

The use of fluctuating asymmetry as a measure of farming practice effects in rodents: A species-specific response



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ABSTRACT

The effects of agricultural intensification on vertebrate populations could vary depending on whether species are habitat specialists or habitat generalists. Organic farming practices are generally considered to be less intensive and more environmental friendly than conventional farming practices and, as a result, these two managements may impact on habitat specialists and habitat generalists in different ways. The effect of environmental and/or genetic stress on populations can be assessed using fluctuating asymmetry (FA) and body condition of animals. We predicted that populations of a specialist species, the Pampean grassland mouse (*Akodon azarae*) would have higher levels of FA and poorer body condition on conventional farms compared to populations of *A. azarae* on organic farms. In contrast, we predicted that populations of generalist species, the corn mouse (*Calomys musculinus*) and the small vesper mouse (*Calomys laucha*) would not show differences in FA or body condition between conventional and organic farms. We examined the expression of FA in the hind foot and used the scaled mass index as a surrogate for body condition. As predicted, we found higher FA in the habitat specialist (*A. azarae*) on conventional farms compared to organic farms, and found no differences in FA among the two generalist species (*C. musculinus* and *C. laucha*). However, we found no differences in body condition for the three studied species between the two managements. Our results suggest that the effect of farming practices on small mammals varies between habitat specialists and habitat generalists. The results of this study provide important insights for the study of asymmetries, both from biological and methodological perspectives. Our results support the idea that the level of FA may be used as an index to assess the effects of farming practices on vertebrate populations.

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1. Introduction

The conversion of natural landscapes in croplands and pastures constitutes the main land cover change worldwide (Foley et al., 2005), and affects habitat quality and suitability at both local and landscape scales. Intensive use of chemical inputs, such as pesticides and fertilizers, and increased levels of disturbances at a local scale not only affects biodiversity on intensively used agroecosystems (Tscharntke et al., 2005) but also on natural landscapes (Geiger et al., 2010; Marchand et al., 2003). Contrarily, extensive farming

practices, that exclude synthetic inputs, and maintain un-cropped border habitats (i.e., organic farming) provide suitable habitats for farmland biodiversity (Benton et al., 2003; Tuck et al., 2014), including plants (Roschewitz et al., 2005), insects (Holzschuh et al., 2007), birds (Beecher et al., 2002) and mammals (Fischer et al., 2011a,b; Macdonald et al., 2007). Thus, these farming practices can counteract the negative effects of agriculture intensification.

The effects of agriculture intensification on populations could vary with the degree of species' habitat specialization. Habitat specialists rely on local habitat quality and are more affected by habitat disturbance than generalist species, which are able to exploit a wider array of habitats and resources (Filippi-Codaccioni et al., 2010; Fischer and Schröder, 2014). Indeed, organic farms and their border habitats support a higher abundance of habitat-specialist small mammals (e.g., *Akodon azarae*) than conventional farms while having little influence on the abundance of habitat generalist

