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Aeronautic behaviour in the wasp-like spider, *Argiope bruennichi* (Scopoli) (Araneae, Argiopidae)

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Aeronautic behaviour, aerial dispersal, ballooning, spiders, *Argiope bruennichi* micrometeorology

Abstract. In only a few decades, *A. bruennichi* has colonized vast areas of continental Europe. This was most likely achieved by the ballooning of young spiderlings. Its original distribution was largely restricted to the Mediterranean. This makes *A. bruennichi* an interesting object for studying the proximate factors, behavioural and micrometeorological, which lead to this rapid mode of dispersal.

After eclosion from their cocoons on sunny days in spring, the spiderlings climb into the top of vegetation. Two modes of take-off can be observed. The most common method is by starting from the top of a grass haulm. However, if many spiderlings have emerged from their cocoons, they will start from a "trapeze", a diffuse construct of silken threads connecting grass blades. In both cases they initiate ballooning by dropping on its dragline.

As no aggregations of orb webs were detected in the direct proximity of the cocoons from which spiderlings eclosed, and their first orb web was only constructed after a ballooning trip, we consider aeronautic behaviour to be an obligatory element of *A. bruennichi*'s life cycle in southern Germany.

With respect to the micrometeorological conditions, it appeared that ballooning activity correlated highly significantly with weather conditions causing thermals, which *A. bruennichi* is apparently able to perceive. The factors which could ultimately be responsible for the rapid invasion of large parts of Europe are discussed briefly.

INTRODUCTION

A. bruennichi has remarkably expanded its original range, the Mediterranean and some isolated localities in Central Europe. In less than 50 years it has invaded vast areas of Europe, avoiding only the northern parts (Guttmann, 1979; Rollard, 1990; Sacher & Bliss, 1990). In southern Bavaria, for example, well established populations of this species have been known since 1965. This makes it attractive for investigating behavioural and ecological questions associated with aerial dispersal, ballooning, in *A. bruennichi.*

Most of the field investigations on ballooning in spiders, however, concern records of trapped ballooning or landing spiders. Therefore, the behaviour before lift-off (pre-ballooning behaviour) and the conditions suitable for it have not been well observed (Weyman, 1993). Vugts and Van Wingerden (1976) observed a positive correlation between ballooning activity of linyphiids and thermals, caused by temperature differences between the top of the vegetation and one meter height. It appeared that solar radiation, which heats the air layer above the vegetation, creates a turbulent air convection. The strong vertical component of the convection is necessary for traveling through the air. In the present study we have investigated the pre-ballooning behaviour and some micrometeorological conditions which may induce ballooning *A. bruennichi.*

METHODS

The study site was a hilly range of grassland in southern Bavaria near Munich. The field experiment lasted from May to early June of 1993. The weather during this period was warmer and sunnier than usual.

Young *A. bruennichi* spiderlings can be found here in their first orb net from the end of April on. They become adults in July. From the middle of August until death in early October the females usually produce one to three egg cocoons. The cocoons contain an average of 300 eggs. In autumn the spiderlings eclose from their eggs and molt once. They hibernate in their cocoon. From the end of April until early May they eclose and become airborne.

For our investigations we used 63 cocoons produced at the study site by *A. bruennichi* females in the autumn of 1992. In addition, 80 cocoons, collected at different localities near Munich, were placed at the study site. The eclosing and starting second-instar spiderlings were counted at twenty-minute intervals. Video film recordings were made to analyze the spiderlings' behaviour. While their behaviour was being observed, micrometeorological data were collected automatically. The ambient temperatures at six heights (0, 13, 33, 55, 98, 197 cm) above ground level, the temperatures of 26 cocoons and the wind speed over the vegetation (55 cm) were measured automatically every ten minutes. Situations with thermals, indicated by the difference between the temperatures above vegetation and 2 m height, were compared with ballooning activity.

