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Hunger induces aeronautic activity in the tropical spider *Cupiennius salei* (Araneae: Ctenidae)

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ABSTRACT   Contrib. Nat. Hist. 12: 1283–1293.
In this study the ballooning frequency of newly hatched fed or hungry spiderlings of the neotropical wandering spider *Cupiennius salei* (KEYSERLING) (Araneae, Ctenidae) was investigated in a wind tunnel experiment. Fully fed spiderlings showed a typical behaviour with common aeronautic activity at certain wind speeds a few days after hatching from the cocoon. If unfed spiders were exposed to the same physical conditions, they showed a higher climbing and ballooning tendency for a much longer period of time. This enhanced successful take-off of hungry spiders indicates that spiderlings balloon in a disadvantageous environment if the stimulating factor hunger is present, and migrate by this means into other habitats (hunger hypothesis).

Keywords: Ballooning, dispersal, age-related, wind-tunnel

Introduction

Ballooning is a form of aerial dispersal widespread among spiders. It is due to the drag induced by air motion on a spider's body and, more importantly, on the silk filament attached to it (Humphrey 1987). The spider-dragline pair is lifted from the ground by the vertical component of the frictional drag, provided this force component at least matches the spider's mass. Horizontal movement is likewise due to the horizontal component of drag (Barth et al. 1991).

Factors influencing aeronautic behaviour can act at three stages in the ballooning process: (1) factors stimulating climbing (biotic or abiotic); (2) factors stimulating "tip-toe behaviour" or "thread-hanging" at the prominent position attained by the climb (abiotic); (3) factors allowing take-off and flight (abiotic). Most research concerning ballooning has examined when, and under what abiotic conditions, the spiders disperse (factor 3), and has not directly investi-

gated biotic factors underlying the motivation of spiders to balloon (see Weyman 1993 for a review).

There are many observations on aeronautic behaviour elicited by certain environmental stresses (e.g. van Wingerden 1977; Duffey 1979). Duffey (1979), for instance, observed mass spider dispersal after drying out of the environment, which had the secondary effect of reducing available prey. Food deprivation was investigated by Legel & van Wingerden (1980) who found that spiders raised individually in conditions of food shortage showed a higher frequency of tip-toe behaviour (factor 2) in the laboratory than fully fed spiders (hunger hypothesis). Weyman et al. (1994, 1995) first presented a significant positive correlation between tip-toe and take-off according to a series of experiments with *Erigone* spiders. This implies that tip-toe in a previous food deprivation experiment (Weyman et al. 1994) was a reliable index of take-off and they concluded that hungry spiders balloon more frequently than fed spiders. However, "take-off within the confines of the laboratory ballooning chamber was not usually possible" (Weyman et al. 1995) and, according to our knowledge, a wind tunnel experiment has still not been performed to prove the hunger hypothesis. There is also still considerable confusion whether juvenile or adult spiders should balloon more frequently or whether there are seasonal trends of ballooning (e.g. Dean & Sterling 1985; Decae 1987; Greenstone et al. 1987; Weyman et al. 1995). All these aspects focus in some way on the hunger hypothesis.

To test the effect of hunger directly on the ballooning frequency, we performed experiments with hatchlings of the neotropical wandering spider *Cupiennius salei,* the most intensively studied spider species (Barth 2001). In this species, many hundreds of spiderlings leave the egg sac within a short period of time, forming a large crowd in the tangle of the threads spun by the female around the egg sac. Contrary to the aggressive behaviour of the adults, the spiderlings tolerate one another during the first days of their life outside the egg sac. After about 3 days, however, their food reserve provided by the yolk is depleted. Now competition for prey begins and cannibalism is common (Melchers 1963). At this stage of their development the spiderlings show dispersal behaviour to escape their predatory siblings and to search for food elsewhere (Barth et al. 1991, Barth 2001). Since *C. salei* grows to a rather big spider (>5000 mg) ballooning as a means of dispersal is restricted to the light first instar (1–2 mg body mass).