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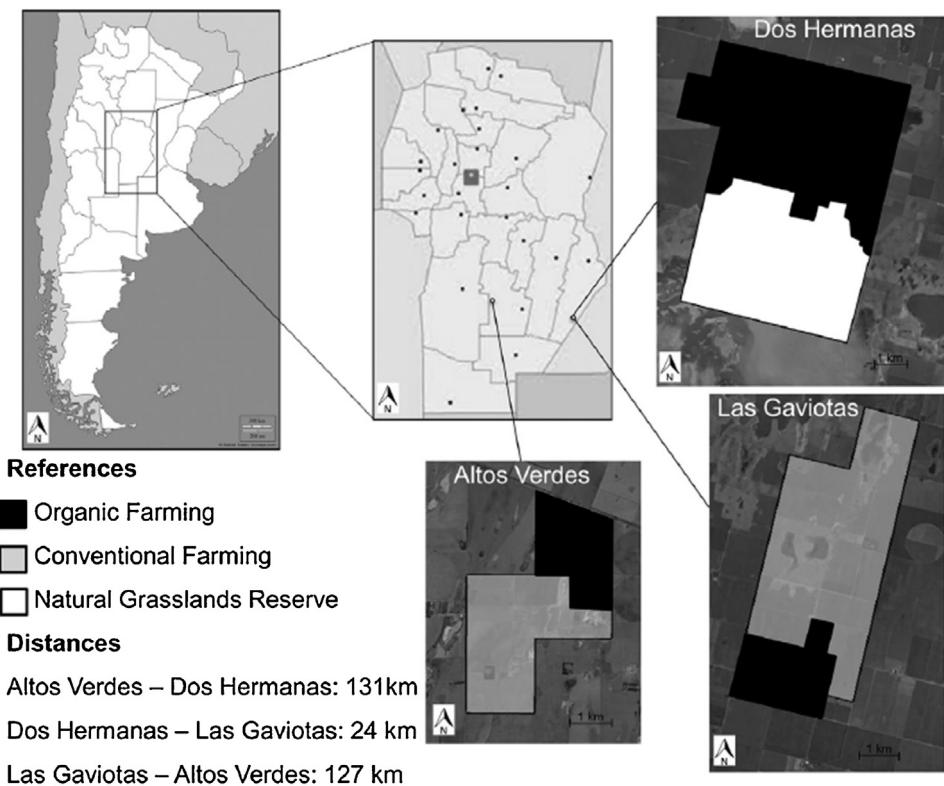


Fig. 1. Study area, agricultural systems of south-eastern Córdoba province with the three study sites (Dos Hermanas, Las Gaviotas and Altos Verdes) that include organic and conventional managements, with distances between them.

species, such as *Calomys musculinus* and *Calomys laucha* (Coda et al., 2015). Moreover, organic farms support higher female reproductive activity than conventional farms by offering high availability of shelter and food (Coda et al., 2014). Different farming practices, then, affect population parameters of small mammals.

Stress caused by agricultural processes can have detrimental effects on vertebrate populations (Marchand et al., 2003). Since developmental precision is negatively affected by a wide range of environmental and/or genetic stressors, the degree of developmental instability – an individual's inability to produce a consistent phenotype in a given environment (Zakharov, 1992) – has been suggested as a reliable indicator of population health (Cuervo and Restrepo, 2007; Lazić et al., 2013; Leary and Allendorf, 1989; Marchand et al., 2003). A frequently used metric of developmental instability is fluctuating asymmetry (FA), which is considered as the only form of asymmetry that can serve as a useful indicator of individuals exposed to environmental/genetic stress (Leary and Allendorf, 1989; Palmer and Strobeck, 1986). Fluctuating asymmetry is defined as small and random deviations from perfect bilaterally symmetrical traits (Ludwig, 1932; Palmer and Strobeck, 1986), and has been widely used to study both environmental and genetic stress (Beasley et al., 2013; Lazić et al., 2013; Leung and Forbes, 1997; Palmer, 1994; Polak and Taylor, 2007). In wild small mammals, high levels of FA are associated with habitat fragmentation (Marchand et al., 2003; Teixeira et al., 2006; Wauters et al., 1996), natural disasters (Hopton et al., 2009) and vegetation removal (Badyaev et al., 2000). Body condition of animals measured as body weight and length can also be used as individual indicators of environmental stress (Peig and Green, 2010, 2009).

In the present study we examined the degree of FA in right and left hind feet and body condition on populations of *C. musculinus*, *C. laucha* and *A. azarae*. We aim to find a reliable tool to infer local dis-

turbance due to human activities in small mammal populations. We predicted that populations of habitat-specialists on organic farms will show lower level of developmental instability and better body condition compared to populations on conventional farms. Populations of generalist species will not show differences in FA and body condition between organic and conventional farms.

2. Materials and methods

2.1. Study area and design

This study was carried out in an agricultural landscape of south-eastern Córdoba province, Argentina (Fig. 1). Here, original flora is restricted to un-cropped border habitats that support both native and invasive herbaceous species. The most frequent crop sequences are wheat–soybean or soybean–maize (as alternate single summer crops per year with a winter fallow) although soybean monoculture as a single yearly summer crop is also a common practice (Puricelli and Tuesca, 2005; Satorre, 2005).