RESULTS

Pre-ballooning behaviour

On dry and sunny periods during the daytime from late April until early June 1993 the second instars of *A. bruennichi* left their egg cocoons and climbed into the upper part of the vegetation. The most common method to become airborne was by starting from

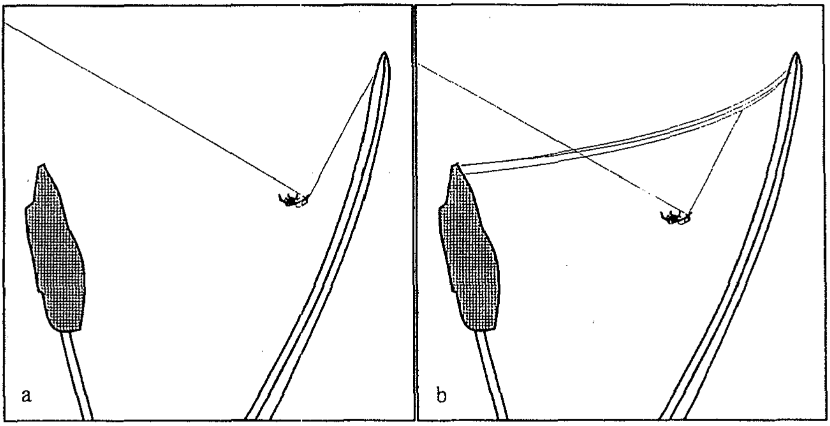

Fig. 1. *A. bruennichi* spiderlings show two alternative methods of take-off: (a) by dropping from the tip of a grass blade; or (b) by dropping from a trapeze of silk connecting the tips of one or more grass haulms which may facilitate the simultaneous lift-off of many individuals.

the top of a grass haulm (Fig. 1a). If many individuals have eclosed, the spiderlings build a "trapeze", a diffuse construct of silken thread connecting grass haulms (Fig. 1b). This form of cooperation facilitates rapid lift-off of many spiderlings over short periods. Then the spiderlings initiated ballooning by dropping about 10 cm on its dragline from the extreme ends of grass haulms or a trapeze. Simultaneously, the spiderlings turned their spinnerets upward and usually produced one line of ballooning silk. If the drag on the ballooning line became strong enough for ballooning, the safety line onto which the spiderlings were hanging broke and they became airborne. It seems that the chelicera were not used for cutting the safety line because they were orientated to the ballooning line (Fig. 2).

"Tip-Toe" behaviour, as defined by Richter (1970), was observed only very rarely. Occasionally, a spiderling's ballooning thread became entangled. By trial and error these spiderlings searched for the best point locally for lift-off in the top of the vegetation. They always used thermals to become airborne.

All the spiderlings of a single cocoon never eclosed in just a few hours. Usually, the spiderlings leave their cocoons in small groups in a period of some days (Fig. 3), the average being 3.8 days. Normally, they try to become airborne about half an hour after

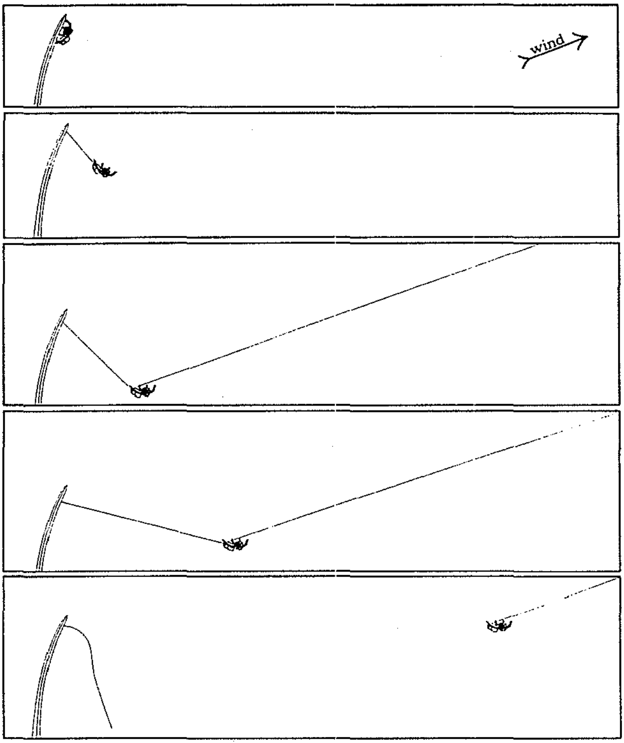

Fig. 2. A schematic presentation of the behavioural sequence of the lift-off from the tip of a grass blade. This usually takes as number seconds.

eclosion, so there was no time-lag related to the 20 min counting interval. Spiderlings which have already left their cocoon but cannot balloon because of unexpectedly adverse weather conditions (high windspeed, rain) may construct a communal web. There they rest until thermals are rebuilt. During the three weeks of the investigation only one communal web was observed. The eclosed A. bruennichi spiderlings did not show any form of cannibalism. The ethogram in Fig. 4 summarizes the possible behavioural elements and sequences involved in the pre-ballooning behaviour of *A. bruennichi.*

An additional laboratory experiment (Follner, 1994) showed how spiderlings may orientate when they try to find a suitable place for lift-off after eclosion from their cocoon. Both positive phototaxis and negative geotaxis play an important role. But negative geotaxis is significantly more important. In the field, both abilities for orientation are always combined.

