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Natural ecotopes of *Triatoma infestans* dark morph and other sylvatic triatomines in the Bolivian Chaco

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Abstract

A survey of natural ecotopes of *Triatoma infestans* dark morph and other triatomine sylvatic species was performed in an uninhabited area of the Bolivian Chaco. Among the 321 triatomines collected by light trapping, only 4 *T. infestans* dark morph specimens were identified. Predominant flying species were *T. guasayana* and *T. sordida* group 2 (51·7% and 37·1% of capture, respectively). The same species prevailed in terrestrial and epiphytic bromeliads where scarce *T. infestans* dark morph nymphal instars were also detected. In parrot nests *T. delpontei* prevailed broadly over other species (90·2% of the capture) and only 4 *T. infestans* dark morph adults were collected. In contrast, *T. infestans* dark morph was the predominant species captured in hollow trees (46·0% of the total collected). The abundance of immature forms (88·2% of the collection) shows that hollow trees constitute a favourable ecotope for this species. Of the 421 trees investigated, 33·7% were positive for triatomines. *T. infestans* dark morph, found inside 15·0% of them, also had higher apparent density than other species (average number of *T. infestans* in positive trees, 2·0 ± 1·6 vs 1·3 ± 0·6 for other species). Light trapping seems to be an efficient method to sample the *T. sordida*–*T. guasayana* complex in that it shows a similar distribution to that observed in natural ecotopes; however, this method is ineffective for the assessment of the local abundance of *T. infestans* dark morph.

Keywords: *Triatoma infestans, Triatoma sordida, Triatoma guasayana,* sylvatic populations, ecology, Bolivia

Introduction

Control of Chagas disease by the elimination of domestic populations of Triatominae has been successful over vast areas of the Southern Cone countries where *Triatoma infestans* is the main domestic vector (SCHOFIELD & DIAS, 1998). Nevertheless, in controlled areas, there are increasing reports of sylvatic triatomines invading human dwellings. Consequently, research activities must focus on originally sylvatic species adapting to peridomestic and domestic habitats. The entomological observations generated will assist in the adaptation of vector control strategies.

With regard to *T. infestans*, Bolivia is the only country where true sylvatic foci are documented. Sylvatic populations have been reported from valleys of Cochabamba and Sucre (TORRICO, 1946; DUJARDIN *et al.*, 1987; BERMUDEZ *et al.*, 1993). More recently, a sylvatic focus was also detected at Caracato, department of La Paz (F. Noireau, unpublished data). These sylvatic populations, which occur always amongst rock-piles, are most likely widespread through Andean valleys between 2400 and 2600 m altitude. Chromatic pattern, isozyme profiles and DNA sequence analysis are similar between domestic and sylvatic Andean specimens but random amplified polymorphic DNA (RAPD) and morphometrics allow them to be distinguished (DUJARDIN *et al.*, 1987, 1997; CARLIER *et al.*, 1996; MONTEIRO *et al.*, 1999).

Besides this Andean focus, another sylvatic *T. infestans* population was recently detected in the Bolivian Chaco (NOIREAU *et al.*, 1997b). The first reported specimens were adults captured in parrot nests and by light trapping. Because of chromatic differences with domestic *T. infestans* (overall darker coloration with small yellow markings on the connexivum), they were named dark morphs (DM). They present morphometric differences but isoenzymatic similarity with domestic *T. infestans*. This suggests that they represent a distinct population (NOIREAU *et al.*, 1997b), a hypothesis recently supported by DNA sequence analysis and cytogenetics (MONTEIRO *et al.*, 1999; F. Panzera, unpublished data).

The same region of the Bolivian Chaco is characterized by the sympatric occurrence of *T. guasayana* with 2 putative cryptic species of the *T. sordida* complex known as groups 1 and 2 (G1 and G2) (NOIREAU *et al.*, 1998, 1999b). Parrot nests in the region often contain ornithophilic triatomines characterized as *T. delpontei* by cytogenetics (F. Panzera, unpublished data). The current work improves the knowledge of these sylvatic species which are all (except *T. delpontei*) considered as candidate vectors because of their ability to colonize artificial structures.

