THE WASP SPIDER *ARGIOPE BRUENNICHI* (ARACHNIDA, ARANEIDAE): BALLOONING IS NOT AN OBLIGATE LIFE HISTORY PHASE

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ABSTRACT.   Aerial dispersal (''ballooning'') of *Argiope bruennichi* spiderlings has been claimed to be an obligate life history trait and a prerequisite for spinning prey-capture webs. If this were true, a ballooning phase would be essential for any laboratory rearing of *A. bruennichi* making rearing protocols particularly elaborate. We tested the significance of ballooning for second-instar spiderlings in the laboratory and showed that the ballooning behavior is not essential for building prey-capture orb webs. Our results also give no evidence for the hypothesis that recent natural selection has changed ballooning behavior in newly founded field populations.

Keywords: Araneae, ballooning experiment, laboratory rearing, web-building behavior.

Ballooning is a common dispersal mechanism for many modern spiders (Coyle 1983; Dean & Sterling 1985; Weyman 1993), and this behavior is particularly important for maintaining genetic cohesion among *Argiope* populations (Ramirez & Haakonsen 1999). The life history of *Argiope* is characterized by ballooning, the aerial transport on wind-blown silk threads. A good example for the importance of ballooning for range expansion is the Palearctic wasp spider *Argiope bruennichi* (Scopoli 1772). The spider is an r-strategist (Guttmann 1979), characterized by high aerial dispersal capability and an ongoing postglacial expansion of its geographical range in Europe (van Helsdingen 1982). Females of *A. bruennichi* produce up to five cocoons in the field, often containing several hundred eggs (Crome & Crome 1961; Köhler & Schäller 1987). The expansion of the species has accelerated in the second half of the last century probably due to factors favoring dispersal by ballooning (Guttmann 1979; Levi 1983; Sacher & Bliss 1990; Scharff & Langemark 1997; Jonsson & Wilander 1999; Smithers 2000). The wasp spider prefers grassy or herbaceous vegetation in open, ephemeral or shrubby sites (Wiehle 1931; Pasquet 1984; Malt 1996) in coarse-grained (patchy) landscapes (Gillandt

& Martens 1980; Sacher & Bliss 1989) and has regionally benefited from an extension of farming production and urbanization (Lohmeyer & Pretscher 1979; Arnold 1986; Nyffeler & Benz 1987). River valleys have been identified as favored dispersal corridors further supporting the importance of ballooning for dispersion (Gauckler 1967; Puts 1988).

Follner & Klarenberg (1995) claimed ballooning to be an obligate phase in the development of *A. bruennichi*. These authors monitored the pre-ballooning and ballooning behavior of spiderlings in a grassland study site near Munich (Germany). Since they never found aggregations of orb webs in the neighborhood of the cocoons from which the overwintering second instar spiderlings eclosed and they only observed the construction of first prey-capture orb webs after a ballooning trip, they concluded ''that aeronautic behaviour in Bavarian populations of *A. bruennichi* is obligatory''. Moreover, these authors suggested that spiderlings, which have hatched from the cocoon, will starve to death, unless they perform a ballooning trip. Ballooning should thus be an obligate phase to switch from a non-predatory, passive phase to one of active predation by spinning prey-capture orbs. Follner & Klarenberg (1995) argued that the obligatory aerial dispersal might be a result of recent natural selection and be the rea-

