The effects of forest fragmentation on the population ecology and natural history of a funnel-web spider

Vanessa Stefani and Kleber Del-Claro*

Institute of Biology, Federal University of Uberlândia, Uberlândia, Minas Gerais, Brazil

(Received 14 June 2013; accepted 23 March 2014; first published online 2 June 2014)

Habitat fragmentation strongly affects the abundance, distribution, body size and population genetics of invertebrates. Urban growth in Brazil has led to severe fragmentation, especially in the Atlantic Forest and savannas. The effects of this fragmentation on the common funnel-web spider Aglaoctenus lagotis were examined in two forest fragments within the interior savanna: a smaller fragment within an urban environment and a larger fragment within a rural environment. The reproductive period occurred in October, coinciding with the beginning of the rainy season, when the species was aggregated in the two forest fragments. The smaller fragment contained a larger population, and the spiders had a larger average prosoma size and web area. The presence of a larger population in a smaller area within the urban centre may reflect a limited dispersal ability, reduced predator abundance or low interspecific competition. The larger prosoma length and web area in the smaller habitat fragment suggest greater resource availability and a higher probability of capturing prey in the urban environment. In both areas, a larger number of capture threads was positively correlated with the presence of inquiline spiders in the webs. The genetic data indicate close similarity between and within the two areas, indicating that the species has low genetic variability or that the areas studied, consistent with their proximity, have separated only recently. Most savannas and forests in midwestern Brazil have recently undergone severe fragmentation, and further studies of this nature are needed.

Keywords: Brazil; Cerrado; inquiline spiders; parental similarity component; spider densities

Introduction

The effects of habitat fragmentation on species abundance and richness in forest communities depend on the biological characteristics of the species, such as their mode of dispersal (e.g. Bierregaard et al. 1992; Hagan et al. 1996). The effects of isolation have been studied in numerous arthropods, including butterflies (Baz and Garcia-Boyero 1995; Brown and Hutchings 1997), bees (Lovejoy et al. 1983, 1986), beetles (Didham et al. 1996, 1998), termites (Souza and Brown 1994) and ants (Miranda et al. 2006). The few studies that have focused on spiders in forest fragments have shown that the populations are strongly affected because fragmentation can dramatically alter the abundance, richness and distribution of individuals, potentially causing local extinctions (Bolger et al. 2000; Venticinque and Fowler 2001; Mestre and Gasnier 2008).

*Corresponding author. Email: delclaro@ufu.br

© 2014 Taylor & Francis
Spiders are diverse in terms of their habitat-selection strategies, prey-capture behaviours and other behavioural traits (Foelix 2011). Environmental alteration due to habitat fragmentation causes changes in the plant community composition and variation in prey availability, influencing the diversity and abundance of spiders (Wise 1993; Gibb and Hochuli 2002). Habitat use, body size, interspecific interactions and inter-population genetic variation may differ in habitat fragments with distinct physical and biological characteristics (Burgess and Uetz 1982; Figueira and Vasconcellos-Neto 1993; Macaranas et al. 2001). Habitat choice is vital for spiders, directly affecting their growth, survival and reproductive success (Riechert and Tracy 1975; Gonzaga 2007).

Increasing habitat fragmentation has been shown to increase the genetic subdivision of populations within a region (Hastings and Harrison 1994; Settele et al. 1996; Harrison and Bruna 1999; Knutsen et al. 2000; Macaranas et al. 2001; Mech and Hallett 2001). In locations that have undergone past fragmentation, remain isolated, and continue to suffer environmental instability, populations are unlikely to be in genetic equilibrium (Colgan et al. 2002). Genetic analyses of populations settled in distinct fragments can determine whether the subpopulations represent a common gene pool, the subpopulation genetic differentiation is correlated with geographic distance, or the subpopulations are in equilibrium (Chang et al. 2007).

In the spider *Pardosa monticola*, Bonte et al. (2003) have suggested that the observed genetic differentiation may be due to both historical gene flow and recent habitat fragmentation. Conversely, in an Australian species of Lycosidae, Colgan et al. (2002) have observed that inter-population divergence is not related to geographical distance, suggesting that the populations were already structured before the anthropogenic fragmentation of the region. Studies clarifying the factors that may affect gene flow among subpopulations of lycosid spiders are essential to understand the impact of habitat fragmentation.

The spider *Aglaoctenus lagotis* (Holmberg 1876) is a common member of Lycosidae in the cerrados (savannas) of central Brazil (Stefani et al. 2011). The cerrados are a threatened ecological ‘hotspot’ (Klink and Machado 2005) whose plant communities have been severely fragmented by urbanization and agriculture (Oliveira and Marquis 2002). Studies of population genetics and species ecology in cerrado fragments are essential for the development of conservation strategies in this biome. The small size of cerrado fragments and the lack of connectivity between them strongly affect populations and necessitate a comprehensive genetic and ecological approach (Krebs 2001).

The present study investigates the hypothesis that two semi-deciduous cerrado–forest fragments of different sizes and isolation levels have affected *A. lagotis* populations in different ways. Biological traits, such as variation in body size and developmental period, and ecological factors, such as abundance, distribution, web size and interspecific interactions, were considered. The genetic similarity of the populations within and between fragments was also evaluated.

### Material and methods

#### Study species

The genus *Aglaoctenus* belongs to the subfamily Sosippinae and includes South American web-building spiders, which are exceptional within the family Lycosidae.
Aglaoctenus species are common throughout southeastern Brazil, occurring in both forest areas and savanna communities. The distribution of *A.lagotis* covers midwestern, southwestern and southern Brazil and extends to Argentina (Santos and Brescovit 2001; González et al. 2013). This species is a lycosid spider that builds a web in the form of a flat sheet, called a ‘capture sheet’, from which emerges a funnel-like tube that ends in a refuge (Riechert 1976; Stefani et al. 2011). In the cerrado, *A.lagotis* occurs in both forests and more closed savannas, and its reproductive period coincides with the beginning of the rainy season (September–October), during spring in the southern hemisphere (Stefani and Del-Claro 2012).

