Exploiting triatomine behaviour: alternative perspectives for their control

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Living in close association with a vertebrate host and feeding on its blood requires different types of adaptations, including behavioural adjustements. Triatomines exhibit particular traits associated with the exploitation of their habitat and food sources and these traits have been the subject of intense analysis. Many aspects of triatomine behaviour have been relatively well characterised and some attempts to exploit the behaviours have been undertaken. Baited traps based on host-associated cues, artificial refuges and light-traps are some of the tools used. Here we discuss how our knowledge of the biology of Chagas disease vectors may help us sample and detect these insects and even increase the efficiency of control measures.

Key words: Chagas disease - vector control - behavioural traits

The diverse lifestyles of the main Chagas disease vector species and the different habitats they live in require multiple tools and specific strategies for interrupting the vectorial transmission of *Trypanosoma cruzi*. Chemical interventions to control triatomine populations are important, but the surveillance of low density infestations inside or near human housings should play a role as well. Among the multiple approaches successfully employed for the control of these insect pests, those based on behavioural traits have not been thoroughly exploited when dealing with triatomines.

Before we consider different possibilities for exploiting the behaviour of Chagas disease vectors, we need to briefly summarise their main behavioural traits, particularly those that are susceptible to being targeted and used for population control. Detailed information on particular aspects of triatomine behaviour can be found in the review article on the chemical ecology of Chagas disease vectors by Cruz-López et al. (2001) and information on the way triatomines obtain and make use of information to find blood sources can be found in the review by Guerenstein and Lazzari (2009).

A brief account of triatomine behaviour

Triatomines spend most of their lives hidden inside refuges, but they leave them when their hosts are resting. Inside human houses and in the nests and burrows of forest-dwelling vertebrates, triatomines are more active at night, with two periods of maximum activity: one just after dusk and another at dawn (Lazzari 1992). These two periods are devoted to finding different resources. The first burst of activity is to seek out a host and the second is to find a refuge to spend the day (Lorenzo & Lazzari 1996, 1998). Other activities, such as mating, oviposition and dispersion, are also performed during one or both of these time periods. Once inside a refuge, they fall into an inactive state, or akinesis, promoted by signals such as assembling pheromones and physical contact with the substrate, as well as by internal circadian clocks. They also "wake up" due to signals from an internal clock to start a new activity cycle (Guerenstein & Lazzari 2009).

When searching for food, triatomines rely on multimodal cues that include physical and chemical signals emitted by warm-blooded vertebrates and the air currents that transport those signals. The presence of a potential host can be revealed by odours that stimulate these insects. This chemical stimulation can trigger an anemotactic response, i.e., the ability to follow air currents that guide them to a host over a long range (Taneja & Guerin 1995, 1997, Guerenstein & Guerin 2001, Barrozo et al. 2003, Barrozo & Lazzari 2004a, b, 2006). When the insect is within a few meters, the heat emitted by the host, particularly infrared radiation, is detected. This increases the amount of information available to the insects not only for spatial localisation, but also for the recognition of the host (Wigglesworth & Gillett 1934, Lazzari & Núñez 1989, Flores & Lazzari 1996, Barrozo et al. 2003). Triatomine bugs are able to distinguish the temperature of different objects and orient themselves towards those that have a temperature characteristic of endothermic hosts (Lazzari & Núñez 1989).

As far as we know, triatomine communication makes use of two different sensory channels: a chemical channel and a vibrational channel. Chemical communication is involved in many aspects of their lives and pheromones promoting assembling, mating and alarm behaviours have been partially characterised (Baldwin et al. 1971, Schofield & Patterson 1977, Lorenzo Figueiras et

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al. 1994, Manrique & Lazzari 1995, Lorenzo Figueiras & Lazzari 1998a, b, Cruz-López et al. 2001, Vitta et al. 2002, 2007, Manrique et al. 2006, Pontes et al. 2008). Vibrational communication associated with stridulation has been described in male-female interactions related to a female's rejection of copulation attempts by males. Stridulation also occurs as a response to mechanical perturbation (Manrique & Lazzari 1994, Roces & Manrique 1996, Manrique & Schilman 2000, Schilman et al. 2001, Lazzari et al. 2006).