We want to test the hunger hypothesis of Legel & van Wingerden (1980) experimentally with spiders of known age and degree of hunger and under controlled conditions of a wind tunnel. In the case of young *C. salei* this hunger hypothesis allows the following predictions:

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- young hatchlings should not balloon (since they still have sufficient yolk),
- when yolk is depleted, ballooning frequency should increase,
- hungry spiderlings should balloon more frequently than satiated animals,
- the resulting ballooning period may be short and age-related,
- ballooning behaviour should be modified by body mass, wind speed and other physical factors (not tested here) such as temperature or air humidity.

Here we present experiments performed to test these predictions and to confirm the hunger hypothesis of Legel and van Wingerden (1980) under the conditions of our test system.

Materials and Methods

Spiders: The juvenile *Cupiennius salei* (Araneae, Ctenidae) used for the study were taken from our permanent breeding stock that originally derived from Melchers' Munich stock (Melchers 1963). The spiders are cultivated under constant conditions: Room temperature of 23 ± 1°C, light/dark regime of L12 : D12 h (artificial light), relative humidity of 70–90%. Adult animals are kept in a glass jar (12 cm diameter x 17 cm height, volume 2 L) with a layer of plaster at the bottom. This layer is watered weekly to keep a high relative humidity. In the present study immature spiders with an age of 1 to 5 days after hatching were used. Hatching is defined as the day when the spiderlings leave their cocoon. The newly hatched spiderlings were kept solitarily in small plastic vials (5 cm diameter x 10 cm height, bottom with a layer of plaster) and received pinhead crickets so they had food ad libitum (experiment 1) or starved (experiment 2).

