerrado, and many of the trees were unburned and supported large amounts of bark lichens and algae. These, together with the large range of tree species and bark types, afford considerably greater potential for psocid colonisation than in cerrado. Many Psocidae were not found elsewhere and some other groups, such as Elipsocidae (*Nepiomorpha*) were found predominantly in



Fig. 8. Numbers of adult Pachytroctidae taken on living and artificially killed (broken branches) foliage of forest trees in the Base Camp area of Central Brazil in various periods from October 1968 - March 1969. (Arrow denotes time of breaking branches; dots = "killed" foliage; squares = living foliage; five trees sampled on each occasion).

this habitat. Most living forest trees supported very few Liposcelidae, but a few species of Embidopsocinae were found under bark.

They were much more numerous on dead trees. An area of dry forest some 30 Km north of the B.C. had been burned and partially felled several months before this survey commenced. Very little regeneration had occurred in this area, and many of the trees had charred and loosened bark. These trees supported large populations of subcortical Psocoptera, especially Embidopsocus and allied genera (Table 7). Embidopsocinae are strongly dorso-ventrally flattened and may be able to resist superficial habitat burning by sheltering in bark crevices. Burning, in this case, had provided a considerable increase in potential habitats for these psocids and, as very few individuals were found in several hours searching on living trees around the burned area, it seems that their abundance on the burned trees could result from relatively unhindered reproduction rather than from numerous immigrations possibly aided by previous removal of most natural enemies. Almost all the trees with loosened bark supported colonies of *Embidopsocus*, including individuals of all instars. In contrast, most other psocids were found in low numbers, were found more commonly elsewhere and are not predominantly or usually subcortical in habitat. Their presence on the burned trees almost certainly resulted from casual imigration, and they included several species representing families with broad habitat ranges, suggesting that they would be effective colonisers. The Echmepteryx, for instance, was found also on dead foliage, palm thatch, litter and on bark during this survey, and a similar species has been recorded from bird nests in Pernambuco (New 1972d).

No clear seasonal trends were detected in the forest Psoptera.

PSOCOPTERA IN LEAF LITTER

Samples of litter from cerrado, dry forest and gallery forest were sifted at approximately weekly intervals, and on any one occasion were taken across asymmetrical valley (Fig. 3). More irregular samples were taken in campos and other forest and cerrado areas.

Campo litter, a mat of dry grass, contained very few psocids (Table 8). Those found included widely distributed primary litter species (those found only in litter and which are not known to breed elsewhere, see New, 1969b) such as *Antilopsocus nadleri* or were found elsewhere in campos. Cerrado and forest litters were composed predominantly of deciduous leaves. Cerrado litter was comparatively sparse, and there were large areas of exposed laterite: samples were taken from the more densely littered areas. Forests had very little bare ground, and a well-developed leaf litter layer.

The numbers of psocids collected from cerrado and forest litter throughout the survey are shown in Fig. 9, in which the total numbers, and numbers of those considered as primary litter frequenters are shown separately.

Total numbers in all three litter types rose rapidly in late September and early October and fell towards the end of October, after which irregular fluctuations occurred, with numbers consistently lower in gallery forest. Much of the September-October peak is composed of 'casual litter frequenters' (here, taken as the difference between 'total' and 'primary' litter psocids but see New, 1969b), which do not regularly breed or inhabit the litter. This peak closely followed the first heavy rainfalls of the wet season, and it is suggested that many psocids were washed off trees at this time and survived for a short time in the litter. This process continued, on a smaller scale, throughout the wet season.

Numbers of primary litter frequenters are comparatively low, although several families are represented (Table 9), and they were highest in September and October. Thereafter, numbers in gallery forest litter rapidly declined, and very few specimens were found from mid-November onwards. During this period, numbers in cerrado and dry forest litter were consistently higher than in gallery forest, although still low. It appeared that seasonal waterlogging of gallery forest litter resulted in local extermination of psocids.



Fig. 9. Numbers of Psocoptera captured in litter samples in three different vegetation types from September 1968 - April 1969. (20 samples of $1/4 \ge 1/4$ m taken on each occasion for each vegetation type).

whilst they persisted in the better drained litter types. Such waterlogging and local flooding of parts of the lower gallery forest are likely to affect many groups of soft bodied or relatively immobile arthropods.

