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Host-feeding sources and habitats jointly affect wing developmental stability depending on sex in the major Chagas disease vector *Triatoma infestans*

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ABSTRACT

Fluctuating asymmetry (FA), a slight and random departure from bilateral symmetry that is normally distributed around a 0 mean, has been widely used to infer developmental instability. We investigated whether habitats (ecotopes) and host-feeding sources influenced wing FA of the hematophagous bug *Triatoma infestans*. Because bug populations occupying distinct habitats differed substantially and consistently in various aspects such as feeding rates, engorgement status and the proportion of gravid females, we predicted that bugs from more open peridomestic habitats (i.e., goat corrals) were more likely to exhibit higher FA than bugs from domiciles. We examined patterns of asymmetry and the amount of wing size and shape FA in 196 adult *T. infestans* collected across a gradient of habitat suitability and stability that decreased from domiciles, storerooms, kitchens, chicken coops, pig corrals, to goat corrals in a well-defined area of Figueroa, northwestern Argentina. The bugs had unmixed blood meals on human, chicken, pig and goat depending on the bug collection ecotope. We documented the occurrence of FA in wing shape for bugs fed on all host-feeding sources and in all ecotopes except for females from domiciles or fed on humans. FA indices for wing shape differed significantly among host-feeding sources, ecotopes and sexes. The patterns of wing asymmetry in females from domiciles and from goat corrals were significantly different; differences in male FA were congruent with evidence showing that they had higher mobility than females across habitats. The host-feeding sources and habitats of *T. infestans* affected wing developmental stability depending on sex.

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1. Introduction

Triatoma infestans (Hemiptera, Reduviidae, Triatominae) is the epidemiologically most important vector of Chagas disease (caused by *Trypanosoma cruzi*) in southern South America. The main habitats of *T. infestans* in rural houses are human-made or -modified structures used as sleeping quarters or for housing domestic animals on which they blood-feed (Cecere et al., 2006; Gürtler et al., 2004; Rabinovich et al., 2011; World Health Organization, 2002). These ecotopes are heterogeneous in size and construction materials; refuge availability for bugs; microclimatic conditions, and resident host species (e.g., humans, dogs, cats, chickens, pigs, and goats).

Weather conditions affect peridomestic bug populations much more than those occupying domestic habitats (Gurevitz et al., 2011; Gürtler et al., 2004; López et al., 1999; Lorenzo et al., 2000; Vázquez-Prokopec et al., 2002). Moreover, the blood meal host species may contribute to the environmental and nutritional stress that each specific type of

habitat exerts on the insects because mammalian and avian blood differ in several respects that affect the haemostatic mechanism (i.e., bird thrombocytes versus mammal platelets) and in other characteristics: hematocrit, viscosity, protein, and water content (Lehane, 2005; Lewis, 1996). In rural villages of Figueroa, in the Argentine Chaco region, bug populations of *T. infestans* occupying distinct habitats differed substantially and consistently in various fitness-related attributes (e.g., blood-feeding rates, host-feeding sources, degree of engorgement and fecundity); chicken coops and domiciles led the ranking of high-quality habitats whereas goat corrals, pig corrals and kitchens were at the other extreme (Gürtler et al., 2014a).

FA has been widely used to infer developmental instability (Palmer and Strobeck, 1986), and its origins are mainly related to environmental factors (Møller and Swaddle, 1997; Parsons, 1990). When asymmetry is slight, random and distributed around a mean of 0, it is often referred to as fluctuating asymmetry (FA). Wing asymmetry may mechanically compromise flight performance and wing function in insect species (e.g., Crespi and Vanderkist, 1997; McLachlan, 1997, 2010). The identified causes of developmental instability in insects include temperature variations, lack of food, and chemical pollution (Bjorksten et al., 2001; Mpho et al., 2001; Talloen et al., 2004; Vishalakshi and Singh, 2008). Asymmetry is expected to influence biological performance directly

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and compromise mechanical functions (Balmford et al., 1993; Dufour and Weatherhead, 1996; Palmer, 1994; but see Leung and Forbes, 1996). Because both sides of bilateral traits develop under the control of an identical genome in the same environment, increased levels of FA may indicate the expression of perturbations accumulated during development (reviewed in Polak, 2003). Resource-limited habitats may constrain the development of an adaptive trait to suboptimal levels, and condition-dependent costs may contribute significantly to observed phenotypic variations in the field.

In Triatominae, higher levels of FA occurred in a domestic rather than in a sylvatic population of *Triatoma sordida* (Dujardin et al., 1999), whereas in *Rhodnius prolixus* under experimental conditions, no differences in the level of FA occurred between simulated sylvan versus domestic conditions (Márquez and Saldamando-Benjumea, 2013). For species within the *Triatoma dimidiata* complex, hybrids had similar FA in wing size and shape as parental groups, and the level of asymmetry in shape varied between villages (Nouvellet et al., 2011). Wing FA usually were greater in males than in females across populations of *T. dimidiata* (Lehmann et al., 2005). To our knowledge, the occurrence of FA in relation to the natural habitats and host-feeding sources of Triatominae has not been investigated.