**Study areas**

This study was conducted at two sites within the municipality of Araguari, Minas Gerais, Central Brazil. The first site, representing an urban area, was the John Kennedy Woodland (JKW; 18°38′35″ S, 48°11′19″ W). This park in the city centre encompasses 11.2 ha of semi-deciduous mesophytic forest, with trees up to 25 m tall and a closed canopy (Figure 1), bordered by cleared areas undergoing vegetative recovery. This woodland is used as a leisure area, and trails and structures are found in its interior, indicating strong anthropogenic interference (Souza and Araújo 2005).

The second site, representing a peri-urban area, is under the permanent protection of the Pica-Pau Country Club (PCC; 18°36′38″ S, 48°11′17″ W). This 28.5-ha site is located 1 km from the periphery of the city and also encompasses a semi-deciduous mesophytic forest, with trees up to 18 m tall and a closed canopy (Figure 1). The two areas are approximately 10 km apart and have similar vegetation. According to Köppen’s classification, the regional climate is of the Aw type. The climate is megathermal, with rains between October and March and a dry period between April and September (see Stefani et al. 2012, for a full characterization of the study sites).

**Abundance and spatial distribution of *Aglaoctenus lagotis***

The abundance and distribution of individuals were surveyed quarterly at both sites (in October 2008 and January, April and July 2009). Ten quadrats (26 m long by 5 m wide) were used, totalling 130 m². The quadrats were located at least 50 m apart. Each *A.lagotis* web found within a quadrat was considered a sampling point, and its position (length and width) within the quadrat was recorded. Morisita’s index (*I*δ) was used to determine the distribution pattern. This index was developed by Morisita (1962) to be independent of the sample mean and the total number of individuals. Values close to one (= 1) indicate a random distribution, values greater than one (> 1) indicate an aggregated distribution, and values less than one (< 1) indicate a regular or uniform distribution. The formula for this index is given by

\[
I\delta = \frac{N\left(\sum_{i=1}^{N} X_i^2 - \sum_{i=1}^{N} X_i\right)}{\left(\sum_{i=1}^{N} X_i\right)^2 - \sum_{i=1}^{N} X_i^2}
\]
Where \( N \) = the total sample number and \( X_i \) = the number of *A. lagotis* webs in the \( i \)th sampling unit.

**Cephalothorax length and sheet length**

During the population surveys, the cephalothorax length of each spider (mm) was estimated using a caliper at a distance of 5 cm from the spider. The sheet area of the web (cm\(^2\)) was calculated as the sheet length (cm) \( \times \) the sheet width (cm). These measurements were taken from the funnel opening without contacting the web. The capture and manipulation of the spiders was avoided to reduce direct interference by the observer in the studied populations. When captured, these spiders rarely remain in the same webs or locations where they originally resided, even when carefully returned by the researcher (pers. obs.). In an unsuccessful capture attempt, the spider
escapes through the bottom of its web funnel and flees below the litterfall. Afterward, the spider may take hours to return to its web (Stefani and Del-Claro, pers. obs.). All of the measurements showed non-normal distributions. Therefore, the Mann–Whitney U test was used for comparisons between the areas. A simple linear regression was performed to estimate the relationship between the sheet area (horizontal capture web) and cephalothorax length of *A. lagotis* individuals. The values were represented as the mean ± standard deviation, followed by the sample n.

**Volume of A. lagotis horizontal capture webs and inquiline spiders**

An *A. lagotis* vertical capture web was selected for sampling when it was seen within a quadrat used in the population survey (Figure 2). The threads of the vertical capture web form a cone shape with an elliptical base. The largest diameter (*dₐ*, 10 cm above the sheet), smallest diameter (*dₖ*, 10 cm below the fixation substrate), and cone height (*h*) were measured (Figure 2). The cone volume was calculated using the following formula:

\[ V = \frac{1}{3} \pi \cdot \frac{d_a}{4} \cdot h \]

For each measured capture web, the inquiline spiders present in the web were observed for 10 min (all-occurrences sampling; Altmann 1974). The number of inquiline spiders associated with the capture threads was recorded, and the spiders were identified. Pearson’s correlation was used to analyse the relationship between the capture-web volume and the number of associated inquiline spiders. All of the samples were non-normally distributed; therefore, the Mann–Whitney U-test was used for the comparative analyses.

**Analysis of genetic similarity**

To determine the degree of genetic similarity between individuals from the two sampling areas, a 10-m by 5-m quadrat was randomly selected in January 2008, and the first 12 individuals sighted within the quadrat were collected. In January 2009, another 12 *A. lagotis* individuals were collected in JKW from the same quadrat used in the previous year. Each individual (collected in 2008 and 2009) was placed in an Eppendorf tube containing a 70% ethylene glycol solution. The genetic analysis employed random amplified polymorphic DNA fingerprinting, which is the method of choice for investigating ecological questions related to population structure in natural environments (see A’Hara et al. 1998). The reactions were performed in a thermocycler (PTC-100) under the following conditions: 40 cycles of 1 min at 92°C, 1 min at 36°C, and 1 min at 72°C, followed by a final extension of 10 min at 72°C. The amplified fragments were separated on a 2.5% agarose gel stained with ethidium bromide, visualized on a UV transilluminator, and photographed using Image Master VDS. The fingerprints were interpreted as binary data based on the presence (1) or absence (0) of each band. The data were analysed using UPGMA (unweighted pair group method using arithmetic means). Fifteen primers were tested, and primer
selection was based on the degree of polymorphism and the reproducibility of the band profile. The results were compared using the Jaccard similarity index, and a genetic-similarity cluster was established.