Wind tunnel: The wind tunnel (Fig. 1) made of perspex had a length of 2.5 m and a width of 0.75 m. The motor (axial van AW1 500E4-A1), which was situated at the right end of the tunnel, sucks the air (max. 140 L s^{-1} = 2.5 m s^{-1}), and its power could be continuously regulated. Inside the wind tunnel, a plastic box with a round plastic platform (∅ 5 cm) surrounded by water, was installed. Two wires bent at the end were fixed to that platform. The plastic box was braced with metal bars outside the wind tunnel to avoid vibrations on the experiment place, produced by the wind tunnel. The hole in the perspex made for that installation was closed with a PVC film. A hot wire anemometer (Schildknecht Thermo Air 2) was also installed inside the wind tunnel, just beside the experimental place. During wind tunnel experiments room temperature was 23–24°C, relative humidity was about 50–60%, artificial light illuminated the tunnel uniformly.
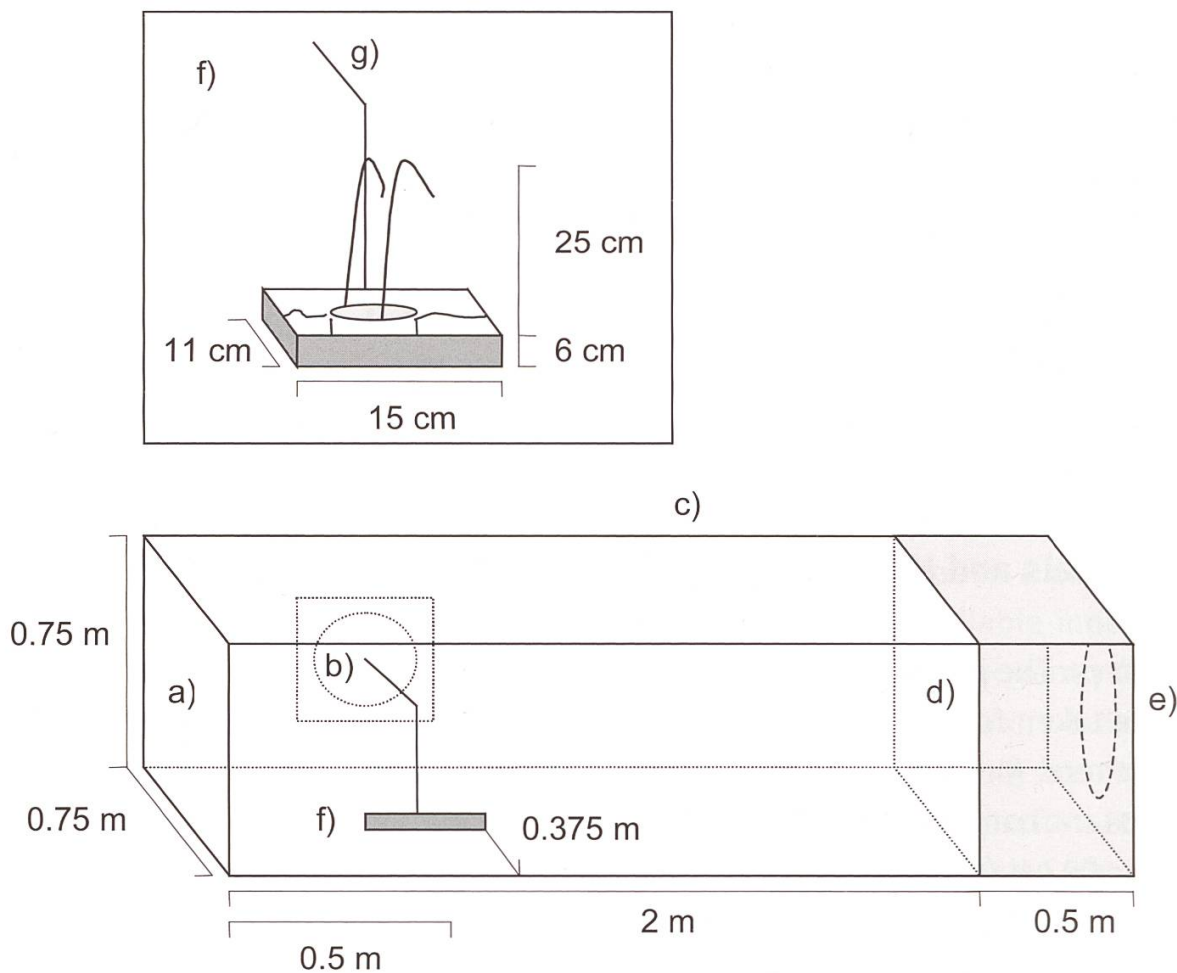
Fig. 1. Wind tunnel. a) coarse net and active carbon filter; b) hole to brace the experiment place outside the tunnel, closed with PVC; c) front part of the wind tunnel made of perspex; d) coarse and fine net spread in front of the motor, back part out of metal; e) motor; f) detailed sketch of the experiment place, round platform in the middle, surrounded by water, two wires installed to allow spiders to balloon; g) holding device for experiment place.