Materials and Methods

Study area

The field work was carried out in the phytogeographical region of the Chaco, in the southern part of the Department of Santa Cruz, Bolivia. The main environmental characteristics of this semi-arid region are: (i) 300-m altitude, (ii) a mean temperature of 26°C, (iii) an average annual rainfall of about 600 mm, and (iv) a marked seasonality, with a dry season from March to October and a wet season the rest of the year. The surveyed area included La Choza (18° 34′ 516″ S; 62° 40′ 108″ W), an uninhabited site located on the way to Izozog, and the surrounding forest. The area is covered by a dense and thick vegetation (elevation 4–6 m) of hardwood trees dominated by *Ruprechtia triflora* with emerging trees up to 12 m high (including *Aspidosperma quebracho-blanco, Chorisia insignis*). In the lowest stratum thorn shrubs, bromeliads and cacti predominate.

Collection of triatomines

The current study was focused on *T. infestans* DM but also included other sylvatic triatomine species endemic to the area. Insects were collected by light-trap at the site of La Choza. The light system consisted of a vertical white cloth simultaneously illuminated by a 12-V fluorescent black light tube and a 150-V mercury vapour light. It was operated by portable generator from sunset to 22:30 for 3–5 successive nights in September 1995, 1996 and 1997, and for 18 nights in September 1998.

Various natural habitats such as bromeliads, parrot nests and hollow trees located near the site were searched

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for the presence of triatomines during September and October 1998. Terrestrial (*Bromelia serra* and *B. hieronymi*) and epiphytic bromeliads (*Tillandsia* spp.) were cut off at the base and systematically dissected. Parrot nests inhabited by *Myiopsitta monacha cotorra* (colonial monk parrot) were carefully dismantled to allow each part to be examined. Mammal-baited traps as described by NOIREAU *et al.* (1999a) were used to capture insects living in hollow trees.

Processing of insects

The collected triatomines were placed in plastic bottles containing filter paper and transported to the laboratory. They were identified by morphology, according to LENT & WYGODZINSKY (1979). Isoenzyme analysis was performed to discriminate nymphal instars and adults of *T. sordida* G1, G2, and *T. guasayana*. All nymphal instars and adults pertaining to this complex were processed for 2 enzyme systems: malate dehydrogenase (MDH, EC 1.1.1.37) and isocitrate dehydrogenase (IDH, EC 1.1.1.42). Both enzyme systems provide a reliable identification of the 3 species (NOIREAU *et al.*, 1998). Although *T. sordida* G2 has not yet received formal nomenclatural recognition as a new species, it will be considered as a putative species in this work. Samples collected in hollow trees were examined for flagellates by direct microscope observation of faeces droplets at ×400 magnification.

Results

A total of 321 triatomines was captured by light-trapping (Table 1). According to their relative abundance, *T. guasayana* prevailed over *T. sordida* G2 and G1 (51·7%, 37·1% and 8·7% of capture, respectively). *T. infestans* DM and *T. delpontei* presented a low abundance (only 4 specimens of each species captured). The sex ratio for the whole collection was close to 1:1.

We searched for triatomines inside 197 terrestrial bromeliads (Table 2). *T. guasayana* and *T. sordida* G2 were the prevailing species (48·9% and 36·2%, respectively). Four nymphal instars of *T. infestans* DM and 3 *T. sordida* G1 specimens were also encountered. A similar distribution of species was observed inside 172 epiphytic bromeliads: *T. sordida* G2 and *T. guasayana* predominated over *T. infestans* DM (8 nymphal instars collected) and *T. sordida* G1 (Table 2). The infestation rate for both types of bromeliads was similar (17·3% for terrestrial bromeliads and 22·1% for epiphytes, respectively). According to the species, the triatomine burden of pooled terrestrial and epiphyte bromeliads is shown in Table 3. The average number of triatomines captured by positive plant was 1·5 ± 0·6. *T. infestans* DM and *T. sordida* G1 were scarcely found (2·2% and 1·9% of bromeliads, respectively). However, *T. sordida* G2 and *T. guasayana* were more frequently detected (in 9·5% of bromeliads for both species). A total of 78·6% of positive bromeliads contained only 1 species while 21·4% contained 2 species.