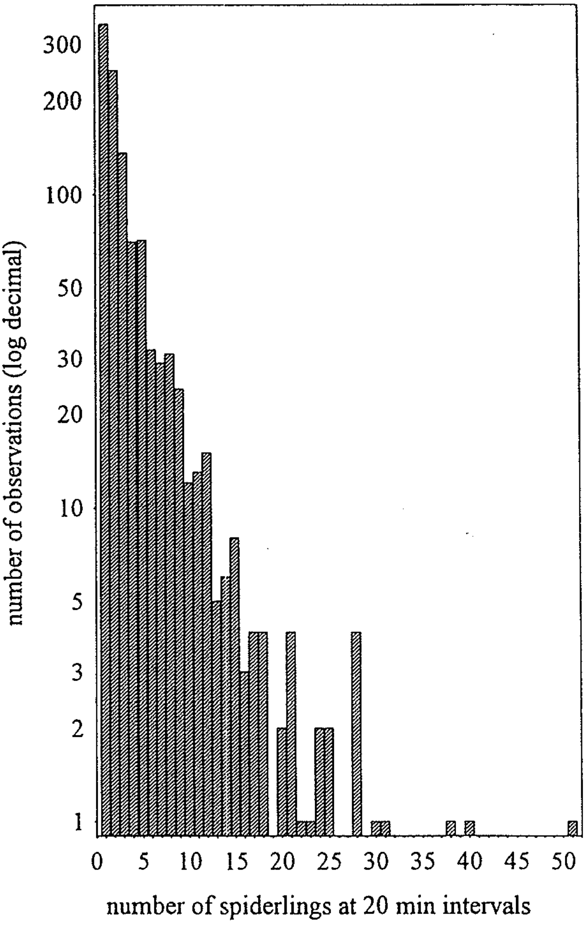

Fig. 3. Frequency of totals of *A. bruennichi* spiderlings eclosing from cocoons during 20min intervals in May, 1993.

As no aggregations of orb webs were detected in the neighbourhood of the egg cocoons from which spiderlings eclosed, and since they only constructed their first orb web after a ballooning trip, we conclude that aeronautic behaviour in Bavarian populations of *A. bruennichi* is obligatory.

Ballooning and micrometeorology

The ballooning activity of *A. bruennichi* showed a highly significant correlation with the thermal indicator ($R_S = 0.509$; $p = 0.00000$; $N = 219$), which represents the instability of the temperature stratification. Instability means that the temperature of an air layer decreases with height faster than the dry adiabatic laps rate (Stull, 1988). A good indicator for this instability is the difference between the temperatures just above the vegetation and a reference at 2 m height, called the thermal indicator (Follner et al. 1995, in prep.). Light wind gusts, 0.5–1.0 m/s, which are continuously generated in turbulent air masses, were important for take-off. A decrease in air temperature in the late afternoon or rain resulted in a collapse of the instable boundary layer and stopped ballooning immediately. Spiderlings of *A. bruennichi* are apparently able to perceive sutiable weather conditions for ballooning trips.