Experimental design: One spider was placed in the middle of the round platform, then the motor was turned on and the desired wind speed adapted. In the following 20 min the spider was observed and its action was recorded. There were several possibilities: (1) the spider stood motionless on the platform, (2) the spider started to move, but did not climb one of the two wires, (3) the spider climbed a wire, but did not balloon, (4) the spider climbed up and ballooned. After 20 min the spider was taken out of the wind tunnel and transferred into alcohol (70%). Later on, its body length and body mass were measured. To determine the body length (defined as front margin of the prosoma to the end of the opisthosoma), a binocular Leica Wild M 10 with an accuracy of ± 0.05 mm was used. Before measuring the wet mass ("drop off mass"), the spider was taken from the alcohol and laid on a paper towel for two minutes. Then the spider was transferred to a balance and weighed with an accuracy of ± 1 µg (Sartorius S4). For data analysis the program Systat was used.

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Experiment 1 (effect of age and wind speed, food available): The spiders were one to five days old, and the behaviour at four different wind speeds (0.75, 1, 1.25, 1.5 m s^{-1}) was analysed. For each age and wind speed 10 spiders were examined, so in total 200 spiders were tested, for a maximum of 20 min each. This experiment was repeated for wind speeds of 1 and 1.25 m s^{-1} and all ages (1–5 days old) with 10 spiders each (= 100 spiderlings). So in total 300 spiders were tested in experiment 1.