**Results**

The abundance of *A. lagotis* was greatest in October 2008 and decreased in January, April, and July 2009 in the two sampling areas (Table 1). The main supports for the web sheets of this species were located near the soil and on top of plant litter, trunks, and fallen branches. For all collections from the two sites, Morisita’s index was > 1, indicating an aggregated distribution (Table 1).
Table 1. Abundance and distribution of *Aglaoctenus lagotis* (Lycosidae) in two vegetation fragments (JKW: John Kennedy Woodland; PCC: Pica-Pau Country Club) in Araguari, Minas Gerais, Brazil. The notation \((I_\delta)\) indicates Morisita’s index.

|                   | First sampling (October 2008) | Second sampling (January 2009) | Third sampling (April 2009) | Fourth sampling (July 2009) |
|-------------------|-------------------------------|-------------------------------|----------------------------|-----------------------------|
|                   | JKW  | PCC  | JKW  | PCC  | JKW  | PCC  | JKW  | PCC  |
| \(n\)             | 376  | 263  | 225  | 192  | 139  | 127  | 105  | 96   |
| Mean ± SD         | 37.6 ± 1.3 | 26.3 ± 9.2 | 22.5 ± 7.3 | 19.2 ± 5.7 | 13.9 ± 3.5 | 12.7 ± 4.6 | 10.5 ± 5.2 | 9.6 ± 3.6 |
| \(I_\delta\)      | 2.34 | 2.63 | 1.94 | 1.97 | 2.44 | 1.99 | 2.28 | 1.3  |
The cephalothorax length of *A. lagotis* individuals varied across the months and study sites (Table 2) and was significantly larger in JKW than in PCC, except in July. The cephalothorax length was smallest in October 2008 and largest in July 2009.

Of the 331 individuals sampled in JKW, only 12 were adult females. Of the 183 sampled in PCC, only five were adult females. Additional webs (eight found within the quadrats at JKW and nine in PCC), which contained female *A. lagotis* individuals with egg sacs, were not sampled because they lacked a sheet area (a prerequisite for measurement). The webs of juveniles were mainly concentrated around old, abandoned adult webs (possibly those of their mothers). The mean sheet area was greatest in July (when the spiders were in the pre-adult stage) and did not differ significantly between the two locations during this month (Table 3). The smallest sheet area was observed in October (when the spiders were in the early instars of development) and differed significantly between the two locations. Significant differences in sheet area were also found in January and April (Table 3).

The cephalothorax length and sheet area were positively correlated in both sampling areas (JKW: $r^2 = 0.554, F = 880, p = 0.0001$; PCC: $r^2 = 0.64, F = 857.5, p = 0.0001$; Figure 3).

The number of vertical capture webs varied across the months and sampling areas, especially in October, when few adults were found. During that month, the majority of the population consisted of juveniles, whose webs did not display vertical threads (Table 4). A significant difference between the study sites was observed only in January. The mean number of inquiline spiders found in the vertical capture webs varied significantly only in July 2009 (Table 5). The number of inquiline spiders in the webs differed significantly between the two sites only in April 2009 (Table 5). Eight species of spiders belonging to three families were identified as inquilines in *A. lagotis* vertical webs. All eight species were found in JKW, while five were observed in PCC (Table 6). The genus *Argyrodes* was the most common inquiline spider (Table 6).

The volume of the horizontal capture web was significantly correlated with the number of inquiline spiders for both JKW ($r = 0.402, p = 0.0001$) and PCC ($r = 0.663, p = 0.0001$) (Figure 4). All of the inquiline species belonging to the families Uloboridae and Pholcidae possessed their own webs but used the webs of *A. lagotis* for support. The inquiline species belonging to the family Theridiidae did not weave their own webs on the host web. The inquiline spiders did not steal prey captured by the host. Rather, they captured prey that had fallen into the horizontal capture web but had not yet been noticed by the host.

Of the 36 *A. lagotis* individuals captured for the genetic analysis, DNA was successfully extracted and amplified from five collected at JKW in 2008, six collected at PCC in 2008, and all 12 collected at JKW in 2009, totalling 23 sampled individuals (Figure 4). The random amplified polymorphic DNA-based Jaccard similarity index for certain individuals collected at the same site in the same year was equal to 0, indicating that these individuals were genetically equivalent (P84 and P83, B83 and B82, B93 and B92, B94 and B95, B99 and B98, B96 and B97; Figure 5). Two individuals collected at JKW in different years also had a Jaccard index equal to 0 (B86, B91). Other pairs of individuals from the same population had Jaccard indices of approximately 0.1 (P81 and P82, B82 and B85). The most notable pair of individuals was B81 and P85, which were from different populations but had similar genetic fingerprints. The Jaccard index indicated that individuals B911, B912, and B910, which were collected in 2009 at JKW, were most closely related to individuals
Table 2. Comparative cephalothorax size (mm) of *Aglaoctenus lagotis* individuals in two vegetation fragments (JKW: John Kennedy Woodland; PCC: Pica-Pau Country Club) in Araguari, Minas Gerais, Brazil.

