
EFFECT OF BODY SIZE AND MATERNAL CARE ON CLUTCH SIZE AND EGG SIZE IN THERIDIIDS

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ABSTRACT

Species-specific life history traits result from the interaction among different factors. In spiders the clutch size and the size of eggs are expected to be influenced by the female body size, but also by other factors such as accessibility to food resources as well as energy and time invested in maternal care. In eight theridiids the female body size of spiders and the maternal care predict the clutch size. The volume of eggs differs among all species and in general those species with little investment in maternal care and larger body size have larger eggs.

Keywords: theridiids, maternal care, clutch size, egg size.

RESUMEN

Efecto del tamaño corporal y el cuidado parental sobre el tamaño de la camada y de los huevos en teridioides. Los rasgos especie-específicos de historia de vida resultan de la interacción entre diferentes factores. En arañas el tamaño de camada y el tamaño de los huevos se espera que estén influenciados por el tamaño corporal de la madre, pero también por otros factores como la disponibilidad de recursos alimenticios, así como la energía y tiempo de cuidado maternal. En ocho teridioides el tamaño corporal de las arañas y el cuidado maternal predicen el tamaño de camada. El volumen de huevos difiere entre las especies consideradas y en general aquellas especies con poca inversión en cuidado maternal y mayor tamaño corporal muestran huevos más grandes.

Palabras clave: teridioides, cuidado maternal, tamaño de camada, tamaño de huevo.

INTRODUCTION

The reproductive success of spiders is strongly influenced by the number of egg batches, clutch size, and egg size that they produce (Morse, 2007). The number of batches a female spider produces along its lifetime varies considerably among species and is likely regulated by a combination of several factors, such as availability of food resource, parasitism, predation, and access and capability to store male gametes (Vollrath, 1987; Godfray *et al.*, 1991; Morse, 2007). For instance in Theridiidae this number varies from one in *Theridion evexum* (Barrantes & Weng, 2007) to up to twenty two in *Latrodectus geometricus* (Bouillon & Lekie, 1961).

The other two factors, clutch size and eggs size, are strongly correlated with the body size of the female spider. The clutch size scales isometrically with female body size, but size of eggs have a negative allometry relative to the female body size (Marshall & Gittleman, 1994); so that small spiders tend to produce smaller clutches but larger eggs, proportional to their body size. There are, however, other factors that could also affect the clutch size in spiders. The amount of food resource a spider could access (e.g., number and size of prey) influences the clutch size and eggs size (Morse, 2007; Fritz & Morse, 1985; Briceño, 1987; Johnson *et al.*, 2014). Half-starved spiders produce smaller clutches, but its effect on eggs size varies across species. In some species there is no effect of food abundance of egg size (Fritz & Morse, 1985; Briceño, 1987), but at least in *Latrodectus hesperus*, well fed females produce larger eggs than those poor fed females (Johnson *et al.*, 2014). The investment in maternal care and life span could also affect the number and size of clutches, as well as the eggs size. Though little is known of the effect of maternal care investment on clutch size, it is expected that the time and energy invested by some spiders (e.g., sub-social spiders) preclude them to produce more clutches during their lifetime. The contrary would happen to solitary spiders, whose reproductive investment is relatively low, or to social species, in which other members of the colony collaborate with the care of the offspring (Christenson, 1984).

Here I explore the effect of maternal care and body size of the female on the clutch size and egg size in eight theridioid species (seven Theridiidae and one Nesticidae). Maternal care varies widely across species in the Theridiidae family, and this behavior presumably correlates with the level of sociality of the species (Viera *et al.*, 2007). A few theridiids are considered solitary (e.g., *Latrodectus* spp., *Steatoda* spp.), other few are social, but the vast majority are sub-social species (Agnarsson, 2004). The maternal care in solitary species is restricted to guard the egg sac in the retreat that also serves for female's protection, but soon after the spiderlings emerge, they are able to build their own webs and capture prey (Eberhard *et al.*, 2008). In sub-social species, maternal care ranges from that in which at least some spiderlings remain for one or two stages in the female web, and she occasionally shares some prey with her offspring, to that in which the female spider actively collects and maintains prey for her offspring for several stages (Barrantes & Weng, 2007; 2009). If maternal care had an effect on clutch size and/or egg size, I expect that those species with higher levels of maternal care (and possibly sub-sociality) would had larger clutches, particularly for iteroparous species, and smaller egg size relative to their female body size, than solitary species. The precosial behavior of spiderlings of solitary species is likely related with a greater development at emergence which in turn is associated with larger eggs (more nutrients for development).

