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Ecological Considerations in Scrub Typhus*

1. Emerging Concepts

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Scrub typhus infection is now known to occur in geographical and ecological areas where its presence was hitherto unsuspected—north and west of the Indus River and in south-eastern Siberia; in semi-desert, montane desert, and alpine terrain high in the Himalayas, as well as in primary jungle. Additional data are presented to support the hypothesis that " ecological islands ", containing basically similar faunas of rodents and ectoparasites, exist on scattered mountains in the Pakistan Himalayas, despite the intervening " barriers " of desert, broad rivers and massive peaks. Since scrub typhus has been demonstrated in some of these isolated areas, it is felt that the infection may exist, unrecognized, in neighbouring countries as well.

A number of larval trombiculid mites, largely species of the subgenus Leptotrombidium, *are believed to be vectors, in addition to the well-known* L. (L.) deliense *and* L. (L.) akamushi. *The host-range of natural infection in ground-dwelling small mammals, especially rodents, is very broad in endemic areas. An important factor of time, and not only of space, may be involved in an endemic locus, the disease undergoing a sequential evolution involving different chiggers and rodents over a period of years. It is pointed out that new irrigation schemes, road construction, and agricultural projects may introduce scrub typhus into an area or greatly increase its endemicity if the infection is already present.*

In the two decades since the Second World War, our concepts of the ecology of scrub typhus infection have undergone profound changes. Scrub typhus, instead of being restricted to the moist tropics, or strictly limited to the summer months if present in a temperate country like Japan, has been shown to occur in a surprising variety of climatic conditions and habitats. These range all the way from truly tropical areas to alpine meadows and even subarctic scree high in the Himalayas, to include regions as diverse in vegetation and rainfall as the equatorial rain-forests, areas of true monsoon extremes, xeric foothills and montane semi-deserts. In Japan, cases of the disease have been noted in cold weather and even in the winter months. Instead of just being an infection characteristic of scrub terrain, i.e., in localities where the activities of man had, within recent years, drastically modified the natural vegetative cover, scrub typhus has now been demonstrated in " undisturbed " situations such as primary jungle, glacial slopes, and foci in the semi-desert. The very name " scrub typhus " is thus a misnomer. The known geographical range has been extended to include the south-eastern tip of Siberia, Korea, the mountains of South Central Asia, and Pakistan west of the Indus River, and there is reason to believe that scrub typhus may be present in Afghanistan, the Tadzhik SSR, Nepal, Tibet, Sinkiang and perhaps eastern Iran. Other species of trombiculid mites besides the classical vectors *Leptotrombidium (Leptotrombidium) akamushi* (Brumpt, 1910) and *Leptotrombidium (Leptotrombidium) deliense* (Walch, 1922) (both formerly placed in the genus *Trombicula*) have been shown to be involved in the epidemiology of scrub typhus. Other genera of chiggers and other kinds of arthropods may also play a role. Natural infection of the causative agent, *Rickettsia tsutsugamushi*, has been demonstrated in a gamut of small mammals previously not incriminated, sufficiently to

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suggest that almost any species of small mammal parasitized by certain groups of trombiculids in an endemic locus may become infected. The extent to which such mammals participate in perpetuating the infectious cycle is unknown. It has also been found that the relative numbers of vector chiggers and hosts may change considerably over the years in any one endemic locus. These and other relevant points about the ecology of scrub typhus will be discussed in this article. Additional data on trombiculid mites as vectors will be presented in another article in this series (Traub & Wisseman, 1988).

Highlights on the ecology of scrub typhus were reviewed by Audy (1961), and details of the classical pattern of epidemiology and natural history of that disease were presented by him in 1949. Some of the earliest observations indicating that scrub typhus could no longer be considered a disease solely of tropical areas or purely a summer phenomenon were made in Japan, as summarized by Sasa (1954) and Tamiya (1958, 1962). The presence of scrub typhus in a country with a very cold winter—namely, Korea—was reported by Jackson et al. (1957), but Kraminskij (1959) later stated that Soviet workers had recognized this in 1946. A surprising northern record was that noted by Soviet scientists in the southern Primorye Territory of Siberia, opposite Sakhalin, as described by Tarasevič (1964) and Tarasevič et al. (1964) and by Kudrjašova et al. (1967), although that area is more temperate than its latitude suggests, since the endemic region is subject to monsoon conditions and the winters are snowless, with frequent warm periods (Tarasevič, 1966). Kalra & Rao (1951) stated that scrub typhus occurred in Kashmir in a relatively temperate climate and Kalra (1947, 1959) made similar observations in the Kumaon Hills for elevations up to 7500 feet (2300 m), but in the absence of details these claims were difficult to evaluate.