Primary litter-frequenting psocids include many species which are apterous, or polymorphic with a high proportion of apterous or brachypterous individuals, and colonisation of gallery litter is unlikely to occur fully by flight. Beck (1972), in his studies of the effects of annual (more severe) flooding on soil arthropods in Amazonian forest regions, found that many forms were subjected to extreme population changes caused by local flooding, but many 'macroarthropods' were able to take refuge by movement to more elevated areas. Psocoptera, part of the 'active meso-fauna' of litter (Fenton, 1947, New, 1969b), may be more akin to Beck's 'macroarthropods' than to the comparatively immobile 'microarthropods', in that many species are active. But, alternatively, many (especially younger nymphs, some of which move around little) are likely to be drowned.

Beck (1972) showed that several of the Oribatid mites he studied had life cycles which were closely adapted to annual rhythms of flooding; some species had eggs that were resistant to flooding, and many were parthenogenetic, a condition that he considered necessary for successful reinvasion of flooded regions from dryer or more elevated areas. One of the most numerous psocids in litter was an apterous *Antilopsocus* (Pachytroctidae), and it is certainly possible that the eggs of this, and of other psocids can resist submersion in water. Their eggs are usually attached to dead leaves or twigs, rather than scattered on soil, and it is also possible that some redistribution occurs by transport of litter down the valley slopes. *Antilopsocus*, of which very few males are known, is parthenogenetic, and several other psocids in litter had sex ratios strongly suggesting that parthenogenesis might occur (Table 9).

The casual litter-frequenters included species of Pachytroctidae, Ectopsocidae, Polypsocidae, Psocidae and Caeciliidae which normally bred on vegetation.

COMPARISON AND DISCUSSION

The tables and foregoing notes clearly indicate that the habitats studied differ widely in the diversity and abundance of their associated psocids, and fuller comparative data are presented in Table 10. In this Table, the extent of species overlap, or similarity, between different vegetation types and habitats, is indicated by use of the 'Sörenson Index' (Sörenson, 1948), in which the degree of similarity between two communities is given by the formula:

$$K = \frac{2c}{a+b}$$

where a is the number of species found only in the first community, b is the number found only in the second community, and c the number of species found in both communities.

Campos are the least diverse community, and also supported fewer total psocids; most psocids were found in forests, and cerrado formed an intermediate level of complexity. This transition is undoubtedly related to the increasing number and diversity of suitable arboreal habitats from campo to forests. Despite this, few species were common in any one vegetation type, and few others were widely distributed in all vegetation types (neglecting the colonial Archipsocidae). This overall picture of the B.C. area was little affected by examination of samples from other areas. The more common cerrado psocids around the B.C. were found also near Xavantina and Brasília, and few species found in the areas were not represented in the B.C. collections (Table 1). Similarly, the forests to the north of the B.C. area yielded psocids of the same species and in similar relative numbers to the B.C. samples. Results from the B.C. sampling programme may, therefore, be representative of a much greater area of Brazil. However, it is likely that many other psocid species occur in the area: several species around the B.C. were found for the first time only in the last few weeks of this survey, and a number of nymphs have not been as-sociated with adults. It is clear that only long term field studies can fully characterise psocid faunas in the tropics.

Although most psocid species within any one vegetation type appeared in samples from several different habitats, several (and in most cases the more abundant) species indicated considerable habitat specificity. These may be regarded as indicators, or dominants within that vegetation type. Thus, the campo grass-frequenting *Caecilius* spp. and the cerrado/cerradão palm tree *Lachesilla* spp. (New 1971b) were amongst the most common species found. Although adults of these were found in other habitats they apparently did not breed elsewhere, and are regarded as useful indicator species for particular habitats. Other *Lachesilla*, *Caecilius* and Pachytroctidae were found on dead foliage in several vegetation types, and their distribution is limited by the availability of a suitable feeding substrate rather than by any purely vegetation characteristic.

There was a conspicuous lack of the species frequenting living foliage. This may partially have been due to the short period of this work but, other than on palm trees, only a few *Caecilius* and *Polypsocus* appeared to utilise this habitat. Intensive searching in forests for egg batches of these groups showed that they occured at very low densities: an average of less than two egg batches per hour of searching were found each month. This situation contrasts markedly with many temperate situations, in which foliage-frequenting psocids are abundant and direct counts of egg batches afford a simple method for assessing population trends (New, 1970a, b, for Britain; unpublished data for Canada and Australia).

