Wild *Triatoma infestans*, a potential threat that needs to be monitored

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The current persistence of Triatoma infestans, *and therefore of Chagas disease transmission, in the Andean valleys of Bolivia and the Gran Chaco (precisely where wild populations of the vector are widespread), indicates a possible relationship between these two occurrences. This paper provides an overview of the current knowledge regarding wild* T. infestans *in Bolivia. The different morphs of the wild vector, their known distributions and some traits of their biology and ecology are presented. Particularly interesting is the considerable behavioural and chromatic plasticity that is displayed by wild* T. infestans. *According to the biogeographic region, different morphs of the vector occur in rupicolous habitats (common form and Mataral morph in Andean wild* T. infestans*) or arboreal ones ("dark morph" populations from the Chaco). The high genetic variability found at the microgeographical scale in Andean wild* T. infestans *favours the hypothesis that the Andes were the centre of origin and dispersal of* T. infestans *throughout South America. The relevant question regarding the origin of domestic populations is also addressed. Finally, current considerations of the epidemiological significance of wild* T. infestans *are discussed in the context of recent discoveries. Even if several observations support the epidemiological risk represented by wild* T. infestans, *the climatic and environmental conditions of their distribution areas would not favour the continued flow of triatomines between sylvatic refuges and domestic environments.*

Key words: Chagas disease - *Triatoma infestans* - sylvatic foci - Bolivia

Triatoma infestans (Reduviidae, Triatominae) was, and still remains, the most important and widespread vector of Chagas disease in South America and it is the target of control programs as part of the Southern Cone Initiative (Dias 2007). The maximum estimated distribution range of *T. infestans*, reached during the 1970s, covered the 12 most populated states of Brazil and vast areas of Bolivia, Southern Peru, Chile, Northern Argentina, Paraguay and Uruguay; current estimates show that the distribution of the vector has been reduced by over 80%, but *T. infestans* foci persist in the highland valleys of Bolivia and in the Gran Chaco Region (Schofield et al. 2006). When the Southern Cone Initiative was launched, in 1991, its expected success relied on some peculiar traits of the vector, in particular its lack of insecticide resistance and its almost exclusively domestic nature, as wild populations had only been detected in the highland valley of Cochabamba, in Central Bolivia (Schmunis et al. 1996). This latter characteristic, which in principle precluded the recolonisation of treated areas by insects from sylvatic environments, was a pivotal argument for undertaking large-scale control campaigns. Recent reports provide evidence that wild populations of *T. infestans* are much more widespread than previously thought, drawing attention to the need for further research on this important and neglected issue, particularly on the role that such wild populations may play in the process of recolonisation of insecticide-treated villages (Noireau et al. 2005). This paper provides an overview of the current knowledge on *T. infestans* wild foci.

Brief history of the discovery of wild *T. infestans* in Bolivia and other Southern Cone countries

Wild *T. infestans* populations were first reported more than 60 years ago on a rocky hill situated in the immediate outskirts of Cochabamba, an important Bolivian Andean city 2,600 m above sea level (asl) (Torrico 1946). During the 1980s, wild *T. infestans* were also documented at other sites in the Cochabamba and nearby valleys (Dujardin et al. 1987, Bermudez et al. 1993). From the late 1990s to the present, new foci have been detected in the Andean departments of Cochabamba, La Paz, Chuquisaca and Potosi (Noireau et al. 2005, Cortez et al. 2007). Wild *T. infestans* populations have also been found outside the Andes, in the lowlands of the Boreal Chaco (Noireau et al. 1997). The existence of wild populations in the Chaco biogeographical region was later suspected in Paraguay (Yeo et al. 2005) and confirmed in the Chaco province of Argentina (Ceballos et al. 2009). Finally, sylvatic colonies of *T. infestans* were recently reported in the Metropolitan Region of Chile (Bacigalupo et al. 2006). These studies shed new light on earlier ones reporting the occasional finding of *T. infestans* specimens in a great variety of sylvatic ecotopes in Argentina, Paraguay and Brazil (Mazza 1943, Velasquez & González 1959, Barretto et al. 1963, Bejarano 1967, Cichero et al. 1984). However, in spite of

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such records, the idea that *T. infestans* did not maintain sylvatic foci became mainstream simply because most specimens had been found in ecotopes relatively close to human dwellings (Usinger el al. 1966).

