2013. The Journal of Arachnology 41:215–218

SHORT COMMUNICATION

Opening and closing of burrows by the Namibian spider *Ariadna* sp. (Araneae: Segestriidae) in a year of heavy rainfall

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Abstract. The *Ariadna* spiders (Araneae: Segestriidae) inhabiting the gravel plains of the Central Namib Desert construct individual burrows with a circular entrance surrounded by a ring of small pebbles; sometimes they close their burrows by a small stone. In the lichen fields, about 20 km east of Walvis Bay (Namibia), there is a consistent population of *Ariadna* spiders that can also use pieces of lichen both in the ring composition and as the plug when the burrow is closed. We sampled and monitored 175 burrows repeatedly between December 1999 and August 2000. In March 2000, an exceptionally high rainfall occurred in the Namib, leading to flooding even in our fieldwork station. We tested whether and to what extent an event of this magnitude could affect burrow closing. We found the rain event increased burrow closure by large, but not small or medium-sized, *Ariadna* sp. We suggest that the flooding event acted as an ecological resource pulse for these spiders.

Keywords: Flooding, lichen-stone fields, Namib Desert, spider population, survival strategies

Spiders of the genus *Ariadna* (Araneae: Segestriidae) inhabiting the gravel plains of the Central Namib Desert dig individual, silk-lined burrows and surround their circular entrances by rings of small quartz stones, suitably selected during the digging activity (Costa et al. 1993, 1995; Henschel 1995). Spiderlings, whose body size is just over a millimeter, simply place a series of sand grains around the mouth of their burrows (Costa et al. 1993, 1995). The features of these rings vary according to the populations and their habitat; in some areas of the Namib Desert, where wide plains rich in lichens occur, pieces of lichen can also be included in the rings.

A spider lurking at the bottom of its burrow keeps the entrance open in order to drag prey inside; the ring items, by transmitting vibrations produced by walking prey, serve as foraging tools allowing spiders to expand their sensory range (Henschel 1995). We observed that these spiders sometime close their burrows, plugging the entrance with a stone or a piece of lichen (Costa et al. 2000), probably as an anti-predatory strategy after consuming prey. The burrows are later reopened when they hunt again.

The Namib Desert is a hyperarid desert stretching from South Africa, through Namibia, and into Angola (Goudie 2002). It is characterized by diurnal high temperature and scanty, irregular rainfall; in the Namib in particular, rainfall is not a predictable factor but does increase from the coast inland (Viles 2005). Mean annual rainfall ranges from 18 mm at Swakopmund, on the coast, to 50 mm at Ganab, located over 100 km inland (Lancaster et al. 1984). In contrast to rainfall, fog is a more predictable factor (Shanyengana et al. 2002). It is heavy along the coast, decreasing inland, and represents an important alternative source of moisture that is crucial for the survival of plants and animals (Costa 1995). Due to the influence of the cold seawater and the frequent occurrence of fog, temperatures are cool and show little diurnal variation along the coast, while there is a nearly continuous high relative humidity. Wind is also a very important component of the central Namib climate, reaching up to 80 km/h and frequently causing sandstorms (Seely 1987). Against this background of low rainfall and coastal fog, every 16–20 years rare rain pulses do occur in the Namib Desert (Hachfeld 2000). In the rainy season of 1999/2000, exceptionally high rainfall occurred in the Central Namib, with 78 mm of precipitation on 24 and 25 March 2000 (Hachfeld 2000).

Our study site, about 20 km east of Walvis Bay, Namibia, along the C14 highway in the Namib Naukluft Park (23°00′32.7″S, 14°43′38.0″E; altitude 46 m), is level and rich in lichens, part of 'Lichen field I' of the Central Namib as defined by Schieferstein & Loris (1992). The ground is made up of fine gravel consisting mainly of quartz stones of many shapes and sizes (Costa et al. 2000). As part of our long-term research on the behavioral adaptations of Namib Desert arthropods, from December 1999 to August 2000 we carried out an eco-ethological survey on a population of an undescribed *Ariadna* species, whose individuals may include quartz stones and/or lichen pieces around the openings of their burrows, sometimes forming a turret (Costa et al. 2000). During the study period, the mean temperature was 18.1°C (min 16.1°C in December 1999, max 20.0°C in January 2000), while the mean humidity was 71.7% (min 59.2% in June 2000, max 80% in February 2000).

The exceptional rain of March 2000 stimulated us to investigate whether and to what extent an event of this magnitude could affect the behavior of burrow closing by *Ariadna* spiders.