|                     | First sampling (October 2008) | Second sampling (January 2009) | Third sampling (April 2009) | Fourth sampling (July 2009) |
|---------------------|--------------------------------|--------------------------------|-----------------------------|-----------------------------|
|                     | JKW | PCC | JKW | PCC | JKW | PCC | JKW | PCC | JKW | PCC |
| **N**               | 331 | 183 | 179 | 130 | 127 | 108 | 72  | 70  |
| **Mean ± SD**       | 1.8 ± 1.2  | 1.76 ± 1.2  | 3.7 ± 0.6  | 3.5 ± 0.4  | 5.1 ± 1.17 | 4.6 ± 0.8  | 8.56 ± 2.36 | 7.35 ± 0.9  |
| **U**               | 3473.1 | 4834 | 8961.5 | 2459.5 | 0.003 | 0.001 | 0.0001 | 0.053 |
| **p**               | 0.003 | 0.001 | 0.0001 | 0.053 |

Note: The *p*-values were obtained using a Mann–Whitney *U* test.
Table 3. Sheet areas (mean ± SD, cm²) of *Aglaoctenus lagotis* webs in two vegetation fragments (JKW: John Kennedy Woodland; PCC: Pica-Pau Country Club) in Araguari, Minas Gerais, Brazil.

|                      | First sampling (October 2008) | Second sampling (January 2009) | Third sampling (April 2009) | Fourth sampling (July 2009) |
|----------------------|------------------------------|--------------------------------|----------------------------|----------------------------|
|                      | JKW                         | PCC                           | JKW                        | PCC                        |
|                      | 331                         | 183                           | 179                        | 130                        |
| Mean ± SD            | 227 ± 143.5                 | 194 ± 186                     | 1074 ± 644                 | 2005 ± 1538                |
|                      | 1074 ± 644                  | 2005 ± 1538                   |                            |                            |
|                      | 127                         | 108                           | 1887 ± 1159                | 2011 ± 1385                |
|                      | 2424 ± 1157                 | 2150 ± 1147                   |                            |                            |
| N                    | 4020                        | 5489                          | 5568.5                     | 2230                       |
| Mean ± SD            | 0.0001                      | 0.001                         | 0.013                      | 0.108                      |

Note: The *p*-values were obtained from a Mann–Whitney *U* test.
P81, P82, P83, and P85, which were collected in 2008 at PCC (Figure 6). These results suggest close genetic similarity between the populations at the two study sites.

Discussion

Our data indicate that the smaller, more human-impacted fragment (the urban site, JKW) supports a larger population of *A. lagotis*, with larger prosoma sizes and web areas. We predicted that these measurements would be greater in the larger and better-preserved fragment, but the results show the opposite. Hence, *A. lagotis* can tolerate a more altered environment. The presence of a larger population in a smaller area within the urban centre may reflect a limited dispersal ability, reduced predator abundance, and/or low interspecific competition (see Schoener and Toft 1983; Gunnarsson 1998; Miyashita et al. 1998; Herberstein and Heiling 2001; Hirai and Matsui 2001).

The life history of *A. lagotis* is marked by seasonal events (Moreira and Del-Claro 2011), and some components of its life cycle occur within a well-defined period. For example, the number of individuals was largest and the cephalothorax length was smallest during October in both areas and in all quadrats. The individuals present in October are juveniles, which disperse at the end of the maternal-care phase and form their first webs near their mother’s (Stefani et al. 2011). Additionally, births begin in October, coinciding with the beginning of the rainy period. Hence, the offspring may obtain more prey, which also increase in abundance during the rainy season. Prey availability is positively correlated with survival and reproductive success in spiders (Uetz 1992) and other arachnids (Del-Claro and Tizo-Pedroso 2009). The body size of spiders is negatively correlated with water loss, indicating that offspring are more susceptible than larger individuals to dry periods (Anderson 1974). Lubin (1978) has observed that orb-weaving spiders occur in higher densities during wet periods, when

![Figure 3. Simple linear regressions between the sheet area of the web and the cephalothorax length of *Aglaoctenus lagotis* individuals in two vegetation fragments (JKW: John Kennedy Woodland; PCC: Pica-Pau Country Club) in Araguari, Minas Gerais, Brazil. The correlation is positive for both sites (p < 0.0001).](image)
Table 4. Comparative volume of capture threads in the webs of *Aglaoctenus lagotis* in two vegetation fragments (JKW: John Kennedy Woodland; PCC: Pica-Pau Country Club) in Araguari, Minas Gerais, Brazil.

|                   | First sampling (October 2008) | Second sampling (January 2009) | Third sampling (April 2009) | Fourth sampling (July 2009) |
|-------------------|-------------------------------|-------------------------------|----------------------------|-----------------------------|
|                   | JKW      | PCC      | JKW        | PCC        | JKW      | PCC        | JKW        | PCC        |
| n                 | 12       | 5        | 225        | 192        | 139      | 127        | 105        | 96         |
| Mean ± SD         | 548 ± 257 | 374 ± 66 | 93.7 ± 49.7 | 204.8 ± 140 | 252.5 ± 128 | 592 ± 477 | 486 ± 320 | 592 ± 276 |
| U                 | 37       | 249.5    | 556        | 680        |
| p                 | 0.461    | 0.001    | 0.085      | 0.09       |

Notes: Volumes are expressed in cm$^3$. The $p$-values were obtained from a Mann–Whitney $U$ test.
Table 5. Comparative abundance of inquiline spiders in the vertical capture webs of *Aglaoctenus lagotis* in two vegetation fragments (JKW: John Kennedy Woodland; PCC: Pica-Pau Country Club) in Araguari, Minas Gerais, Brazil. The *p*-values were obtained using a Mann-Whitney U test.