Experiment 2 (effect of hunger): For this experiment the juvenile spiders did not receive any food. As in experiment 1, all ages (1–5 days old) and four wind speeds (0.75, 1, 1.25, 1.5 m s^{-1}) were tested, with a total of 200 spiderlings, for each wind speed and age 10 spiders. The results of experiment 2 (no food available) were compared with those experiment 1 (food available).

Results

The spiderlings which were kept together in the glass jar (food available, experiment 1) showed a decreasing mass until their third day after hatching. At the fourth day, they had a significantly larger average mass than at the days before (Mann Whitney U-test, $p < 0.05$, N=300). The body size of the spiderlings of this experiment showed no significant differences during the first five days after hatching (Mann Whitney U-test, $p > 0.05$, N=300) (Fig. 2). In experiment 2, where no food was available, the mass of the spiders got smaller every day, as expected (Mann Whitney U-test, $p < 0.05$, N=200). The body size in experiment 2 was in the first four days each day significantly different from the one before (Mann Whitney U-test, $p < 0.05$, N=200) (Fig. 3). The body size and mass of all spiders ballooning in these experiments were not different from those of the spiders which showed no aeronautic activity (size: Kruskal Wallis, $p = 0.305$, N=500, mass: Kruskal Wallis, $p = 0.585$, N=500).

To compare food availability and aeronautic activity, the percentage of spiders ballooning in experiment 1 (food available, N=300) are shown versus experiment 2 (no food available, N=200) (Fig. 4). The spiders which had food during the whole experiment (experiment 1, Fig. 4a) showed a low ballooning activity (3%) on the first two days and on the last two days (day 4: 5%, day 5: 7%). A marked increase occurred on the third day of their life (23%, Kruskal Wallis, $p < 0.05$). In experiment 2 (no food available), the ballooning activity of day 1 was also low (8%, Kruskal Wallis, n. s.), but already on the second day, dispersal by ballooning became more common than in experiment 1 (20%, Kruskal Wallis, $p < 0.05$). The third day showed a high ballooning level in the same range as in experiment 1 (20%, Kruskal Wallis, n. s.), but on the
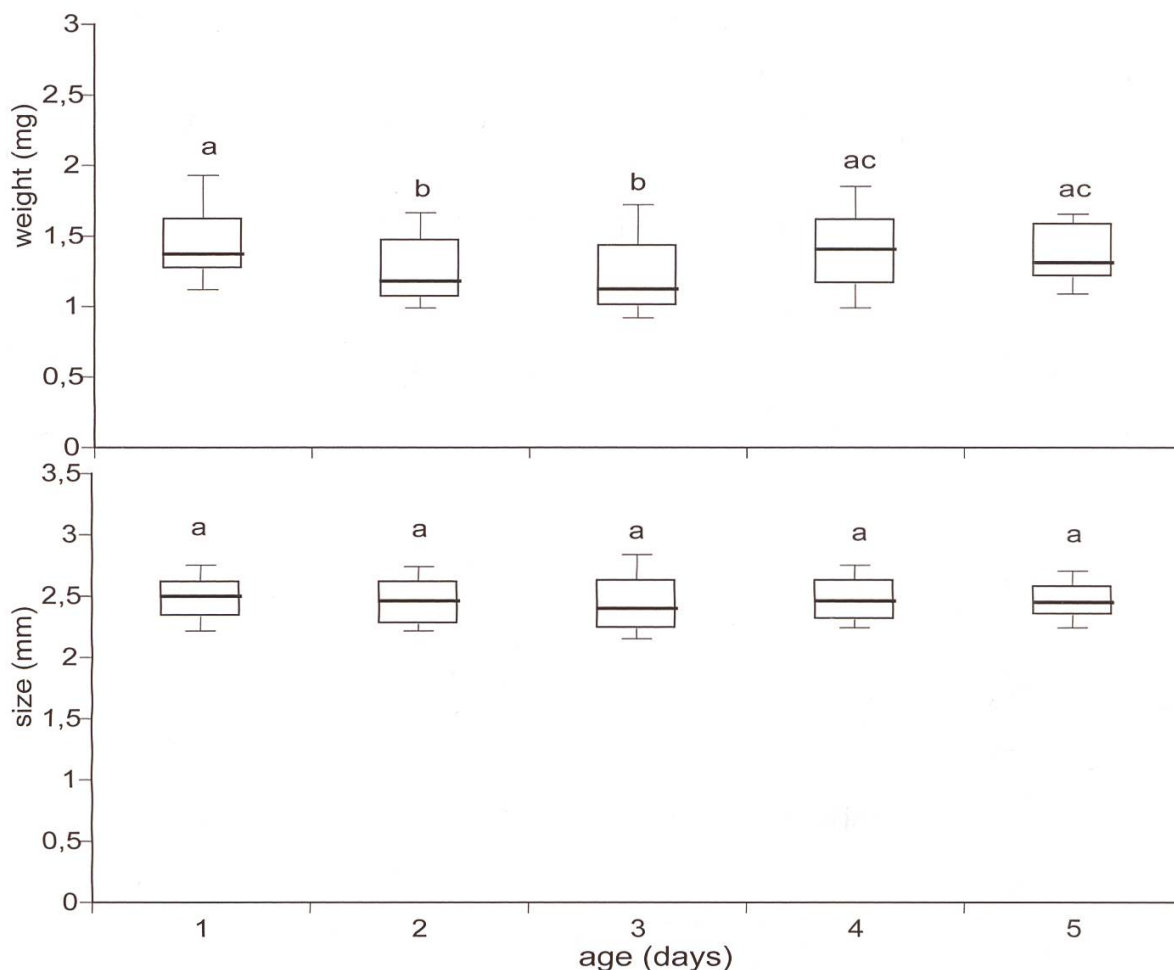
Fig. 2. Body mass and size of the spiders of experiment 1 (food available, N=60, total N=300) during the first 5 days of their life. Different letters indicate significant differences (Mann Whitney U-test).