No species were shown to undergo obligatory generations in both litter and on trees each year. Again, this may be due to the short survey period, but the low density of living foliage-frequenting species and general lack of seasonal deciduousness suggests that such 'secondary litter-frequenters' (New, 1969b) may be scarce. Nevertheless, the extent of movement between habitats was in some cases very marked. In particular, many of the 'dead foliage' species appeared opportunistic and capable of colonising wherever dead foliage was available. Several of these, notably Pachytroctidae. appeared to breed continuously in litter and on trees. Dispersal peaks of some other species, notably the campo *Caecilius*, did not extend the range of habitats frequented, but probably served for interchange of psocids between different parts of their existing habitat range. In this case, the dispersal peak appeared to be very well defined, and may be of regular annual occurrence. Irregular burning of campo and cerrado occurs in central Brazil, and such groups of animals as Psocoptera, which have comparatively low vagility, may undergo regular extension of distribution from similar unburned areas. In the case of campos, burning often occurs towards the end of the dry season (August), and by January-February, have regenerated to the extent that sufficient older grasses are present to support Psocoptera.

The large numbers of Embidopsocinae found on burned forest trees may exhibit a different kind of fire-resistance mechanism, through their ability to shelter in narrow bark crevices. Some of this subfamily were found also in cerrado, and it is possible that some of the pyrophytic adaptations of cerrado/cerradão trees may serve to protect some insects from climatic extremes. In particular, thick furrowed bark and sheathing leaf bases may offer protection against both desiccation and being washed off trees during rains.

This latter feature apparently accounts for the presence of 'casual' psocids in leaf litter at the beginning of the wet season, and this may also constitute a seasonal dispersal pattern. Most of these 'casual litter-frequenters' in forest regions were found in low numbers on the trees (although the canopies were not sampled, and could harbour more psocids. From the few trees which were cut, and samples of foliage and bark examined for eggs, it seemed that psocids were scarce in canopies as well as at lower levels). but were 'dead foliage' species, which could probably survive in non-flooded litter. Others, especially nymphs of 'living-foliage' psocids, are likely not to survive under these conditions. It is implied that a considerable proportion of the arboreal psocids populations may be killed through the effect of seasonal rains in flood-prone areas. Cerrado litter is dryer and sparser than forest litter, and a higher proportion of 'casual' psocids may survive and reenter trees. However the changes in relative abundance of primary litter-frequenting psocids in cerrado and forest litters coincided with flooding (Fig. 9) This is clearly a situation in which local extermination can be caused by a climatic event of fairly regular annual occurrence.

Fire and flood may also destroy natural enemies of psocids. This was particularly noticeable in the burned forest area, where ants were very scarce. Ants, notably species of *Crematogaster*, appeared to be the most frequent predators of psocids in central Brazil, and they were directly responsible for the destruction of several large colonies of Archipsocidae observed (New, in press c), in which situation they bit holes through the webs and removed psocids. Other predators recorded with psocid prey during this work included Reduviid bugs (only once outside domestic situations), spiders (twice), and a Chrysopid larva. In addition, it can be inferred that such predators as grounddwelling larvae of Myrmeleontidae and Ascalaphidae occasionally take psocid prey: both readily accepted them in captivity. Numerically these, and other possible predators, are greatly inferior to ants, and more restricted in habitat.

Parasitism was extremely low in the psocids examined. No evidence of Braconid parasitism was found, in contrast to psocids in North America (Sommerman, 1956; Loan & New, 1972) and in Britain (Broadhead & Wapshere, 1966; New, 1970c), and no adult Euphorine Braconidae were collected. Egg parasitism was also low and, although only small numbers of eggs were collected, only four specimens of *Alaptus* (Mymaridae) were reared — a figure which represents less than one per cent parasitism of samples examined. It thus appears, from the limited data available, that ants may be the most important natural enemies of psocids in central Brazil, and that parasitism by Hymenoptera has very little effect on psocid populations.

Although most species of Psocoptera for which data are available appear to be continuously brooded in Brazil, some seasonal effects due to climate or to the availability of particular food substrates may determine seasonal peaks or the relative abundance of particular species in different parts of their habitat range. Climate and food are generally recognised as amongst the most important factors determining insect phenology in tropical regions (see Gibbs & Leston, 1970).