In this region, the small mammal assemblage is mainly represented by the Cricetidae rodents *C. musculinus*, *Calomys venustus*, *C. laucha*, *A. azarae*, *Akodon dolores*, *Oxymycterus rufus* and *Oligoryzomys flavescens* (Simone et al., 2010). Rodent species were ranked from generalists to specialists considering species-specific habitat specialization; ranging from habitat generalist (species that occur in almost all habitats within the agriculture landscape) to habitat specialist (species that occur in habitats with high vegetation cover); *C. musculinus*, *C. laucha*, *A. azarae*, *O. flavescens*, *C. venustus*, *A. dolores* and *O. rufus* (Martínez et al., 2014).

Three farms were sampled: Las Gaviotas (Postel S.A., 33°50'S, 62°39'W), Dos Hermanas (Rachel and Pamela Schiele Foundation, 33°39'S, 62°30'W) and Altos Verdes (Huanqui S.A., 33°18'S,

Table 1

Distribution of the trap lines by year, season, management (O: organic; C: conventional) and farm.

| | 2012 | | | | 2013 | | | | | |
|--------------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|
| | Summer | | Autumn | | Spring | | Summer | | Autumn | |
| Altos Verdes | O 4 | C 10 | O 7 | C 10 | O 5 | C 7 | O 7 | C 9 | O 8 | C 10 |
| Dos Hermanas | O 8 | C – | O 8 | C – | O 7 | C – | O 8 | C – | O 8 | C – |
| Las Gaviotas | O 3 | C 11 | O 3 | C 11 | O 3 | C 9 | O 2 | C 10 | O 3 | C 10 |
| Total | O 15 | C 21 | O 18 | C 21 | O 15 | C 16 | O 17 | C 19 | O 19 | C 20 |

63°51'W) (Fig. 1). Dos Hermanas comprises a natural grassland reserve of 1922 ha and a productive area of 2101 ha organically managed since 1992 (Fig. 1). Las Gaviotas (1689 ha) and Altos Verdes (1010 ha) are managed with organic and conventional practices (Fig. 1); organic plots have been maintained for over 10 years, and occupy 330 ha and 664 ha in Las Gaviotas and Altos Verdes, respectively. While under organic practices weeds were mechanically controlled using disk plough, chisel plough, roll and weeder, farms under conventional management used herbicides (glyphosate, atrazine, acetochlor, nicosulfuron, 2,4-D, chlorimuron and metolachlor). Other external inputs as fertilizers (sulfur, urea and ammonium) and insecticides (chlorpyrifos, alphametrin, cyclopropane carboxylate, endosulphan and lambdacyalothrine) are regularly used in conventional plots, while fungicides (Epoxiconazole, Pyraclostrobin, Azoxystrobin, Difenoconazol) are used as required. During this study, the main crops grown were soybean and maize, both in organic and conventional farms. Organic production is certified by private companies, OIA (Organización Internacional Agropecuaria, 2015) for Las Gaviotas and Argencert (2015) for Altos Verdes and Dos Hermanas.

Our study was conducted in border habitats of organic and conventional farms, 1.5–2.5 m wide vegetation strips located in the margins of plots. In conventional farms, frequent intentional or unintentional spraying of broad-spectrum herbicides on border habitats (De la Fuente et al., 2010; Ghersa et al., 2002) results on low vegetation volumes comprised mainly by plant litter (Coda et al., 2015, 2014). On the other hand, border habitats on organic farms have higher green vegetation cover and height (Coda et al., 2015, 2014).

Capture, mark and recapture (CMR) trapping sessions were seasonally conducted, over two weeks in each session. Altos Verdes was sampled during the first week and Dos Hermanas and Las Gaviotas during the second week; for each week, trapping was conducted during four consecutive nights. A total of 84 and 97 trap lines were placed in border habitats of organic and conventional farms, respectively (Table 1). Each line consisted of 20 traps similar to Sherman live-traps, with one trap every 10 m in the middle of a border. Traps were baited with a mixture of peanut butter and cow fat. The minimum distance between lines was 300 m to avoid correlation between neighbouring lines. Trapped animals were identified, sexed, weighed and ear-tagged, and we registered body and tail length for each individual.