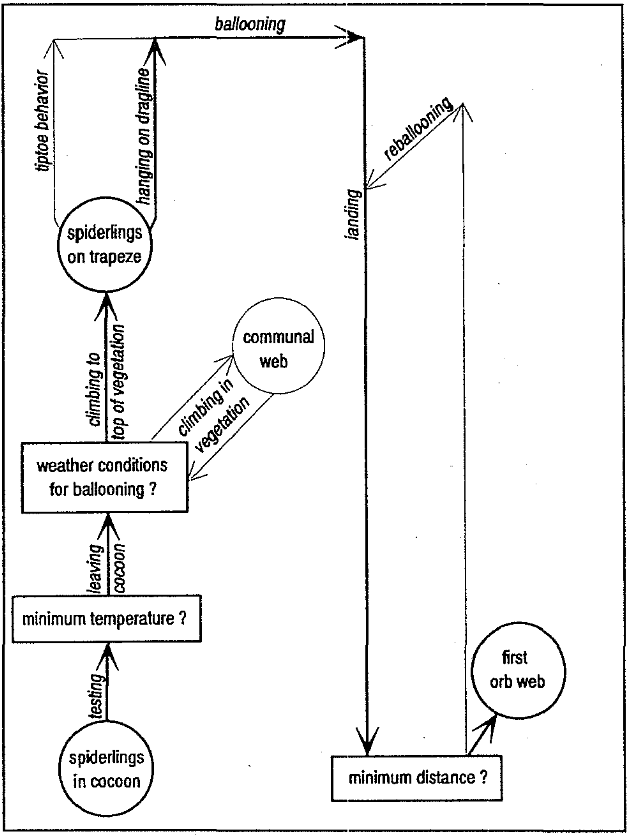

Fig. 4. Ethogram of the ballooning behaviour in *A. bruennichi*. Bold arrows indicate major behavioural sequences; thin arrows represent rare behavioural sequences.

DISCUSSION

Aeronautic behaviour is an obligatory part of the life cycle in southern Bavarian populations of *A. bruennichi.* This result is surprising for us because we could not find any corroborating reports in the literature stating that ballooning could be obligatory. Our results differ from those of Tolbert (1977) on two North American *Argiope* species, *A. aurantia* (Forskal) and *A. trifasciata* (Lucas). Their spiderlings can be reared successfully after eclosion from their cocoons without having ballooned at all. We may infer that in contrast to *A. bruennichi,* aeronautic behaviour in the other two *Argiope* species is not obligatory.

It would be very interesting to know whether ballooning is obligatory in long established populations of *A. bruennichi* in the Mediterranean. We believe that new populations established during a period of expansion, such as those in southern Bavaria, are always founded by individuals which have ballooned. Therefore, these populations may be selected for this behaviour.

A pilot experiment to investigate the minimum ballooning distance achieved by ballooning in *A. bruennichi* spiderlings (Follner & Klarenberg, unpublished) suggests that a small portion of any source population lands in its original habitat. Three of the 200 to 300 spiderlings which ballooned were recovered within two hours at distances of 3.7 m, 4.4 m and 29.7 m from the point of release in their first orb web. One of them, which travelled only 1.4 m, ballooned again. This indicates that obligatory ballooning does not necessarily lead to an emptying of a local population. In addition, there may be an influx of ballooning spiderlings from neighbouring populations.

The incidence of obligatory ballooning in spiders may be linked to the stability of the habitat, as proposed by Richter (1970). He demonstrated that those *Pardosa* species which live in rare or instable habitats show a higher dispersal activity than *Pardosa* species of relatively stable habitats. *A. bruennichi* lives in fallow land, an extremely variable habitat, both temporally and spatially. So it is forced to use an efficient dispersal mechanism to reach suitable areas. Nevertheless, ballooning may be very risky for individual spiderlings. The weather conditions during eclosion from their cocoons may not always be suitable for ballooning. Apparently, *A. bruennichi* has evolved a strategy which compensates the risks of adverse weather in spring by eclosing in many small groups over a period of several days or by constructing a communal web for resting during adverse weather, as Tolbert (1977) reported for *A. aurantia.*

We could only observe aeronautic behaviour in the second-instar spiderlings of *A. bruennichi.* The adult females are relatively stationary (Crome & Crome, 1961). Because of their body-weight adult females do not disperse by air. Moreover, it is most improbable that all the arachnologists who investigated *A. bruennichi* overlooked ballooning in later instars.

The results of the weather conditions used by *A. bruennichi* for ballooning corroborate earlier results in linyphiids (Vugts & van Wingerden, 1976). Only the maximum of windspeed for ballooning of 3 m/s could not be found, simply because windspeed was generally lower during the period of the study. Based on estimations of the speed of dispersal by *A. bruennichi* during the process of colonization of southern Germany by *A. bruennichi* (Guttmann, 1979; Follner, 1994), it appears that ballooning spiderlings could travel at least a number of kilometers. However, there are no reliable field data on the travelling distances of these spiderlings. This could be one of the most interesting questions for further investigations.

Apart from the proximate factors which induce ballooning, it remains to be seen which factors are ultimately responsible for the rapid colonization of wide areas of Europe. It would be particularly intriguing to know whether a change in climate could have influenced the rapid expansion of *A. bruennichi.* We may hypothesize that global warming (Peters & Lovejoy, 1992) is one of the determinants which has enabled *A. bruennichi* to complete its life-cycle successfully in more northern regions of Europe.

Ballooning seems to be very important ecologically, for both short and long range dispersal in spiders (Weyman, 1993). Consequently, it ensures survival in the temporally and spatially varying habitats used by *Argiope bruennichi.*

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