MATERIAL AND METHODS

I collected the first egg sac (first two for *Latrodectus geometricus* and *Achaearanea tepidariorum*) and the adult females of seven Theridiidae species and one Nesticidae in the Costa Rican Central Valley. Females of all species (except *Helvibis longicauda*) were collected as juveniles or pre-adults and maintained in the lab, and then paired when they reached adulthood; lab conditions are described in Barrantes & Weng, 2007; 2009; Eberhard *et al.*,

2008. To reduce the effect of different feeding conditions, I fed all female spiders with a blowfly –Calliphoridae– (2/3 to 3/4 the spider size) every other day.

I dissected the egg sacs and counted the total number of eggs. I took pictures of each egg from a sample or sometimes from the entire clutch under the dissecting microscope and then measured the longest and shortest diameters of each egg, using Image J 1.49. I then calculated the volume of each egg (using the equation for a spheroid) and the mass using the equation described by Anderson (1990): $EM = aED^b$; EM- egg mass; ED- egg diameter; a- a proportionality constant; b- the exponent of the function. I also measured the cephalothorax width as a proxy of the female body size. For *Helvibis longicauda* I measured the eggs and spider size in the Parque Estadual Intervales, Atlantic Forest, in south-eastern São Paulo State, Brazil.

I ranked species into five categories based on investment of maternal care of each species (Table 1); species may change of rank with more information. I also included semelparous and iteroparous species into three categories based on the number of batches each species is known to produce (G. Barrantes, unpubl. data): A- one or two batches, B- between 3 and 8 batches, and C- > 8 batches. I obtained information on maternal care from adult females I maintained in lab conditions and published work (Table 1); part of this information is also included in Barrantes & Eberhard, 2007; Barrantes & Weng, 2007; 2009. I then proceeded to estimate the effect of the female body size, degree of maternal care, and batch category on two response variables: clutch size and egg size (volume and mass), using General Linear Models (GLM). I selected the “best model” based on Akaike Information Criterion (AIC). Using AIC is particularly important when models run on small samples, as is the case in this study. I used the R statistical language, version 3.0.1 (R Development Core Team, 2013) for all statistical analyses. I \log_{10} transformed variables to normalize the residuals.

RESULTS

The size of spiders correlated directly with their clutch size (Fig. 1a-b), but the model that best explained the clutch size of the eight species also included the effect of maternal care (Table 2). The model with both factors (female body size and maternal care) explained 13% more of the variance of the clutch size than the model that included only the female body size (both factors: $r^2 = 0.75$, spider size: $r^2 = 0.62$). The magnitude of r^2 was taken in this case as an approximation of the explained variance (Zuur *et al.*, 2009).

The volume of eggs varied widely across species (Table 3), and increased, but not significantly, with females' size ($b = 3.93$, $p = 0.1458$, $r^2 = 0.20$; Fig. 1c). *Achaearanea tessellata* had tiny eggs and the residuals corresponding to this species were far beyond the normality limit. Running the analysis without *A. tessellata* highly improved the adjustment of the model ($b = 2.18$, $p = 0.0520$, $r^2 = 0.47$; Fig. 1d). For those species for which I measured the volume of eggs of two individuals, they also differed significantly (Table 3). *Latrodectus geometricus* had the largest eggs, followed by *Gaucelmus calidus*, while *A. tessellata* and *A. studiosus* had the smallest eggs (Fig. 1); the other species had an intermediate size of eggs.