Another important biological trait of triatomines is the ability of adults to disperse over long-ranges at night (Lehane & Schofield 1977, 1981, Schofield et al. 1991, 1992, Vazquez-Prokopek et al. 2004, Gurevitz et al. 2006). Flying triatomines are attracted to artificial lights, including those of houses (Schofield & Matthews 1985, Minoli & Lazzari 2006, Carbajal de la Fuente et al. 2007). Undoubtedly, this is a key factor leading to their colonisation of anthropic environments.

Some of the methods currently used to monitor and control Chagas disease vectors can be seen as means of exploiting the aforementioned behaviours. For instance, government programs promoting the improvement of houses aim to reduce the number of potential refuges available for insects, forcing them to remain exposed to predators and pesticides. This can hinder the establishment of domiciliary colonies. Triatomines need to find dark and narrow places to rest in close contact with the substrate during the day. In the same sense, Gomez-Núñez and Maria boxes act as artificial refuges, providing protection, physical contact and darkness (Gomez-Núñez 1965, Wisnivesky-Colli et al. 1988).

Live host-baited traps used for sampling triatomines in sylvatic habitats are another example of techniques that take advantage of triatomine behaviour. These traps exploit the host searching behaviour of the insects by attracting them (Noireau et al. 1999, 2002). Other devices have been proposed that use baker's yeast as a source of carbon dioxide and other volatile substances (Guerenstein et al. 1995, Lorenzo et al. 1998, 1999, Pires et al. 2000, Pimenta et al. 2007).

Other biological characteristics of triatomines can be exploited to control their populations or to detect their presence in houses as well as in their natural habitats. We will discuss some of them as well as the possibility of putting them into practice, but first we should mention some general principles of Triatomine behaviour.

Using insect behavioural traits

Taking advantage of a pest's behaviour for control purposes has revealed itself to be a successful, even efficient, strategy in many cases. Examples of its effectiveness in controlling different species of insects are abundant in the literature. Insects of various orders (i.e., Lepidoptera, Diptera), with different lifestyles (i.e., culture pests, haematophagous flies) living in different environments (i.e., cultures, open savannah areas, forests, buildings) have been the target of different behavioural control strategies (Shorey & McKelvey 1977, Greenblatt & Lewis 1983).

Exploiting triatomine activity

Triatomines acting as vectors for Chagas disease are essentially nocturnal. Even though the activity patterns for all relevant species have not been characterised, the major vectors, *Triatoma infestans* and *Rhodnius prolixus*, have a bimodal pattern of activity (Constantinou 1979, Lazzari 1992). Triatomines leave their refuges at dusk to search for food and to find refuges for the next day (Lorenzo & Lazzari 1998). During this period of time, it is thought that they stay away from both hosts and refuges, probably performing their diuresis in a protected place away the shelter. It has also been shown that these insects do most of their feeding and are most sensitive to some host signals in the early night hours (Barrozo et al. 2004, Bodin et al. 2008).

Because of their activity patterns, triatomines are not only more exposed and active at night, but they are also more vulnerable to mechanical and chemical attacks. Their vulnerability to chemical attacks is due to the distension of their abdominal cuticle (Ianowski et al. 1998), which becomes more fragile and permeable to pesticides just after feeding (Fontan & Zerba 1992). Preliminary experiments performed recently in *T. infestans* also showed that their sensitivity to insecticides is much higher at night (I Amelotti et al., unpublished observations).

This evidence suggests that chemical control measures may be more efficient when they are applied at night because this assures that the triatomines will come into direct contact with active chemicals. Even though insecticides may remain active for long periods of time, it is possible for these bugs to avoid treated surfaces. It is obvious that spraying at night may not always be possible for practical reasons. This is especially true when an infestation calls for the intervention of qualified technical teams. However, when spraying is performed by local people living in infested houses, the application of insecticides or the manual search for triatomines in the night hours is recommended.

