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The infra-red (IR) landscape of *Triatoma infestans*. An hypothesis about the role of IR radiation as a cue for Triatominae dispersal

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ABSTRACT

This paper presents the infrared (IR) emission spectrum of hosts and habitats of *Triatoma infestans* in the chaco region of NW Argentina, representing the first attempt to correlate the natural infrared stimulus with the known behaviour of these blood-sucking insect, vectors of *Trypanosoma cruzi* – causative agent of Chagas disease. The study was carried out in two rural villages of La Rioja Province (Argentina). A FLYR i40 camera was used to obtain IR pictures which were analyzed to determine the thermal range for humans, domestic animals, building materials, and general background emissions. From sunset to the first hours of night, the thermal contrast between hosts and their landscape rises, increasing the likelihood that hosts could be differentiated by the vector. However, some building materials, can retain high temperatures during the night, which might add attractiveness to the presence of hosts. The results suggest that the most attractive habitats for dispersing bugs would be those at short distance, with high CO2 emission and strong IR radiation indicative of host presence. Goats corrals may be the most attractive habitat to disperse, within the domestic habitat. Dispersal would be favoured in periods of low atmospheric water saturation when IR perception is highest. In the IR band, the potential host and habitat discrimination available for the insects fits well with their known sensory capacities and observed dispersive behavior. Research in this area could be of considerable interest in relation to vector surveillance, epidemiology of Chagas disease transmission, and to develop new methods to minimise triatomine colonisation of new habitats.

1. Introduction

The main characteristics of Triatominae (Hemiptera, Reduviidae) reflect their almost exclusive dependence on vertebrate blood as food-source, mainly from birds and mammals, but little is known about their mechanisms of orientation to a vertebrate host. CO_2 has long been known to act as an alertant for hungry bugs, but alone seems to have only week attractant effects (Barrozo and Lazzari, 2004, 2006). Ammonia appears to evoke both activation and attractant behaviour (Taneja and Guerin 1997) and both CO_2 and ammonia seem to synergise the attractant effects of some short-chain carboxylic acids such as lactic (Barrozo and Lazzari, 2004).

Since the early experiments of Wigglesworth and Gillett (1934) however, heat has been recognised as an important factor for host-finding by Triatominae bugs, and seems to be the primary cue evoking the proboscis extension response that brings the mouthparts in contact with host skin (Flores and Lazzari 1996; Ferreira et al., 2007). At short distances, *T. infestans* will try to bite any objects at a temperature similar to that of a living host (Lorenzo et al., 1999). Behavioural experiments indicate that Triatominae exhibit very high thermal sensitivity, and they can detect and orient to thermal sources with a surface temperature close to that of warm blooded animals (Guerestein and Lazzari, 2009).

Orientation to the heat source depends on the bug having intact antennae (Wiggleswoth and Gillet, 1934; Lazzari and Nuñez, 1989) where heat receptors are present (Bernard, 1974; McIver and Siemicki, 1984; Catalá, 1994; Catalá and Schofield, 1994; Lazzari and Wicklein, 1994; Insausti et al., 1999). Barth (1952) discovered the cave organ, a particular organ deeply placed inside the antennal pedicel of adult Triatominae. According to Barth's hypothesis, the cave organ is an infrared receptor. Lazzari (1990) and Lazzari and Wiklein (1994) found a response of cave cells to thermal stimuli. The absence of this organ on nymphs (Catalá, 1997) reinforces the idea that the cave is only necessary for the adults who probably use this receptor on activities like habitat or host selection during flight. New details of its morphology support the hypothesis of an olfactory function of the cave organ of Triatominae, associated to infrared perception (Catalá et al., 1998).

Heat emanated from mammals and birds may contact the bug sensory system by temperature gradient of the air around the host (conduction), by convective air currents ascending from the host body (convection), or by absorption of radiant heat at wavelengths in the infra-red region of the spectrum (radiation). Infrared (IR)

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waves are not perceived by humans but some snakes and vampire bats possess specialised sensory organs devoted to IR detection. After the discovery of perception of radiant heat by snakes (Bullock and Cowles, 1952), Callahan (1965) proposed that IR was the key medium for insect communication and navigation. IR perception has since been observed for heteropterans displaying phytophagous and pyrophilous activity, as well as in some Coleoptera (Schmitz et al., 1997; Takács et al., 2009). However, Triatominae are the only group of haematophagous insects for which IR perception and response has been demonstrated: in *T. infestans* (Lazzari and Nuñez, 1989; Wiesinger, 1956) and in *Rhodnius prolixus* (Schmitz et al., 2000), which implies the ability to assess, from any relative position, the heat emitted by a potential host, without perturbation by wind, a factor affecting conduction gradients and convective currents.