FIELD SURVEYS

On the basis of preliminary surveys specifically undertaken to determine the faunal affinities of endemic rodents and ectoparasites, field teams of the University of Maryland School of Medicine prognosticated that scrub typhus was present in West Pakistan in areas which were remote both physically and ecologically from known foci and in terrain where its presence had never been suspected and where known vectors and reservoirs were absent. As reported by Traub et al. (1967), these hypotheses were correct, and *R. tsutsugamushi* was isolated from mammalian tissues or from chiggers: (*a*) in the mountains of the Kaghan Valley from elevations as high as 10 500 feet (3200 m), where snow remains on the ground 10 months of the year; (*b*) from a gerbil in the semi-desert plains of Multan; (*c*) in the mountain-desert of Gilgit, north of the Indus River; and (*d*) in the plains of Lahore. In that study it was reported that scattered throughout the extremely desolate and barren stretches of the Gilgit Agency are " ecological islands " on tops of mountains or in valleys watered by glacial streams, where may be found many of the same mammals and ectoparasites that occur miles away in moist parts of the Himalayas. It therefore seemed likely that infections associated with these mammals and mites, fleas and ticks in the Kaghan Valley would be found on other of these isolated " ecological islands ". More recent, unpublished data indeed indicate that, for example, scrub typhus infection also exists west of the Indus in various parts of Swat, in mountains separated by miles of desert and broad rivers from known endemic foci, and in the midst of the semi-desert region of Malakand. According to this hypothesis, the high mountains do not uniformly serve as true barriers to the rodents and their ectoparasitic and enzootic faunas, but instead represent upward thrusts of the Himalayas in the Pliocene which rent asunder what had been continuous stretches of forests in the Tertiary Period, and thereby isolated foci in which relicts of former eons survive today. As xeric conditions developed on the rain-shadow side of the mountain masses, deserts and semi-deserts were formed, encouraged by erosion stimulated by man's activities, thus providing additional barriers and further isolating the " faunistic islands " with their " oasis scrub typhus ". For these reasons and because of basic affinities regarding many of the rodents and insectivores and of their mites, ticks and fleas, it seems probable to us that similar foci of scrub typhus (and tick typhus, etc.) exist in at least the border areas of the countries surrounding West Pakistan, and that other infections known in the latter regions also occur in Pakistan, albeit unrecognized as yet.

Earlier studies had suggested that the name scrub typhus was in reality a misnomer, and that chiggers other than *L. deliense* and *L. akamushi* may participate in the natural history of this infection. The demonstration of *R. tsutsugamushi* in indigenous forest-rats and in a Malayan species of chigger of the genus *Euschoengastia* Ewing, 1938, led to a belief in a " jungle cycle " of scrub typhus (Traub et al., 1950).

It was then shown that human cases can occur in outbreak form in such terrain, even in the dry season when vector mites are scarce and when very few cases are occurring in the classical types of terrain (Traub, 1962), thereby lending substance to unverified wartime reports of such occurrences (Traub, 1949). *Leptotrombidium pallidum* (Nagayo et al., 1919) and *L. scutellare* (Nagayo et al., 1921) are regarded as important vectors in Japan, particularly in the fall and winter, as reported by Asanuma et al. (1959), Tamiya (1962) and Kumada (1959). Jackson et al. (1957) likewise incriminated *L. pallidum* in Korea, and Kudrjašova & Tarasevič (1964) recovered strains from this species in Siberia, as well as from a mixture of *L. pavlovskyi* (Schluger, 1948) and *Neotrombicula japonica* (Tanaka, 1916) and in addition demonstrated transtadial infection in *L. pavlovskyi*. *L. orientale* (Schluger, 1948) is another suspect vector (Asanuma et al., 1959; Tarasevič et al., 1964), while *Leptotrombidium arenicola* Traub, 1960, is also regarded as important in this respect (Traub, 1960). Yu & Lin (1957) reported *Euschoengastia indica* (Hirst, 1915), *Acomatacarus* sp. and *(Walchia)* as serving as natural sources of infection or as possible vectors.