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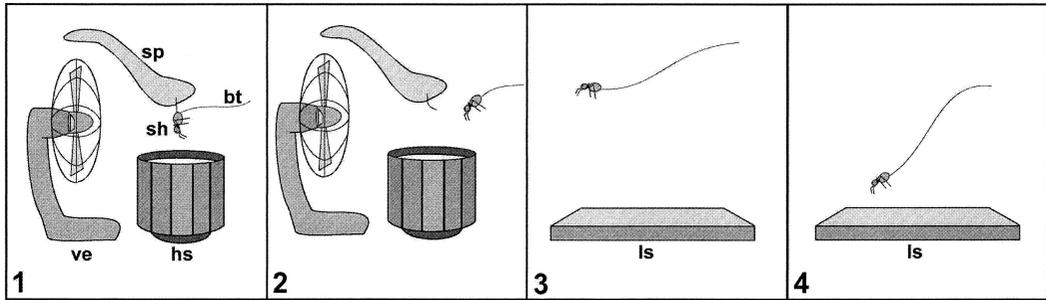
Figures 1–4.—Design and course of the ballooning experiment. The spiderlings were placed on a spatula (sp) and exposed to a light air current by a fan (ve) and heat source (hs), which were placed at the left edge of a lab bench (240 cm). After cutting the drag line the spiderlings became airborne to land on the lab bench, which served as a landing strip (ls). 1. Pre-ballooning behavior: sp = spatula; ve = ventilator (light breeze); hs = heat source (25 Watt lamp, distance to spatula = 20 cm); sh = spiderling hanging from a dragline; bt = ballooning thread. 2. Initial ballooning phase. 3. Airborne spiderling: ls = ''landing strip'' (lab bench of 240 cm length). 4. Landing phase.

son behind the swift expansion of the species. New populations which are established during a period of expansion are always founded by individuals, which have ballooned.

If ballooning were a truly obligate phase, it would not only be important for natural selection but also be important for any rearing protocol for *A. bruennichi*. Allowing for ballooning in a rearing procedure might easily render laboratory breeding unfeasible as it could prove to be too time-consuming and laborious. However, an obligate ballooning phase has never been observed before, neither in other *Argiope* nor in the generally well studied *A. bruennichi*. Tolbert (1976, 1977) studied ballooning behavioral elements of *A. trifasciata* (Forskål 1775) and *A. aurantia* Lucas 1833. He concluded from field and laboratory observations that ''it is unnecessary for spiderlings of either *Argiope* species to engage in aerial dispersal before building an orb web'' (Tolbert 1977), which is an obvious discrepancy to Follner's and Klarenberg's (1995) claims. We here test the significance of ballooning for the construction of the first prey-capture web in the laboratory by comparing spiderlings reared under two experimental conditions, one with and one without ballooning.

We collected cocoons of *A. bruennichi* (*n* = 6) in dry and semi-dry grasslands northeast of Halle (Saale) in late April 2002 (Germany, 160 m a.s.l., 51°33′31″ N, 011°52′49″ E). They were maintained in the lab in individual glass vials (9 cm diameter, 13 cm height, coated with fine gauze) at 23 ± 2 °C and mist-sprayed with water every two days to avoid desiccation. The vial bottom was covered with initially wet cellulose wadding (1 cm). Second-instar spiderlings hatched from the cocoons in early May.

One day after hatching we simulated individual ballooning for 60 spiderlings (10 from each cocoon) by exposing the spiderling on a spatula to an air stream generated by a heat source and a fan (see Figs. 1–4 for details of the experimental design). We observed behavioral elements in the pre-ballooning phase in detail and noticed its mode. When the spiderling became airborne, we tracked it and retrieved it at the ''landing strip'' (Figs. 3, 4). The ballooning experiment was repeated immediately (re-ballooning) for each individual to satisfy a possible ''ballooning drive'' (see Tolbert 1977). The spiderlings had to actively participate in this experiment by showing the entire sequence of pre-ballooning and ballooning behavior (Figs. 1–4).