IR cues are unexplored in the natural ecotopes of Triatominae, and there is no clear evidence for the role of IR radiation in their long range dispersal. A casual observation in a field experiment suggested that combined CO_2 and IR emission had been responsible for the attraction of *T. infestans* some 800 m away from its release point (Schofield et al., 1992). More recently, Milne et al. (2009) found that heat alone or combined with CO_2 was a consistent attractant for *R. prolixus* and *Triatoma dimidiata* – even more than odorant cues – but they do not check the emission of IR in their experiment. It seems plausible however, that IR cues are involved in the dispersive and colonisation behaviour of Triatominae in their natural habitats. As a first step, we analyse here the magnitude and range of infra-red radiation from human as well as domestic animals and their habitats, in rural villages where *T. infestans* commonly infests houses and peridomestic habitats. The interrelationship between the IR emission and the known sensory and behavioural capacities of *T. infestans*, is discussed.

T. infestans occurs in seven countries of the southern cone of Latin America and is the main vector of *Trypanosoma cruzi* – causative agent of Chagas disease. In large areas of Argentina, Bolivia, and parts of Paraguay, rural houses can be heavily infested with *T. infestans,* both inside the houses and in peridomestic areas such as goat corrals, chicken coops, rabbit cages, and storerooms, that in many cases are just a few metres from the house (López et al., 1999; Ceballos et al., 2005; Cecere et al., 1997; Catalá et al., 2004; OMS, 2002). *T. infestans* becomes active at night, moving between habitats flying or walking (Abrahan et al., 2011) searching for food and colonising new sites. Dispersal of triatomines among habitats is an important factor influencing the long-term success of vector-control interventions due to the fact that dispersing bugs can re-colonise habitats treated with insecticide, initiating new cycles of colonisation and disease transmission (Schofield and Matthews, 1985; Cecere et al., 1997; Porcasi et al., 2007).

2. Materials and methods

2.1. Study area

The selection of the rural houses for the present study was based on the presence of abundant peridomestic *T. infestans* populations (Porcasi et al., 2007) and the owners' cooperation in allowing access to their homes. On the other hand, two others studies about *T. infestans* dispersion had been carried out simultaneously in these houses (Hernández et al., 2011; Abrahan et al., 2011).

Two small rural villages: Patquia Viejo (550 masl) and Salinas de Busto (1100 masl), about 90Km apart, were visited during 27–28 January 2009, to carry out a thermographic study. These localities are in La Rioja province, Independencia Dept., in the hot semi-arid zone of NW Argentina (Fig. 1a). The inhabitants are mainly subsistence farmers. Each house is made with adobe or cement bricks and roofed with straw and mud, or metal sheets, and represents a complex environment with a domestic zone where people rest and cook, and a peridomestic area where they breed different animals, mainly goats, pigs, chickens and other fowl (Fig. 1b). In general, chicken coops are low rectangular structures, delimited by wood or wire with a rudimentary thatched roof. Some cardboard, old clothes and plastic sheets may complement the habitat. Sometimes the chickens roost in trees. The goat corrals (Fig. 1c) are generally made with tree branches horizontally intertwined, with a covered area where kids are kept. Cement bricks for walls with sheet metal roofs, have been included recently in an effort to avoid triatomine infestation of the goat corrals (Gorla et al., unpublished).

The distance between chicken coops and goat corrals is variable (30–80 m). In all houses, the chicken coop is nearer to human habitations than the goat corral. The average size of a goat herd was 80–100 animals per corral, including kids, at the time of the insect collection. Each chicken coop had 8–10 chickens.

2.2. Thermography of the rural landscape, late afternoon and early night (6 PM to 10 PM)

January is high summer in this region with sunset close to 8 PM. From 6 PM to 10 PM more than 200 images were taken with an IR camera (FLIR i40). The period 8 PM to 10 PM (sunset to early night) accords with the peak flying time of *T. infestans* under natural conditions in central Argentina (Schofield et al., 1992; Vazquez-Prokopec et al., 2006). Data from the last hours of afternoon (6 to 8 PM) indicated the IR emissions prior to this dispersal period. Additional data of humidity, air temperature and wind, were recorded with a portable meteorological station (Weather Monitor II, Davis Instruments) each half an hour, at the same period of time.

Excluding humans and other hosts, all other elements on the images were considered as "general landscape".

2.3. Image processing

The FLIR i40 infrared camera (wavelength range of 7–14 μm, http://www.FLIRi40.com) was selected because following Wien's law for thermic radiations, the human skin (and other homoeotherms) at 32 °C has its maximum emission between 9 and 10 μm (Grant, 1949).

