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Flying sand-dwelling spiders: aerial dispersal in *Allocosa marindia* and *Allocosa senex* (Araneae: Lycosidae)

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Abstract. Aerial dispersal in spiders or ballooning is typically considered to occur during the day by juvenile instars or small-sized adults. *Allocosa marindia* Simó, Lise, Pompozzi & Laborda, 2017 and *Allocosa senex* (Mello-Leitão, 1945) are two nocturnal wolf spiders that inhabit coastal sandy beaches of South America. As mothers of both species emerge from the burrows during the night to disperse the spiderlings, we expected that aerial dispersal of spiderlings could occur during that period. Our aim was to test ballooning occurrence in both species during day and night under laboratory conditions, using as a positive control, the wolf spider *Schizocosa malitiosa* (Tullgren, 1905). We examined ballooning behavior of once-molted spiderlings of *A. marindia*, *A. senex* and *S. malitiosa*, under diurnal and nocturnal conditions, recording observations in a container with grasses and sand as substrate. We exposed the spiderlings to air flow and recorded occurrences of climbing the grass, dropping on dragline and tip-toeing (pre-ballooning behaviors). The three species performed pre-ballooning behaviors during the day but also in the night, and the occurrences of these behaviors varied both within and among species. More events of pre-ballooning behavior were observed during the day than during the night. However, we found differences in the number of events of tip-toeing and dropping on dragline according to the time of the day. We discuss the possibility that microhabitat conditions could affect ballooning propensity particularly in the three coastal wolf spiders.

Keywords: Ballooning, wolf spider, tip-toe, drop on dragline, coastal environment

Aerial dispersal is a central trait affecting the life history of spider species (Bonte & Dahirel 2017). Along with other biotic and abiotic factors, aeronautic behavior can shape species distributions and population structures (Muñoz et al. 2004; Papadopoulou et al. 2009; Gillespie et al. 2012). It allows species to colonize remote habitats and experience rapid range shifts during unfavorable environmental conditions (Muñoz et al. 2004; Papadopoulou et al. 2009; Peterson 2009; Gillespie et al. 2012; Travis et al. 2013).

Ballooning is commonly known as the mechanism for aerial dispersal in spiders (Foelix 2011). By means of silk threads, spiders can travel throughout the air, moving from few meters to many kilometers away from their birth site (Decae 1987; Weyman et al. 2002; Bell et al. 2005; Bonte 2013). This behavior is widespread among araneomorph spiders and has rarely been described in mygalomorphs (Decae 1987; Bell et al. 2005; Coddington 2005; Ferretti et al. 2013). With few exceptions (Weyman et al. 2002; A. Aisenberg, pers. obs.), aerial dispersal is restricted to juvenile instars or to spiders with small adult sizes (e.g., linyphiids) (Greenstone et al. 1987; Weyman 1993). In general, ballooning occurs during daylight in warm dry days, and when wind speed is low (< 3 m/s) (Richter 1970; Vugts & Van Wingerden 1976; Bishop 1990; Greenstone 1990; Weyman 1993; Duffey 1998; Reynolds et al. 2007).

The most frequently known pre-ballooning behavior is the stereotypical 'tip-toeing' (i.e., after climbing to a high point the spider places itself in front of an air stream, stretches the legs, raises the opisthosoma and produces silk threads until taking-off) (Richter 1970; Decae 1987). Another mechanism is the 'dropping on dragline', during which the spider climbs to a high point, drops from attached lines of silk and swings in the wind. When the silk lines break, the spider becomes airborne (see Decae 1987, Eberhard 1987 for other pre-ballooning behaviors).

As with any other dispersal mechanism, ballooning will help to avoid inbreeding, competition for resources, and unfavorable environmental conditions (Decae 1987; Bonte et al. 2006). Moreover, other factors like starvation and overcrowding have also shown to stimulate ballooning behaviors (Duffey 1998; Mestre & Bonte 2012; Bonte 2013). However, because spiders can control when to balloon but not where they are going to land, aerial dispersal has a potential cost of landing in unsuitable habitats. Hence, the performance of ballooning will depend of the trade-off between costs and benefits (Bell et al. 2005; Bonte 2013). Theoretical and empirical studies in several organisms have shown that the temporality of the habitat and its spatial distribution are main factors shaping dispersal strategies (Southwood 1962; McPeek & Holt 1992; Travis & Dytham 1999). Thus, unpredictable and unstable habitats may select for higher dispersal rates either in continuous or fragmented areas (Southwood 1962; McPeek & Holt 1992; Travis & Dytham 1999; Travis et al. 2013). Studies of spiders agree with those predictions (see Richter 1970; Greenstone 1982; Bonte et al. 2006, for examples of lycosids of the genus *Pardosa* C.L. Koch, 1847). In addition, Bonte et al. (2003b) showed that ballooning in spiders is negatively related to habitat specialization in fragmented habitats.