We divided our 50 × 80 m fieldwork area into 160 5×5-m squares using a grid system composed of nylon string and wooden stakes. From 19 to 27 December 1999, we located and marked 175 spider burrows with numbered flags. We recorded the burrow entrance diameter (measured with a Vernier caliper, measurement error = 0.05 mm), the status of the entrance (open or closed), and counted stones and lichen pieces placed around the lip of the burrow entrance by the spiders. Then in five different months (15 January, 9 February, 19 April, 15 May and 9 August), we ascertained whether each burrow was open or closed (data for all 175 burrows were collected in one day for each sampling). Since these spiders tend to remain in the same burrows and widen the walls of them as they grow (Henschel 1995), it is possible to assume that the diameter of the burrow entrance is age-dependent as also occurs with other spiders (Carrel 2003). Assuming that the measures of burrow entrance diameter correlate to spider age, we sorted the 175 diameters into three size classes: 'small' (spiderlings, diameter less than 3.0 mm, $n = 62$), 'medium' (sub-adults, diameter greater than or equal to 3.0 mm and less than 4.5 mm, $n = 46$), and 'large' (adults, diameter greater than or equal to 4.5 mm, $n = 67$). Since the long-lived Namibian *Ariadna* spiders widen their burrows by less than 1 mm per year (Henschel 1995), we have considered the variation of the diameter of the sampled burrows to be negligible during our study period (nine months), also taking into account that such variation, from a monthly sampling to the next one, was comparable to the measurement error, and so we do not consider those data here.

We evaluated whether the ring composition (number of stones or pieces of lichen) correlated with the burrow diameter. Then, to test the influence of the rainfall on opening and closing of burrows, we a) assigned the value 0 to each open burrow and the value 1 to each closed burrow, b) grouped the monthly data into three time variables [time 1, pre-rain (data from December 1999, January and February 2000), time 2, immediately post-rain (data from April) and time 3, months-after rain (data from May and August)] and reduced the influence of the differences in the number of months in the three time periods by using mean values for each individual; c) used a mixed design, repeated measures ANOVA, with one between-group effect (size-class) for time 1, time 2 and time 3 and one within-subject effect (time period) on the opening/closing behavior data from time 1, time 2 and time 3. To compare the status of burrows between the first (December 1999) and the last (August 2000) samplings, we used McNemar's test for paired-sample nominal scale data. Statistical analyses were conducted using SPSS for Windows (version 18.0).

We found that the number of pieces of lichen and diameter of the entrance burrow were positively correlated ($r = 0.60$, $P < 0.001$); the regression line ($y = -0.71 + 0.89x$) had a significant slope ($P \ll 0.001$).

Repeated measures ANOVA showed a highly significant difference in closed burrows between the three size-classes ($F = 12.16$; $df = 2, 172$; $P \ll 0.001$). Moreover, the interaction of time and size class was also significant ($F = 30.45$; $df = 3.86, 331.80$; $P \ll 0.001$). Post-hoc Bonferroni comparisons showed that the number of closed burrows was significantly different between small and medium burrows ($P < 0.02$) and small and large burrows ($P \ll 0.001$), while medium and large burrows did not differ. Rainfall significantly increased the closing behavior overall ($F = 15.28$; $df = 1.93, 331.80$; $P \ll 0.001$). Post-hoc Bonferroni comparisons revealed significant differences between time 1 and time 2 ($P \ll 0.001$) and between time 2 and time 3 ($P \ll 0.001$), but no significant differences between time 1 and time 3 (Table 1). Finally, the McNemar's test showed no significant difference in number of closed burrows between the first and the last sampling ($n = 66$ and $n = 75$ respectively) ($\chi^2 = 0.93$).

Our results on closing/opening frequency of *Ariadna* burrows over time (Fig. 1, Table 2) suggest that 1) the heavy rainfall of March 2000 influenced the closing/opening of burrows in some spiders; 2) once the rain event ended, adults tended to keep their large burrows closed for weeks, whereas smaller spiders opened their burrows soon thereafter, if they closed them at all; 3) the proportion of open small burrows increased over time (rising from 0.2 to 0.5); 4) the proportion of closed medium size burrows (0.5) did not change significantly over time.