fourth day, the ballooning tendency remained high, in contrast to experiment 1 (15%, Kruskal Wallis, $p<0.05$). The fifth day showed a lower percentage of spiders ballooning (10%, Kruskal Wallis, n. s.).

The highest ballooning frequency was found at a wind speed of 1 m s^{-1} (Fig. 4b). At a low wind speed (0.75 m s^{-1}), only few spiders in experiment 2 ballooned (4%). With availability of food, ballooning did not start till 1 m s^{-1} (13%) and decreased with increasing wind speed (1.25 m s^{-1}: 10%, 1.5 m s^{-1}: 4%). A significantly stronger ballooning tendency resulted if no food was available: at a wind speed of 1 m s^{-1}, 24% of spiders showed aeronautic activity, but it also decreased with increasing wind speed (1.25 m s^{-1}: 18%, 1.5 m s^{-1}: 12%). So a stronger ballooning tendency for spiders receiving no food was found at each wind speed (Kruskal Wallis, $p<0.05$).
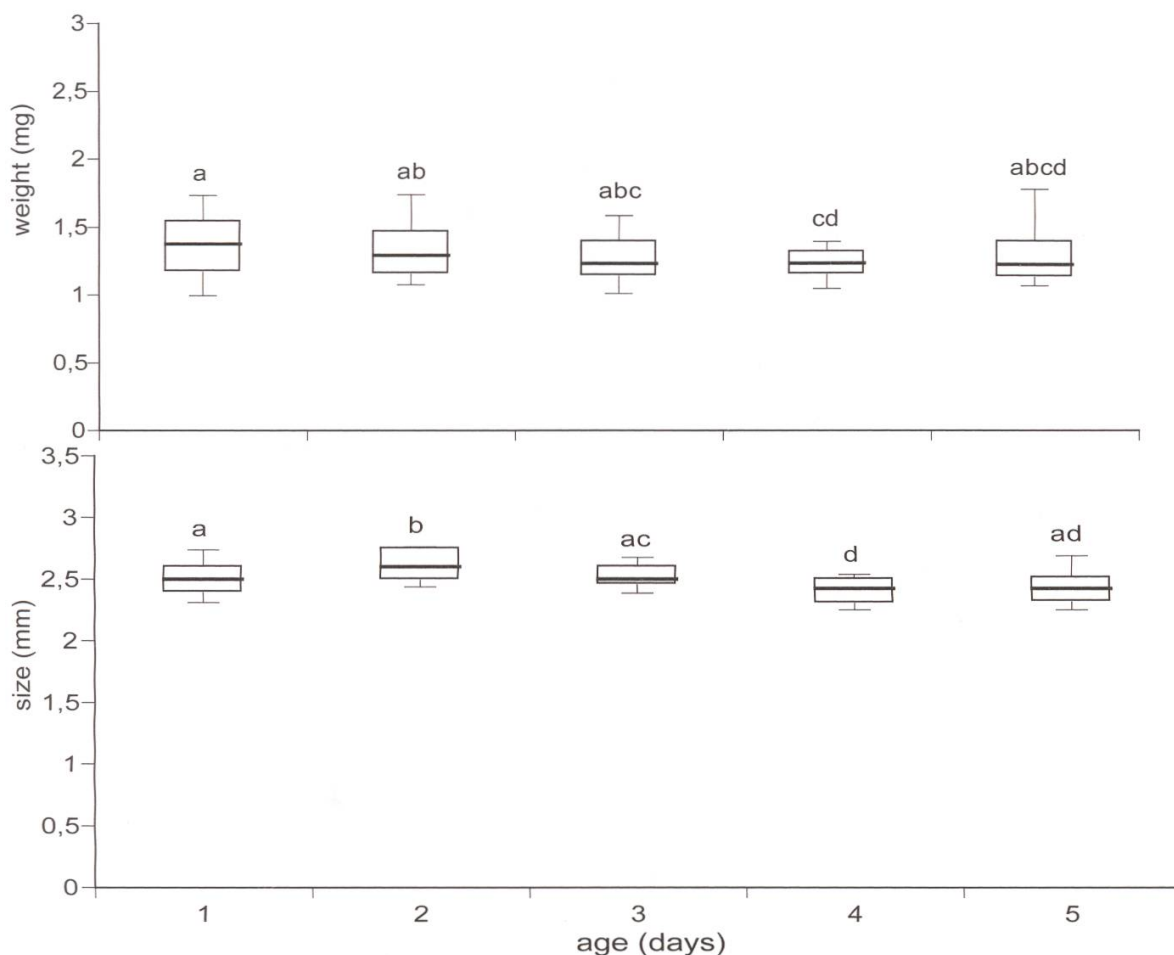
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Fig. 3. Body mass and size of the spiders of experiment 2 (no food, N=40, total N=200) during the first five days of their life. Different letters indicate significant differences (Mann Whitney U-test).

Discussion

Food-receiving spiderlings (experiment 1): Hatchlings do not balloon, since they still have sufficient yolk (Barth et al. 1991). In the study of Barth et al. (1991) with *Cupiennius getazi,* yolk was depleted 9 days after hatching. The young *C. salei*, however, showed predatory behaviour already 3 days after leaving their egg sac, which was indicated by a decreasing body mass from day 1 to 3, and a significantly heavier mass on day 4. So the yolk of spiderlings of *C. salei* was probably depleted on day 3 and ballooning in experiment 1 was most frequent on that day. Already on day 4, ballooning activities were low again because several biological factors stimulating ballooning obviously were not strong enough any more.