The nocturnal sand-dwelling wolf spiders *Allocosa marindia* Simó, Lise, Pompozzi & Laborda, 2017 and *A. senex* (Mello-Leitão, 1945) are distributed throughout the coasts of rivers, lakes and the ocean shores of Argentina, Brazil and Uruguay (Capocasale 1990). Both species are strictly associated with sandy coastal shores and are considered good bio-indicators of those environments (Ghione et al. 2013). They construct burrows in the sand where they shelter during the cold months and during daylight, becoming active during the summer nights (Costa 1995; Costa et al. 2006). Both species exhibit a reversal in sex roles and sexual size dimorphism expected in spiders; thus, females are smaller than males and they seek and initiate courtship (Aisenberg et al. 2007; Aisenberg & Costa 2008). Mating occurs inside male burrows and females lay their egg-sac there, exiting during the night when it is time for progeny dispersal (Aisenberg 2014), with the spiderlings on their dorsum as it is typical for this family (Foelix 2011). These species have sympatric distributions, but *A. senex* is most frequently found in open sandy areas with scarce psammophile native vegetation, whereas *A. marindia* is associated with sandy areas showing greater abundance of native and exotic vegetation (Costa et al. 2006; Aisenberg et al. 2009, 2011; Ghione et al. 2013). Moreover, the two species differ in the continuity of their distributions: *A. senex* has a continuous distribution whereas *A. marindia* shows a more irregular and patchy distribution throughout the coastline of Uruguay (Bidegaray-Batista, pers. obs.). Due to their extraordinary morphological, ecological and behavioral adaptations to inhabit sandy coasts, both species are promising models to study ballooning propensity and shed light on the evolution of dispersal strategies in spiders.

Here, we study the propensity to exhibit ballooning behavior during day and night in *A. marindia* and *A. senex* under laboratory conditions. As a positive control, we examined ballooning behavior in the similar-sized wolf spider *Schizocosa malitiosa* (Tullgren, 1905), which inhabits neighboring anthropic habitats and shows high propensity for aerial dispersal (Capocasale & Costa 1975; Carlozzi et al. 2014). We predicted that both *Allocosa* would exhibit ballooning behavior during the night, when the dispersal of spiderlings occurs in nature. We also expected to find differences in ballooning occurrence between the three species, accordingly to the degree of stability of their microhabitats. As both *Allocosa* species inhabit sand coastal habitats which are considered unpredictable and unstable, we predicted higher ballooning propensity in these species compared to *S. malitiosa*.

METHODS

During February 2014, we collected 4 females of *A. marindia*, 5 females of *A. senex* and 4 females of *S. malitiosa* carrying spiderlings on the dorsum. *Allocosa* females were collected at San José de Carrasco, Canelones, Uruguay (34°50′46.71″S, 55°58′17.65″W), while the females of *S. malitiosa* were collected at Marindia, Canelones, Uruguay (34°46′52.15″S, 55°49′30.18″W).

We maintained the females with their progeny under laboratory conditions in individual cylindrical containers of 6.7 cm diameter and 7.5 cm height, with sand as substrate and water provision. We waited until the spiderlings molted and descended from their mother on their own initiative. Then we separated the spiderlings in small groups for the trials. We formed groups of 5 in *A. marindia*, and of 3 in *A. senex* and *S. malitiosa*. We decided to form larger groups in *A. marindia* because they showed lower activity than the other species, making them easier to record in a higher number (A. Carlozzi, unpublished data).

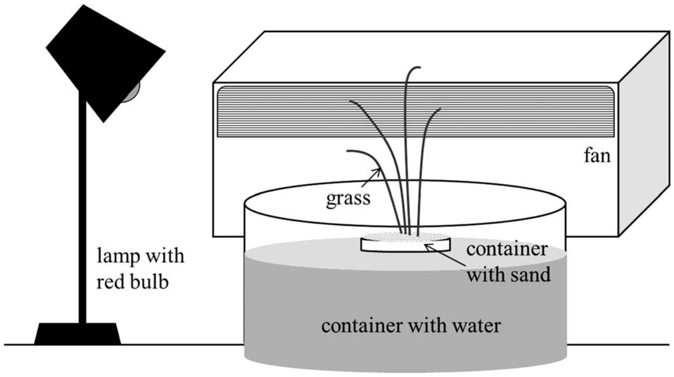

Figure 1.—Experimental set-up.