| First sampling (October 2008) | Second sampling (January 2009) | Third sampling (April 2009) | Fourth sampling (July 2009) |
|------------------------------|-------------------------------|---------------------------|---------------------------|
|                              | JKW                           | PCC                        | JKW                        | PCC                        | JKW                        | PCC                        | JKW                        | PCC                        |
| n                            | 12                            | 5                          | 225                        | 192                        | 139                        | 127                        | 105                        | 96                         |
| Mean ± SD                    | 2.8 ± 1.53                    | 3.4 ± 1.6                  | 2.6 ± 1.53                 | 3.1 ± 1.6                  | 2.65 ± 1.5                 | 3.47 ± 1.4                 | 4.23 ± 2.22                | 4.36 ± 2.4                 |
| U                            | 33                            | 631.2                      | 441.5                      | 904.5                      |
| *p*                          | 0.74                          | 0.33                       | 0.002                      | 0.68                       |
more prey is available, while spiders that build sheet-type webs and other three-dimensional structures are more abundant during dry periods, when prey is more scarce. According to Lubin (1978), orb-weaving spiders are more susceptible to desiccation and require greater amounts of energy to rebuild their webs daily, while more permanent webs enable spiders to persist during periods when food is scarce.
Our results show that the abundance of *A. lagotis* declines from October onward, indicating high mortality during development in the natural environment and corroborating the laboratory-based observations of Moreira and Del-Claro (2011). Various factors that do not exist in artificial environments (such as the laboratory) may influence spider mortality in natural environments, including temperature variations, disease, food scarcity, the availability of web-building sites, competitive interactions, predation, and parasitism.

The spider populations in the two forest fragments showed an aggregated distribution. Importantly, the distribution of an *A. lagotis* population over time is associated with its habitat occupancy and use. As individual spiders grow in size, their webs increase in area and height, suggesting that progressively larger and taller webs are necessary to capture sufficient prey to maintain individual biomass. Hence, habitat occupancy during the development of *A. lagotis* may vary according to the selective pressures of the environment. Habitat selection in ‘sit-and-wait’ predators, such as some web-weaving spiders, may determine individual performance because these animals move to new sites only once or a few times during their lives (Riechert 1976; Ward and Lubin 1993). Site selection is therefore a vital decision, influencing the distribution of the population within the habitat and profoundly affecting individual growth, survival and reproductive success (Riechert and Tracy 1975). An aggregated distribution may also improve the probability of prey capture because larger prey organisms may collide with the capture threads of two or more webs and fall into a third. Finally, an aggregated distribution may represent a defence against predators. Many webs show interconnected threads that can transmit information between individuals in separate webs (Uetz and Hieber 1994).

The cephalothorax length and sheet area of *A. lagotis* were always larger in JKW compared with PCC. This result suggests that the spiders at JKW encounter greater
resource availability, with a higher probability of capturing prey, and consequently have larger body sizes. According to Dearn (1977), the life strategies of populations represent different ways of allocating energy to maximize success in a particular environment. Studies have indicated that spider populations from different locations may vary in some life-history parameters due to pressure from environmental factors that interact differently in each location (Oxford 1993). As observed in *A. lagotis*, body size is positively correlated with sheet area. For many spider species, prey abundance in the environment is positively correlated with growth rates and other parameters (Viera et al. 2007). Roush and Radabaugh (1993) have demonstrated experimentally that *Pholcus phalangioides* (Pholcidae) spiders build denser webs (by adding more threads and increasing the dimensions of the web) in situations with

Figure 6. Cluster analysis of genetic similarity between *Aglaoctenus lagotis* individuals from two vegetation fragments in Araguari, Minas Gerais, Brazil. For each individual, the uppercase letter indicates its location (B: John Kennedy Woodland; P: Pica-Pau Country Club), the first numeral indicates the collection year (8: 2008; 9: 2009), and the subsequent digits indicate the collection number of the spider within the sampling quadrat.
greater prey availability than in situations where food is scarce. Our observations confirm that \textit{A.\ lagotis} constructs the supports for its web sheet on the lower strata of its habitat. The webs are found predominantly on the herbaceous stratum, suggesting that these spiders require appropriate supports for web construction and substrates for refuge construction to be available in this stratum, corroborating the results of Sordi (1996).

Despite the low variation between the study sites in the number of inquiline spiders associated with the vertical capture web (except in April), these variables were positively correlated: the larger the volume of the vertical web, the bigger the number of inquiline spiders. According to our observations, inquiline spiders in \textit{A. lagotis} vertical capture webs do not steal captured prey; rather, they reside in the webs and exploit items that are not captured by the host. According to Vollrath (1987), webs are capture structures that are much longer than the bodies of their builders; hence, they generate opportunities for inquiline species to approach items that are not being guarded and/or manipulated by the host. Many inquiline spiders take advantage of other benefits, such as protection from natural enemies, that the host webs provide (Gonzaga 2007). The most common genus of inquiline spiders in the webs was \textit{Argyrodes}, which belongs to the subfamily Argyrodinae. This group generally exploits other spiders to obtain their food by stealing stored prey or web threads or even attacking the host directly (Agnarsson 2004). The interactions between Argyrodinae species and their hosts are not limited to stealing prey. These inquiline spiders may also attack the host while it is involved in ecdysis or may capture small insects that the host has not detected (Whitehouse 1986). Therefore, more behavioural and biological data are needed to assess the relationships of the identified species of parasitic spiders found in the vertical capture webs of \textit{A.\ lagotis}.

Our results also show that there is a strong parental-similarity component among \textit{A.\ lagotis} individuals in the study region. The genetic data suggest that this species has low genetic variability or that the areas studied, consistent with their proximity, have separated only recently. This separation is due to rapid urbanization.