Table 1. Description of the maternal care showed by the species included in this study. I refer to first instar spiderlings as the first instar outside the egg sac.

| Maternal care category/ species | Description/species | References |
|---------------------------------|---|--|
| 1- Lowest cost | Adult females guard the egg sac until spiderlings emerge, but no further care is provided by the female. Spiderlings disperse and construct their own functional webs a few hours after emergence. Many egg sacs produced (>8): <i>Latrodectus geometricus</i> C.L. Koch, 1841. | Forster & Forster, 1973; G. Barrantes (unpubl. data) |
| 2- Low cost | Egg sac guarding. Spiderlings remain in their mother's web between one to two weeks. Adult female provides no food nor regurgitates to the offspring, but provides unfertile eggs for spiderlings inside egg sac to feed (e.g., <i>A. tepidariorum</i>). First instar spiderlings are capable of constructing its own webs if separated from the mother's web. Egg sacs (3 to 8): <i>Gaucelmus calidus</i> Gertsch, 1971, <i>Achaearanea tepidariorum</i> C.L. Koch, 1841, <i>Nesticodes rufipes</i> (Lucas, 1846). | Valerio, 1974; G. Barrantes (unpubl. data). |
| 3- Moderate cost | Egg sac guarding. Spiderlings remain in their mother's web more than two weeks; some spiderlings remain in the web until they reach second or third instar after emerging from the egg sac, and feed often on mother's prey. First instar spiderlings may or may not be capable of constructing its own webs if separated from the web. Occasional matrophagy occurs. Egg sacs (3 to 8): <i>Achaearanea tesselata</i> Keyserling, 1884, <i>Helvibis longicauda</i> Keyserling, 1891. | Barrantes, 2007; Barrantes & Weng, 2007; 2009 |
| 4- High cost | Egg sac guarding. Spiderlings remain in the mother's web at least to the third or fourth instar. In some species spiderlings may remain in the web after their mother dies. Adult female captures prey and regurgitates for spiderlings to feed upon; in some species spiderlings cooperate in prey capture. In some species the adult spider opens up the egg sac for spiderlings to emerge. First instar spiderlings are incapable of constructing their own webs. Adult females produced from one to three egg sacs: <i>Anelosimus studiosus</i> (Hentz, 1850). | Viera et al., 2007; Barrantes & Weng, 2009 |
| 5 - Highest cost | Egg sac guarding. Spiderlings remain in the mother's web at least to the third or fourth instar. Adult female captures prey for spiderlings; spiderlings do not cooperate in prey capture. In some species, adult spider needs to open up the egg sac for spiderlings to emerge. First instar spiderlings are incapable of constructing its own webs if separated from the mother's web. Adult females produced from one to two egg sacs. Some species accumulate dead prey prior spiderlings emerge for them to feed upon: <i>Theridion evexum</i> Keyserling, 1884. | Barrantes & Weng, 2007 |

Table 2. Effect of female body size and maternal care on clutch size of eight theridiid spiders. Variables were \log_{10} transformed.

| Effect | Coefficient | SE | T | P |
|---------------|-------------|------|------|---------|
| Intercept | 0.70 | 0.38 | 1.83 | 0.12666 |
| Cephalothorax | 3.37 | 0.75 | 4.47 | 0.00659 |
| Maternal care | 1.29 | 0.65 | 1.98 | 0.10484 |

The median of egg volume decreased with each species investment in maternal care (Spearman correlation: $r_s = -0.83$, $p = 0.0112$, $n = 8$).

The volume of eggs and the mass (calculated with Anderson's equation) had nearly the same values, and were highly correlated for all the theridiid species included in this study (Table 4). Hence, for comparative studies, volume or mass of eggs provide the same information on maternal investment. However, if eggs deviate from a spherical form, I considered the volume a more appropriate measurement of the egg content, since Anderson's equation considers only one value for the diameter of the egg (possibly the mean between the longest and shortest diameters). In case the form of the egg deviates substantially from spherical the mass of the egg would be overestimated.