Following the experiments, the ''ballooners'' were kept in the same unheated indoor room with windows admitting indirect natural light. They were housed in groups (*n* = 20) in three gauze covered glass terraria (50 × 30 × 31 cm; 25 ± 3 °C; 65 ± 10% RH) and fed ad libitum 45–50 live *Drosophila melanogaster* once a day. Every two days we sprinkled the inside surfaces of the terraria with water. This prevented desiccation and allowed for
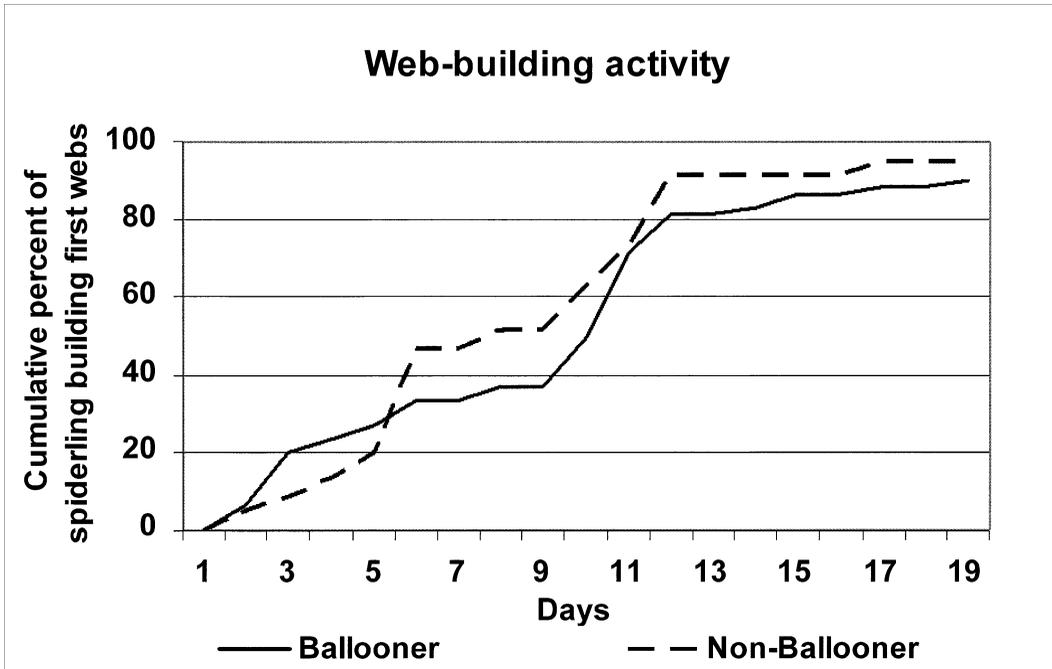
Web-building activity

Figure 5.—Web-building activity of the *A. bruennichi* spiderlings during laboratory rearing for both ballooners and non-ballooners.

normal drinking behavior of the spiderlings. The bottoms of the terraria were covered with a layer of commercial, pasteurized potting soil (3 cm) with grass tufts, some dry twigs and wooden skewers to enhance the number of potential attachment points for web building.

A control group of spiderlings ($n = 60$) was treated in the same way, but without the ballooning procedure (''non-ballooners''). In both groups (ballooners vs. non-ballooners) spiderlings and orb webs were noted three times daily at 6 a.m., 12 p.m. and 6 p.m. to ensure individual based data sets. The rearing period was cut off after 19 days when all the surviving individuals had spun their first prey-capture orb-webs.

Voucher specimens are deposited in the Entomological Collection of the Martin-Luther-University Halle-Wittenberg (Zoological Institute), Germany (identification number 2568).

The web-building activity of the spiderlings increased in both the ballooners and the non-ballooners over time and reached $90 \pm 5\%$ for ballooners ($n = 54$, three terraria) and $95 \pm 5\%$ for non-ballooners ($n = 57$, three terraria) within a period of 19d (Fig. 5). The differ-ences in the web-building activity (Fig. 5) were not statistically significant between the two groups of spiderlings (Kruskal-Wallis test, $P = 0.7515$; tested for daily built-first webs). The mean latency time for web-building (time from hatching from the cocoon to the construction of the first prey-capture web) was 8.61 ± 4.28 days and 8.18 ± 3.60 days for ballooners ($n = 54$) and non-ballooners ($n = 57$) respectively. This difference was not statistically significant (t-test, $P = 0.56$).

Although mortality increased in the second half of the observation period (Fig. 6), it did not exceed 22% at the end of the experiment (ballooners: $21.7 \pm 2.89\%$, $n = 13$, non-ballooners: $20.0 \pm 8.66\%$, $n = 12$, difference not significant, t-test, $P = 0.77$). The surviving animals caught prey in their orb webs and showed normal development with up to four molts within the experimental time.