Known distribution range of wild *T. infestans*

Recent field surveys have revealed that wild *T. infestans* populations are much more widespread throughout Bolivia (and also in neighbouring countries) than previously thought. This discovery was largely the result of a simple trapping system that provided an effective way to detect the presence of *T. infestans* in hard-to-reach terrestrial and arboreal sylvatic habitats (Noireau et al. 1999, 2002). If we overlay the reported locations of wild *T. infestans* on the biogeographic regions of Bolivia, the highland foci are clearly located in the Inter-Andean Dry Forest, whereas the lowland foci occur in the Gran Chaco Region. The case for a wide distribution of wild *T. infestans* within these biogeographic regions is strengthened by the increase in the number of surveys that were often successful in detecting sylvatic populations. The wild populations of the Andes and the Chaco seem to be geographically isolated; no sylvatic *T. infestans* foci have been found to date in the Andean foothills (the Tucuman-Bolivian Forest and Chaco Serrano biogeographic regions). Because wild *T. infestans* have a wide distribution throughout the Bolivian Andes and the Gran Chaco, the notion of foci should be interpreted as geographically restricted records, which probably represent point occurrence data from a more widespread population. The distribution of wild *T. infestans* may not be restricted to small areas, but may extend to all of the biogeographic regions mentioned above. A new idea of great consequence is the existence of sylvatic *T. infestans* in periurban environments, as demonstrated in Cochabamba. In this large Andean city (> 500,000 inhabitants, 2001 census), soaring urbanisation in the southern zone disregards the occurrence of wild *T. infestans* that are readily captured in the immediate outskirts of new settlements.

The different morphs of wild *T. infestans* and some traits of their biology and ecology

The sylvatic ecology and the role of wild *T. infestans* in the transmission of *Trypanosoma cruzi* are still poorly understood despite the number and diversity of foci recorded. Wild Andean *T. infestans* occur chiefly in rocky outcrops, which, regardless of their size, represent suitable refuges for the species. These Andean populations of *T. infestans* display a chromatic pattern (Table) similar to that of their domestic counterparts in all of the Southern Cone countries, except for some populations named "Mataral morphs", which are found in the South-Eastern Cochabamba department (~1,800 m asl) and are larger, with noticeably different marks on the connexivum (Cortez et al. 2007). In the Cotapachi region of the Cochabamba Valley, we collected nymphs and adults of *T. infestans* in 30% of the outcrops where *Thylamys* marsupials and rodent species of *Bolomys*, *Philotys* and *Akodon* find shelter. A yearly pattern of the population-stage structure, which is characterised by only one emergence peak of young nymphs that corresponds to the production of one generation a year, was found in Andean wild *T. infestans* (Cortez et al. 2007). Mammal hosts and insects both presented very high levels of *T. cruzi* infection (> 60%). In spite of the prevalence of both *T. cruzi* lineages (TCI and TCII) in the domestic cycle in the Cochabamba Valley, only TCI seems to be transmitted between wild small mammals and *T. infestans* (Cortez et al. 2006, 2007). Rupicolous (inhabiting rocks) *T. infestans* populations that were recently found in the north Potosi department (Toro Toro area) are interesting, because they live in fissures in cliffs where the red-fronted macaw (*Ara rubrogenys*) and other birds nest (M Baune, personal communication). In contrast, wild *T. infestans* from the Chaco (< 400 m asl) are arboreal (inhabiting trees). Their overall darker coloration ("dark morph") distinguishes them from the other forms of *T. infestans*, either domestic or sylvatic (Noireau et al. 1997, 2005). They are found inside the trunks of emergent trees, in hollows occupied by blue-fronted parrots (*Amazona aestiva*). The very low

TABLE

The different morphs and geographic populations of wild *Triatoma infestans* and some traits of their bioecology

Name	Common morph	Common morph	Mataral morph	Dark morph
Distinguishing morphochromatic traits with the common morph	-	-	Large size (> 30 mm), great yellow markings on the connexivum	Overall dark coloration, small yellow markings on the connexivum
Area of endemism	Inter-Andean, dry Forest (> 2,000 m asl)	Toro Toro area, inter-Andean Dry Forest (~2,000 m asl)	Inter-Andean dry forest, southeastern Cochabamba department (~1,800 m asl)	Lowlands of the Gran Chaco (< 400 m asl)
Habitat	Rocky outcrops	Cliffs	Rocky outcrops	Hollow trees
Preferential host-feeding	Small mammals	Birds (probably parrots)	Probably small mammals	Birds (probably parrots)
Trypanosoma cruzi infection rates	High	Low	High	Low

asl: above sea level.

T. cruzi infection rate detected in the dark morph (2.5%) supports its ornithophilic tendency (Noireau et al. 2000, Ceballos et al. 2009). The stage-structure pattern of the dark morph population is still unknown. Although domestic *T. infestans* produce two generations a year in the warm climate of the Chaco (Gorla & Schofield 1989), fluctuations in host availability in wild habitats might put the dark morph at a disadvantage and lead to an increased development time.