DISCUSSION

The clutch size and the size of eggs are influenced by both the size of the female spider and the investment of spiders in maternal care. In arthropods the size of females correlates positively with their reproductive capabilities, with large females producing more or larger eggs (Blanckenhorn *et al.*, 2007; Sánchez-Quirós *et al.*, 2012). In spiders this pattern is common for many species (Foellmer & Moya-Laraño, 2007). However, other factors may also affect both reproductive traits (clutch size and egg size), and this study suggests that the time and resources the spiders invest in maternal care affect both traits.

The maternal care of the solitary *L. geometricus* is restricted to the construction and guarding of the egg sac (Forster & Forster, 1973). During the first days (*ca.* 5 days) the female remains close and nearly continually touching the egg sac with one of her first legs, possibly to reduce the impact of egg parasites. However, after emergence the spiderlings abandoned the egg sac and the tunnel retreat to construct their own total functional webs. This precocious behavior would be only possible if eggs contain a large amount of resources necessary for a greater morphological and/or behavioral development of spiderlings (Walker *et al.*, 2003). From the group of species included in this study *T. evexum* represents the opposite extreme in maternal care. The female produces one egg sac (occasionally two) during her lifetime, which she has to open up for the spiderlings emergence. The spiderlings remain in their mother web until they reach the fourth instar, and during this period the adult female provides prey (often storing death prey) for them (Barrantes & Weng, 2007; 2007 (2008); 2009). The investment of maternal care of the other species ranges between *L. geometricus* and *T. evexum* (Table 1).