Exceptional rain events can change the landscape and endanger survival in desert environments, compelling arid-adapted organisms to resort to alternative strategies (Cloudsley-Thompson 1983). Indeed, adults of *Ariadna* spiders in this work appeared to cope with the flooding by plugging their burrows long-term with a stone or a lichen piece. It remains to be determined whether small and medium size spiders exhibit the same behavior on a short-term basis, such as during the downpour itself and a few days thereafter.

It is well known that many terrestrial arthropods are able to withstand prolonged submersion in water (Cloudsley-Thompson 1958). Interestingly, a closely related species, *Ariadna bicolor* (Hentz, 1842), was shown to survive long periods of experimental submersion,

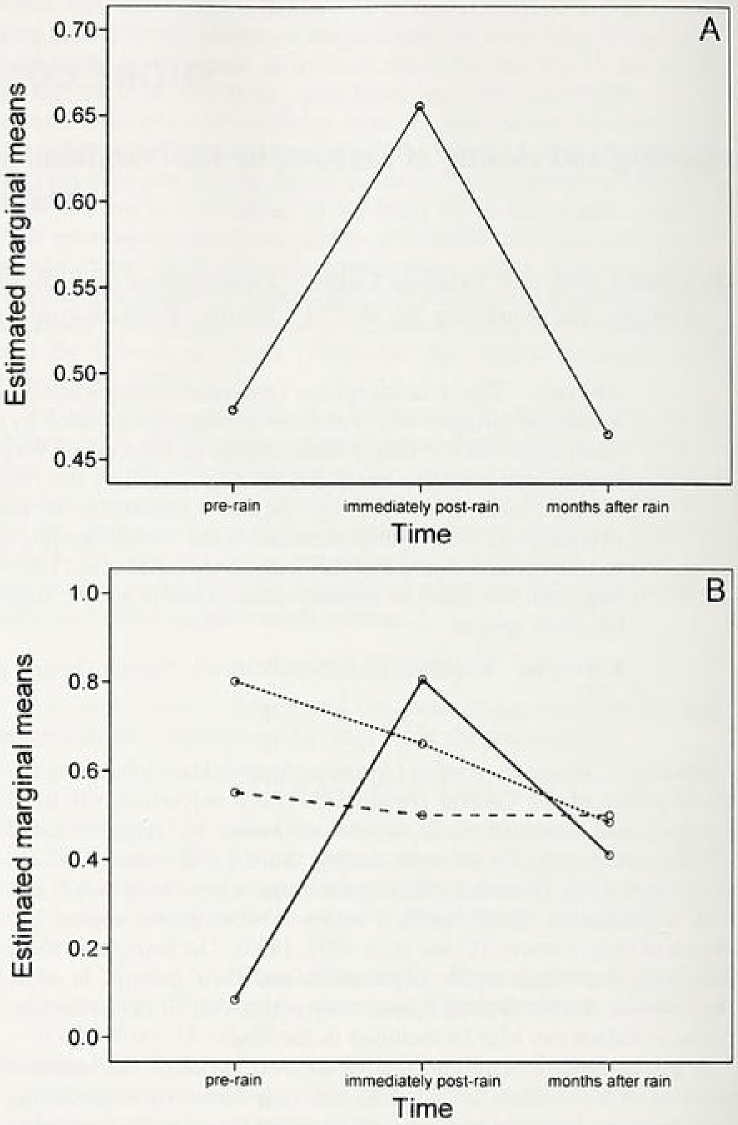

Figure 1.—Plot of estimated marginal means of proportions of closed burrows of *Ariadna* sp. in the three different time periods with respect to rainfall of March 2000: A) all 175 burrows, B) each size class. Values in the graphs refer to the mean values of closed burrows as specified in Table 2. Symbols for graph B: dotted line = small burrows, dashed line = medium burrows, continuous line = large burrows.

Table 1.—Post-hoc Bonferroni comparisons for rainfall effect based on estimated marginal means of all *Ariadna* closed burrows.

(I) Time	(J) Time	Mean difference (I–J)	SE	*P*
pre-rain ($m = 0.461$)	immediately post-rain	−0.177*	0.042	0.000
	months-after rain	0.014	0.037	1.000
immediately post-rain ($m = 0.674$)	pre-rain	0.177*	0.042	0.000
	months-after rain	0.191*	0.037	0.000
months-after rain ($m = 0.460$)	pre-rain	−0.014	0.037	1.000
	immediately post-rain	−0.191*	0.037	0.000

Table 2.—Statistical parameters of proportions of closed burrows of the *Ariadna* sp. inhabiting a Namibian gravel-lichen plain according to mm-size class of the entrance diameter and the different time periods (pre-, immediately post- and months-after rain).