The dissection of 46 parrot nests showed that *T. delpontei* prevailed over *T. sordida* G1 (90·2% vs 6·3%, respectively). Only 4 *T. infestans* DM and 1 *T. sordida* G2 were also collected (Table 2). Except for *T. delpontei* which exhibited a great number of nymphal instars, only adult forms were detected for other species. *T. delpontei* was encountered inside 26 nests (56·6%) and *T. sordida* G1 inside 5 (10·9%). The 4 adult forms of *T. infestans* DM were captured inside 3 nests.

From a total of 732 bait-traps suspended in hollow trees, 160 (21·9%) collected live triatomines adhering to the tape. The distribution by species and age structure of the 276 captured triatomines is shown in Table 2. *T. infestans* DM was the predominant species (46·0% of the 276 triatomines captured), followed by *T. guasayana* (23·2%) and *T. sordida* G2 and G1 (17·0% and 13·8%, respectively). A great number of nymphal instars was collected, particularly of *T. infestans* DM and *T. sordida* G1 (88·2% and 71·1%, respectively). From a total of 421 trees investigated, 142 were positive for triatomines (33·7%). According to triatomine species, the apparent triatomine burden of infested trees is shown in Table 4. The average number of triatomines captured by positive tree was 1·9 ± 1·4. *T. infestans* DM, found inside 15·0% of trees, presented the highest apparent density: the average number of specimens captured by positive tree (2·0 ± 1·6) was greater than for any other species ($P <$ 0·05) while the mean burdens for *T. sordida* G1, G2 and *T. guasayana* were similar. Most positive trees contained only 1 species (73·3%) while 23·2% had 2 species and 5 (3·5%) 3 species. Forty-five trees contained only *T. infestans* DM (31·7%) while 18 (12·7%) had *T. infestans* DM associated with another species.

The distribution of *T. sordida* G1, *T. sordida* G2 and *T. guasayana* adults did not differ significantly between captures performed by light-trapping, in bromeliads and hollow trees. In contrast, only 4 *T. infestans* DM were collected by light-trapping in spite of their abundance in hollow trees.

Faecal samples from 134 triatomines collected in hollow trees were examined by microscopy for flagellates. Only 2 (2·5%) *T. infestans* DM were positive. The infection rate of other species is summarized in Table 5.

Discussion

Ecological studies of Triatominae in areas where endemic species are hard to discriminate on morphological traits show the importance of using molecular tools for an accurate characterization. This is particularly so for the *T. sordida*–*T. guasayana* complex (NOIREAU *et al.*, 1998) and other Triatominae such as the *Rhodnius* genus (DUJARDIN *et al.*, 1991). In the Bolivian Chaco, multilocus enzyme electrophoresis allows reliable discrimination between 2 biological species pertaining to the *T. sordida* complex and named groups 1 and 2 (NOIREAU *et al.*, 1998). Later, this partition was confirmed by RAPD, morphometrics, cytogenetics and crossing experiments (J. P. Dujardin, B. Bastrenta, L. Garcia, F. Panzera and F. Noireau, unpublished data). Because these *T. sordida* groups could exhibit different behaviour, ecologicial studies should take the distinct population subdivision into consideration.

Light-trapping seems to be an efficient method to sample the *T. sordida*–*T. guasayana* complex as it shows

Table 1. Distribution of Triatominae captured by light-trapping in the Bolivian Chaco

Species	No. (%) of males	No. (%) of females	Total (%) of capture
T. sordida G1	9 (32·1)	19 (67·9)	28 (8·7)
T. sordida G2	68 (57·1)	51 (42·9)	119 (37·1)
T. guasayana	79 (47·6)	87 (52·4)	166 (51·7)
T. infestans DM	1 (25·0)	3 (75·0)	4 (1·2)
T. delpontei	3 (75·0)	1 (25·0)	4 (1·2)
Total	160 (49·8)	161 (50·2)	321 (100)

DM, dark morph. See the text for details of the methods used.