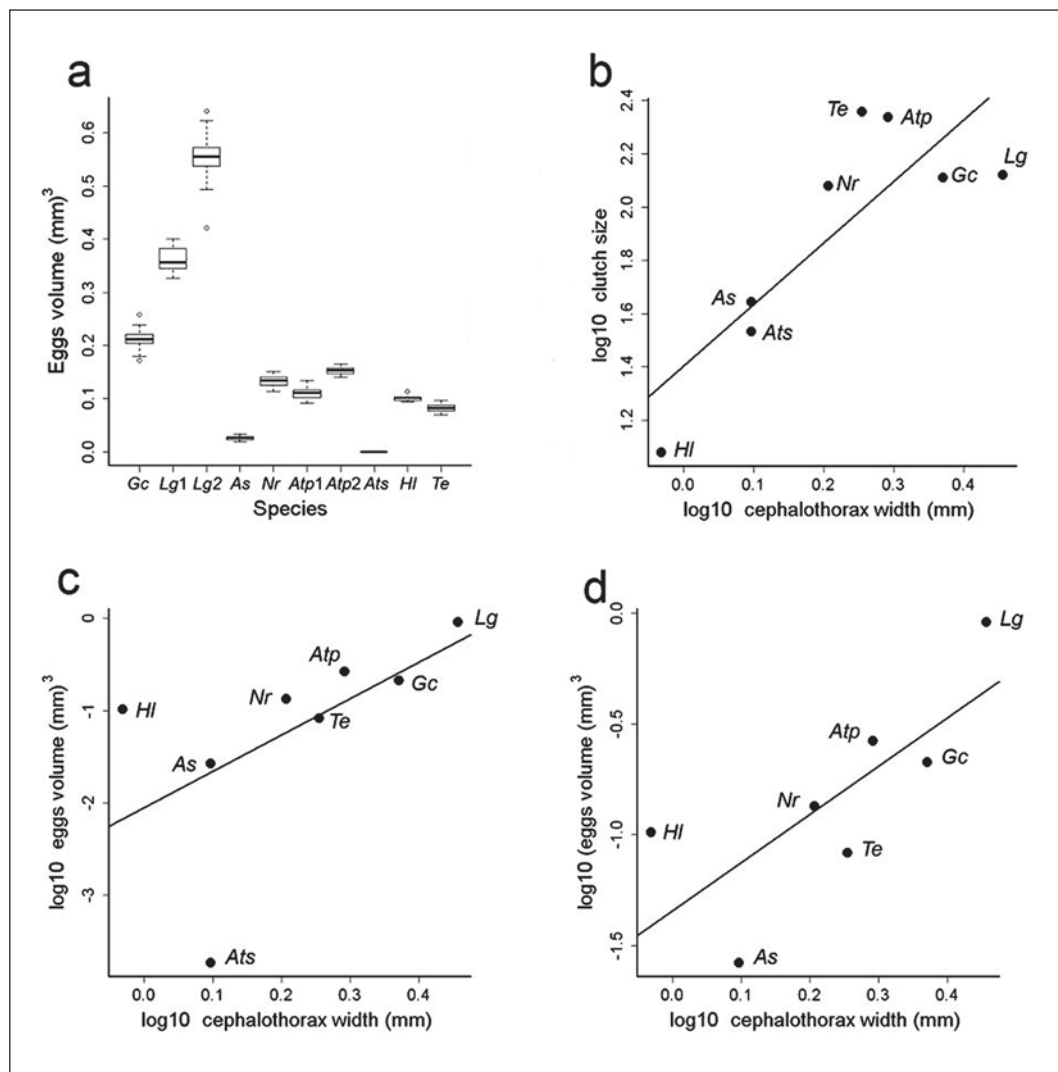


Fig. 1. Volume of eggs and relationships between female body size vs. clutch size and egg volume. a- The median volume of eggs varies largely across the eight theridiid species (Gc: *Gaulcemus calidus*; Lg: *Latrodectus geometricus*; As: *Anelosimus studiosus*; Nr: *Nesticodes rufipes*; Atp: *Achaearanea tepidariorum*; Ats: *Achaearanea tessellata*; Hl: *Helvibis longicauda*; Te: *Theridion evexum*). b- Size of clutch size increases with spider size. c- Median volume of eggs increases with spider size. d- The same relationship excluding *A. tessellata*.

Table 3. Effect of female body size on eggs size (volume) of eight theridiid spiders. Variables were \log_{10} transformed. Full names of species are included in Fig. 1.