Group	Time	Mean	Std. Error
small	pre-rain	0.801	0.038
	immediately post-rain	0.661	0.058
	months-after rain	0.484	0.048
medium	pre-rain	0.551	0.044
	immediately post-rain	0.5	0.067
	months-after rain	0.5	0.056
large	pre-rain	0.084	0.036
	immediately post-rain	0.806	0.056
	months-after rain	0.41	0.046

especially when maintained in their silk-lined burrows (Rovner 1987). Rovner's report led us to predict that our spiders do not close the entrance of their burrows to avoid the direct contact with rainwater; rather, we think that burrow-plugging could prevent the destruction of the spider's home and the expenditure of energy necessary to its subsequent reconstruction. Indeed, previous observations carried out on *Ariadna* sp. living in areas near Gobabeb (Namibia) (Costa et al. 1993), showed that after a sudden storm in March 1993, several burrow entrances appeared closed with silk and sand and their ring stones scattered. Spiders spent the whole night rearranging their burrow and replacing the stones around the mouth.

The *Ariadna* sp. population of the present study lives in a habitat very rich in lichens. Lichens, an important component of biological soil crusts, act in soil stabilization and in increasing primary production (Lalley & Viles 2005). They play an especially important function in hyperarid areas, such as the Namib Desert, where fog events are regular and sporadic, heavy rainfall occurs (Lalley et al. 2006). Lichen communities are often species-rich and densely crowded with complex biotic interactions (Wessels et al. 1979; Tuba et al. 1998). They provide a milieu that enables the arthropod community to survive extended periods of desiccation within a thallus micro-habitat (Seaward 2008). Not surprisingly, in the burrow-surrounding rings of adult *Ariadna* spiders, the number of pieces of lichen exceeds the number of stones, as the correlation analysis indicated. In our opinion, these animals can avoid desiccation due to fog moisture retained by lichens and receive a trophic benefit from lichenophagous prey.

Brief rain pulses, lasting at most several hours, as is characteristic in the Namib Desert, affect the population growth of organisms like soil-dwelling microfauna (Schwinning & Sala 2004). Researchers have also pointed out (Yang et al. 2008) that rain events act as "resource pulses" that are especially important in xeric environments such as deserts, which are described by Noy-Meir (1973) as "pulse-drive ecosystems." Hence, our results lead us to hypothesize that the heavy rain of March 2000 did not pose a real risk for *Ariadna* spider survival and, on the contrary, that it likely served as a hydrating resource pulse.

Ariadna spiderlings responded to rain differently than adults, possibly because they need to forage frequently. Their burrows are shallow and almost always surrounded only by sand grains; therefore, the rainwater, in addition to the fog moisture, makes sand still more compact, reducing the risk of burrow collapse caused by high winds that characterize the area. Unlike adults, spiderlings cannot survive for long periods without feeding. By opening their small burrows shortly after a rain event, they can benefit from the increased probability of intercepting tiny mites or springtails that live on the soil surface of the Namib Desert (André et al. 1997) and are washed by rainwater into the spider burrows. In other words, we hypothesize that rain pulses can turn into immediate "trophic resource" pulses (Yang et al. 2008) for the *Ariadna* spiderlings.

Finally, "medium size" subadult spiders did not show temporal changes in their burrow opening/closing activity. This perhaps occurred due to a reduced risk of collapse of their burrows and the impelling necessity to gain from the prey the energy required for their molts.

More research is necessary in order to make clear many aspects of the biology of this undescribed *Ariadna* species. Its life cycle is as yet poorly understood. Moreover, we failed to collect any male specimens, so species determination was not possible. Knowing that the Central Namib Desert is a hotspot of endemism for many vertebrates and invertebrates (Simmons et al. 1998; Prendini & Esposito 2010), we suspect that our *Ariadna* sp. might turn out to be another endemic arthropod.

ACKNOWLEDGMENTS

We would like to thank the Ministry of Environment and Tourism, Namibia, for a permit to work in the Namib-Naukluft Park and to collect some specimens of *Ariadna*. We would also like to express our thanks to Prof. Claudio Barbaranelli, University of Rome, for helpful discussion and advice with statistical analysis. We especially thank the Associate Editor, Dr. Linden Higgins, and two anonymous reviewers for providing constructive critiques of the manuscript. Financial support was provided by the Ministry of University and Scientific Research of Italy.

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Manuscript received 16 January 2013, revised 4 May 2013.