Using our protocol, we could initiate the full sequence of ballooning behavior promptly in every experiment. The *A. bruennichi* spiderlings always showed an identical sequence of pre-ballooning and ballooning behavior (Fig. 1–4). When exposed to the heat from the lamp, they displayed the ''ballooning drive''
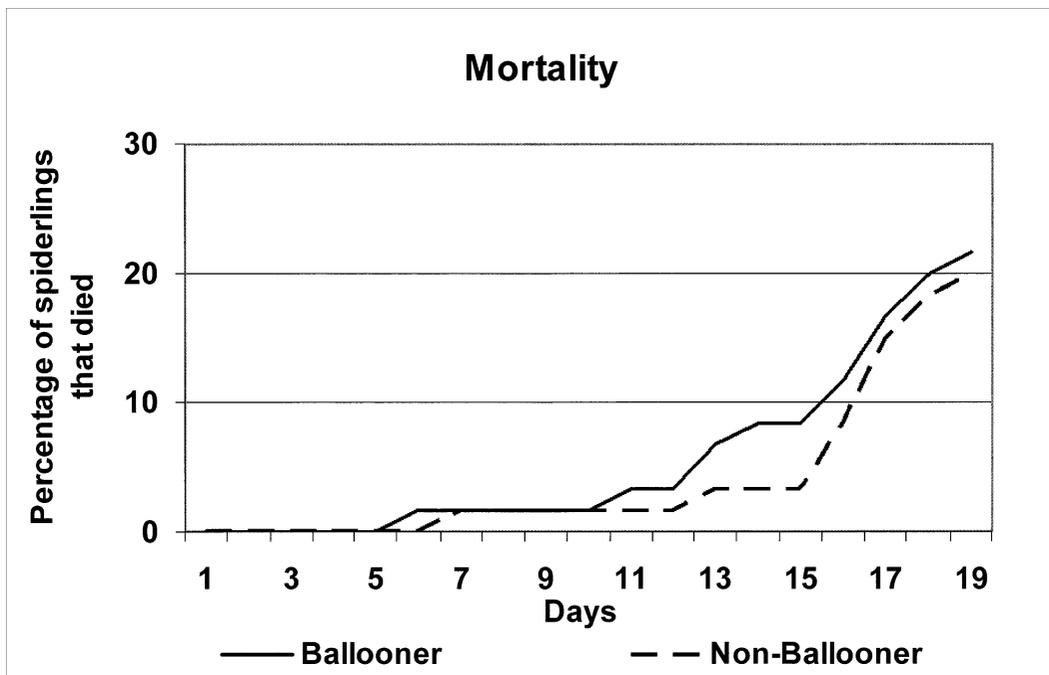
Mortality

Figure 6.—Mortality of the *A. bruennichi* spiderlings during laboratory rearing.

behavior. Individuals walked to the margin of the spatula, spooled out a dragline and dropped down hanging from the line. While suspended and holding on to the drag line, they let out an additional line of 50–100 cm ballooning silk (Fig. 1). When this was lifted by the breeze generated by the fan and the heat source, the spiderlings cut the dragline and became airborne (Figs. 2, 3). After landing (Fig. 4) they hauled in the ballooning line, formed it with the legs into a silk blob and finally ate the silk, bringing the ballooning behavioral sequence to completion.

Tolbert (1977) observed two modes of preparation for ballooning in sympatric field populations of *A. trifasciata* and *A. aurantia*. A spiderling attempting to become airborne climbed to the top of some blade of grass or other structures and adopted the typical ''tip-toe'' posture by depressing the cephalothorax and elevating the opisthosoma. Multiple silk lines were then exuded from the spinnerets. When moving air generated sufficient silk, the spiderling became a ''ballooner'' (Nielsen 1932; Richter 1970; Eberhard 1987). Alternatively, the spiderling could become airborne by dropping and hanging from a dragline, spinning a ballooning thread, which then grad-

ually lifted and lengthened in the breeze. The ballooner then cut the dragline and floated off into the air (Nielsen 1932; Bristowe 1939).