| Comparison | Coefficient | SE | T | P |
|---|-------------|------|---------|-----------|
| <i>L. geom.</i> 01 – <i>L. geom.</i> 02 | 0.19 | 0.00 | 40.21 | <0.000001 |
| <i>L. geom.</i> 01 – <i>A. tepid.</i> 01 | -0.25 | 0.00 | -53.81 | <0.000001 |
| <i>L. geom.</i> 01 – <i>A. tepid.</i> 02 | -0.21 | 0.00 | -44.22 | <0.000001 |
| <i>L. geom.</i> 01 – <i>H. longicauda</i> | -0.26 | 0.01 | -28.47 | <0.000001 |
| <i>L. geom.</i> 01 – <i>T. evexum</i> | -0.28 | 0.00 | -57.61 | <0.000001 |
| <i>L. geom.</i> 01 – <i>A. tessellata</i> | -0.36 | 0.01 | -52.22 | <0.000001 |
| <i>L. geom.</i> 01 – <i>A. studiosus</i> | -0.34 | 0.00 | -63.04 | <0.000001 |
| <i>L. geom.</i> 01 – <i>N. rufipes</i> | -0.23 | 0.00 | -49.22 | <0.000001 |
| <i>L. geom.</i> 01 – <i>G. calidus</i> | -0.15 | 0.00 | -31.48 | <0.000001 |
| <i>L. geom.</i> 02 – <i>A. tepid.</i> 01 | -0.45 | 0.00 | -97.28 | <0.000001 |
| <i>L. geom.</i> 02 – <i>A. tepid.</i> 02 | -0.41 | 0.00 | -86.83 | <0.000001 |
| <i>L. geom.</i> 02 – <i>H. longicauda</i> | -0.45 | 0.01 | -49.79 | <0.000001 |
| <i>L. geom.</i> 02 – <i>T. evexum</i> | -0.47 | 0.00 | -99.54 | <0.000001 |
| <i>L. geom.</i> 02 – <i>A. tessellata</i> | -0.56 | 0.01 | -80.92 | <0.000001 |
| <i>L. geom.</i> 02 – <i>A. studiosus</i> | -0.53 | 0.00 | -101.14 | <0.000001 |
| <i>L. geom.</i> 02 – <i>N. rufipes</i> | -0.42 | 0.00 | -92.86 | <0.000001 |
| <i>L. geom.</i> 02 – <i>G. calidus</i> | -0.35 | 0.00 | -73.13 | <0.000001 |
| <i>A. tepid.</i> 01 – <i>A. tepid.</i> 02 | 0.04 | 0.00 | 9.31 | <0.000001 |
| <i>A. tepid.</i> 01 – <i>H. longicauda</i> | -0.01 | 0.01 | -0.94 | 0.348 |
| <i>A. tepid.</i> 01 – <i>T. evexum</i> | -0.03 | 0.00 | -5.93 | <0.000001 |
| <i>A. tepid.</i> 01 – <i>A. tessellata</i> | -0.11 | 0.01 | -16.12 | <0.000001 |
| <i>A. tepid.</i> 01 – <i>A. studiosus</i> | -0.08 | 0.00 | -16.23 | <0.000001 |
| <i>A. tepid.</i> 01 – <i>N. rufipes</i> | 0.02 | 0.00 | 5.17 | <0.000001 |
| <i>A. tepid.</i> 01 – <i>G. calidus</i> | 0.10 | 0.00 | 21.82 | <0.000001 |
| <i>A. tepid.</i> 02 – <i>H. longicauda</i> | -0.05 | 0.01 | -5.58 | <0.000001 |
| <i>A. tepid.</i> 02 – <i>T. evexum</i> | -0.07 | 0.00 | -14.81 | <0.000001 |
| <i>A. tepid.</i> 02 – <i>A. tessellata</i> | -0.15 | 0.01 | -22.21 | <0.000001 |
| <i>A. tepid.</i> 02 – <i>A. studiosus</i> | -0.13 | 0.00 | -24.19 | <0.000001 |
| <i>A. tepid.</i> 02 – <i>N. rufipes</i> | -0.02 | 0.00 | -4.28 | <0.0001 |
| <i>A. tepid.</i> 02 – <i>G. calidus</i> | 0.06 | 0.00 | 12.48 | <0.000001 |
| <i>H. longicauda</i> – <i>T. evexum</i> | -0.02 | 0.01 | -2.08 | 0.038160 |
| <i>H. longicauda</i> – <i>A. tessellata</i> | -0.10 | 0.01 | -9.70 | <0.000001 |
| <i>H. longicauda</i> – <i>A. studiosus</i> | -0.07 | 0.01 | -7.96 | <0.000001 |
| <i>H. longicauda</i> – <i>N. rufipes</i> | 0.03 | 0.01 | 3.48 | 0.000584 |
| <i>H. longicauda</i> – <i>G. calidus</i> | 0.11 | 0.01 | 11.96 | <0.000001 |
| <i>T. evexum</i> – <i>A. tessellata</i> | -0.08 | 0.00 | -11.85 | <0.000001 |
| <i>T. evexum</i> – <i>A. studiosus</i> | -0.06 | 0.00 | -10.54 | <0.000001 |
| <i>T. evexum</i> – <i>N. rufipes</i> | 0.05 | 0.00 | 10.94 | <0.000001 |
| <i>T. evexum</i> – <i>G. calidus</i> | 0.13 | 0.00 | 26.80 | <0.000001 |
| <i>A. tessellata</i> – <i>A. studiosus</i> | 0.03 | 0.01 | 3.60 | 0.000387 |
| <i>A. tessellata</i> – <i>N. rufipes</i> | 0.13 | 0.01 | 19.57 | <0.000001 |
| <i>A. tessellata</i> – <i>G. calidus</i> | 0.21 | 0.01 | 30.54 | <0.000001 |
| <i>A. studiosus</i> – <i>N. rufipes</i> | 0.11 | 0.00 | 20.81 | <0.000001 |
| <i>A. studiosus</i> – <i>G. calidus</i> | 0.18 | 0.00 | 35.00 | <0.000001 |
| <i>N. rufipes</i> – <i>G. calidus</i> | 0.08 | 0.00 | 16.94 | <0.000001 |