The Chinese have reported natural infection of *R. tsutsugamushi* in *Ixodes* ticks (Kuang-Leih et al., 1959; Yuan et al., 1959), but there is little evidence that ticks play any significant role in the ecology of scrub typhus. (In fact, Japanese workers (Tamiya, 1962) failed to infect ticks experimentally with *R. tsutsugamushi*.) It is similarly difficult to evaluate the epidemiological potential of Tiflov's report (1959) that fleas can maintain infection with *R. tsutsugamushi* for 11 days and transmit the rickettsiae by biting.

CHIGGERS AS VECTORS OF SCRUB TYPHUS

It is apparently much easier to demonstrate the presence of *R. tsutsugamushi* in a pool of chiggers containing numbers of *L. deliense* than in those consisting of other genera and species from the same area. Thus, Trishnanda et al. (1966) reported the inoculation of 84 pools of chiggers, representing 17 pools of *L. deliense*, and 67 pools containing 6 species in 4 other genera of chiggers. The 6 rickettsial strains isolated were all from the samples with *L. deliense*. Similarly, in the only known hyperendemic scrub typhus area in West Pakistan, and the only locality studied where *L. deliense* was present (Traub et al., 1967), Nur Ahmad & Burney (1962) had reported that one of three attempts to isolate *R. tsutsugamushi* from pools of chiggers was successful. Our own unpublished results in this particular site were comparable, in marked contrast to observations in the mountains, deserts and other areas where *L. deliense* was absent—and where the bulk of the chigger pools were collected. Thus, the over-all strain-recovery rate for chiggers (from all areas) was 1 isolation in 60 attempts (1.7%) (Traub et al., 1967). Even when isolation was attempted from mammalian tissues, the isolation rate in West Pakistan was higher in localities where *L. deliense* occurred, namely, 21 out of 96 (22%) as against 42 out of 606 (7%) (Traub et al., 1967). In Thailand, where *L. deliense* was always present in the areas studied, the strain-recovery rate from tissues was 16% (Trishnanda et al., 1966).

It seems significant that nearly everywhere where sufficient numbers of ground-dwelling rodents were tested in West Pakistan, it was possible to demonstrate natural scrub typhus infection, regardless of habitat. In that study, infection was reported for the first time for 5 genera and 6 species of rodents, out of a total of 11 species of mammals found positive and 17 tested. A broad host range of natural infection with *R. tsutsugamushi* in indigenous small mammals was also reported in northern Queensland, Australia, by Cook et al. (1967), including the marsupial *Isoodon* and rats such as *Uromys*, *Melomys* and *Rattus*.

There is one aspect of the ecology of scrub typhus that is apparently frequently overlooked—namely, the factor of *time* in contrast to that of *space*. Scrub typhus is a prime example of a disease with a " natural nidality," as Pavlovskij (1946) used the term, and in fact, the endemic foci can be so localized that a sharp outbreak may affect only certain groups of men in a highly limited area while sparing others apparently equally and simultaneously exposed in the same locus (Philip, 1948, 1949; Audy, 1949). So small are some of these infective sites that what had been regarded as " typhus islands " were shown to actually be " mite islands " a few feet in extent where vector trombiculid mites occurred in small patches on the ground (Philip et al., 1949; Audy, 1961), or in clusters on debris a few inches above the ground (Gentry et al., 1963). However, important as this spatial factor is, scrub typhus infection is also a dynamic, flexible process undergoing a sequential evolution of its own, involving different trombiculids and rodents in any one focus over a period of a few years. It is this latter type of change that accounts for what appear to be contradictory findings in the chigger (or rodent) population in the same site studied some years apart. For instance, Hubert & Baker (1963a) stated that in 1963 " This field was infested with . . . *Leptotrombidium* (*Leptotrombidium*) *akamushi* " but that " *L.* (*L.*) *deliensis* does not occur in this habitat in Malaya ", when speaking of lallang grass (*Imperata cylindrica*) where Traub & Dowling (1961), 6 or 7 years earlier, had collected about 9 times as many *L. deliense* as *L. akamushi.* This phenomenon is discussed further on the basis of observations made incidentally by the senior author in Malaya during studies of the United States Army Medical Research Unit (Malaya) on the prevention of scrub typhus, undertaken intermittently during the period 1948-59.