Argiope bruennichi can display both pre-ballooning modes. However, the drop and dragline mediated ballooning seems to be more frequent (Follner & Klarenberg 1995). In the field, second-instar spiderlings usually attach the draglines to tips of grass blades or they use silk threads which connect the tips of grass haulms as attaching points (Follner & Klarenberg 1995). In our experiments, we offered individual spiderlings optimal starting conditions, and we never observed the tip-toe ballooning mode. Follner (1994) suggested that ''tip-toe'' might be a tactical alternative for individuals in unfavorable starting points (e.g., overcrowded tips of grass blades).

Our results show that it is not necessary for spiderlings of *A. bruennichi* to engage in aerial dispersal before building a prey-capture web. While ballooning is frequent in the field (Follner & Klarenberg 1995), it is clearly not an obligate part in the development of this species. In spite of the rapid expansion of the species over the past decades and the potential importance of aerial dispersal for colonizing new habitats, the role of ballooning in *A.*

bruennichi does not differ from *A. trifasciata* and *A. aurantia* where this phase in life history is also not obligate (Tolbert 1977).

The mortality of about 20% after 19 days in both experimental groups (difference statistically not significant) suggests that rearing of *A. bruennichi* spiderlings to adulthood may be challenging. Our rearing method based on a diet with *Drosophila melanogaster*, similar to Müller & Westheide (1993), worked well for our purpose, where we only tested the effects of ballooning in second-instar spiderlings on their ability to make their first web.

On average, more then eight days elapsed before *A. bruennichi* spiderlings began to build their first prey-capture web. This appears to be a surprisingly long period, because the animals can only feed once the first web is built. We cannot exclude that this is a laboratory artifact, for example due to unattractive sites for web construction. However, the long latency did not interfere with the rearing regime. The animals appeared to be well adapted to temporary starvation because the mortality was low in this phase (Fig. 6). Also in the field, the spiderlings do not immediately start with prey-capture web construction (Follner & Klarenberg 1995) and endure extended periods of starvation. *Argiope* spiderlings easily survive several days nearby their cocoons, sometimes with communal meshworks of interlocking dragline threads (''communal tangles'') (Tolbert 1976, 1977; Follner & Klarenberg 1995) where they find shelter until favorable weather or microclimate conditions allow for ballooning (Tolbert 1977; Follner & Klarenberg 1995; see also Suter 1999 for physics of ballooning).

Argiope spiderlings actively select suitable web sites by ballooning, re-ballooning or walking (Enders 1973; Tolbert 1977; Follner & Klarenberg 1995). Also in this nonpredatory phase the spiderlings must avoid starvation. Tolbert (1976) kept *A. aurantia* spiderlings in the laboratory without food and water. Mortality remained moderate in these experiments for several days and only increased distinctly about two weeks after hatching.

The behavioral ballooning sequence could be easily triggered under artificial conditions in our study, suggesting that it will also occur in the field whenever environmental conditions allow. Therefore dispersal and population structure will be primarily driven by mi-

croclimatic conditions in the local habitats. The local persistence of non-emigrants (non-ballooners and short-distance ballooners) in *A. bruennichi* populations might facilitate aggregated dispersion patterns, just as in weather phases which are unfavorable for aerial dispersal. Given ballooning is a less effective means of long distance dispersal than previously thought (Roff 1981; Decae 1987; Wise 1993; Bonte et al. 2003), this could also explain the genetic differentiation among habitat patches in other *Argiope* species (Ramirez & Haakonsen 1999).

The role of natural selection in range expansion has recently been discussed for insects in the context of global warming (e.g., Pimm 2001; Thomas et al. 2001). However, improving environmental conditions at range margins can initiate range extensions purely on the basis of ecological, physiological and population-dynamic processes not requiring any evolutionary change (Thomas et al. 2001; see also Coope 1995; Williamson 1996). Our results are in line with these views and reject the hypothesis of Follner & Klarenberg (1995) that evolutionary processes have changed ballooning behavior in newly founded populations.

ACKNOWLEDGMENTS

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