Experimental studies have demonstrated the usefulness of genetic analyses in fragmented habitats. Genetic data can illustrate spatial population differentiation (Ramirez and Haakonsen 1999; Kronforst and Fleming 2001) or demonstrate that habitat fragmentation has reduced gene flow (Knutsen et al. 2000). Members of Lycosidae generally have one or two generations per year (Schaeffer 1987); \textit{A.\ lagotis} has only one (Moreira and Del-Claro 2011). Hence, several generations have already passed between the studied fragments since their isolation. Many of the spiders collected in the same locations and years showed high genetic similarity. Because the calculated dispersion index indicated an aggregated distribution in January, these initial groupings most likely comprised siblings that had remained near each other. The JKW population showed high intra-population similarity, except for certain individuals who were more similar to individuals from PCC. Hence, the duration of isolation of these populations was insufficient to alter their genetic similarity.

Population studies in spiders generally associate the genetic structure with the dispersal rate of each species (Colgan et al. 2002; Vandergast et al. 2004; Johannessen et al. 2005; Bidegaray-Batista et al. 2007). Analysing three populations of \textit{Metepeira ventura}, Ramirez and Fandino (1996) have attributed the large variability and weak genetic structure to the dispersal capacity of these araneids, suggesting that individuals of this species (at least the juveniles) can disperse by ballooning. Ramirez and
Haakonsen (1999) have inferred the same phenomenon for *Argiope trifasciata*, demonstrating that this pattern is relatively common in this family. The offspring of *A. lagotis* most likely disperse through the litterfall after their birth, resulting in the aggregation of their webs around the maternal webs. This species shows no evidence of ballooning. Ballooning is rare in Lycosidae spiders due to their larger body size compared with members of other families, such as Araneidae and Theridiidae, which use this method as their primary dispersal mode. Hence, lycosid spiders typically undertake short-distance trips when migrating to other fragments (Richter 1970).

Tropical savannas and semi-deciduous forests once occupied 25% of the Brazilian territory, but less than 8% of this area is preserved today. Although spiders and invertebrates are highly abundant and diverse in these ecosystems, which dominate midwestern Brazil, little knowledge exists concerning the effects of habitat fragmentation on natural populations of these organisms (Del-Claro et al. 2013). Studies such as this one, which focuses on an important group of predators that control the natural populations of many invertebrates and serve as food for higher trophic levels, must be replicated for various groups to better understand the effects of habitat fragmentation on invertebrate populations in the cerrado region.

**Acknowledgements**

We thank the president, directors and employees of the Clube Pica-Pau (Woodpecker Club) for authorizing this research in their permanent preservation area. We also thank the municipal government of Araguari, the environmental department, and the employees of the John Kennedy Woodland Park (Parque Bosque John Kennedy) for their assistance in this study.

**Funding**

KDC thanks the National Counsel of Technological and Scientific Development (Conselho Nacional de Desenvolvimento Científico e Tecnológico; CNPq) [grant numbers 473055/2012; 72046/2011; 301248/2009]. VS thanks the Coordination for the Improvement of Higher-Education Personnel – National Post-Doctoral Plan (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Plano Nacional de Pós-Doutorado; CAPES-PNPD) [grant number 2556/2011].

**References**

Agnarsson I. 2004. Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneoidea, Theridiidae). Zool J Linn Soc. 141:447–626.

A’Hara S, Harling R, McKinlay R, Topping C. 1998. RAPD profiling of spider (Araneae) DNA. J Arachnol. 2:397–400.

Altmann J. 1974. Observational study of behavior: sampling methods. Behaviour. 49:227–266.

Anderson JF. 1974. Responses to starvation in the spiders *Lycosa lenta* Hentz and *Filistata hibernalis* (Hentz). Ecology. 55:576–583.

Baz A, Garcia-Boyero A. 1995. The effects of forest fragmentation on butterfly communities in Central Spain. J Biogeogr. 22:129–140.

Bidegaray-Batista L, Macías-Hernández N, Oromí P, Arnedo MA. 2007. Living on the edge: demographic and phylogeographical patterns in the woodlouse-hunter spider *Dysdera lancerotensis* Simon, 1907 on the eastern volcanic ridge of the Canary Islands. Mol Ecol. 16:3198–3214.
Bierregaard Jr RO, Lovejoy TE, Kapos V, Santos AA, Hutchings RW. 1992. The biological dynamics of tropical rainforest fragments. Bioscience. 42:859–866.

Bolger DT, Suarez AV, Crooks KR, Morrison SA, Case TJ. 2000. Arthropods in urban habitat fragments in Southern California: area, age, and edge effects. Ecol Appl. 10:1230–1248.

Bonte D, Lens L, Maelfait J, Hoffmann M, Kuijken E. 2003. Patch quality and connectivity influence spatial dynamics in a dune wolfspider. Oecologia. 135:227–233.

Brown Jr KS, Hutchings R. 1997. Disturbance, fragmentation, and the dynamics of diversity in Amazonian forest butterflies. In: Laurance WF, Bierregaard RO, editors. Tropical forest remnants: ecology, management, and conservation of fragmented communities. Chicago (IL): University of Chicago Press; p. 91–110.

Burgess JW, Uetz GW. 1982. Social spacing strategies in spiders. In: Witt PN, Rovner JS, editors. Spider communication: mechanisms and ecological significance. Princeton (NJ): Princeton University Press; p. 317–351.

Chang J, Song D, Zhou K. 2007. Incongruous nuclear and mitochondrial phylogeographic patterns in two sympatric lineages of the wolf spider Pardosa astrigera (Araneae: Lycosidae) from China. Mol Phylogenet Evol. 42:104–121.

Colgan DJ, Brown S, Major RE, Christie F, Gray MR, Cassis G. 2002. Population genetics of wolf spiders of fragmented habitat in the wheat belt of New South Wales. Mol Ecol. 11:2295–2305.