In situations where opportunistic colonisation by psocids can occur at irregular intervals, as on to dead foliage, inadequate sampling (especially samples taken over a small area) can lead to misleading interpretations. A superficial appearance of discrete psocid generations may be caused by increasing age structure of successive samples from the same area or same trees following a single colonisation, and larger samples are needed to overcome such local effects. The occurrence of discrete generations can be inferred only in such species as the cerrado Amphigerontia, in which samples taken over a wide area without exception showed that species were absent for a period and nymphs appeared in several samples during the same following period. Together, cerrado samples gave a uniformly increasing age structure for the Amphigerontia populations. Many Psocids lay eggs in batches; synchronised hatching and subsequent nymphal aggregation (of up to about 40 individuals in some genera) may also bias interpretations. In such situations, samples must be sufficiently broadly based to ensure that several such groups are included - differing ages of different nymphal groups strongly indicates that the species is continuously brooded.

The presence of alternative habitats can also produce the superficial appearance of discrete generations over part of a habitat range — the *Lachesilla* associated with *Borreria* in cerrado, for example — and indeed, it appears that many species of tropical psocids may occupy their maximum habitat range for only part of a year, some areas being rendered unsuitable or inaccessible, and the feeding substrates being replaced in particular areas at different times or the year.

Examination of acetate peels of foliage showed that, in general, living foliage bore very little adventitious material. This was especially so for the xerophytic cerrado foliage. Slightly greater amounts of potential psocid food were found on forest foliage but much of this appeared to be of casual origin (bark flakes, dust etc.) rather than constituting microfloral successions. Dead foliage, and foliage killed by breaking branches developed more conspicuous fungal associations within a few weeks and, especially in damper forest areas. these apparently enabled rapid colonisation by psocids, and some normally bark-frequenting Entomobryid Collembola to occur. The difference in colonisation rate between Pachytroctidae and Lachesillidae could imply differential food preferences related to a microfloral succession. Gut contents of both families were grossly similar, and it is possible that the sensory or 'habitat finding' mechanisms of the two families differ. No work on the sensory mechanisms involved in habitat selection by psocids has yet been published.

Litter foliage in forests also supported considerable amounts of fungi and, of 40 peels examined, over half the area of 34 was covered by fungi and debris. In contrast, much of the cerrado litter had less potential psocid food than did dead leaves on trees (similar situation for cerrado palm foliage was recorded by New, 1971b), possibly related to increased desiccation caused by reflectance from laterite. Although cerrado litter psocid populations are low, several species frequented this habitat throughout this study.

This study revealed several major differences from temperate psocid species (see Broadhead, 1958; Broadhead & Thornton, 1955; Broadhead & Wapshere, 1966; New, 1970a, 1971a), most of which undergo discrete generations, often with an egg or nymphal diapause throughout the winter. Europe and North America support much better-defined faunas of Psocoptera frequenting living arboreal foliage, and several of these show seasonal population peaks related to the amounts of potential food available. Interchange of these between habitats is largely dependent on seasonal deciduousness. Many temperate bark-frequenting psocids are rare, as in Brazil, but particular genera may be abundant at particular times of the year (*Mesopsocus, Elipsocus*). A comparatively small litter fauna is found and, in general, this is not subjected to regular flooding.

Most biological studies on temperate region Psocoptera have emphasised their occurrence on one, or a range of, tree species rather than their overall community structure. In Brazil, such distinctions were not made, as many trees were scarce and the flora extremely diverse. Nevertheless, the northern temperate region division between species predominantly found on broadleaved trees and those found mainly on conifers may be analogous to the 'palm tree/rest of cerrado' situation in that distinct ecological groups (usually comprising few species) appear to be severely limited to particular kinds of tree.

Although there are differences in the abundance and likely effects of natural enemies, it seems that food availability may be a major factor affecting distribution and abundance of psocids in both tropical and temperate regions, and that provision of a suitable food supply can result in population peaks in Brazil (*Lachesilla* on *Borreria*) which are analogous to some found on foliage in temperate regions (*Ectopsocus briggsi*, for example, see New 1970a). But food is relatively sparse on many kinds of foliage, apparently does not increase markedly with time, and most psocids occur in only small numbers. Further work on habitat specificity of tropical psocids should emphasise more detailed feeding and host selection studies.

SUMMARY

This work represents a first attempt to study habitat limitation of Psocoptera on different vegetation types and in leaf litter in Brazil. Of the vegetation types sampled the sequence 'campo — cerrado — forests' supported increasingly diverse psocid faunas, related to the increase in abundance of arboreal habitats.