Each image was analysed with the software QuickReport 1.1 (FLIR Systems, 2007). Emissivity was kept at 0.96. For each picture analysis, humidity was adjusted following the meteorological station data (in situ) at the time the image was registered.

Within the image of each host the lowest and the highest temperature values were identified. Mean temperature values were considered not appropriate as estimators of the whole host temperature. The thermal properties of the three main materials (wood, adobe bricks and cement bricks) comprising each habitat were assessed separately.

3. Results

3.1. Climate

Table 1 shows data registered by the portable meteorological station during the experimental period (6–10 PM).

3.2. Humans (Fig. 2 a,b and 3)

The clothes that cover the human body produce a partial blockage of IR radiation, which leads to a wide thermal range of 23.3–34.6 °C. The highest values correspond to naked skin, as of face and arms.

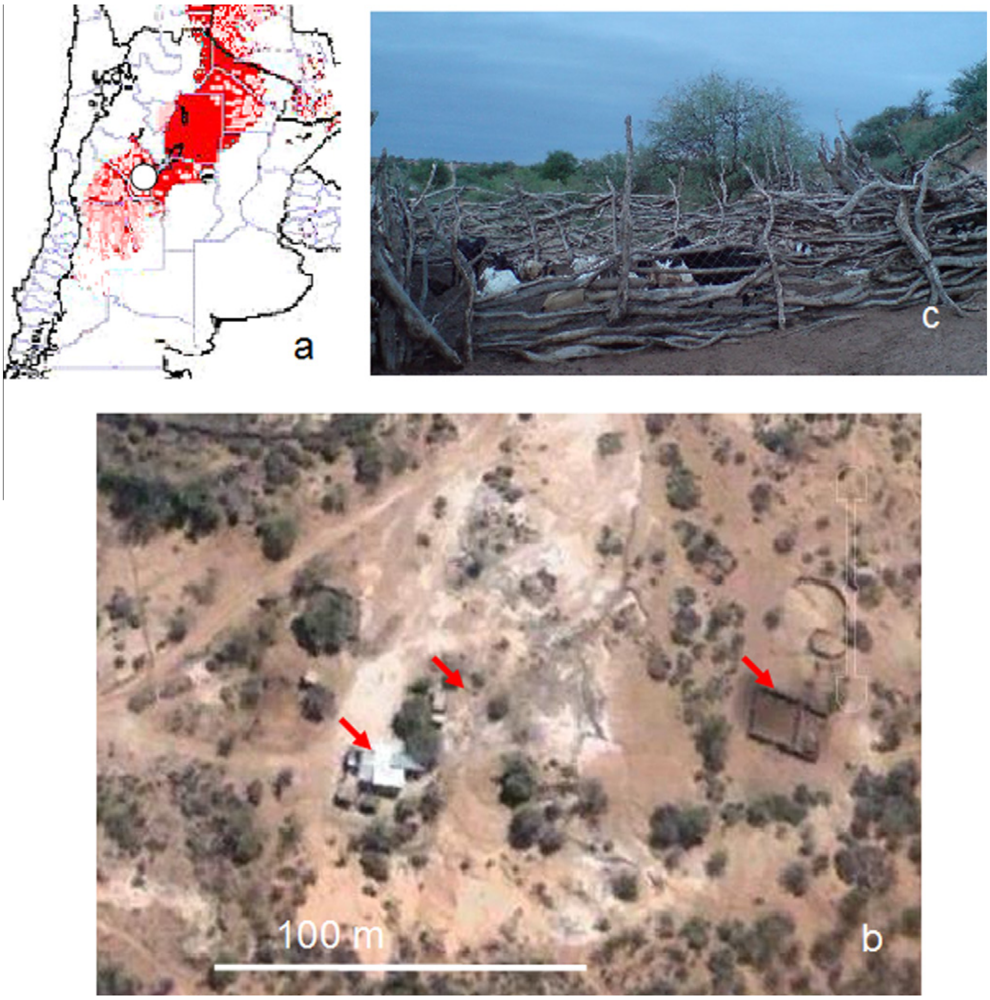

Fig. 1. The study area. (a) Map showing the estimated distribution of *Triatoma infestans* in the Gran Chaco and Andean Valleys. (b) Goat corral in Independencia Department, La Rioja, Argentina. (c) A house and its peridomestic area (Patquia Viejo, Google Earth 2006). From left to right the arrows point to house, chicken coop and goat corral.

Table 1
Meteorological data obtained *in situ* from the two studied localities: Patquia Viejo and Salinas de Busto (La Rioja, Argentina), during the daily study period (6–10 PM).