Aeronautic activity is also limited by several physical factors such as wind speed (Humphrey 1987). In our experiments, ballooning was most frequent at wind speeds of 1 m s^{-1} and 1.25 m s^{-1}. We observed spiderlings of experiment 1 hiding behind the experiment place at a wind speed of 1.5 m s^{-1}. Also Barth et al. (1991) reported a marked decrease of ballooning behaviour at a wind
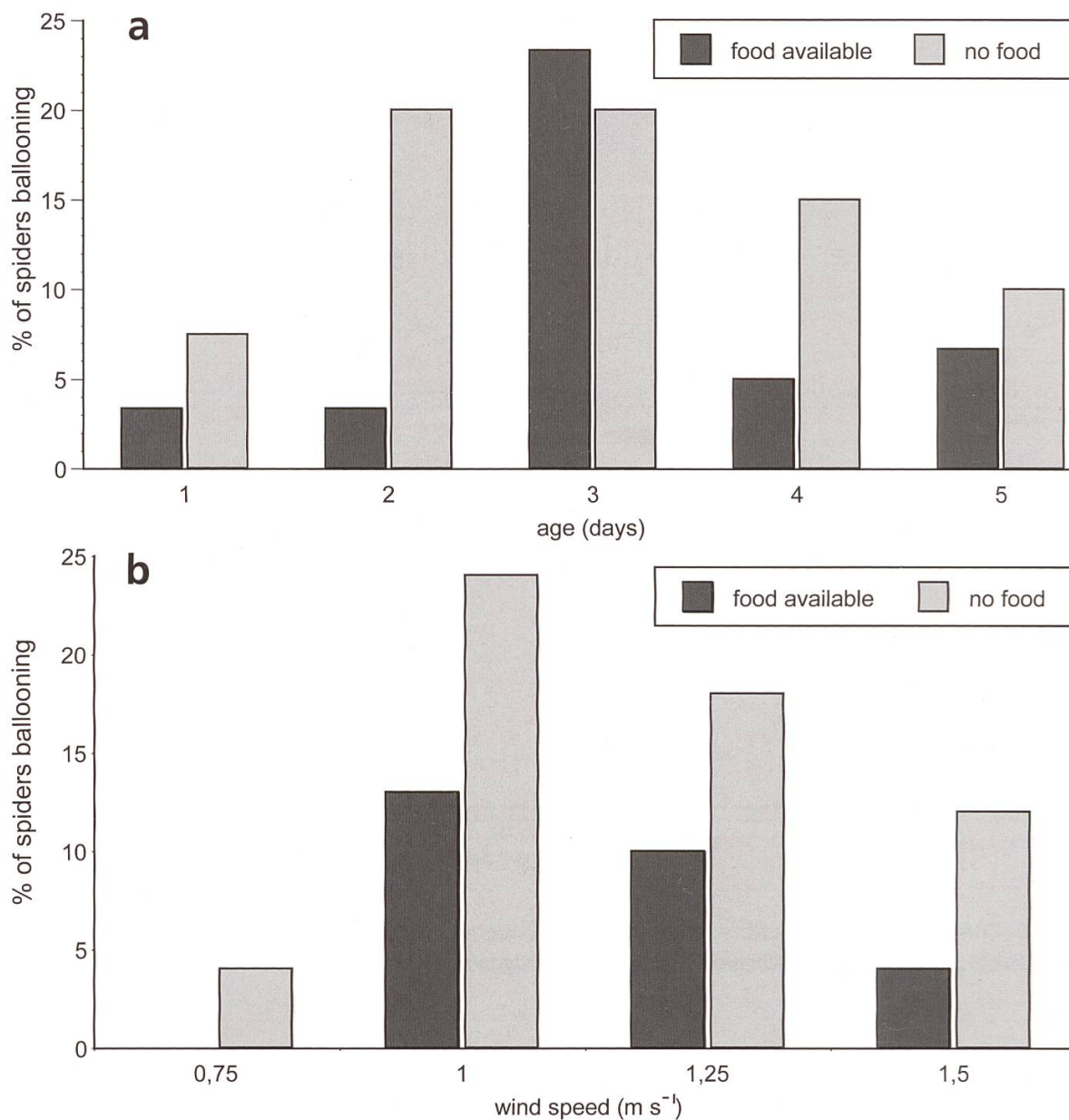
Fig. 4. Percent of spiders ballooning at a) different ages and b) different wind speeds in experiment 1 (food available, N=300) and experiment 2 (no food available, N=500), compare text.

speed of 1.5 m s^{-1} for spiderlings of the closely related species *C. getazi*. The reduced ballooning tendency on day 4 and 5 might be explained by the higher body mass because the mass of a spider, its body mass and the silk are, in combination with wind velocity, the determining parameters which mechanically constrain the ballooning activity (Humphrey 1987). Although even at day 4 and 5 the average body mass was far below 2 mg, where the body mass of the vast majority of ballooning spiders is located (Greenstone et al. 1987). So we conclude that aeronautic activity should not be limited by the body mass of these spiderlings.