Dearn JM. 1977. Variable life history characteristics along an altitudinal gradient in three species of Australian grasshopper. Oecologia. 28:67–85.

Del-Claro K, Stefani V, Lange D, Vilela AA, Nahas L, Velasques M, Torezan-Silingardi HM. 2013. The importance of natural history studies for a better comprehension of animal-plant networks. Biosci J. 29:439–448.

Del-Claro K, Tizo-Pedroso E. 2009. Ecological and evolutionary pathways of social behavior in Pseudoscorpions (Arachnida: Pseudoscorpiones). Acta Ethol. 12:13–22.

Didham RK, Ghazoul J, Stork NE, Davis A. 1996. Insects in fragmented forests: a functional approach. Trends Ecol Evol. 11:255–260.

Didham RK, Lawton JH, Hammond PM, Eggleton P. 1998. Trophic structure, stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. Philos Trans R Soc B Biol Sci. 353:437–451.

Figueira JEC, Vasconcellos-Neto J. 1993. Reproductive success of Latrodectus (Theridiidae) on Paepalanthus bromelioides (Eriocaulaceae): rosette size, microclimate and prey capture. Ecotropicos. 5:1–10.

Foelix RF. 2011. Biology of spiders. 3rd ed. Oxford (NY): Oxford University Press.

Gibb H, Hochuli DF. 2002. Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biol Conserv. 106:91–100.

Gonzaga M. 2007. Socialidade e cuidado. In: Gonzaga MO, Santos AJ, Japyassú HF, editors. Ecologia e comportamento de aranhas. Rio de Janeiro: Editora Intericiência; p. 185–208.

González M, Peretti AV, Viera C, Costa FG. 2013. Differences in sexual behavior of two distant populations of the funnel-web wolf spider Aglaocinus lagotis. J Ethol. 31:175–184.

Gunnarsson B. 1998. Bird predation as a sex- and size-selective agent of the arboreal spider Pityohyphantes phrygianus. Funct Ecol. 12:453–458.

Hagan JM, Haegen WMV, McKinley P. 1996. The early development of forest fragmentation effects on birds. Conserv Biol. 10:188–202.

Harrison S, Bruna E. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography. 22:225–232.

Hastings A, Harrison S. 1994. Metapopulation dynamics and genetics. Annu Rev Ecol Syst. 25:167–188.

Herberstein ME, Heiling AM. 2001. Positioning at the hub: does it matter on which side of the web orb-web spiders sit? J Zool. 255:157–163.
Hirai T, Matsui M. 2001. Attempts to estimate the original size of partly digested prey recovered from stomachs of Japanese anurans. Herpetol Rev. 32:14–16.

Johannesen J, Lubin Y, Lauß T, Seitz A. 2005. Dispersal history of a spider (Stegodyphus lineatus) across contiguous deserts: vicariance and range expansion. Biol J Linnean Soc. 84:739–754.

Klink CA, Machado RB. 2005. Conservation of the Brazilian Cerrado. Conserv Biol. 19:707–713.

Knutsen H, Rukke BA, Jorde PE, Ims RA. 2000. Genetic differentiation among populations of the beetle Bolitophagus reticulatus (Coleoptera: Tenebrionidae) in a fragmented and a continuous landscape. Heredity. 84:667–676.

Krebs CJ. 2001. Ecology, the experimental analysis of distribution and abundance. San Francisco (CA): Benjamin Cummings.

Kronforst MR, Fleming TH. 2001. Lack of genetic differentiation among widely spaced subpopulations of a butterfly with home range behaviour. Heredity. 86:243–250.

Lovejoy TE, Bierregaard RO, Rankin JM, Schubart HOR. 1983. Ecological dynamics of forest fragments. In: Sutton SL, Whitmore TC, Chadwick AC, editors. Tropical rainforest: ecology and management. Oxford (NY): Blackwell Scientific Publishing; p. 377–385.

Lovejoy TE, Bierregaard RO, Rylands AB, Malcom JR, Quintela CE, Harper LH, Brown KS, Powell AH, Powell GVN, Schubart HOR, et al. 1986. Edge and other effects of isolation on Amazon forest fragments. In: Soulé ME, editor. Conservation biology: the science of scarcity and diversity. Sunderland: Sinauer Associates; p. 257–285.

Lubin YD. 1978. Seasonal abundance and diversity of web-building spiders in relation to habitat structure on Barro Colorado Island, Panama. J Arachnol. 6:31–51.

Macaranas JM, Colgan DJ, Major RE, Cassis G, Gray MR. 2001. Species discrimination and population differentiation in ants using microsatellites. Biochem Systemat Ecol. 29:125–136.

Mech SG, Hallett JG. 2001. Evaluating the effectiveness of corridors: a genetic approach. Conserv Biol. 15:467–474.

Mestre LAM, Gasnier TR. 2008. Populações de aranhas errantes do gênero Ctenus em fragmentos florestais na Amazônia Central [Populations of Ctenus wandering spiders in Amazonian forest fragments]. Acta Amazonica. 38:159–164.

Miranda M, Andrade VB, Marques GDV, Stefani V. 2006. Mirmecofauna (Hymenoptera: Formicidae) em fragmento urbano de mata mesófila semidecídua [Ant fauna (Hymenoptera: Formicidae) in an urban fragment of semi-deciduous mesophytic forest]. Rev Bras Zool. 8:49–54.

Miyashita T, Shinkai A, Chida T. 1998. The effects of forest fragmentation on web spider communities in urban areas. Biol Conserv. 86:357–364.

Moreira VSS, Del-Claro K. 2011. Oviposition and post-embryonic development of Aglaoctenus lagotis (Araneae: Lycosidae). Zoologia. 28:565–570.