Locality	Temperature C Mean (min–max)	Humidity% Mean (min–max)	Wind speed km/h Mean (min–max)
Patquia Viejo	26.2	58.5	4.19
January 27, 2009	(24.1–29.4)	(51–67)	(0–9.7)
Salinas de Busto	27.03	37.7	5.4
January 28, 2009	(25.6–28.7)	(32–45)	(4.8–6.4)

3.3. Non-human hosts (Fig. 2 c–f and 3)

Body temperatures of domestic animals ranged between 22.8 and 38.3 °C, depending on body region and skin cover. Bird feathers constitute an excellent IR isolator, so that birds have the highest temperatures on legs and head, with maximum temperature (38.3 °C) registered for the periocular zone. Surface temperatures for mammals (dogs, goats and rabbits) ranged between 22.8 and 37.4 °C, with a maximum for goat udder, nose and eyes.

3.4. Building materials (Fig. 4)

Wood, adobe and cement bricks, are the most frequent materials of the rural houses. Thermography of the rural houses and their surroundings – between 6 and 10 PM – shows the termal changes of these materials during afternoon and early night. Adobe was the most thermo-stable material (27 to 29 °C) and cement the most variable (27 to 39 °C). The temperature of wood varied between 28 and 32 °C. However as building materials have lower emissivity than animals (wood 0.89, cement 0.92, bricks 0.85) it should be considered that values of temperature should be a bit higher (less than 1 °C).

3.5. Background temperatures (Fig. 5)

Excluding humans and other hosts, all other elements on the images were considered as "general landscape". The main components were buildings, vegetation, rocks, ground, and other materials derived from human activities (tools, vehicles, etc.). Minimum and maximum temperatures were extracted from the images. The atmosphere temperature was considered only up to a few meters above the ground, where *T. infestans* develops its dispersive activities. (Schofield et al., 1992). The landscape temperature varied between 28 and 41 °C at late afternoon and 24 to 32 °C at dawn and early night.

3.6. Background and host

During the afternoon the high temperatures of building materials, ground, rocks and other landscape components are similar to

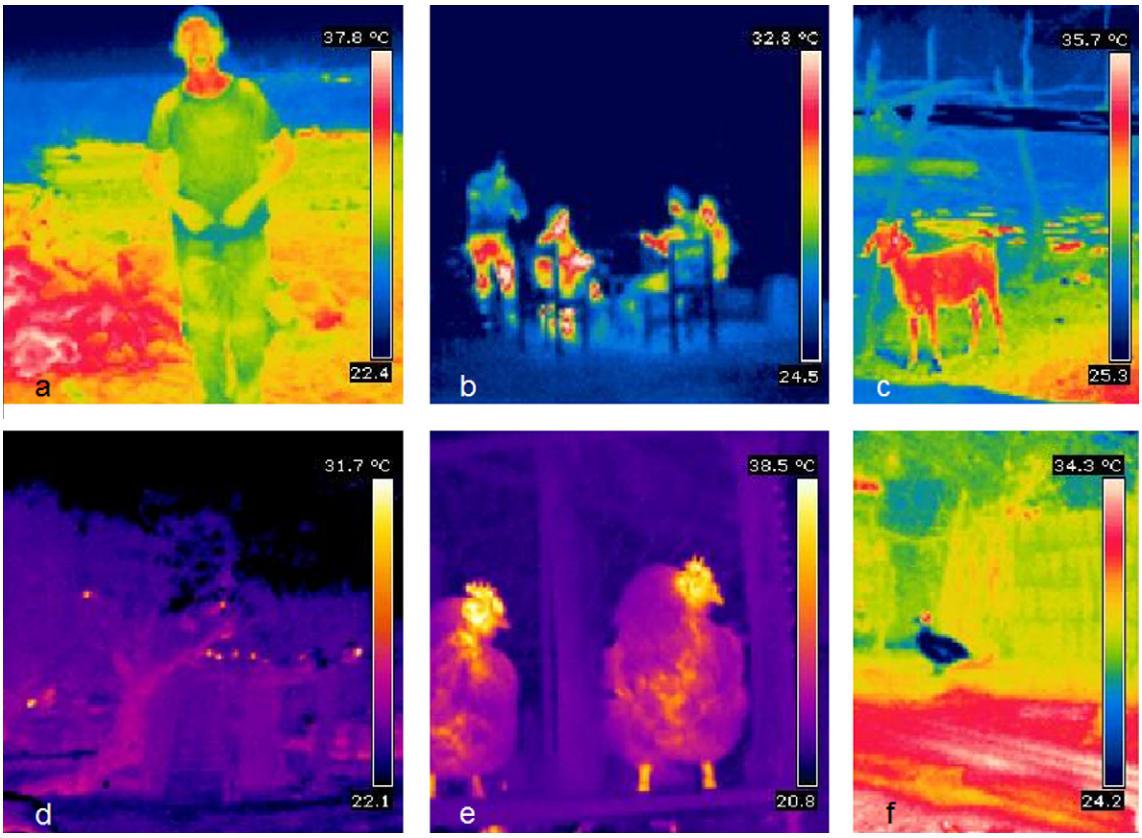

Fig. 2. Thermal images of hosts. (a) 7 PM, a young man. (b) 9 PM, a group of humans sat at their house courtyard. (c) 6:30 PM a goat calf. (d) 10 PM, chickens sleeping on a tree. (e) 5 PM two chickens. (f) 6 PM, a duck. The colour palette of pictures are indicative of temperature range according to the scale at right.