Spiderlings of *Cupiennius salei* showed a preballooning behaviour which has been called "drop and swing dispersal behaviour" by Barth et al. (1991). The spiderling, dropping and dangling from its dwelling plant on its dragline,

swings in the wind. In the experiment of Barth et al. (1991) with *C. getazi*, this behaviour was the only aerial dispersal behaviour. In our experiments, this behaviour was commonly followed by the rupture of the dragline and by ballooning. The same type of preballooning was also observed in 10 other spider species belonging to 9 different families (Decae 1987, Eberhard 1987). This indicates the importance of posture (Suter 1992) and that it is not possible to transfer our observations even to congeneric species, or to generalize it for all spiders, though many other species may behave similarly.

Starving spiderlings (experiment 2): In experiment 2, aeronautic activity (take-off) was observed significantly more often than in experiment 1, although all physical conditions stayed the same, except the body mass of the spiders, which decreased with increasing age in the second experiment. Hunger is considered to be the most important motivation for this behaviour. Ballooning activity of hungry spiders was higher on days 1, 2, 4 and 5, and at all wind speeds. With reduced body mass and same surface, the needed buoyancy force (van Wingerden & Vugts 1979) for successful aeronautic activity gets smaller, so ballooning is possible at lower and higher wind speeds (Humphrey 1987). If the body mass was the only limiting factor, then ballooning should also increase linearly from day 2 on. But ballooning in experiment 2 was high on day 2 and 3, and decreased on day 4 and 5. The increased ballooning tendency on wind speeds at 0.75 m s^{-1} and 1.5 m s^{-1} of hungry spiderlings indicated that also unfavourable wind speeds could be used for aeronautic activity.

Spiderlings of *C. salei* showed in their first days after hatching a clearly defined stage within which ballooning occurs. This period was strongly influenced by food reserve level: when yolk was depleted, frequent aeronautic activity was observed, resulting in a short developmental period of high ballooning frequency. Within this period, ballooning can be modified by wind speed, as reported by several other investigations (Richter 1970, Roff 1991). Bishop (1990) found no significant effect of wind direction or velocity (within the 3 m s^{-1} limit) on ballooning, but the rate of fluctuation in wind direction was negatively correlated with the number of spiders ballooning. Because fluctuation in wind direction and turbulence in general increase in a wind tunnel with increasing wind speed (Gersten 1991, Barth et al. 1991), this might be a further explanation for reduced aeronautic tendency on 1.5 m s^{-1}.

Our results clearly indicated that hunger is not only a stimulating factor for the first (climbing) and the second stage (drop in the wind) of preballooning behaviour (Legel & van Wingerden 1980, Weyman et al. 1994). It also enhanced successful take-off in combination with hunger, although wind speeds were not always optimal. Spiderlings could balloon accordingly

despite disadvantageous physical conditions (too low or high wind speeds) if a strong biotic stimulating factor such as hunger forced them to. In the case of *C. salei* (a species which rapidly becomes too heavy for ballooning) this results in a short and age-related period of high ballooning activity in which a relevant part of the population migrates to other habitats with hopefully better living conditions (Whittingham et al. 2001). For spiders, no generalisation on a preferred time of ballooning can be given because an unadvantageous period may occur in all habitats and seasons even if some habitat-specificity can be found (e.g. Bonte et al. 2003). These results confirm earlier statements that the offer of additional food and high biodiversity (e.g. by set-asides or ecological compensation areas, Nentwig 2000) reduces the need for ballooning and thus augments the abundance of spiders as general predators within an integrated pest control concept.

Acknowledgements

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