Table 2. Distribution of triatomines collected in natural ecotopes in the Bolivian Chaco

Ecotope	Species	No. of nymphs	No. of males	No. of females	No. of adults	Total (%) of capture
Terrestrial bromeliad	*T. sordida* G1	1	2	0	2	3 (6·4)
	T. sordida G2	0	9	8	17	17 (36·2)
	T. guasayana	0	16	7	23	23 (48·9)
	T. infestans DM	4	0	0	0	4 (8·5)
	Total	5	27	15	42	47 (100)
Epiphytic bromeliad	*T. sordida* G1	1	0	3	3	4 (7·3)
	T. sordida G2	0	9	13	22	22 (40·0)
	T. guasayana	1	9	11	20	21 (38·2)
	T. infestans DM	8	0	0	0	8 (14·5)
	Total	10	18	27	45	55 (100)
Parrot nest	*T. sordida* G1	0	2	7	9	9 (6·3)
	T. sordida G2	0	1	0	1	1 (0·7)
	T. guasayana	0	0	0	0	0
	T. infestans DM	0	3	1	4	4 (2·8)
	T. delpontei	69	33	27	60	129 (90·2)
	Total	69	39	35	74	143 (100)
Hollow tree	*T. sordida* G1	27	7	4	11	38 (13·8)
	T. sordida G2	9	21	17	38	47 (17·0)
	T. guasayana	3	30	31	61	64 (23·2)
	T. infestans DM	112	5	10	15	127 (46·0)
	Total	151	63	62	125	276 (100)
All ecotopes	*T. sordida* G1	29	11	14	25	54 (10·4)
	T. sordida G2	9	40	38	78	87 (16·7)
	T. guasayana	4	55	49	104	108 (20·7)
	T. infestans DM	124	8	11	19	143 (27·4)
	T. delpontei	69	33	27	60	129 (24·8)
	Total	235	147	139	286	521 (100)

DM, dark morph. See the text for details of the methods used.

Table 3. Triatomine burden in bromeliads in the Bolivian Chaco

Species	No. (%) of positive bromeliads	No. of triatomines	Mean no. (SD) of triatomines per positive plant	Range of density
T. sordida G1	7 (1·9)	7	1·0 (0·0)	1
T. sordida G2	35 (9·5)	39	1·1 (0·3)	1–2
T. guasayana	35 (9·5)	44	1·3 (0·5)	1–3
T. infestans DM	8 (2·2)	12	1·5 (0·8)	1–3
All species	70 (19·0)	102	1·5 (0·6)	1–3

The values given are combined results from 197 terrestrial bromeliads and 172 epiphytic bromeliads.
DM, dark morph.

Table 4. Apparent triatomine burden in trees in the Bolivian Chaco

Species	No. (%) of positive trees	No. of triatomines	Mean no. (SD) of triatomines by positive tree	Range of density
T. sordida G1	32 (7·6)	38	1·2 (0·5)	1–3
T. sordida G2	40 (9·5)	47	1·2 (0·4)	1–2
T. guasayana	50 (11·9)	64	1·3 (0·6)	1–4
T. infestans DM	63 (15·0)	127	2·0 (1·6)	1–11
All species	142 (33·7)	276	1·9 (1·4)	1–12

DM, dark morph.

a similar distribution to that observed in natural ecotopes such as hollow trees and bromeliads. Moreover, it confirms the dispersive flight ability of these species as reported by SCHOFIELD *et al.* (1991), WISNIVESKY-COLLI *et al.* (1993) and NOIREAU *et al.* (1999b). However, the light-trapping of *T. infestans* DM seems ineffective to assess the local abundance of this species. As suggested by studies on domestic populations, *T. infestans* has a lesser propensity to flight than *T. sordida* (SCHOFIELD *et al.*, 1992). WISNIVESKY-COLLI *et al.* (1993) reported that *T. guasayana* females attracted to light were slightly more numerous than males. In our

Table 5. Infection by flagellates of triatomines collected in hollow trees in the Bolivian Chaco

Species	No. examined	No. positive	% positive
T. sordida G1	22	2	9·1
T. sordida G2	16	0	0·0
T. guasayana	15	2	13·3
T. infestans DM	81	2	2·5
Total	134	6	4·5

DM, dark morph.

study, a similar result was observed in *T. guasayana* and *T. sordida* G1. On the contrary, the capture of males by light-trapping was greater in *T. sordida* G2. These collections performed during the end of the dry season discard the idea of a temporal sex ratio modification where males are more common early in the season and females at the end, as observed by EKKENS (1981) for *T. rubida* in Arizona.