Morisita M. 1962. I σ-Index, a measure of dispersion of individuals. Res Popul Ecol. 4:1–7.

Oliveira PS, Marquis RJ. 2002. The Cerrados of Brazil. Ecology and natural history of a neotropical savanna. New York: Columbia University Press.

Oxford GS. 1993. Components of variation in population size in the spider Enoplognatha ovata (Clerck) sensu stricto (Araneae: Theridiidae). Bull Brit Arachnol Soc. 9:193–202.

Ramirez MG, Fandino LB. 1996. Genetic variability and gene flow in Metepeira ventura (Araneae, Araneidae). J Arach. 24:1–8.

Ramirez MG, Haakonsen KE. 1999. Gene flow among habitat patches on a fragmented landscape in the spider Argiope trifasciata (Araneae: Araneidae). Heredity. 83:580–585.

Richter CJJ. 1970. Aerial dispersal in relation to habitat in eight wolf spider species (Pardosa, Araneae, Lycosidae). Oecologia. 5:200–214.

Riechert SE. 1976. Web-site selection in the desert spider Agelegenopsis aperta. Oikos. 27:311–315.
Riechert SE, Tracy CR. 1975. Thermal balance and prey availability: bases for a model relating web-site characteristics to spider reproductive success. Ecology. 56:265–284.

Roush RS, Radabaugh DC. 1993. Web density is related to prey abundance in cellar spiders, Pholcus phalangioides (Fuesslin) (Araneae: Pholcidae). Bull Brit Arachnol Soc. 9:142–144.

Santos AJ, Brescovit AD. 2001. A revision of the South American spider genus Aglaoctenus Tullgren, 1905 (Araneae, Lycosidae, Sosippinae). Andrias. 15:75–90.

Schaeffer M. 1987. Life cycles and diapauses. In: Nentwig W, editor. Ecophysiology of spiders. Chapter E, I. Berlin: Springer-Verlag; p. 331–347.

Schoener TW, Toft CA. 1983. Dispersion of a small-island population of the spider Metepeira datona (Araneae: Araneidae) in relation to web-site availability. Behav Ecol Sociobiol. 12:121–128.

Settele J, Margules C, Poschlod P, Henle K. 1996. Species survival in fragmented landscapes. Amsterdam: Kluwer Academic Publishers.

Sordi SJ. 1996. Ecologia de Populações da aranha Porrinosa lagotis (Lycosidae) nas Reservas Mata de Santa Genebra, Campinas (SP) e Serra do Japi, Jundai (SP) [Population ecology of the spider Porrinosa lagotis (Lycosidae) in forest reserves in Santa Genebra, Campinas, SP and Serra do Japi, Jundai, SP]. [Doctoral thesis]. Unicamp, Campinas.

Souza JP, Araújo GM. 2005. Estrutura arbustivo/arbórea do subosque de clareiras e áreas sob dossel fechado em floresta estacional semideciduas urbana em Araguari – MG [Structure of understory woody species in gaps and closed-canopy sites of an urban seasonal semi-deciduous forest in Araguari, MG]. Biosci J. 21:93–102.

Souza OFF, Brown VK. 1994. Effects of habitat fragmentation on Amazonian termite communities. J Trop Ecol. 10:197–206.

Stefani V, Del-Claro K. 2012. Oviposition and post-embryonic development of Aglaoctenus lagotis (Araneae: Lycosidae). Zoologia. 28:565-570.

Stefani V, Del-Claro K, Silva LA, Guimarães B, Tizo-Pedroso E. 2011. Mating behaviour and maternal care in the tropical savanna funnel-web spider Aglaoctenus lagotis Holmberg (Araneae: Lycosidae). J Nat Hist. 45:1119–1129.

Uetz GW. 1992. Foraging strategies of spiders. Trends Ecol Evol. 7:155–159.

Uetz GW, Hieber CS. 1994. Group size and predation risk in colonial web-building spiders: analysis of attack abatement mechanisms. Behav Ecol. 5:326–333.

Vandergast AG, Gillespie RG, Roderick GK. 2004. Influence of volcanic activity on the population genetic structure of Hawaiian Tetragnatha spiders: fragmentation, rapid population growth and the potential for accelerated evolution. Mol Ecol. 13:1729–1743.

Venticinque EM, Fowler HG. 2001. Local extinction risks and asynchronies: the evidence for a metapopulation dynamics of a social spider, Anelosimus eximius (Araneae, Theridiidae). In: Bierregaard Jr RO, Gascon C, Lovejoy TE, Mesquita R, editors. Lessons from Amazonia: the ecology and conservation of a fragmented forest. New Haven: Yale University Press; p. 187–198.

Viera C, Japyassú HF, Santos AJ, Gonzaga MO. 2007. Teias e forrageamento [Webs and foraging]. In: Gonzaga MO, Santos AJ, Japyassú HF, editors. Ecologia e comportamento de aranhas [Ecology and behavior of spiders]. Rio de Janeiro: Editora Interciência; p. 45–65.

Vollrath F. 1987. Kleptobiosis in spiders. In: Nentwig W, editor. Ecophysiology of spiders. Chapter C, V. Berlin: Springer-Verlag; p. 264–273.

Ward D, Lubin Y. 1993. Habitat selection and the life history of a desert spider, Stegodyphus lineatus (Eresidae). J Anim Ecol. 62:353–363.

Whitehouse MEA. 1986. The foraging behaviours of Argyrodes antipodiana (Theridiidae), a kleptoparasitic spider from New Zealand. NZ J Zool. 13:151–168.

Wise DH. 1993. Spiders in ecological webs. Cambridge: Cambridge University Press.