Campo, without trees, supported few psocid species but some grassfrequenting Caeciliidae were characteristic of this vegetation type and did not breed elsewhere. Few species were common in, or peculiar to, cerrado or forests, but several of the more common species showed marked habitat specificity during the eight months of this study. Some Lachesilla spp. and Pachytroctidae frequented dead foliage, for example, and their distribution was limited by that of such a suitable feeding substrate. Most species of Psocoptera were apparently continuously brooded, but seasonal peaks may be produced by seasonal availability of feeding substrates (i) as function of an annual plant life-cycle or (ii) as affected by seasonal flooding. Seasonal dispersal peaks, possibly related to flooding, may facilitate interchange of some species (Caecilius) between different isolated areas, but some other species are more opportunistic colonisers, and fly actively over much of the year. Burning of forests may enable large populations of subcortical psocids to develop on superficially burned trees, probably due in part to removal of natural enemies. Feeding, dispersal and habitat limitation of Brazilian psocids is briefly discussed.

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Table I. Location of collecting trips made outside the Base Camp (B.C.) area in Brazil, and Psocoptera collected.

Area	Dates	Habitats Sampled	Total Psocids	No. Species	No. species not found at B.C.
R. Suia Missu	9-13.x.68	Forest litter	89	9	1
11	18-24.xi.68	11 U	26	3	0
	u	Forest foliage	17	6	0
Xavantina	21-26.i.69	Gallery forest			
		living foliage	34	6	1
u	11	Gallery forest			
		dead foliage	65	5	?1
u	\$1	Gallery forest			
		subcortical	25	4	0
u	u	Cerradão			
		dead foliage	58	5	0
11	n	Dead palms	94	13	2
Brasília	27-29.iv.69	Cerrado	106	14	0

Table II. Numbers and incidence of adult psocids captured on camps vegetation in the Base Camp area, September 1968-April 1969. (presence denoted by '+')

						Mo	onths				
					196	8			196	9	
	Species		Total No.	s.	о.	N.	D.	Ј.	F.	м.	А.
(a)	Grasses										
	Lachesilla	А	17	+			+	+	+	+	
	11	в	11						+		
	Caecilius	Α	367	+	+	+	+	+	+	+	+
		в	109	+	+	+	+	+	+	+	+
	11	С	18		+		+	+	+		
(b)	Paepalanthus										
	Liposcelis	D	5			+			+		
	Pachytroct	es E	3 16			+		+			
	Lachesilla	A	78	+	+	+	+	+	+	÷	
	11	в	8				+	+	+		
	Archipsoco	psis	168	+	+	+	+	+	+	+	÷
	Polypsocus	A	1		+						

Table III.Numbers of adult Lachesilla'A' captured in various
habitats around the Base Camp, September 1968-
April 1969.

Habitat	No. Lachesilla	Total for Vegetation Type
Campo - grasses	17	
" - Paepalanthus	78	99
" - litter	4	
Cerrado - palms	21	
" - Borreria	522	554
" - other	11	
Gallery forest - dead foliag	e 8	
Dry forest - dead foliage	22	[:] 4 0
Forests - litter	6	
" - other	4	

Table IV. Psocoptera found on palm trees and in other cerrado habitats in the Base Camp area, September 1968-April 1969.

SPECIES

FOUND ELSEWHERE

Echmepteryx	A	/	dead foliage, litter
11	в	/	litter
Liposcelis	А	/	litter
11	в	1	under bark, litter
Embidopsocus	Е	1	under bark of dead trees
Neurostigma di	spositum	/	dead foliage, rarely litter
Epipsocus taitu	bai	/	dead bark, forest litter
E. brasilianus		/	bark
E. roesleri		1	bark
E. niger		/	campo, swept
E. ctenatus		x	single specimen
Caecilius A		/ }	
" B		/	campo, casual on palms
" C		/	
" E		/ '	dead foliage, thatching
Blaste brasilier	nsis	. x }	
B. alfineta		x	single specimens
Psococerastis i	interrupta	x	
Trichadenotecn	um <u>sinuatum</u>	1	dry forest, bark

Table V. Total numbers of Psocoptera (adults + nymphs) captured on vegetation in different habitats in the Base Camp area from September 1968 to April 1969.