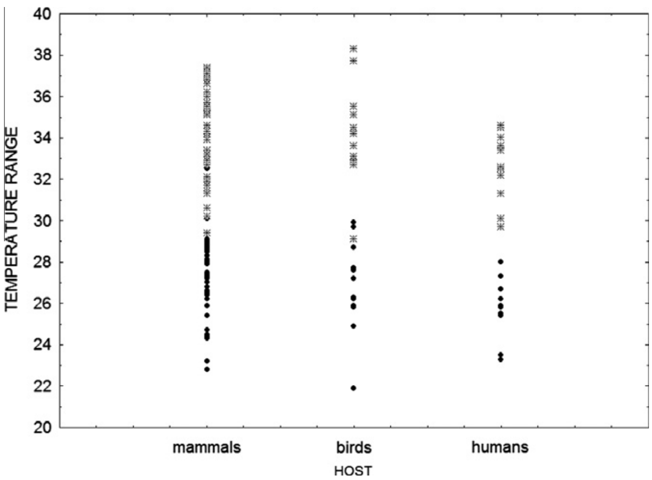

Fig. 3. Temperature of hosts. Minimum (black circles) and maximum (astericks) temperatures observed for humans, birds and mammals.

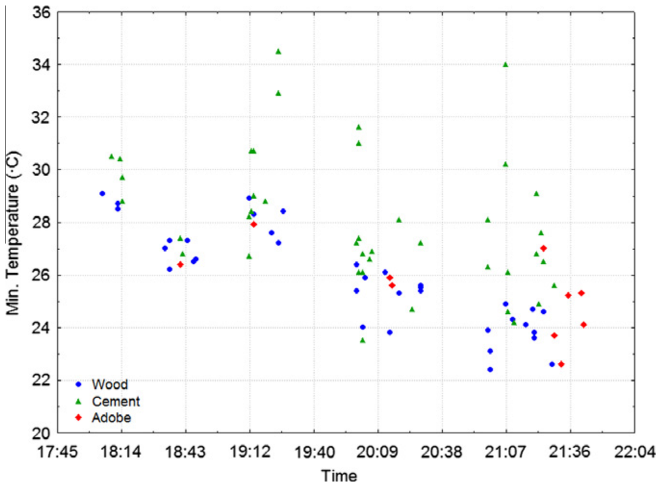

Fig. 4. Minimum temperature of building materials and their variations 6 to 10 PM.

those of hosts and did not allow to clear discrimination of hosts as a different element of the landscape. During dawn and early night however, the temperature of landscape components drops quickly and the hosts can be differentiated by their IR radiation (Fig. 6).

3.7. Size of the IR source

Figs. 7 and 8 show houses and peridomestic dwellings thermographed at short (Fig. 7a and b) and long distances (5–300 ms from the observer, Fig 7c and d, Fig. 8b), illustrating that detection of IR emission is reduced by distance. However, house lights are a good IR emitters (Fig. 8) and other pictures (not shown here) indicate that each type of light produces a distinctive radiance with temperatures fluctuating from 21.7 to 38.5 °C (minimum) to 34.3 to 95.8 °C (maximum).

4. Discussion

The present work is the first analysis of the natural IR radiation of rural villages infested by *T. infestans*, analyzed under the

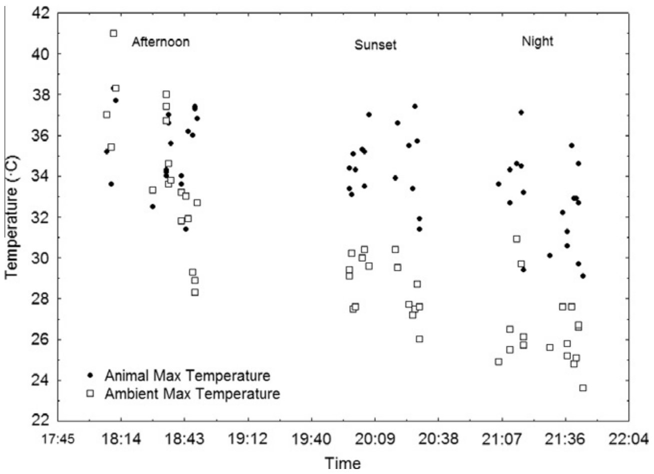

Fig. 5. Relationship between host and ambient temperature. Animal maximum temperature (black squares) and ambient maximum temperature (open squares) during afternoon, sunset and early night.