CHIGGERS AND THEIR RODENT HOSTS IN RELATION TO HABITAT

The nature of the terrain in these various Malayan foci and the methods for collecting chiggers have been mentioned previously (Philip et al., 1949; Traub & Frick, 1950; Traub & Dowling, 1961). Suffice it to state that: (1) 6 of these areas in Selangor are discussed, 2 at Seaport Estate and 4 at Subang; (2) chiggers were collected by examining both wild-caught rats and laboratory rats that had been exposed in pens; and (3) both snap-traps and live-traps were used in collecting the rats. During the periods under consideration, about 90% of the chiggers studied were either *Leptotrombidium deliense* or *L. akamushi*; the remainder belonged to other genera. The Seaport areas were both known to be hyperendemic loci where old rubber trees, surrounded by wartime scrub, were being replaced by saplings. In one section, designated as " shrubs ", there was still an abundance of scrubby, bushy growth, in contrast to the " lallang " sector, which had been cleared several years previously and where lallang was accordingly plentiful. At Subang, Area A had been the source of an outbreak of scrub typhus a few weeks before the field-study commenced and was a virtually pure stand of *Paspalum* and other grasses used for fodder on a site that had been forest a year earlier. Areas B and C were plots used by Traub & Dowling (1961) in their insecticide studies and consisted of a mixture of lallang, herbs and shrubs next to a forest reserve; both had been covered with trees before the land was cleared in the practice of " shifting cultivation ". Area C had been deforested for 1 year and Area B for 2 years. The margins of these fields were being cleared and burned annually as the study proceeded, and the periphery therefore consisted of the " youngest " scrub and lallang and the centre of the oldest lallang. Since lallang is the commonest " climax type " of vegetation in this part of Asia, the middle blocks were almost pure stands of dense, tough, old *Imperata.* Area D, which had mistakenly been thought to have been the scene of a large outbreak of scrub typhus in 1946, had actually been converted from forest to gardens in 1940 and was a solid stretch of old lallang when first studied in 1948.

Data on the relative proportions of the various major groups of chiggers or rats noted in these areas are presented in Fig. 1–3. The year the original cover of natural forest or cultivated " rubber forest " was cut is considered as Year Y and the number of years subsequent to that event that the various sites were studied is indicated as Y+2 or Y+5, etc. (These figures therefore do *not* represent calendar years denoting when tests were made.) From Fig. 1 it can be seen that for 1 or 2 years following the clearing of the forest, *L. deliense* outnumbered *L. akamushi* on wild rats by at least 4 to 1, or else was the only one of the two vectors present. However, in the 3-year-old lallang sector of Seaport, *L. akamushi* was much more prevalent than *L. deliense* and was more abundant than in other sites of the same ecological age. In fields that were in their fourth or fifth year since clearing (and where lallang accordingly covered most of the area in the process of ecological succession of plants), *L. akamushi* was already the dominant species, and in older plots, *L. deliense* was scarce or absent. The data from white rats released in pens in these foci (Fig. 2) follow a similar pattern. Thus, areas in which *L. deliense* originally predominated or was present alone, *L. akamushi* became successively more numerous with the passage of time.

It is of interest that at essentially the same time there was an analogous change in the relative numbers of the major species of rats in these foci, as shown in Fig. 3. Thus, in plots that had been deforested within the past 2 years, *Rattus argentiventer* Robinson & Kloss, 1916, was either the only rat trapped or else constituted the great majority of those collected. In contrast, *R. jalorensis* Bonhote, 1903,[1] was apparently absent or uncommon in scrub and lallang fields that were under 3 years of age, but

[1] There is some confusion about the correct name to apply to this species. The name we use, and *Rattus rattus jalorensis*, are the names most commonly seen in the medical literature. Harrison (1966) now refers to this species as *Rattus tiomanicus jalorensis.*

FIG. 1

RELATIVE PERCENTAGES OF *LEPTOTROMBIDUM DELIENSE* AND *L. AKAMUSHI* ON WILD RATS TRAPPED AT SEAPORT ESTATE AND SUBANG, MALAYA