In this study we measured the occurrence and amount of wing size and shape FA as well as the patterns of asymmetry in *T. infestans* populations collected in five well-defined ecotopes (i.e., domiciles, storerooms, chicken coops, pig corrals, and goat corrals) from three rural communities in Figueroa, for which we also had information on their individual blood meal sources (human, chicken, pig and goat blood) (Gürtler et al., 2014b). Genetic and phenotypic evidence support that *T. infestans* populations are strongly structured, with a high population differentiation detectable at a small spatial scale (Brenière et al., 1998; Schachter-Broide et al., 2004). Based on this evidence, we assumed that the adult triatomines included in this study most likely developed in the habitats where they were collected; did not have differences in factors intrinsic of the development of each sex, and most likely blood-fed on the local host identified. The expected pattern of symmetry is the result of a particular environment (habitat and food source) during nymphal development. We tested the following hypotheses based on background evidence: 1) repeated blood-feeding on hosts differing in blood quality (i.e., mammals and birds) would modify the occurrence and pattern of FA; 2) bugs from more instable, open peridomestic ecotopes (i.e., kitchens, goat corrals and pig corrals) suffering more extreme fluctuations would show higher amounts of FA than bugs from domiciles; 3) patterns of asymmetry across ecotopes for each sex would differ according to habitat stability and adult bug mobility (Ceballos et al., 2005; Gürtler et al., 2014a).

2. Materials and methods

2.1. Study area

Field work was carried out in October–November 2003 in three neighboring rural communities: Barrio Nueva Esperanza (BNE), Bajo Cequeira (BC) and Vaca Huañuna (VH) from Figueroa Department (27° 23' S, 63° 29' W), Santiago del Estero Province, Argentina, described elsewhere (Cecere et al., 2006). The study area was endemic for Chagas disease, with high levels of house infestation with *T. infestans* and reports of acute human cases of *T. cruzi*, and had been sprayed with pyrethroid insecticides by vector control personnel three years before the current study. A cross-sectional survey of house infestation was conducted before conducting a new community-wide insecticide spraying campaign (Cecere et al., 2006). The three selected study communities included 184 houses which had multiple peridomestic structures with specific construction patterns (Cecere et al., 2006). Domiciles, storerooms and kitchens were made of adobe walls and thatched roofs. Chicken coops were built with walls made of wood sticks or mud bricks and thatched or wood-stick roofs. Goat corrals

were usually made of piled thorny shrubs and vertical posts, and pig corrals had solid walls and roofs of wooden planks or trunks.

2.2. Insects

A total of 64 domestic or peridomestic sites (i.e., 20 in BNE; 18 in BC, and 26 in VH) harbored adult *T. infestans* collected by timed-manual searches with a dislodging aerosol (data shown in Gürtler et al., 2014a). All bugs were kept frozen at -20°C upon arrival to the laboratory in Buenos Aires. Identification of the host-feeding sources of each bug was conducted via a direct ELISA against human, dog, cat, chicken, pig, goat and murid rodent (rat or mouse) serum antigens with high sensitivity and specificity values as described (Gürtler et al., 2014a). From the pool of samples we selected all female and male adult insects ($n = 196$) that had unmixed blood meals on a given host species or bug collection habitat for wing asymmetry analysis using geometric morphometry. Bugs that fed on dog, cat, or murid rodent were excluded from the analyses due to their small sample size.

2.3. Metric data

Wings were mounted between microscope slides and cover slips as described in Schachter-Broide et al. (2004). Photographs of each pair of wings were taken using a digital camera (Sony MVC-CD300, US) and a stereo-microscope (Zeiss SV11, Germany). We used landmark-based geometric morphometry. Ten type-I landmarks positioned at vein intersections were collected and expressed as x,y coordinates in Cartesian space. The position of each landmark was described elsewhere (Schachter-Broide et al., 2004).

2.4. Size and shape variation

Centroid size (CS) was used as the size variable for comparison of wing asymmetry between groups. CS is a single variable of size that integrates different axes of growth and is measured as the square root of the sum of the squared distances between the center of the configuration of landmarks and each individual landmark (Bookstein, 1991).

To obtain Procrustes coordinates, a full Procrustes Analysis superimposition algorithm was applied (Rohlf, 1990; Rohlf and Slice, 1990). The full Procrustes fit analysis optimally translates, rotates and uniformly scales the objects to obtain a similar placement and size by minimizing a measure of shape difference (sum of the squared deviations) between landmarks (Rohlf, 1990).

2.5. Asymmetry assessment

For the analysis of asymmetry (“matching symmetry” according to Mardia et al. (2000), as opposed to “object symmetry”), we first reflected all configurations from one wing side to their mirror images (Klingenberg and McIntyre, 1998; Klingenberg et al., 2002). Separate landmark configurations were digitized twice in images of both wings of each individual for the estimation of measurement error (Palmer, 1994). For each combination of host-feeding source, ecotope and sex, configurations were superimposed by using a full Procrustes fit (Klingenberg and McIntyre, 1998). In addition to possible fluctuating asymmetry (FA), two other types of bilateral asymmetry are expected to occur: directional asymmetry (DA), which occurs whenever there is on average a greater development of a character on one side of the plane of symmetry relative to the other; and antisymmetry (AS), which is detected by a bimodal distribution of signed differences with a zero mean. Unlike DA, FA and AS are non-directional asymmetries. Antisymmetry and DA are believed to have a significant genetic basis (Carter et al., 2009; Palmer and Strobeck, 1986; Pelabón and Hansen, 2008; Van Valen, 1962), and are presumably unrelated to developmental stability (Palmer, 1994).

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