Particularly interesting is the considerable behavioural and chromatic plasticity displayed by wild *T. infestans*. According to the biogeographic region, the vectors occur in rupicolous (rock-piles or cliffs) or arboreal habitats, unlike almost all other triatomine species, which show a marked preference for a type of habitat. Similarly, we observed obvious chromatic differences between rupicolous specimens (common form and Mataral morph) and between the Andean and arboreal *T. infestans* from the lowlands (dark morph populations but also *Triatoma melanosoma*) (Martinez et al. 1987).

The origin of *T. infestans* as a species

Since wild populations were initially found in the Bolivian highlands, Andean *T. infestans* are generally assumed to represent the most ancient form (Usinger et al. 1966, Schofield 1988). The detection of wild *T. infestans* in the Boreal Chaco in the late 1990s challenged the traditional view that the Andean valleys in Bolivia were the only centre of origin and dispersal of *T. infestans* throughout South America. The most ancient populations may be those of the dry, subtropical Chaco forest in South-Eastern Bolivia, Paraguay and Northern Argentina (Carcavallo et al. 2000). This Chacoan proposal is also based on the broader biogeographical patterns of the species group to which *infestans* belongs. However, recent findings based on allozymes, genome size and nuclear rDNA favour the Andean hypothesis (Dujardin et al. 1998, Panzera et al. 2004, Bargues et al. 2006). This would imply that the dark morph populations, which exhibit an important reduction of heterochromatin and DNA amounts as well as a considerable degree of genetic isolation, represent a direct expansion from the Andean populations (Monteiro et al. 1999, Giordano et al. 2005, Piccinali et al. 2009). However, the occurrence of at least one recolonisation of a sylvatic habitat from a domestic population in the Chaco was not discarded (Panzera et al. 2004, Bargues et al. 2006). The detection of the Mataral morph of *T. infestans* in the inter-Andean Chaco (i.e., intermediate between the high Andean valleys and the Chaco) further complicates the question.

The origin of *T. Infestans* domestic populations

The introduction of *T. infestans* into domestic environments would have been a consequence of a vector transition from rodent burrows to the cave-like habitations of pre-Columbian peoples, where the microclimatic conditions were not too dissimilar (Usinger el al. 1966). Later, Schofield (1988) put forward the traditional speculation of *T. infestans* adaptation to the synanthropic environment as a consequence of the domestication of wild guinea pigs, one of its natural hosts, by Andean tribes in approximately 5,000 BC. After this first step of adaptation to the domestic environment, *T. infestans* would then have dispersed throughout other countries of South America, apparently in association with human migrations, ultimately reaching Brazil during the 20th century (Schofield 1988). A further speculation, based this time on the passive dispersal of sylvatic *T. infestans*, has been recently put forward. It involves organised human social activities, in particular maize production and storage in the Cochabamba valley (MR Cortez et al., unpublished observations). The spread of the vector would have been a consequence of the transport and distribution of maize hosting the associated fauna (wild rodent populations and insects) throughout distant provinces of the Inca Empire.

Microgeographic genetic diversity of wild *T. infestans*

Until recently, *T. infestans* populations were believed to have low levels of genetic variability (Schofield 1988, Guhl & Schofield 1996). Most studies were based on allozymes and reported low polymorphism as inferred from results on two or three polymorphic loci (Pereira et al. 1996, Dujardin et al. 1998). Recent studies based on mitochondrial or nuclear gene sequences from domestic populations detected higher levels of genetic variation than expected (Giordano et al. 2005, Bargues et al. 2006, Piccinali et al. 2009). To assess the genetic variability in a wild *T. infestans* population, a mitochondrial cytochrome b (Cytb) gene fragment was sequenced in insects sampled from a very small area (< 1 km^2) in the Cochabamba valley, at 2,700 m asl. The results showed high genetic variability: seven haplotypes were identified in 38 triatomines analysed (P Kengne & F Noireau, unpublished observations). Among the sylvatic haplotypes, two of them were also found in domestic insects from the Sucre Region (Giordano et al. 2005). The detection of seven haplotypes in wild *T. infestans* from a limited area supports the evolutionary theory, which predicts higher genetic variability in the ancestral wild populations than in their domestic derivatives (Dujardin et al. 1999).

