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Short communication

New insights on the spread of *Triatoma infestans* from Bolivia—Implications for Chagas disease emergence in the Southern Cone

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ABSTRACT

Triatoma infestans, now eliminated from most of South America by control campaigns, has been and still is the main Chagas disease vector due to its ability to colonize rural dwellings. The traditional hypothesis put forth to explain *T. infestans* adaptation to the synanthropic environment rests on the domestication of wild guinea pigs, one of its natural hosts, by Andean tribes about 5000 BC. Here we present two new hypotheses, based on organized human social activities. The first involves maize production, storage and distribution during the Inca period. Maize granaries could host wild rodent populations that would attract sylvatic *T. infestans* that were later dispersed during maize distribution. The second hypothesis is associated with the contemporary Urkupiña Virgin festival, near Cochabamba, where thousands of pilgrims gather for rituals in an area that is part of a sylvatic *T. infestans* focus, thus favoring the contact with the insects and leading to their passive dispersal.

1. Introduction

Triatoma infestans (Reduviidae, Triatominae) has been and still is the most important and widespread domestic vector of Chagas disease in South America. A high degree of adaptation to domiciles enabled its passive spread in association with human migrations, leading to the dissemination of the disease from restricted endemic areas in the Andes Mountains to the entire Southern Cone region of Latin America up to northeastern Brazil, affecting an estimated 18 million people (Noireau et al., 2009). Consequently, *T. infestans* became the target of large-scale campaigns started in the 1960s in various countries (Dias et al., 2002).

2. Domestication and dispersal of *T. infestans*

While the maximum distribution of the vector had, during the 1970s, reached the 12 most populated states of Brazil, in addition to vast areas of Bolivia and Argentina, southern Peru, northern Chile, Paraguay, and Uruguay, current estimates show that its distribution has been reduced by over 80%, reflecting the success of the interventions (Schofield et al., 2006). Nowadays, domestic *T. infestans* mostly persists in the Andean valleys of Bolivia and in the Gran Chaco region where several wild populations have been detected (Noireau et al., 2000, 2005; Cortez et al., 2007; Ceballos et al., 2009). The Andean valleys in Bolivia are traditionally believed to represent the center of origin and dispersal of *T. infestans* throughout South America, although the detection of wild populations in the Chaco has come to challenge this view (Dujardin et al., 1998; Carcavallo et al., 2000). Most genetic data, however, favor a Bolivian highlands origin for *T. infestans* (Dujardin et al., 1998; Panzera et al., 2004; Bargues et al., 2006). *T. infestans* dispersal history has been inferred from archaeological findings, historical records, and population genetics analyses (Panzera et al., 2004; Bargues et al., 2006; Schofield, 1988). These studies point to two different dispersal lines from the Bolivian highlands, one toward Peru and another in the direction of Chilean lowlands, Paraguay, Argentina, Uruguay and Brazil. The traditional hypothesis involves an initial vector-domiciliation process, followed by passive human-mediated spread (Schofield, 1988). It is well established that *T. infestans* arrived in northern Uruguay in the beginning of the 20th century, and reached the Northeast of Brazil in the 1970s (Panzera et al., 2004). However, the early events, which led to the passive dispersal of *T. infestans*, remain obscure.

In order to explain the adaptation of *T. infestans* to human dwellings, Usinger et al. (1966) put forward the hypothesis that insects could have made the transition from rodent burrows to cave-like habitations of pre-Columbian humans fairly easily, due to the microclimatic similarities between both structures. However,