Table 4. Correlation between volume and mass of eggs calculated with the equation provided by Anderson (1990). Mean and standard deviation (sd) are included for volume and mass.

| Species | <i>r</i> | <i>p</i> | Volume | SD vol. | Mass | SD Mass |
|---------------------------|----------|----------|--------|---------|------|---------|
| <i>G. calidus</i> | 0.99 | <0.00001 | 0.21 | 0.02 | 0.22 | 0.02 |
| <i>L. geometricus</i> 01 | 0.97 | <0.00001 | 0.55 | 0.04 | 0.56 | 0.04 |
| <i>L. geometricus</i> 02 | 0.98 | <0.00001 | 0.36 | 0.02 | 0.37 | 0.02 |
| <i>A. studiosus</i> | 0.98 | <0.00001 | 0.03 | 0.00 | 0.03 | 0.00 |
| <i>N. rufipes</i> | 0.99 | <0.00001 | 0.13 | 0.01 | 0.14 | 0.01 |
| <i>A. tepidariorum</i> 01 | 0.99 | <0.00001 | 0.11 | 0.01 | 0.12 | 0.01 |
| <i>A. tepidariorum</i> 02 | 0.89 | <0.00001 | 0.15 | 0.00 | 0.16 | 0.00 |
| <i>A. tessellata</i> | 1.00 | <0.00001 | 0.11 | 0.01 | 0.11 | 0.01 |
| <i>H. longicauda</i> | 0.98 | <0.00001 | 0.09 | 0.01 | 0.09 | 0.01 |
| <i>T. evexum</i> | 0.98 | <0.00001 | 0.08 | 0.01 | 0.08 | 0.01 |

The size of eggs varies also within species. For both *L. geometricus* and *A. tepidariorum* the size of eggs differ between individuals (Fig. 1; Table 3). There are several factors that may affect intra-specific variation in the size of eggs. For instance, age in female birds affect the egg size; young and old female birds tend to lay smaller eggs than those with an intermediate adult age (Gill, 2007). In some spiders (e.g., *Nephila cornuta*) the number of eggs in each batch decreases with the order in which the egg sacs are produced (Gertsch, 1949), but in general the effect of age on the number of eggs is unexplored in spiders. Availability of prey is thought to affect the size of eggs, and the clutch size, at least in some species (Briceño, 1987; Walker *et al.*, 2003; Johnson *et al.*, 2014). However, information of the effect of prey availability on both, size of eggs and clutch size, is unknown for most species.

Both the clutch size and eggs size of theridiids have positive allometry ($b > 1$) relative to the female body size, which differ from other results (Anderson, 1990; Marshall & Gittleman, 1994). One possibility is that each family has its own allometric relationship, but when data of different families is combined, a more general pattern obscures these particular relationships, as it occurs when the allometry of the brain relative to body size of different groups of animals is analyzed (Eberhard & Wcislo, 2011). Another possibility is that the small number of species, and small sample size for each of the species included in this study could produce a relationship that is not representative for the entire theridiids.

Results of this study suggest that both, clutch size and eggs size are influenced by female body size and species-specific life history traits. For instance, semelparity vs. iteroparity, life span, and investment in maternal care are factors that could interact and affect either the clutch size, egg size or both. Finally, values of volume and mass of eggs are nearly the same as long as eggs are spherical or nearly so.

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