In the Argentinean Chaco, sylvatic *T. guasayana* colonizes bromeliads, cacti and tree cavities (WISNIVESKY-COLLI *et al.*, 1997). Except for cacti (not considered in this study), the same ecotopes are infested in the Bolivian Chaco. In bromeliads and hollow trees, nymphs were collected in low numbers (1 and 3 specimens, respectively) whereas previous studies reported their greater abundance in such ecotopes (WISNIVESKY-COLLI *et al.*, 1997; NOIREAU *et al.*, 1999b). Nevertheless, the presence of nymphal instars allows particular ecotopes to be considered as breeding sites.

Both *T. sordida* groups were collected in bromeliads and hollow trees, although our observations suggest that bromeliads are not important breeding sites since we found no nymphal instars amongst these plants. By contrast, our finding of numerous nymphs in tree cavities suggests that these constitute a favourable ecotope for both species. In spite of the greater abundance of *T. sordida* G2 in this area, *T. sordida* G1 adults largely predominate over G2 in parrot nests but the absence of nymphal instars calls into question the role of these nests as breeding sites. The detection of *T. sordida* G1 in parrot nests opens the idea of passive transport of eggs of this species among the feathers of parrots, which could help to explain the wider distribution of this group. The capture of *T. delpontei* in nests occupied by parrots confirms previous reports of ABALOS & WYGODZINSKY (1951), CARCAVALLO & MARTÍNEZ (1985) and SALVATELLA *et al.* (1993). Until now, *T. delpontei* has not been reported from Bolivia, possibly owing to misidentification as *T. platensis*.

In hollow trees, 88·2% of collected *T. infestans* DM were nymphal instars. The abundance of immature forms shows that hollow trees certainly constitute a very favourable ecotope for this species. The vertebrate hosts living in such hollow trees were not investigated but we observed rodent faeces in various cavities suggesting a possible association between *T. infestans* DM and rodents. In Andean foci, sylvatic *T. infestans* were found associated with *Galea musteloides*, the wild guinea-pig (BERMUDEZ *et al.*, 1993). *T. melanosoma*, a species closely related to *T. infestans*, was captured under tree bark in its sylvatic habitat (A. Martínez, unpublished data) and the similarity of habitat between *T. infestans* DM and *T. melanosoma* suggests that both species share ecological traits regarding habitat and related fauna. The infrequent detection of young nymphal stages in bromeliads (7 stage 1, 3 stage 2 and 2 stage 3) makes us question the significance of these habitats as breeding sites, and the finding of only occasional adults of *T. infestans* DM in parrot nests suggests that these are also not the preferred breeding site of this species.

As reported by FORATTINI *et al.* (1973) and NOIREAU *et al.* (1997a), *T. sordida* does not form large colonies in artificial structures. A similar observation was reported by WISNIVESKY-COLLI *et al.* (1993) in relation to *T. guasayana* in Argentina. Their inability to build up significant populations may be due to the fact that both species rarely complete more than 1 generation per year (SCHOFIELD, 1994). Our data obtained in bromeliads and hollow trees, where only small colonies of these species were observed, support this biological trait. In contrast, *T. infestans* forms large populations in domestic/peridomestic structures where it generally completes 2 generations per year (SCHOFIELD, 1994). This reproductive ability was also reflected in sylvatic ecotopes such as hollow trees where *T. infestans* colonies are larger than those of *T. sordida* and *T. guasayana*. Moreover, laboratory studies demonstrate that *T. infestans* females lay more eggs than *T. sordida* and *T. guasayana* (CARCAVALLO & MARTÍNEZ, 1985). Differences of oviposition also may explain the size difference between populations of these species in artificial or sylvatic habitat.

T. sordida G1 and *T. guasayana* collected in hollow trees were found infected by flagellates. A previous analysis performed by polymerase chain reaction on faecal samples of *T. sordida* and *T. guasayana* from the same area indicates that these flagellates were probably *Trypanosoma cruzi* (NOIREAU *et al.*, 1999b). *Triatoma infestans* DM was also infected by flagellates but its infection rate (2·5%) was lower than observed in sylvatic Andean populations: 73% in Cochabamba according to BERMUDEZ *et al.* (1993) and 100% in Caracato according to F. Noireau (unpublished data).