hypothesis that this natural stimulus fits well with the known behaviour of these vectors and could be an important guide to their dispersive activities. Being independent of air turbulence and propagated in the form of waves in all directions, heat radiation remains an effective cue at dawn and dusk when thermal contrast against a background is greatest (Baierlein, 1999). Lorenzo et al. (1999) proposed that objects at a temperature in the range between a couple of degrees above ambient levels and about 47 °C would be considered a host by *T. infestans,* even independently of other host cues such as odours and CO_2 (Guerestein and Lazzari, 2009). Figs. 5 and 6 show how, from sunset to the first hours of night, the thermal contrast between hosts and their landscape rises, increasing the likelihood that hosts could be differentiated by the vector. This fits well with the nocturnal activity pattern of *T. infestans,* both in terms of its walking and flying activity (Vazquez-Prokopec et al., 2006; Guerestein and Lazzari, 2009; Abrahan et al., 2011).

During the two days that the experiment was carried out, mean temperature and humidity as well as wind speed were indicative of optimal conditions for dispersive behaviour of *T. infestans*, which was corroborated by a simultaneous experiment in the area (Abrahan et al., 2011). It is well known that certain weather conditions affect Triatominae dispersion. Temperatures below 23 °C, rain and winds of more than 5 km/h have a negative effect on *T. infestans* dispersion (Gurevitz and Ceballos, 2006). Results obtained by Abrahan et al. (2011) from Los LLanos, indicate that nights with active flight and walking dispersal of *T. infestans* were characterised by a lower maximum relative humidity 65%.

Different skin covers (feathers, hair or clothes) attenuate the host skin emissions producing a complex pattern for each animal (Figs. 2 and 3). Goats and dogs provide a larger area of temperatures over 30 °C, compared to chickens and ducks. This also suggests that a herd of goats would be more attractive than a single animal, not only for the amount of radiant heat but also the synergistic effect of exhaled CO_2 (and perhaps other odours) – as recently demonstrated by Milne et al. (2009) for *T. dimidiata* and *R. prolixus*. Traps using CO_2 and heat to mimic a mammal host have been created for mosquitoes control (Kline and Lemire, 1995), and a trap supplied with CO_2 and heat succeeded in capturing *T. infestans* in field and laboratory experiments in Bolivia (Ryelandt et al., 2011). Then, if we consider the IR and CO_2 amount produced in a single habitat, it seems likely that dispersing *T. infestans* may orient more easily to a goat corral than to a chicken coop, or even to a human house. The high number of *T. infestans* frequently found in goat corrals seems to support the hypothesis that these are the most attractive habitat for this species (Ceballos et al., 2005).

The IR radiation from domestic buildings materials could be also a synergistic factor when added to IR, CO_2 and odours emanating from humans, other mammals and birds resting within. Here we show that some building materials, especially cement blocks, can retain high temperatures during the night, which might add attractiveness to the presence of hosts. During dusk and early night, the temperature of wood and adobe decreases down to 30 °C and may be less attractive to Triatominaes than cement walls, especially during hot nights when the general landscape temperature is also higher. This raises questions in terms of control of Triatominae through habitat management, for example whether a goat corral made of cement bricks is more attractive for dispersant bugs, or is a goat herd better protected from Triatominae by a wood fence rather than a wire fence? (see Fig. 9). Distance is another factor to be considered, since efficiency of IR capture decreases as the inverse square of distance to the source, suggesting that spatial management of the peridomestic environment could have a strong influence on recolonisation by the bugs.

Atmospheric absorption may also diminish the amount of radiation that would be perceived by the insect. In air the main IR window is from 7 to 14 µm wave length (Kemp, 1962), and of the primary constituents of the atmosphere, water vapour is the principal attenuator of IR radiation (Hackforth, 1960). Thus, if the bugs are using IR as orientation cue, then to disperse during periods when the water saturation is lowest, would increase their efficiency of IR capture (Callahan, 1965). Consistent with this, it is known that *T. infestans* dispersal activities are affected by high humidity values even when temperature and wind speed appear optimum (Abrahan et al., 2011). Ekkens (1981) showed that low relative humidity is one of the most important physical factors promoting flight of *Triatoma rubida uhleri* and *Triatoma recurva* in Arizona (USA). Similarly, field captures of *Triatoma protracta* in