Vegetation	n Type	Living Foliage	Dead Foliage	Bark	Total
Cerrado	Individuals	46 + 102	493 + 1164	138 + 741	677 + 2007
	Species	8	17	45	58
Cerradão	Individuals	96 + 72	608 + 1830	408 + 972	1112 + 2974
	Species	11	16	62	71
Forests	Individuals	208 + 412	1652 + 1906	2280 + 3015	4140 + 5333
	Species	7	29	104	108

 Table VI.
 Numbers of the more common Cerrado Psocoptera

 found on trees (excluding Palmaceae) around the

 Base Camp, September 1968 - April 1969. (Adults + nymphs)

Species		Living Foliage	Dead Foliage	Bark	Total
Echmepteryx	в	0 + 1	46 + 130	0 + 9	46 + 140
	С	0 + 0	18 + 57	3 + 11	21 + 68
Pachytroctes	в	8 + 0	132 + 364	11 + 130	151 + 494
11	С	0 + 0	59 + 168	68 + 40	117 + 208
" ye	oung nymphs	5	49		49
Epipsocus bras	silianus	0 + 0	·0+2	4 + 39	4 + 41
Caecilius D		17 + 52	38 + 76	0 + 0	55 + 128
Lachesilla. B		0 + 0	57 + 1.59	0 + 0	57 + 159
Amphigerontia	1	0 + 0	1 + 0	40 + 126	41 + 126

			N	0.	
	Psocids		Burned Forest	Unburned Forest $*$	Other habitats
	Echmeptery	<u>x</u> B	38	6	Cerrado, foliage
**	Embidopsoc	inae	1258	16	and bark Cerrado, cerradão under bark, litter
	Liposcelis	в	119	5	domestic
	н	С	27	0	Cerrado litter
	н	D	62	11 }	Cerrado, cerradão:
	н	G	7	0	litter, bark
	11	nymphs	204	17	
	Pachytrocte	<u>s</u> A	7	1	dead foliage
	11	в	18	7	dead foliage
	"	D	64	0	"", domestic
	<u>Psoquilla</u> m	arginepunctata	11	0	domestic
	Lachesilla	С	7	0	Cerrado, dead foliage
	Archipsocus	tenebricosus	0	1	palm thatch
	A. gibberop	hallus	1	0	palm thatch
	A. modestu	s	. 0	13	none
	Archipsocop	osis inornata	11	2	Camp, forest litter, bark, palm thatch
	Caecilius 1	D	2	0	palm thatch

Table VII. Psocoptera found under bark of burned and unburned forest trees, and their presence elsewhere.

* These samples are not strictly comparable with the burned trees, but adequately indicate the relative abdunance of different taxa.

** Eight taxa are represented, including two new genera.

Table VIII. Total numbers (adults and nymphs) of Psocoptera found in campo litter in the Base Camp area, September 1968 - March 1969.

					Month				
Species		s.	о.	N.	D.	J.	F.	M.	Total
Echmeptery	x B	1	0	7	0	5	0	0	13
Liposcelis	A	3	2	4	11	3	0	1	24
н	D	1	7	8	4	0	0	0	20
Antilopsocu	s nadleri	2	0	2	7	0	0	0	11
Caecilius	A	2	6	11	5	0	2	0	26
н	в	0	1	0	4	0	0	0	5
Lachesilla	в	0	1	0	0	4	9	0	14
Archipsoco	psis inornata	0	2	0	7	3	2	0	14

Table IX.Incidence and characteristics of the more common
primary litter-frequenter in areas around the Base
Camp, September 1968 - April 1969.

Species	Total Adults	Sex Ratio (ơ :Չ)	Comments
Pteroxanium A	11	0:11	Brachypterous
Liposcelis F	34	11:23	Apterous
Pachytroctes D	16	0:16	Dimorphic - 9 apterous, 7 macropterous
Antilopsocus nadleri	46	3:43	Apterous
Ectopsocus A	5	3:2	Macropterous

Table X. Sörenson indices of similarity between psocids collected in different habitats and in different vegetation types around the Base Camp, September 1968 - April 1969.

(a) <u>Totals</u>					
No. Species	Vegetation type:	Campo	Cerrado	Cerradão	Forests
12	Campo		.267	.176	.142
63	Cerrado			.817	.607
79	Cerradão				.835
115	Forests				

(b) Foliage	Foliage only			Sorenson Index			
No. Species	Vegetation type:	Campo	Cerrado	Cerradão	Forests		
9	Campo		.452	.387	.279		
22	Cerrado			.772	.714		
22	Cerradão				.679		
34	Forests						

(c) Litter on	ly		Sõrenson Index			
No. Species	Vegetation type:	Campo	Cerrado	Cerradão	Forests	
8	Campo		. 538	.316	.255	
18	Cerrado			.737	, 492	
20	Cerradão				. 537	
47	Forests					