2.2. Fluctuating asymmetry

Adult individuals belonging to three rodent species (*C. musculinus*, *C. laucha* and *A. azarae*) were used in fluctuating asymmetry analyses. Rodents were captured between spring 2012 and autumn 2013 in organic and conventional farms. For each individual, right and left hind feet were measured to nearest 0.01 mm using a digital Mitutoyo Digimatic series 500 caliper. Following Wauters et al. (1996), to investigate measurement errors (repeatability of the measure), three independent measurements were made of both hind feet following the protocol: left-right, right-left, left-right (the caliper was zeroed after each measurement). All morphometric

measurements were taken by one person only (JC). A one-way ANOVA was calculated with foot length as dependent variable and each individual as a class (sample size in each class = 3). We then calculated r_1 , the coefficient of intraclass correlation (Sokal and Rohlf, 1981); when r_1 is high, variation among individuals is much larger than variation within individuals. The mean estimate of left and right hind foot length was calculated for each individual and used to determine the absolute level of FA (unsigned left minus right hind foot length). We performed a two-way mixed ANOVA in which individual and side were included as random and fixed effects, respectively (Palmer, 1994). The interaction effect was also included. Significance of this term indicates that asymmetry is significantly greater than measurement error whereas significance of the side term (tested over the interaction mean square) suggests the presence of directional asymmetry (Palmer, 1994). In addition, we inspected the distribution of the signed asymmetry. Normality was evaluated using Shapiro-Wilk test, and deviation from a zero mean using one sample *t*-tests. Trait size dependence was examined by linear regression analyses of absolute FA on weight (to test for dependence on total body size) and on hind foot length (to test for dependence on trait size). In order to evaluate FA, we performed a mixed ANOVA with sex and management included as fixed effects and farm as random effect. All interaction effects were included. Data of both *C. musculinus* and *A. azarae* were square-root transformed to satisfy homoscedastic assumption. Data of *C. laucha* were not homoscedastic, therefore a Mann-Whitney *U* tests was used.

2.3. Body condition

Body condition of adult individuals belonging to the three mentioned rodent species were analysed in relation to farming practices. The individuals were captured between summer 2012 and autumn 2013 in organic and conventional farms. In order to avoid weight overestimation in relation to pregnancy, we only considered male individuals. For each individual, body weight and body and tail lengths were registered. We calculated the scaled mass index (Peig and Green, 2010, 2009) as a surrogate for body condition: $SM_i = Mi[LO/Li]^{bSMA}$, where Mi and Li are the body mass and body length of the individual i , respectively, LO is the arithmetic mean of body length and $bSMA$ is a scaling exponent derived from the standardized major-axis (SMA) regression of body mass on body length. We performed a one-way mixed ANOVA in which the scaled mass index was the dependent variable, management was included as fixed effect and year and farm were included as random effects. Since data of *C. laucha* were not homoscedastic, a Mann-Whitney *U* tests was used.

All the analyses were performed using R 3.0.2 software (R Development Core Team, 2013).

3. Results

3.1. Fluctuating asymmetry

A total of 199 adult individuals were trapped in 8480 trap nights (Table 2). All coefficients of intraclass correlation were higher than

Table 2

Number of individuals (males and females) used in Fluctuating Asymmetry analyses, coefficients of intraclass correlation (C.C.I.) in right and left hind foot with their 95% confidence intervals (CI), individual-side interactions, normal distribution of hind foot signed asymmetry and mean equal to zero of signed asymmetry in *C. musculinus*, *C. laucha* and *A. azarae*.