Y	SEAPORT ESTATE SHRUBS L.D.	SHRUBS L.A.	LALLANG L.D.	LALLANG L.A.	SUBANG AREA "A" L.D.	AREA "A" L.A.	AREA "B" L.D.	AREA "B" L.A.	AREA "C" L.D.	AREA "C" L.A.	AREA "D" L.D.	AREA "D" L.A.
Y+1	80%	20%	—	—	100%		—	—	100%		—	—
Y+2	80%	20%	—	—	100%		90%	10%	90%	10%	—	—
Y+ 2-3	60%	40%	—	—	100%		80%	20%	80%	20%	—	—
Y+3	50%	50%	20%	80%	—	—	75%	25%	70%	30%	—	—
Y+4	—	—	25%	75%	30%	70%	30%	70%	40%	60%	—	—
Y+5	20%	80%	10%	90%	15%	85%	20%	80%	—	—	—	—
Y+6	—	—	—	—	5%	95%	5%	95%	10%	90%	—	—
Y+8	20%	80%	10%	90%	—	—		100%		100%	—	—
Y+10	—	—	—	—	(NIL)	(NIL)	5%	95%	(NIL)	(NIL)	(NIL)	(NIL)
Y+12	—	—	—	—	—	—	(NIL)	(NIL)	—	—	(NIL)	(NIL)

(solid black) and L.D. = *L. deliense*.
(horizontal hatching) and L.A. = *L. akamushi*.
(black bar) = No data for period.
Y = Year in which forest-cover was removed; Y+2 = 2 years after removal of cover, etc.

achieved dominance in such areas that were 5 or more years of age. (The third most abundant species, *R. exulans* Peale, 1848, was only occasionally collected, and its numbers did not vary significantly or consistently.)

In our opinion, these changes in the faunas of chiggers and rats in endemic foci can be explained by a hypothesis based upon observations already reported on the habitats and habits of the vector mites and of their rat hosts. Thus, the distribution of *L. deliense* throughout its range is definitely associated with existing or former forest-cover or woody scrub vegetation (Traub, 1949; Traub et al., 1967; Hubert & Baker, 1963a), including primary

FIG. 2

RELATIVE PERCENTAGES OF *LEPTOTROMBIDIUM DELIENSE* AND *L. AKAMUSHI* ON LABORATORY RATS EXPOSED IN PENS AT SEAPORT ESTATE AND SUBANG, MALAYA

Y	SEAPORT ESTATE				SUBANG							
	SHRUBS		LALLANG		AREA "A"		AREA "B"		AREA "C"		AREA "D"	
	L.D.	L.A.	L.D.	L.A.	L.D.	L.A.	L.D.	L.A.	L.D.	L.A.	L.D.	L.A.
Y+1	80%	20%	—	—	100%		—	—	100%		—	—
Y+2	75%	25%	—	—	100%		80%	20%	95%	5%	—	—
Y+ 2-3	65%	35%	—	—	100%		75%	25%	80%	20%	—	—
Y+3	55%	45%	30%	70%	75%	25%	70%	30%	60%	40%	—	—
Y+4	50%	50%	35%	65%	50%	50%	40%	60%	40%	60%	—	—
Y+5	20%	80%	20%	80%	20%	80%	30%	70%	—	—	—	—
Y+6	—	—	—	—	—	—	10%	90%	—	—	—	—
Y+8	—	—	10%	90%	—	—	—	—	—	—	—	—
Y+10	—	—	—	—	—	—	—	—	(NIL)	(NIL)	(NIL)	(NIL)
Y+12	—	—	—	—	—	—	—	—	—	—	(NIL)	(NIL)

and L.D. = *L. deliense*.
and L.A. = *L. akamushi*.
= No data for period.
Y = Year in which forest-cover was removed; Y+2 = 2 years after removal of cover, etc.

jungle in the lowlands (Traub, 1949), foothills (Traub et al., 1950; United States Army Medical Research Unit (Malaya), 1960), and montane forest (Traub & Audy, 1954). In contrast, *L. akamushi* is associated primarily with open grassland (Audy, 1958b; Hubert & Baker, 1963a). It is also well established that *L. deliense* and *L. akamushi* are much more likely to be found in relatively moist habitats or in rainy periods, than in dry sites or during droughts (Traub & Frick, 1950; Audy, 1961; Hubert & Baker, 1963b). As for the mammals, Harrison (1954) made the significant observation that rats inhabiting lallang, particularly *R. argentiventer*, fed upon termites to a large degree, and he

FIG. 3

RELATIVE PERCENTAGES OF WILD-CAUGHT RATS, *RATTUS ARGENTIVENTER*, *R. JALORENSIS* AND *R. EXULANS*, AT SEAPORT ESTATE AND SUBANG, MALAYA