Except for research on Andean populations of *T. infestans* in Bolivia (TORRICO, 1946; DUJARDIN *et al.*, 1987; BERMUDEZ *et al.*, 1993), very few studies have considered sylvatic foci. Former reports indicate that *T. infestans* was occasionally found in sylvatic conditions in Argentina (MAZZA, 1943; BEJARANO, 1967), Paraguay (VELASQUEZ & GONZÁLEZ, 1959) and Brazil (BARRETTO *et al.*, 1963). Despite these reports, it was considered that *T. infestans* did not maintain sylvatic foci in these areas because most specimens were found in ecotopes relatively close to human dwellings (USINGER *et al.*, 1966). In a review dedicated to such records, BEJARANO (1967) mentions eggs, nymphs and adults collected in a great variety of ecotopes such as rocks, trunks of fallen trees, hollow trees, shelters or burrows of marsupials and rodents and bird nests. The important investigation of *T. infestans* sylvatic populations must be again considered in non-Andean areas after the detection of a new focus in the Bolivian Chaco.

Isolation between sylvatic and domestic *T. infestans* populations from Andean valleys of Bolivia is strongly indicated by field experiments combined with morphometric studies as well as RAPD analysis (CARLIER *et al.*, 1996; DUJARDIN *et al.*, 1997). In the Chaco, continuous exchange of insects between sylvatic and domestic habitats also seems unlikely because of the marked chromatic and morphometric differences as well as differences in mitochondrial DNA and chromosome banding (MONTEIRO *et al.*, 1999; F. Noireau & J. P. Dujardin, unpublished data; F. Panzera, unpublished data). However, the capacity of *T. infestans* DM to invade domestic habitats is still unknown because the current study was performed in an uninhabited area. Further field studies carried out in an inhabited site would allow the determination of whether *T. infestans* DM presents a trend toward domesticity. At last, the detection of sylvatic *T. infestans* in the Bolivian Chaco leads to questions about the ancestral population of this species (CARCAVALLO, 1998), when it was classically considered that Andean populations represented the original sylvatic focus (SCHOFIELD, 1988).

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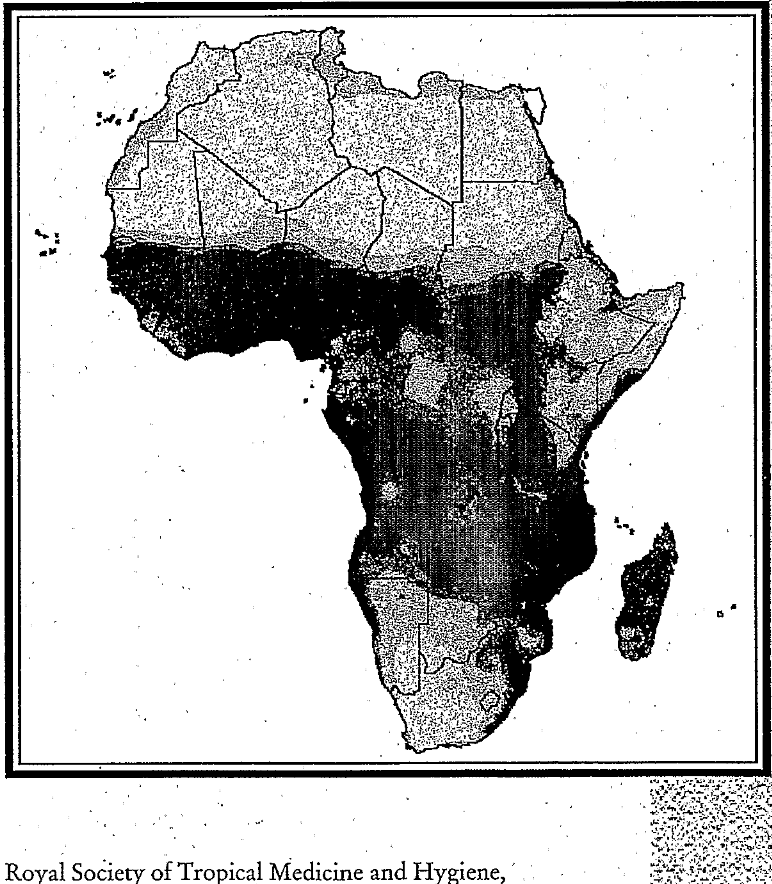

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