| | | <i>C. musculinus</i> | <i>C. laucha</i> | <i>A. azarae</i> |
|-----------------------------|--------------|----------------------|---------------------|---------------------|
| Individuals (males/females) | Organic | 62 (42/20) | 18 (11/7) | 28 (15/13) |
| | Conventional | 41 (21/20) | 30 (23/7) | 20 (12/8) |
| C. C. I. | Right (CI) | 0.908 (0.885–0.926) | 0.786 (0.716–0.844) | 0.870 (0.819–0.909) |
| | Left (CI) | 0.856 (0.823–0.885) | 0.855 (0.804–0.896) | 0.808 (0.742–0.861) |
| Individual-side interaction | F | 1.501 | 1.826 | 1.768 |
| | Df | 205 | 95 | 95 |
| | p | 0.003 | 0.002 | 0.004 |
| Normal Distribution | W | 0.990 | 0.919 | 0.975 |
| | p | 0.650 | 0.003 | 0.935 |
| $\mu = 0$ | T | -0.155 | 0.573 | 0.082 |
| | p | 0.877 | 0.570 | 0.398 |

Table 3

Statistical results obtained from linear regressions of unsigned fluctuating asymmetry on weight and hind foot length.

| | Weight | | | Hind foot length | | |
|---------------------------|--------|--------|-------|------------------|--------|-------|
| | F | r | p | F | r | p |
| <i>Akodon azarae</i> | 0.278 | -0.016 | 0.600 | 0.077 | -0.020 | 0.783 |
| <i>Calomys musculinus</i> | 0.695 | 0.003 | 0.407 | 0.487 | -0.005 | 0.487 |
| <i>Calomys laucha</i> | 4.142 | 0.063 | 0.048 | 0.924 | -0.002 | 0.341 |

0.78. The individual-side interaction term was significant for the three species (Table 2). The distribution of hind foot signed asymmetry in *C. musculinus* and *A. azarae* did not depart from normality with mean zero while in *C. laucha* the distribution differed from a normal distribution but the mean did not differ from zero (Table 2).

Linear regression of unsigned FA on weight and hind foot length revealed no body size dependence for *A. azarae* and *C. musculinus*. For *C. laucha*, unsigned FA was related with weight but not to hind foot length, the r value for this regression was low (Table 3).

There were no significant differences in FA of *C. musculinus* between managements ($F_{1,102} = 0.117$, $p = 0.734$) and sex ($F_{1,102} = 0.396$, $p = 0.531$). Likewise in *C. laucha*, there were no difference in FA between managements ($W = 284.5$, $p = 0.766$) and sex ($W = 227.5$, $p = 0.821$) (Fig. 2A). For *A. azarae* there was no difference in FA between sexes ($F_{1,47} = 0.069$, $p = 0.794$), but individuals had a higher FA in farms under conventional than under organic management ($F_{1,47} = 5.854$, $p = 0.020$) (Fig. 2A).

3.2. Body condition

A total of 224 adult males were trapped in 12000 trap nights and used for body condition analysis (Table 4). There was not an effect of management on scaled mass index in either of the three species, *C. musculinus* ($F_{1,105} = 0.153$, $p = 0.696$), *C. laucha* ($W = 699$, $p = 0.303$) and *A. azarae* ($F_{1,35} = 0.298$, $p = 0.590$) (Fig. 2B).

4. Discussion

The degree of FA of morphological traits may provide a valuable indicator of environmental and/or genetic stress in animal popula-

Table 4

Number of adult males belonging to the three captured species in organic and conventional farms used in body condition analyses.

| Species | Organic | Conventional |
|---------------------------|---------|--------------|
| <i>Akodon azarae</i> | 17 | 19 |
| <i>Calomys musculinus</i> | 48 | 58 |
| <i>Calomys laucha</i> | 49 | 33 |