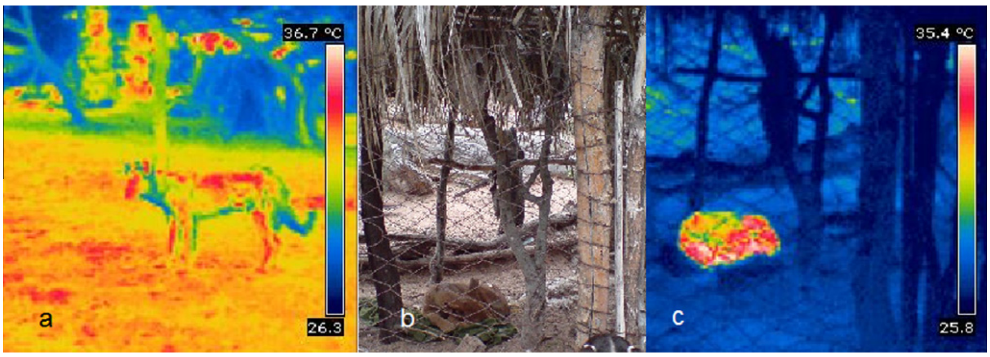

Fig. 6. Relationship between host and ambient temperature. (a) 6 PM dog and ambient share similar temperatures. (b) 8 PM sleeping dog, normal picture. (c) 8 PM sleeping dog, thermal picture, the temperature of the ambient is lower than that of dog body.

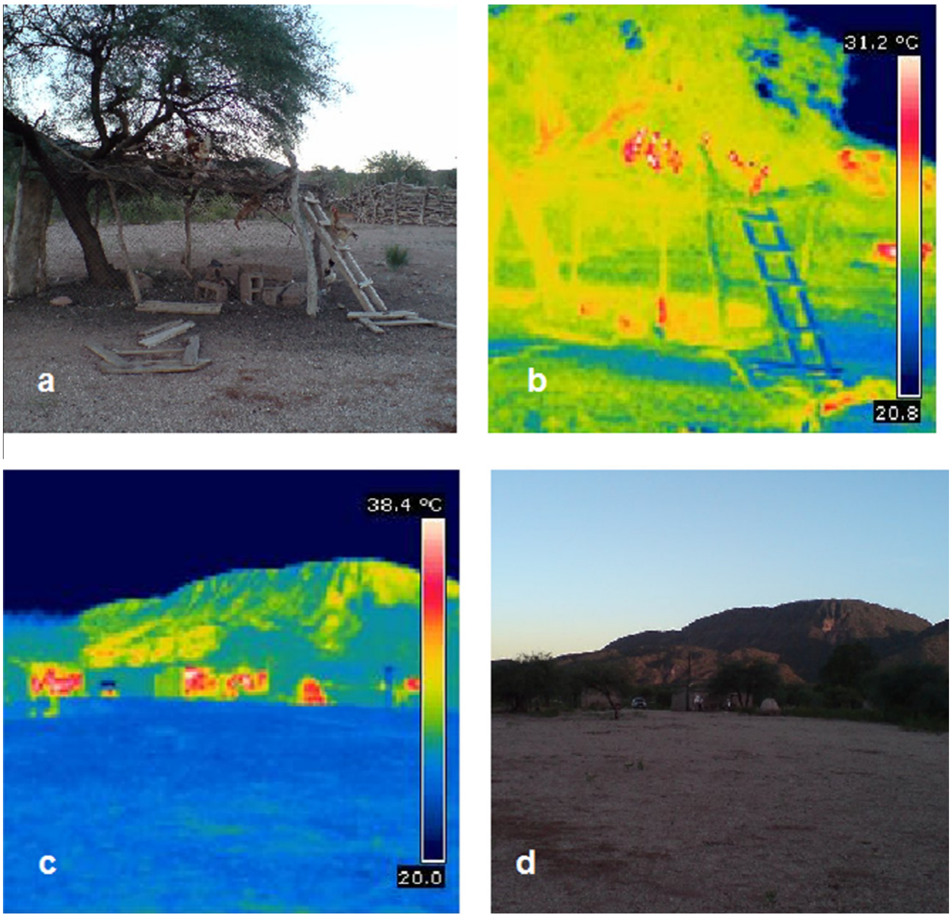

Fig. 7. (a) A chicken coop photographed at 8 PM (dawn) in La Torre. (b) Thermal image, chickens can be distinguish above the roof and inside the coop. (c) Houses and peridomestic dwellings in La Torre, 8 PM, thermal image. (d) Same landscape, normal image. Hotest elements of the landscape in red and white(For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