Y	SEAPORT ESTATE				SUBANG AREA "A"				SUBANG AREA "B"				SUBANG AREA "C"			
	TOTAL NO.	R.A.	R.J.	R.E.	TOTAL NO.	R.A.	R.J.	R.E.	TOTAL NO.	R.A.	R.J.	R.E.	TOTAL NO.	R.A.	R.J.	R.E.
Y+1	77	95%		5%	25	100%			—	—	—	—	29	100%		
Y+2	62	90%		10%	47	90%	10%		240	80%	15%	5%	91	82%	15%	3%
Y+ 2-3	94	93%	7%		62	81%	19%		493	61%	36%	3%	321	68%	30%	2%
Y+3	123	78%	20%	2%	77	69%	31%		397	64%	33%	3%	425	12%	91%	7%
Y+4	—	—	—	—	—	—	—	—	540	13%	82%	5%	408	5%	90%	5%
Y+5	72	25%	54%	13%	56	7%	93%		372	3%	90%	7%	—	—	—	—
Y+6	—	—	—	—	50	6%	94%		566	4%	92%	4%	365	6%	88%	6%
Y+8	108	5%	79%	16%	—	—	—	—	675	2%	93%	2%	416	4%	90%	6%
Y+10	—	—	—	—	—	—	—	—	175		96%	4%	81		89%	11%
Y+12	—	—	—	—	—	—	—	—	24		100%		—	—	—	—

and R.A. = *R. argentiventer*.
and R.J. = *R. jalorensis*.
and R.E. = *R. exulans*.
= No data for period.
Y = Year in which forest-cover was removed; Y +2= 2 years after removal of cover, etc.

also noted that at Seaport Estate, *R. jalorensis* tended to replace *R. argentiventer* in time (Harrison, 1957). Other data indicate how the behavioural pattern of rats influences their ecological distribution in the Malaysian area. In the original studies at Seaport Estate, it was observed that *Rattus rattus diardi* could be trapped only in or very close to huts, and never in the fields or wasteland, where *R. argentiventer* was prevalent and apparently kept other species from their territory. In nearby Singapore, however, where *R. argentiventer* is presumably absent (Audy, 1961; Harrison, 1966), *R. r. diardi* is the dominant rat in lallang and other wasteland and fields, while the niche in houses is occupied by the imported, larger and fierce *R. norvegicus*.

According to our hypothesis, then, the rats inhabiting the lallang in recently cleared areas feed largely on termites which live in the decaying roots of the great trees that had formerly covered the area. The termites rapidly establish colonies in the underground stumps and roots and live there for years, and the tunnels remaining after the roots are eaten or become decomposed are then used by rats for shelters and runways and no doubt provide suitable conditions for *L. deliense*. Thus, despite an environment that superficially appears barren and hostile because of lack of shade and a dearth of rodent-food such as fruits, seeds and insects, rats such as *R. argentiventer* can thrive at this particular stage of the ecological succession. Moreover, this species of rat is large and aggressive enough to keep competitors, *R. r. diardi* and *R. jalorensis*, from its territory. Our chigger and host data suggest that after 3–5 years, as the roots decay completely and the termites feeding on them become scarce, and as pure lallang takes over more and more of the habitat, there is an exodus of *R. argentiventer*, thereby permitting *R. jalorensis* to enter from the periphery. As conditions become modified in the microhabitats, the numbers of *L. deliense* also decline, except in highly localized favourable sites with moisture and shade. *R. jalorensis*, it would seem, fare well for a few years, but their numbers fall as their sources of food, such as passion-fruit, seeds and underground insects, become harder to find, as the inedible lallang becomes dominant, and as soil conditions change. In the earlier stages of this succession, ground-birds such as quail, which often harbour large numbers of *L. akamushi* (Philip et al., 1949; Audy, 1958a) are plentiful and undoubtedly seed the ground with engorged chiggers often acquired elsewhere and acquire newly emerged larval trombiculids in the lallang habitat. *L. akamushi* then becomes the dominant species in the grassfields. Later, as the ecological succession leads to large stretches of pure lallang 6 or more years in age (8 or 10 years after the trees were felled), the chigger population becomes minimal, and at times, nil, except for localized pockets where ground-birds or mammals such as wild-boar, may have nested or lived or where seepage and scrubby bushes occur.