We followed the experimental design described by Richter (1970) (Fig. 1). Each group of individuals was placed in a cylindrical plastic container of 7 cm diameter and 10 cm height, with sand as substrate and four leaves of *Panicum racemosum* grass (Poaceae). The container was centered inside a bowl of 21 cm diameter and 10.5 cm height with water, to prevent potential escape of the spiderlings. We generated a continuous airflow at a rate that averaged 2.47 ± 0.16 m/sec. We measured the airflow with a handheld digital anemometer (Benetech GM816), at the middle of the grass that was closer to the airflow device. The air was generated by a fan directed upwards at an angle of 45° (Fig. 1). This breeze speed has been indicated as adequate for displaying ballooning by spiderlings of other wolf spider species (Richter 1970; Greenstone 1982). Each trial was run for 15 minutes after placing each group of spiderlings at the sand of the container.

We performed trials during the day between 12 am and 9 pm, and during the night between 9.30 pm and 6.30 am, under a 40 watt red light bulb. All the trials were carried out during summer of the Southern Hemisphere. We tested a total of 60 spiderlings of *A. marindia* (25 spiderlings at diurnal and 35 at nocturnal trials), 135 of *A. senex* (75 spiderlings at diurnal and 60 at nocturnal trials), and 132 of *S. malitiosa* (75 spiderlings at diurnal and 57 at nocturnal trials). The age of the spiderlings, measured in days since leaving the mother's dorsum, was 5.77 ± 3.71 days (range: 1–13). Temperature and humidity data under laboratory conditions are summarized in Table 1.

For each trial, we recorded by direct observation the number of occurrences of the behaviors: climbing the grass, tip-toeing, dropping on dragline and ballooning. We compared the total number of events of climbing the grass, dropping on dragline and tip-toeing between diurnal and nocturnal trials, and between species. Also, we tested for significant interactions among the behaviors and time of the day, and among the behaviors and species identity, using generalized linear mixed-effects models under a negative binomial distribution. The species identity, trial time (day vs. night) and its interaction were set as fixed-effect factors while the variable 'mother' was set as a random factor (because maternal effects have been shown to affect ballooning behavior, Mestre & Bonte 2012). Furthermore, to test for changes in the prevalence of dropping on dragline or tip-

Table 1.—Temperature and humidity conditions during the experimental trials for each species, during the day and night. All data are presented as mean values with their corresponding standard deviations.

	Temperature (°C)	Humidity (%)
A. marindia	Day: 27.40 ± 1.14	Day: 65.56 ± 4.29
	Night: 26.94 ± 0.11	Night: 72.30 ± 5.50
A. senex	Day: 26.61 ± 1.21	Day: 73.20 ± 6.70
	Night: 26.59 ± 0.48	Night: 75.00 ± 2.90
S. malitiosa	Day: 31.19 ± 2.90	Day: 70.60 ± 4.83
	Night: 33.00 ± 0.00	Night: 74.80 ± 4.55

toeing events in each trial in the different species and according to the time of the day, we built a mixed-effects binomial model, considering each of the species, timing (day vs. night) and its interaction as fixed-effect factors and the variable ‘mother’ as a random factor.

Temperature was added as a fixed-effect continuous factor to all the full models created in order to disregard any effect of this variable in our results. The general procedure was to build full models (including all potential effects) and compare these models to reduced models (removing one factor at a time) using likelihood ratio tests (e.g., Zuur et al. 2009). In case of finding differences between the species or an interaction between time and species, we performed multiple comparison post hoc tests. The modelling was made using the glmer function in lme4 package (Bates et al. 2015) in R software (R core Team 2016). The selection of the probability distribution in which to frame our analysis and accomplishment of assumptions were performed following standardized methods for generalized linear models (Zuur et al. 2009).

Voucher specimens were deposited in the collection of Sección Entomología, Facultad de Ciencias, Uruguay.