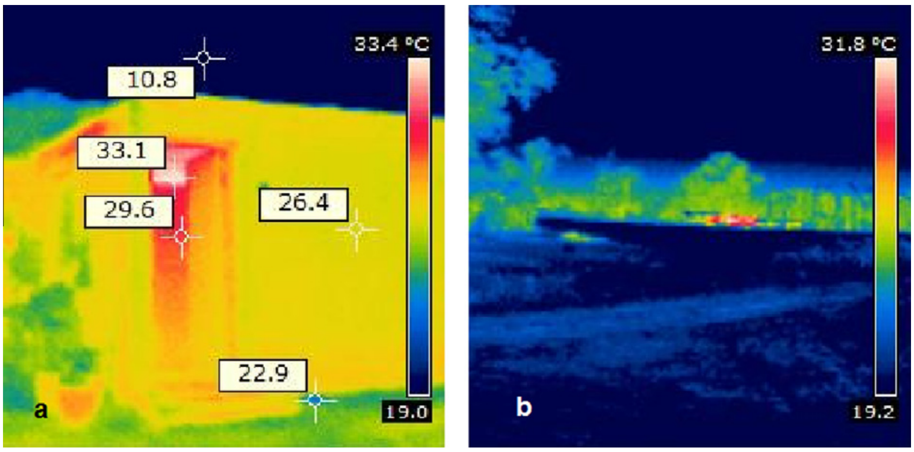

Fig. 8. Effect of distance on IR source size. 10 PM. Thermal images of two houses. (a) 3 ms from the observer (note the light inside the room). (b) 200 ms from the observer.

California peak when humidity was no more than 40–70%, within the first hour after dark (Sjogren and Ryckman, 1966). Other Triatominaes from the Amazon basin, seem to disperse more actively during the dry hot season (Castro et al., 2010).

The sensory and behavioural capabilities of *T. infestans* – described by other authors – and the patterns of IR emission in the rural domestic landscape described here, seem to support the hypothesis that IR radiation emitted by hosts and their habitats is an important factor in the dispersal behaviour of this species. In the IR band, host and habitat discrimination is available for the insects, they have adequate sensory systems to detect these wavelengths, and laboratory experiments indicate that heat – as IR – is an important cue in host-finding. If so, we can deduce that the most attractive new habitats for dispersing bugs would be those at short distance, with high CO_2 emission and strong IR radiation indicative of host presence, and that dispersal would be favoured in periods of

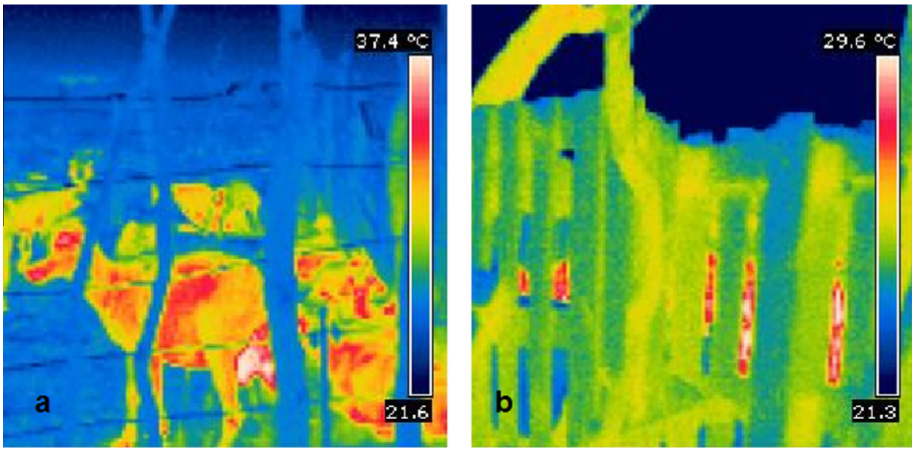

Fig. 9. Building materials on goat corral fences. 10 PM. (a) Wire fence. (b) Wood fence.

low atmospheric water saturation when IR perception is highest. Goats corrals may be the most attractive habitat to disperse, within the domestic habitat of this region. On the other hand, human habitations seems to be less attractive. This is in agreement with the house infestation rates detected by our research team (2009, unpublished observations), reporting that after 3 years of insecticide application in the area, infestation of human dwellings was very low (less than 1%) despite the fact that peridomestic structures continued to be infested (more than 30%). These peridomestic dwellings may be also more attractive than the house for sylvatic species as *Triatoma guasayana*, even when their dispersive rate in the zone was higher than for *T. infestans* (Abrahan et al., 2011).

More research in this area of knowledge, could be of considerable interest in relation to vector surveillance, epidemiology of Chagas disease transmission, and potentially to develop new methods to minimise Triatominae colonisation of new habitats.

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