Dispersal ability of wild *T. infestans* at high altitude

The key question regarding the threat represented by wild populations of *T. infestans* is whether they can recolonise insecticide-treated villages and thus jeopardise control efforts. Therefore, it is essential to assess the dispersal of wild *T. infestans* and the extent of gene flow between sylvatic and domestic populations. In a dispersal study performed in the Cochabamba valley at 2,700 m asl, the detection of restricted gene flow between close, but distinct, sylvatic sites (rocky outcrops) was consistent with the hypothesis that the vectors do not disperse by flying at high altitude (Richer et al. 2007). Some studies on the ability of *T. infestans* to fly under more favourable conditions (in the lowlands of the Chaco) pointed out that this species showed flight potential on a village-wide scale and in sylvatic environments (Schofield et al. 1992, Noireau et al. 2000, Vazquez-Prokopec et al. 2006). However, the results of Richer et al. (2007) suggested that, at 2,700 m asl in the Andes, wild *T. infestans* gradually disperse over a small distance by walking within a "patch", which might be characterised as a continuous land cover with all necessary resources for the persistence of triatomine populations (Gustafson & Gardner 1996). On the other hand, when the land cover is disrupted by human activities (e.g., building of dwellings and peridomestic structures, land or livestock farming), triatomine bugs encounter an unsuitable environment and cannot spread to separate patches by walking. However, the results of this highlands study probably cannot be extended to regions with different environmental conditions. Consequently, it is essential to determine the role that wild *T. infestans* populations may play as potential sources of reinfestation in the different ecoregions where they are found.

Current arguments regarding the epidemiological significance of the wild *T. infestans*

The following question deserves to be asked: does a relationship exist between the persistent vector infestation in certain areas and the occurrence of wild *T. infestans*? In other terms, do wild *T. infestans* threaten to recolonise insecticide-treated areas? There are increasing reports of wild triatomine species invading human dwellings in areas where domestic vector populations have been targeted by chemical control interventions. In certain cases, the initial phenomenon of the intrusion of adult bugs into households may continue until the establishment of domestic breeding colonies (Noireau et al. 1994, 1995). Why would wild *T. infestans* be excluded from such a process even though this species has successfully adapted to domestic environments in the past? Several observations support the epidemiological risk represented by wild *T. infestans*: (i) Currently, domestic *T. infestans* still persists in only the Andean valleys of Bolivia and in the Gran Chaco Region; interestingly, wild populations of *T. infestans* are widespread throughout these precise regions; (ii) Another argument is based on mitochondrial genetic variability (COI and Cytb genes). Various haplotypes are shared by both domestic and sylvatic Andean populations (Monteiro et al. 1999, Piccinali et al. 2009). Moreover, and as previously mentioned, two Cytb haplotypes isolated from wild triatomines in Cochabamba are also shared by domestic insects from Cochabamba and Sucre; (iii) The Mataral form, found in sylvatic environments in the south-eastern Cochabamba department, is also colonising houses of the same region (F Noireau, unpublished observations); (iv) *T. infestans* was, without any doubt, the triatomine species that displayed the most successfully completed process of domestication. It began this process in Bolivia, probably in the Andean mesothermic valleys, before spreading by passive transportation associated with human activities (Schofield 1988, Bargues et al. 2006). It is difficult to give credit to the hypothesis that sylvatic forms of *T. infestans* would have become restricted to their natural habitat since then, whereas many other sylvatic species are currently involved in a process of domestic intrusion.

However, current evidence does not support a continued flow of *T. infestans* between sylvatic refuges and domestic environments. In the Andes, climatic factors may hamper the process of domestic intrusion by wild *T. infestans*. Between 1,700-2,800 m asl, the altitude range where *T. infestans* wild populations are widespread, the crepuscular coldness restricts flight dispersal. In the Chaco, certain environmental characteristics might hamper the process of domestic intrusion by the dark morph. Emergent trees, which offer stable refuges for the vectors that live in parrot nests located within trunks, have become scarce in the vicinity of the villages and only persist in areas free of environmental damage caused by humans. Moreover, intensive hunting of parrots would also lead to the destruction of nests and the extinction of triatomine colonies. Consequently, the *T. infestans* dark morph would persist in preserved and remote wooded areas and would be scarce near human settlements.

As a whole, these observations suggest that the climatic and environmental conditions of their distribution areas would not favour a continued flow of triatomines between sylvatic and domestic environments, even if wild *T. infestans* retained its potential to invade and colonise human dwellings. Contrary to *Rhodnius prolixus*, for which a continued flow between palm trees and houses has been revealed (Fitzpatrick et al. 2008), only unusual circumstances would generate a continued transfer of *T. infestans* from the natural to the domestic environment. The direct consequence will be the need to use suitable hypervariable genetic markers to detect this restricted gene flow.

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