RESULTS

We summarize data about the total number of events in which the pre-ballooning behaviors “dropping on dragline” and “tip-toeing” were followed by ballooning in Table 2. Temperature did not affect the total number of pre-ballooning behaviors (pooling dropping on dragline plus tip-toeing events) observed (likelihood ratio test: *Chisq* = 2.58, df = 1, *P* = 0.11). We observed higher counts of pre-ballooning behaviors per trial during the day (mean ± SD = 2.7 ± 2.4) than during night (mean ± SD = 2.1 ± 1.2) (likelihood ratio test: *Chisq* = 25.7, df = 3, *P* = 1.1 x10^{-5}), and a different number of pre-ballooning behaviors per trial were displayed between species (likelihood ratio test: *Chisq* = 20.3, df = 4, *P* = 0.0005). Furthermore, day-night effects depended on the species (significant interaction, likelihood ratio test: *Chisq* = 11.0, df = 2, *P* = 0.004). During the day *A. senex* produced more pre-ballooning behaviors per trial than *S. malitiosa* (posthoc comparison: *Z* = -2.85, *P* = 0.01), whereas the number of pre-ballooning behaviors per trial in *A. marindia* did not differ from the others (Z = -0.19, *P* = 0.18 compared with *A. senex* and Z = -1.7, *P* = 0.84 compared with *S. malitiosa*). However, during the night, the number of pre-ballooning events per trial was similar between all the species (*A. senex* versus *A. marindia:* Z = -0.55, *P* = 0.57*; A. senex* versus *S. malitiosa:* Z = 1.3, *P* = 0.46; and *A. marindia* versus *S. malitiosa:* *Z* = 1.4, *P* = 0.46) (Fig. 2). *Allocosa senex*

Table 2.—Total number of events in which the pre-ballooning behaviors dropping on dragline (DD) and tip-toeing (TT) were followed by ballooning (B) for each species and diurnal/nocturnal trials. Total number of trials is shown in parentheses.

Species	DD + B Diurnal trials	DD + B Nocturnal trials	TT + B Diurnal trials	TT + B Nocturnal trials
A. senex	7 (25)	4 (20)	3 (25)	1 (20)
A. marindia	1 (5)	3 (7)	0 (5)	0 (7)
S. malitiosa	7 (25)	10 (19)	9 (25)	1 (19)

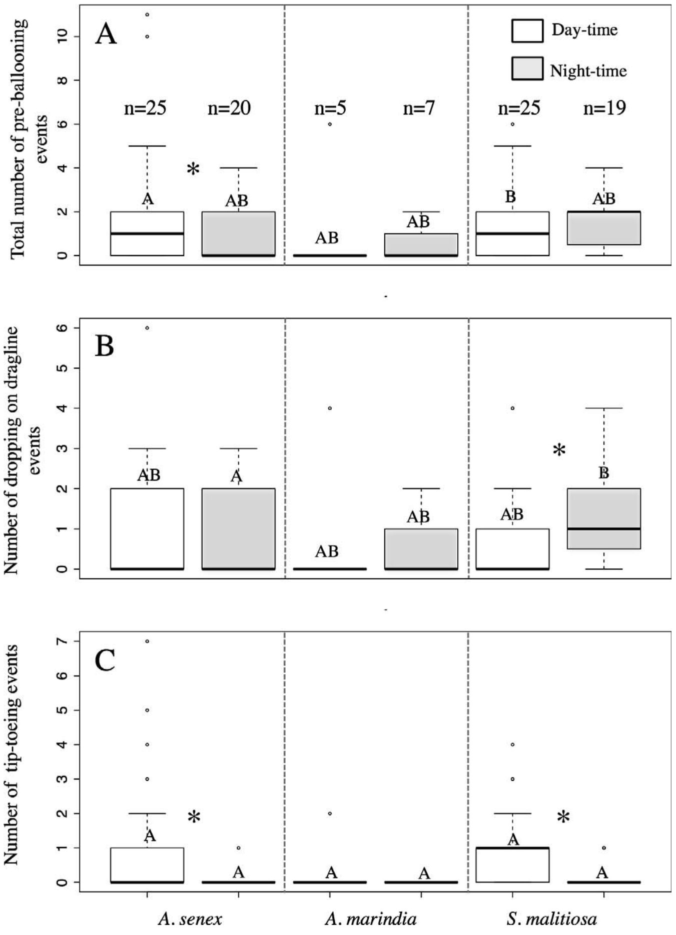

Figure 2.—Box and whiskers plots of the total number of pre-ballooning events per trial: (A) dropping on dragline + tip-toeing, (B) dropping on dragline events, and (C) tip-toeing events, recorded for *A. senex*, *A. marindia*, and *S. malitiosa* during day and night trials (shown by light and dark boxes, respectively). The total number of trials in each treatment (n) is shown in panel A, above each box. Open cirlces represent outliers. The results of mixed-effects negative binomial models testing effects of species and trial times are summarized in the plots as follows: in each panel, significant differences between species are represented by different letters; significant differences between day and night trials are indicated by an asterisk within each species in each panel. Only statistical differences in which $P < 0.05$ are reported in the graph.