Hubert & Baker (1963a) undoubtedly had correctly identified the chiggers in their respective sites but were unaware of the changes wrought by time when they wrote: "The finding of the marked difference in habitats [at Subang] of *L.* (*L.*) *akamushi* and *L.* (*L.*) *deliensis* departs clearly from the existing concept that these mites exist together in a grassland-scrub habitat". At the time of their study, the Subang fields were in their sixth to ninth years after the felling of the forest, and hence at the stage favourable to *L. akamushi*, in contrast to earlier years. The time-factor also accounts for such statements as: "A number of lallang fields studied appeared to lack *L.* (*L.*) *akamushi*" (Hubert & Baker, 1963b), and for the failure of other workers in Malaya to find these chiggers in what appeared to be typical fields of *Imperata cylindrica*, resembling those heavily infested elsewhere. (The chemical and physical properties of the soil are other factors that affect the chigger population, but are beyond the scope of this article, although these, too, may vary in time as the type of vegetative cover changes.)

Despite the advances in our knowledge of the natural history of scrub typhus indicated in this article, there are sufficient hints that we still have much to learn—about its true geographical and ecological distribution, and about the vectors and reservoirs in newly discovered areas and even in the relatively well-studied foci. This is especially important nowadays, when tremendous physical changes are being wrought by man in many parts of the world by the construction of dams in hydroelectric or irrigation schemes, and as vast stretches of forest are cleared to open new agricultural lands, or as roads are cut across mountains and jungles. Concomitant changes in the ecology of such areas are inevitable, and as was shown repeatedly during the Second World War, scrub typhus is often a phenomenon arising out of man's activity. It was the conversion of jungle to roads or camps and the abandonment of well-groomed gardens that produced the scrub terrain that has given this disease its name (Audy, 1949, 1961). Thus, the huge, newly constructed Mangla Dam in Pakistan is fairly close to the hyperendemic foci in the plains of Sialkot, and as the irrigation programme develops and converts former xeric habitats to agricultural land, rats and chigger-vectors may spread alongside the new canals and introduce scrub typhus infection, if, indeed, it is not already present (Traub et al., 1967). Medical experts should always be included among the officials in charge of planning major projects which affect the ecology of plants and animals on a regional scale.

RÉSUMÉ

Depuis la fin de la deuxième guerre mondiale, les conceptions concernant l'écologie du typhus de brousse se sont profondément modifiées. L'affection peut se rencontrer dans un grand nombre de régions différant par les conditions de climat et d'habitat, comme par exemple les territoires situés au nord et à l'ouest de l'Indus, le sud-est de la Sibérie ou les zones montagneuses du Pakistan, où sa présence n'était pas soupçonnée. La gamme des zones propices va de régions typiquement tropicales aux prairies alpines et aux pentes montagneuses à climat subarctique. Les travaux personnels des auteurs, comme ceux d'autres chercheurs,

plaident en faveur de l'existence d'« îlots écologiques » qui bien que séparés par de hautes montagnes, des déserts ou de larges cours d'eau renferment des populations de rongeurs et d'ectoparasites de type semblable favorables à l'éclosion de foyers d'infection. De tels îlots ont été identifiés dans l'Himalaya, au Pakistan, et il est probable qu'il en existe également dans les pays voisins.

Outre les vecteurs classiques du typhus de brousse, *Leptotrombidium (Leptotrombidium) akamushi* et *L. (L.) deliense*, beaucoup d'autres agents, appartenant en général au sous-genre *Leptotrombidium*, sont vraisemblablement capables de transmettre l'infection. Le rôle des Ixodes n'est pas confirmé. Dans les régions d'endémicité, on décèle l'infection naturelle chez une grande variété de petits mammifères, spécialement des rongeurs. Lors de l'étude écologique du typhus de brousse, on doit tenir compte non seulement des particularités géographiques — existence de très petits foyers d'infection résultant de la prévalence très localisée d'un vecteur — mais aussi d'un facteur « temps », le caractère de la maladie se modifiant dans un même foyer au cours des années suivant les fluctuations des populations de vecteurs ou du réservoir de virus.

S'appuyant sur de nombreux exemples, les auteurs montrent que l'ouverture de nouvelles routes, la mise en valeur des terres ou la réalisation de projets d'irrigation, en modifiant l'habitat, risquent d'ouvrir de nouveaux territoires à l'expansion de l'infection ou d'accroître son ampleur là où elle existe déjà.

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