Exploiting triatomine communication

A great deal of work has been done concerning triatomine communication. The triatomine vibratory channel hardly seems exploitable for pest control and its use for detecting the presence of hidden bugs in walls and roofs by detecting their vibrations has not yet been investigated. In any case, its application could be very limited given that it would require sophisticated techniques and expensive equipment to be a feasible control method.

The use of pheromones for attracting insects or disturbing their communication during sensitive periods of their life, for example their mating period, has been used as a tool for controlling different insect pests. Several instances where pheromones are used in triatomine communication have been identified. These instances are related to mating, alarm, assembling and substrate-marking behaviours. Among them, the aggregation signals present in triatomine faeces appear to be the most promising for triatomine control for several reasons: (i) faeces samples can be easily obtained from rearing facilities, since the paper or cardboard sheets usually used as substrates are a rich source for triatomine waste; (ii) modern chemical methods should be able to unravel the composition of these pheromones and eventually produce synthetic versions of them; (iii) the pheromones remain effective for almost two weeks (Lorenzo Figueiras & Lazzari 2000); (iv) the way triatomines convey information using the pheromones found in faeces is understood (Lorenzo & Lazzari 1996); (v) pheromones in faeces are able to attract and assemble triatomines in an unspecific fashion (Lorenzo Figueiras & Lazzari 1998a, 2002, Pires et al. 2002, Vitta et al. 2007); (vi) pheromones in faeces are used in the context of finding shelters (Lorenzo & Lazzari 1996).

Artificial refuges baited with the chemicals composing the aggregation signal appear to be a control solution that deserves attention. Current box sensors are able to detect the presence of wandering bugs, but their efficiency could be improved by associating them with a lure that actively recruits triatomines. The chemical composition of this signal appears to be common to several species of triatomines, and synthetic mixtures of these compounds have been shown to be capable of luring triatomines into artificial shelters (MG Lorenzo, unpublished observations).

Exploiting triatomine habitat selection

As indicated above, the chemical environment associated with a refuge (i.e., the presence of aggregation signals) is important for inducing aggregation in triatomines. In addition, the physical properties of the refuge are also known to play a role in shelter selection. Refuges offering intense physical contact due to their intricate surfaces appear to be the most appropriate. The microclimate inside the refuge also seems to affect the selection of a place to rest (Lorenzo & Lazzari 1999). Nevertheless, controlling temperature or relative humidity inside an artificial shelter does not seem feasible for a low-cost field device. Adequate materials that tend to reduce humidity may be a suitable alternative. Finally, dark surfaces have been proven to be preferred by inactive triatomines and this should be taken into account when designing artificial refuges (Reisenman et al. 2000).

Exploiting triatomine dispersion

Triatomines are able to undertake relatively long dispersive flights and the attraction of triatomines to artificial light sources has also been widely reported. From an epidemiological point of view, attraction to light plays an important role in the invasive process of triatomines into human dwellings. What causes these photophobic insects to be attracted to artificial lights remained puzzling until recently? New evidence suggests that a change in the sign of the phototactic response to punctual lights takes place after the imaginal moult (CR Lazzari et al., unpublished observations). This means that triatomines do not invade houses by chance or due to navigational errors as would be expected in the case of amenotactic error. On the contrary, triatomines are actively attracted by incandescent lamps (Minoli & Lazzari 2006). This means that every dispersing individual, not just a fraction of them, could actively approach lights and eventually settle in houses.

Sampling insects using light traps has been a common practice for many years. Several studies have been done to determine the types of light source that are most appropriate for these practices. Results to date have revealed that white light bulbs and even portable light sources (battery or fuel operated) are quite efficient for this purpose (Carbajal de la Fuente et al. 2007). More work is needed to analyse whether their efficiency could be improved by adjusting the light wavelength of the lamps or adding spectral filters to them.

Exploiting triatomine host-seeking

Triatomines, like many other blood-sucking insects, are attracted by different physical and chemical host-associated cues. Heat, water vapour and odours released by vertebrate hosts allow triatomines to detect their presence, localise them in space and orient to their position. In addition to the cues emitted by hosts, air currents play two major roles: they disperse these signals and offer triatomines directional cues about the source of stimuli (odour-modulated anemotaxis).