performed significantly higher number of pre-ballooning behaviors during the day trials (2.9 ± 3.0 events) than during the night trials (1.9 ± 1.2 events) (posthoc comparison: $Z = -3.71$, $P = 0.0002$) (Fig. 2). However, *A. marindia* and *S. malitiosa* did not show significant differences between day and night trials (posthoc tests: $Z = -1.0$, $P = 0.31$ and $Z = 0.01$, $P = 0.99$, respectively).

We did not find statistical differences in the number of climbing the grass events observed between species (likelihood ratio test: *Chisq* = 3.6, df = 2, $P = 0.16$). Trial time and this behavior was not related to temperature in our dataset (likelihood ratio test: *Chisq* = 0.52, df = 1, $P = 0.46$).

We observed more dropping on dragline events per trial during the night (mean ± SD = 1.0 ± 1.1) than during the day (mean ± SD = 0.8 ± 1.3) (likelihood ratio test: *Chisq* = 12.2, df = 3, $P = 0.007$). However, this behavior differed between species (likelihood ratio test: *Chisq* = 14.3, df = 4, $P = 0.006$), as the day–night differences depended on the species (significant interaction on likelihood ratio test *Chisq* = 12.2, df = 2, $P = 0.002$). While during the night all the species displayed similar numbers of dropping on dragline events per trial (posthoc tests: *A. senex* versus *A. marindia:* $Z = -0.7$, $P = 0.47$; *A. senex* versus *S. malitiosa:* $Z = 1.5$, $P = 0.31$; and *A. marindia* versus *S. malitiosa:* $Z = 1.6$, $P = 0.31$), during the day *S. malitiosa* tended to perform more dropping on dragline than *A. senex* (note the marginal P value in posthoc tests: *A. senex* versus *A. marindia:* $Z = -1.0$, $P = 0.56$; *A. senex* versus *S. malitiosa:* $Z = -2.1$, $P = 0.09$; and *A. marindia* versus *S. malitiosa:* $Z = -0.4$, $P = 0.68$). Moreover, *A. senex* showed a tendency (note the marginal P value) to make more dropping on dragline during the day than during the night ($Z = -1.8$, $P = 0.06$), while *S. malitiosa* showed the opposite pattern with more dropping on dragline events observed during the night ($Z = 2.54$, $P = 0.01$). *Allocosa marindia* did not show significant differences in this behavior between day and night ($Z = -1.2$, $P = 0.24$) (Fig. 2).

Opposite to the pattern of dropping on dragline behaviors, the tip-toeing events occurred in higher numbers per trial during the day (mean ± SD = 0.87 ± 1.5) than during the night (mean ± SD = 0.08 ± 0.28) (likelihood ratio test: *Chisq* = 44.2, df = 1, $P = 2.9 \times 10^{-11}$). Although initially the likelihood ratio test suggested differences between species (likelihood ratio test: *Chisq* = 7.6, df = 2, $P = 0.02$), posthoc comparisons did not show differences between any of the species (posthoc tests: *A. senex* versus *A. marindia:* $Z = -1.5$, $P = 0.36$; *A. senex* versus *S. malitiosa:* $Z = -1.4$, $P = 0.36$; *and A. marindia* versus *S. malitiosa:* $Z = 0.8$, $P = 0.41$). This is likely attributed to the fact that there is only one observation of night tip-toeing in one trial for *A. senex,* one for *S. malitiosa*, and none for *A. marindia* (Fig. 2).

Consistent with the aforementioned patterns, we found that individuals performed a higher proportion of dropping on dragline per trial (implying a lower proportion of tip-toeing) during the night (mean ± SD = 93.2 ± 0.84 %) than during the day (mean ± SD = 49.9 ± 1.6 %)) (*Chisq* = 33.6, df = 1, $P = 6.5 \times 10^{-9}$). However there were no significant differences between the species (*Chisq* = 0.5562, df = 2, $P = 0.75$) or a significant interaction between time and species (*Chisq* = 0.26, df = 2, $P = 0.87$).