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the most recognized hypothesis argues that vector adaptation may have been a consequence of the domestication of wild guinea pigs (most likely *Cavia tschudii*), one of its natural hosts (Usinger et al., 1966). This might have been accomplished as early as 5000 BC by mountain tribes in the Andean region of today's Peru, Chile, and Bolivia (Wing, 1986). Since pre-Columbian times, the domestic *cuy* (*Cavia porcellus*) is considered a delicacy, in addition to its importance in both folk medicine and rituals (Gade, 1967). Although speculative, such an explanation is plausible, provided that the association between *T. infestans* and *Cavia* actually occurs in the sylvatic environment (Bermudez et al., 1993). It is worth mentioning though, that man and triatomine vectors live together regardless of the nature of their dwellings, at least the last 9000 years (2000 years before the accepted date for guinea pig domestication), as shown by a 40% prevalence of *T. cruzi* infection in Chilean mummies, even in regions where the guinea pig has never been domesticated, such as Minas Gerais, Brazil (Lima et al., 2008). However, recent insights from archaeological findings and religious rites lead us to propose two new hypotheses on the dispersal of wild, instead of domestic, *T. infestans*.

Fig. 2. Present-day reconstruction of granary storage units (*Qollqas*) at Cotapachi during the Inca Empire. The archeological circular bases remains of more than 2400 *Qollqas* give the area the title of second largest Inca storage center yet recorded. Stockpiles of maize could have hosted small wild mammals (today abundant in this area), and associated triatomine fauna.

3. First hypothesis: wild *T. infestans* dispersal during pre-Columbian times

Historical reconstruction of the Cotapachi archeological site, located in the Cochabamba valley, currently considered the most important *T. infestans* sylvatic focus in Bolivia, raises the possibility that dispersal of wild *T. infestans* might have occurred independently of the *Cavia*-domestication event. Cotapachi (2750 m asl; 17°26′S, 66°17′W) is a highland rural area situated 20 km west of Cochabamba city, with abundant rocky outcrops that provide perfect refuge for abundant wild *T. infestans* populations (Cortez et al., 2007). In the late Inca period (first half of the fifteen century), the valley of Cochabamba was a productive maize agricultural region, and Cotapachi one of the most important among the maize storage sites scattered throughout the Inca Empire (Fig. 1). The surplus maize was stored in granary units called *Qollqas* (see recent tentative reconstruction in Fig. 2) built on the southern hill of Cotapachi (Jenkins, 2001). Today, the circular bases of more than 2400 *Qollqas* are still visible, for which Cotapachi has been given the title of second largest Inca storage center yet recorded. It seems natural to postulate that stockpiles of maize hosted small wild mammals (abundant in this area) together with their associated triatomine fauna. Among the rodent species recently collected at Cotapachi, *Phyllotis osilae* was the most frequent, and a high proportion shows *Trypanosoma cruzi* infection (Cortez et al., 2006). This species has generalist feeding habits and easily becomes adapted to synanthropic conditions. There is good evidence for long-distance llama-caravan maize transportation from Cotapachi to Cuzco, Peru, and to the southern and southeastern borders of the Inca Empire (Wachtel, 1982). So, we may reasonably envision a scenario where triatomines associated with wild rodents were transported with the maize, and redistributed through distant provinces of the Inca Empire. Once transported to their final destination and deposited with the corn in domestic or peridomestic premises, the sylvatic vectors could still feed on their natural hosts (the geographic range of rodent and marsupial hosts associated with wild *T. infestans* at Cotapachi covers as well north-western Argentina, Chile and Peru) but also explore the new feeding possibilities on humans and their synanthropic animals. This would greatly multiply opportunities for direct contact between vectors and humans, thus increasing the possibilities of domicile adaptation. This explanation precludes the need for a natural host serving as a bridge between sylvatic and domestic habitats.

Fig. 1. Aerial view of the Cotapachi study site. (A) Location of an important maize storage center of the Inca Empire, characterized by the presence of storage units called *Qollqas*. (B) Location of the Cotapachi *Cerro* (hill) where the annual Urkupiña Virgin syncretic religious festivities take place. (C) Areas from where wild *T. infestans* specimens have been collected.