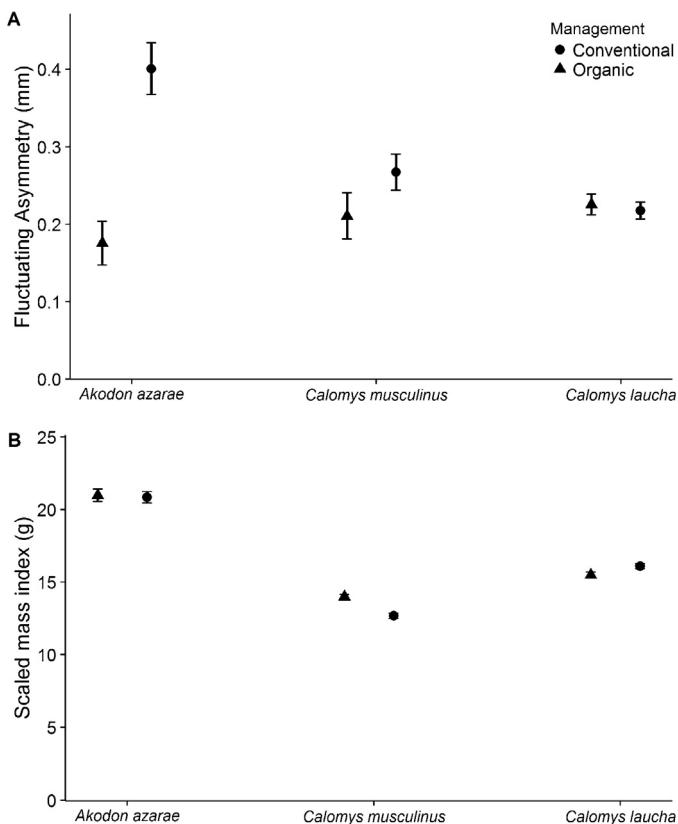


Fig. 2. Degree of fluctuating asymmetry (FA) (Mean \pm SE) of hind foot length (A) and scaled mass index (Mean \pm SE) (B) in three species, *A. azarae*, *C. musculinus* and *C. laucha*, in conventional and organic farms.

tions (Lazić et al., 2013; Leary and Allendorf, 1989; Wauters et al., 1996). A large number of studies have shown a positive relationship between FA and environmental stress in populations of rodents

(Marchand et al., 2003; Nunes et al., 2001; Oleksy et al., 2004; Teixeira et al., 2006; Wauters et al., 1996).

We used a non-invasive technique to measure FA in live wild rodents and assessed the effects of farming practices on developmental instability. This technique has the advantage of obtaining morphological data without sacrificing individuals. Although sample size of the specialist species *A. azarae* was small, higher FA values were observed in this species within conventional farms. Contrary, there were no differences in FA of the generalist species *C. musculinus* and *C. laucha* between managements.

The anthropogenic stress produced by conventional farming through external inputs of synthetic pesticides and soluble fertilizers increase developmental instability in animal populations. In Argentina, anthropogenic disturbances produced by conventional farming results in high levels of stress since weed control depends almost exclusively on the use of total herbicides that affects border habitats (De la Fuente et al., 2010; Ghersa et al., 2002; Satorre, 2005). On the other hand, organic farming is characterized by a mechanical control of weeds, do not use synthetic fertilizers or pesticides, and do not intentionally manage border habitats. Thus, it is generally thought to be more environmentally friendly than conventional farming, resulting in lower level of stress on animal populations. The better quality and suitability of crop fields and border habitats for small mammals in organic farms has just been found in Argentinian agroecosystems (Coda et al., 2015, 2014). Thereby, borders and crops of organic farms are high quality habitats that provide resources for persistence and reproduction of rodent populations.

The lower FA reported for *A. azarae* individuals from organic farms may be explained by the greater possibility of dispersion in more continuous and higher quality habitats. Studies developed in European agroecosystems suggest that organic farms offer more resources, and sustain higher abundance and richness of invertebrates and weeds, both in border habitats and within crop fields (Frieben and Kopke, 1995; Hole et al., 2005; Macdonald et al., 2000). Considering that conventional farms have less resources (coverage and food) and higher percentages of arable land (Coda et al., 2015), crop fields could not connect suitable habitats for small mammal nor provide shelter from predators (Cittadino et al., 1998; Coda et al., 2015, 2014; Gomez et al., 2011; Sheffield et al., 2001). Contrarily, organic farms have more resources, both in border habitats and crop fields, and less percentage of arable land, potentially increasing habitat connectivity.