DISCUSSION

Our results showed that *A. marindia*, *A. senex* and *S. malitiosa* can perform ballooning behavior during the day but also during night hours. Interestingly, although adults and juveniles of both *Allocosa* species are inside their burrows during the day (Costa 1995), our results suggest that once-molted spiderlings would balloon or at least be able to balloon also during the day. This aerial dispersal ability found in both *Allocosa* species is in agreement with recent phylogeographic studies, which revealed an absence of genetic differentiation and high connectivity among populations of both species (Bidegaray-Batista et al. 2017; Postiglioni 2015). However, pre-ballooning frequencies varied both within and among species and also between day and night.

Though the three wolf spiders inhabit the sandy coasts of Uruguay, *A. senex* is more common in sand dunes with scarce native vegetation, while *A. marindia* is more frequent in sandy areas with higher abundance of native and exotic vegetation (including shrubs and trees), and *S. malitiosa* inhabits continuous areas with more vegetation and human constructions (Costa et al. 2006; Ghione et al. 2013). Microhabitat characteristics such as the vegetation coverage could negatively affect the incidence and speed of air currents perceived by the spiderlings, determinant factors for triggering ballooning behavior (Weyman et al. 2002). *Allocosa senex* showed higher number of pre-ballooning events compared to *S. malitiosa* during the day, but did not show differences with *A. marindia*. The high occurrence of ballooning in *A. senex* during the day could be related with the harshness and unpredictability of their habitat (Aisenberg 2014; Jorge et al. 2015), characteristics that can promote aerial dispersal in spiders (Southwood 1962; Greenstone 1982; Bell et al. 2005). On the other hand, the degree of continuity or fragmentation of the habitat can determine the possibilities of aerial dispersal of a spider species, population or individual (Bonte et al. 2006). Moreover, species showing a strict association with a certain habitat (in our case *Allocosa*) are expected to show lower frequencies of aerial dispersal compared to species with more generalist distributions (Bonte et al. 2003b). These two last hypotheses do not agree with the results of the present study. Hypotheses of how habitat fragmentation, harshness or stability can affect ballooning occurrence in spiders can be difficult to test and interpret in contexts in which more than one of those characteristics apply, as occurs in our situation, so results should be analyzed cautiously.

In the present study, carried out under controlled laboratory conditions, the three species were able to balloon at night, under red light. According to a recent study by Postiglioni et al. (2017), *Allocosa* balloons at night also in the field. According to this, light conditions would not be the main factor triggering ballooning occurrence in *A. senex*, *A. marindia* and *S. malitiosa*. However, most studies testing aerial dispersal in spiders have been carried out during daylight (Richter 1970; Yeargan 1975; Greenstone 1982, 1990; Suter 1999). Moreover, Bishop (1990) performed a field study to test spider aerial dispersal by placing sticky traps in a forest canopy and found that ballooning occurred only during the day. Though thermal conditions and the appropriate air flow necessary for ballooning diminish after sunset, the night would not prevent the occurrence of ballooning (Weyman et al. 2002). The meteorological conditions determining ballooning occurrence in both *Allocosa* species and in *S. malitiosa* remain to be further studied.

Though both tip-toeing and dropping on dragline have been reported as pre-ballooning behaviors (Decae 1987; Barth et al. 1991), we found differences in the number of events of those behaviors between the day and the night. In this study, we found more dropping on dragline events during the night and more tiptoeing during the day. Dropping on dragline is a pre-ballooning behavior, but it can also occur in other contexts to avoid predation, when the spider starts to build a web, or as a consequence of overcrowding. However, the three spiders tested in this study are wolf spiders that do not construct webs or perform pre-bridging behavior. Moreover, as we show in Table 2, dropping on dragline was followed by ballooning in some observations, corroborating that this behavior was not misunderstood as pre-ballooning behavior. The dissimilarities in the number of events of tip-toeing and dropping on dragline according to the time of the day remain to be further studied.

Other factors that can affect aerial dispersal behavior in spiders are the individual nutrition status, mother condition, feeding history and temperature breeding conditions during juvenile stages (Bonte et al. 2003a; Mestre & Bonte 2012). In the current study, we did not control those variables, the body size and weight of the spiderlings or of their mothers, so the influences of those characteristics in *A. marindia*, *A. senex* or *S. malitiosa* remain to be studied further. Moreover, despite that the trials for *A. marindia* contained five individuals versus three individuals in the rest of groups this did not translate into more ballooning events observed in the trials of *A. marindia*, disregarding a potential increase in the number of observed ballooning per trial with increasing number of individuals. Though aerial dispersal in spiders is an extraordinary phenomenon, much work still needs to be done in order to determine the factors triggering this behavior.

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