Our knowledge about the effects of vertebrate cues on triatomine behaviour as well as on the detection thresholds makes these cues useful for capturing triatomines. Two different approaches have been tested to date. The first one uses a live host as bait in a relatively simple capture device known by triatomine field researchers as a Noireau's trap. These simple devices are efficient for capturing sylvatic triatomines in natural ecotopes. One reason these traps are so efficient is that they use the "ideal bait", a real host. Vertebrates are sources of a complex mixture of stimuli that include signals from different sensory modalities that attract triatomines. Even though imitating the performance of a real host is difficult, for practical and ethical reasons it would be helpful to find alternative baits to replace live hosts. Attempts have been made to use baker's yeast as a lure since it is a cheap and easy to handle source of carbon dioxide and other host volatiles. Although some successful tests have been conducted in laboratory conditions, field tests are still necessary to assess their efficiency. A drawback to using yeast cultures as baits is that they are short-lived and, being liquids, are difficult to use in vertical or narrow places.

Other baits and traps have been proposed, but they remain to be tested under rigorous laboratory and field conditions. Almost none of them, however, exploit the response of triatomines to warm objects, probably because it is difficult to incorporate a durable and inexpensive source of heat into a trap.

In conclusion, in addition to intervention measures such as improving the walls of rural houses and adjusting the time of insecticide spraying, two types of devices seem to be promising for the control, surveillance and sampling of triatomines. These devices are based on triatomine shelter utilisation and host-seeking behaviour. Judging by the utility of sensor boxes and Noireau's traps, these alternatives seem to be quite promising. Nevertheless, the chance of success for developing novel and efficient capture or detection devices can be increased if some basic principles are taken into account: (i) we will probably never be able to develop bait that is more attractive than a real living host. Therefore, the best option would be to imitate a host as closely as possible to attract triatomines; (ii) given the first principle, any artificial bait will be more efficient in the absence of real hosts; (iii) triatomines are eclectic and opportunistic in their feeding behaviour. We should look for general attractants such as heat, CO_2, or fatty acids, rather than for specific cues associated with particular host species; (iv) triatomines, as other haematophagous insects, make use of multimodal cues to locate hosts. Thus, combinations of physical and chemical stimuli, even if more difficult to standardise, will have a better chance of attracting these bugs; (v) triatomines make parsimonious use of information. This means that the same odour may have different interpretations depending on the context in which it is presented. For instance, isobutiric acid is the main component of the alarm signals of several species and is also released by hosts (Guerenstein & Guerin 2001, Manrique et al. 2006). Depending on its concentration and the presence of other volatile compounds, triatomines can be attracted or repelled by its presence; (vi) a deep knowledge of the biology of triatomines is indispensable, especially the behavioural and temporal context of potential signals. Without this knowledge, we risk using supposedly attractive cues in inappropriate situations; (vii) in order to have a real significance for triatomines, attractants need to be presented in precise combinations and not simply thrown together. The statement "the more attracting cues we associate with a device, the better it will work" is simply not true.

Triatomine excrement finely illustrates how behavioural manipulation traps should be conceived. Even though the attractiveness of triatomine faeces has been well established (Schofield & Patterson 1977, Lorenzo Figueiras et al. 1994), associating them with pitfall traps that require that the insects to fall inside proved to be ineffective (Guerenstein et al. 1995). A close inspection of triatomine behaviour revealed that they were effectively attracted to trap surroundings by their faeces. Nevertheless, faecal odours were unable to induce triatomines to fall into traps as they usually did when the trap was baited with host-related signals (Guerenstein et al. 1995). This is quite logical given that we are proposing that specific insect behaviours, i.e., falling after odours, are usually associated with host search (when wandering triatomines let themselves fall on a host from ceilings). However, this behaviour cannot be triggered in the context of refuge search. They do not enter shelters by jumping inside. Thus, the behavioural context associated with each particular signal must be known and taken into account to increase the chances of success. Otherwise, our designs will be meaningless and the chances of success will be significantly reduced.

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