The occurrence of the specialist species *A. azarae* in more vegetated and stable habitats is in line with previous studies of this species (Andreó et al., 2009; Busch et al., 2001; Gomez et al., 2015). Marchand et al. (2003) found that individuals belonging to the specialist species *Myodes glareolus* had lower degree of FA in the more extensive and more connected hedges of undisturbed areas than in fragmented hedgerows of disturbed areas. As mentioned, intensive agricultural methods of conventional management produce crop fields with scarce weed cover and managed border habitats that do not connect suitable habitats for small mammals. This lack of habitat connectivity can result on small, more or less isolated sub-populations suffering both genetic and environmental stress (Wauters et al., 1996). This would be the case of *A. azarae* in conventional farms since analyses of genetic spatial structure showed that the presence of barriers as crop fields limits dispersal of this species in agroecosystems, resulting on increased consanguinity (Vera, 2014).

Further, small mammals in organic farms may profit from a higher food supply related to the lack of use of agrochemicals. Contrarily, the decrease in availability of food resources due to the use of agrochemicals in conventional farms could produce nutritional stress and consequently higher FA values in the specialist species *A. azarae*. Some experimental studies have shown that nutritional

stress causes larger development asymmetries in birds and rodents (Anciaes and Marini, 2000; Nunes et al., 2001; Sciulli et al., 1979; Swaddle and Witter, 1994). However, we found that *A. azarae* had similar body condition under both managements. This finding could be a result of analysing only males to avoid biases related to pregnant females. Considering the high costs associated with pregnancy, lactation and young guarding, females generally invest more in their offspring than males, and typically compete with each other for food and space to rear offspring, whereas males mainly compete for access to estrous females (Steinmann et al., 2009; Trivers, 1972). Indeed, *A. azarae* females have higher consumption of invertebrates as a source of proteins to meet both energetic and nutrient requirements for reproduction (Bilenco and Kravetz, 1998). Thus the effects of farming management should be more apparent in females' body condition. On the other hand, sample size might be darkening clear statistical effects of farming on body condition.

Individuals of *C. musculinus* and *C. laucha* did not show differences in both FA and body condition between managements. Both species have been described as the most opportunistic and generalist species of the assemblage, since they show wider habitat and trophic niche, and occur in almost all habitats within the agriculture landscape (Martínez et al., 2014). Generalist species are able to exploit different habitats and resources, while specialist species are dependent on habitat quality and susceptible to habitat disturbances (Filippi-Codaccioni et al., 2010; Fischer and Schröder, 2014). Thus, the former may not be affected by environmental stressors such as habitat fragmentation or chemicals utilized in agroecosystems, and they may benefit from agricultural changes (Busch et al., 2001; Gonzales Fischer et al., 2012). The lack of genetic spatial structure observed in *C. musculinus* suggests that habitat fragmentation in agroecosystems does not represent a barrier to dispersal (Sommaro, 2012). Thus, contrarily to *A. azarae*, its populations seem to maintain higher levels of gene flow despite of habitat fragmentation.

5. Conclusions

In summary, our results suggest that the effects of farming practices on small mammals would vary with the degree of specialization of species. We found that individuals of the specialist species *A. azarae* had higher values of FA under conventional management while there were no differences in generalist species *C. musculinus* and *C. laucha*. Besides, these results support the idea that the level of FA may be used as an index of stress in conservation biology. Thus, the results obtained in this study would provide important insights for the study of asymmetries, both from a biological and a methodological perspective. Moreover, there are few studies in small mammals that assess FA without sacrificing animals. To our knowledge, this is the first study to investigate the effect of farming practices on FA in small mammal through a no-invasive technique. However, our results should be carefully considered since a single trait was used to assess FA, several studies suggest that to obtain an accurate evaluation of developmental instability multiple traits should be required. Although, the use of a single trait enables us to find differences in the specialist species, could not be enough to establish the absence of the effect of management on generalist species. It is possible that to highlight the effects of management in those species more tolerant to human disturbances more traits and a large sample size should be taking into account.

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