4. Second hypothesis: current dispersal through the pilgrimage to the Urkupiña Virgin

The second hypothesis derives from a syncretic religious event, the festival of the Urkupiña Virgin, held every August in Quillacollo, near Cochabamba. During three days an estimated half million pilgrims (including thousands from northern Argentina) gather at the city to pray for wealth and material goods, and to participate in traditional dancing parades. Urkupiña is a former pilgrimage place that soared up in the 1970s. The festival, which has become a national event in the last years, is, in fact, a combination of Catholic devotion to the Virgin and pre-Columbian Andean rituals to the fertility goddess Pachamama. On the third day, the pilgrims will

Fig. 3. Pilgrims extracting stones during the 2007 festival devoted to the Urkupiña Virgin at the sacred *Cerro* (hill) of Cotapachi, Quillacollo, Cochabamba. The event is held every August, with the participation of an estimated half million pilgrims. The existence of natural sylvatic *T. infestans* populations in the *Cerro* favors the possibility of human contact with local vectors, which might ultimately lead to their passive dispersal.

visit the sacred *Cerro* (hill) of Cotapachi, where they excavate huge boulders and break off smaller rocks using picks and hammers (Fig. 3). These rocks symbolize the material goods they will request from the Virgin in prayer (Díaz-Barriga, 2003). In addition, the pilgrims eat, drink, play music, dance, and so spend the entire day at this location. Since this *Cerro* forms part of the sylvatic focus of *T. infestans* described by Cortez et al. (2007), it is highly probable that not only would insects and eggs become caught in the pilgrim's clothes and belongings, but also that unnoticed small nymphs would actively crawl onto them to be later passively carried away. The repeated excavations at this religious site, and thus removal of insect habitat, throughout more than 40 years of rituals would have likely contributed to a gradual decrease in wild vector population density in the *Cerro*.

The possibility of a contemporary passive dissemination of wild *T. infestans* from Quillacollo to other regions in Bolivia and northern Argentina is a point that deserves close attention. The launching of the Southern Cone Initiative in the early 1990s relied on two pivotal arguments: (i) that true sylvatic populations only occurred in the Cochabamba region of central Bolivia, and were isolated from nearby domestic populations; and (ii) that domestic vector populations would be genetically depauperate (Dujardin et al., 1987; Schofield, 2000). While reduced variability would render domestic insect populations incapable of developing insecticide resistance, ecological isolation of scarce sylvatic populations would rule out the possibility of reinfestation of treated villages, making domestic *T. infestans* easy target for insecticide control interventions. This ideal scenario, however, seems not to withstand scientific scrutiny. Available data contradict the former assumption by revealing the existence of extensive *T. infestans* sylvatic foci in the Andean valleys of Bolivia and the Chaco region of Bolivia and Argentina (Noireau et al., 2005; Ceballos et al., 2009; Noireau, 2009). The latter is equally likely to be rejected, as genetically variable wild insects would be delivered straight into homes. The detection of previously unsuspected *T. infestans* sylvatic foci has led scientists to investigate the potential threat these populations might pose to local vector control programs.

Although morphometry and antennal structure data suggest separation between sylvatic and domestic insects (Dujardin et al., 1997; Abrahan et al., 2008), such characters are known to be subject to environmental selective pressures that might confound the interpretation of the results obtained. Alternatively, neutrally evolving mitochondrial DNA markers have been used to compare sylvatic and domestic *T. infestans* populations to evaluate the epidemiological relevance of the former. Various cytochrome *b* haplotypes are shared by domestic and wild Andean populations (Monteiro et al., 1999; Piccinali et al., 2009). Interestingly, in Bolivia, haplotype diversity was higher in domestic than in sylvatic insects (Piccinali et al., 2009). The same sharing of cyt *b* haplotypes between wild and domestic *T. infestans* was observed in samples from Cochabamba and Sucre (Noireau, 2009). However, haplotype sharing *per se* is not proof of gene flow. Future studies designed specifically to address this issue are required. The use of the more variable microsatellite markers would certainly shed light on the issue.

5. Conclusions

The two non-mutually excluding hypotheses describe possibilities of human dispersal of wild *T. infestans* that may have been operating from pre-Columbian times to these days. Moreover, they do not depend on fortuitous events, but instead, are based on human organized social activities.

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