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Phenological and meteorological determinants of spider ballooning in an agricultural landscape

Déterminants phénologiques et météorologiques du ballooning *chez les araignées en contexte agro-écosystémique*

Manon Simonneau [a,*], Cyril Courtial [a], Julien Pétillon [b]

[a] *Groupe d'étude des invertébrés armoricains, antenne Bretagne, campus de Beaulieu, 263, avenue du Général-Leclerc, 35042 Rennes cedex, France*

[b] *Université de Rennes-1, EA 7316, campus de Beaulieu, 263, avenue du Général-Leclerc, 35042 Rennes cedex, France*

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ABSTRACT

Spiders are known to commonly use aerial dispersal, so-called ballooning, especially at juvenile stages. They produce a silk thread that allows them to rise up in the air to disperse, which serves as inbreeding avoidance or to find an optimal over-winter habitat. Studies of phenology, species and meteorological factors associated with aerial dispersal have been limited to laboratory settings, with few data obtained under natural settings and no studies to date executed in France. To understand aerial dispersal, we conducted daily sampling between 2000 and 2002 at a height of 12 m. For adults, high proportions of "ballooners" were observed during four seasonal peaks, with dispersal most prevalent during summer, while for juveniles dispersal was protracted across summer and fall. Linyphiidae is the most abundant family among the 10,879 individuals caught. We show a significant and negative influence of high wind speeds on ballooning, an effect that increased even under low temperatures (< 19 °C). At wind speeds greater than $4\,m{\cdot}s^{-1}$ dispersal becomes difficult, and is almost impossible beyond $5.5\,m{\cdot}s^{-1}$. Ballooning ability is reported for the first time for several species. This study increases our knowledge on aerial dispersal in spiders in an agricultural context. Such behaviour can be seen as a survival strategy to escape from a disturbed and unstable landscape.

RÉSUMÉ

Les araignées sont connues pour pratiquer la dispersion aérienne, appelée *ballooning*, plus particulièrement aux stades juvéniles. Elles émettent un fil de soie leur permettant de s'élever dans les airs et de se disperser pour la reproduction et la recherche d'un site d'hivernage notamment. La phénologie, les espèces et les facteurs météorologiques impliqués ont déjà été étudiés, mais principalement en laboratoire. Ce phénomène reste peu connu en conditions naturelles, notamment à l'échelle française, puisqu'aucune étude n'y a encore été menée à ce jour. Pour comprendre la dispersion aérienne, des échantillons journaliers ont été prélevés entre 2000 et 2002 à une hauteur de 12 m. Chez les adultes, de

* Corresponding author.
E-mail address: manon.simonneau@gmail.com (M. Simonneau).

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fortes proportions de « ballooneurs » ont été observées au cours de quatre pics saisonniers, la dispersion étant la plus importante en été, alors que chez les immatures la dispersion était prolongée à travers l'été, puis a chuté. La famille des Linyphiidae est la plus abondante parmi les 10 879 individus capturés au total. Nous montrons également l'influence négative du vent sur le *ballooning*, accentuée sous de faibles températures (< 19 °C). Au-delà de 4 m·s^{-1}, la dispersion devient rare, voire presque impossible au-delà de 5,5 m·s^{-1}. Ce comportement a ainsi été illustré chez des espèces pour qui il n'était pas encore renseigné. Cette étude a donc permis d'accroître les connaissances sur la dispersion aérienne des araignées, et ce en contexte agro-écosystémique. Le *ballooning* peut alors être vu comme une stratégie de survie dans un paysage perturbé et instable.

1. Introduction

Dispersal is a frequent process engaged by almost all species, animals and plants alike. It has strong evolutionary and ecological implications on the spatial structure of meta-populations [1,2], particularly *via* gene flow in a context of habitat fragmentation [3–7]. The effects of dispersal are thus important for fauna and flora for a variety of reasons, preventing population homogenization, and reducing inbreeding, intraspecific competition and predation. Dispersal has also been defined as a "bet-hedging" strategy, or risk spreading, allowing individuals to move out of unstable environments [8–16] or habitats of marginal quality.

In addition to ground dispersal, some spider species use aerial dispersal strategies commonly called "ballooning" [17–19]. In addition to araneomorpha spiders, other Arachnids, trap-door spiders (Mygalomorpha) and acarid juveniles (e.g., Ixodidae and Tetranychidae) disperse by flight [14,20]. Ballooning has been defined as a passive dispersal enabled by the emission of a silk thread and subsequent transport in air currents [14,21,22] during which individuals lack control of direction, speed, and distance [21,23,24], contributing to the so-called "aerial plankton" [15,24,25]. Ballooning is divided into three phases: the ascent to a high point of the vegetation, the adoption of a specific body posture ("tiptoe" behaviour) and rising into the air [14,23,24].

Previous ballooning studies have focused on species initiation of pre-dispersal behaviour and on the effect of meteorological factors, but this research was primarily conducted under laboratory conditions. Juveniles are supposed to display this behaviour more frequently, mainly because of physiological conditions undergone during early development [26,27]. The weight of the individuals also plays an essential role [21,24], as climbing-up and dispersing in the air become more difficult concomitant to weight increase [18,28]. Moreover, stenotopic species, i.e. narrowly dependent on a habitat type, are less inclined to perform ballooning, in contrast to those who settle a variety of habitats (eurytopic species) [21]. Costs of dispersal are indeed higher for stenotopic species, because of reduced chance for dispersal success. Ballooning is especially important for survival in fragmented and/or disturbed habitats [21,30], such as agroecosystems [8,11,13,29,31–33]. Ballooning also plays a key role in limiting within-populations inbreeding, and promotes gene flow by dispersal to genetically different populations. Furthermore, dispersal allows spiders to prevent intraspecific competition rising from over-population [11,13,19,27,34].

Besides the endogenous parameters and those related to habitat characteristics, meteorological factors, particularly wind speed and air temperature [23,35–38], are believed to play an important role in the initiation of ballooning. A wind speed threshold beyond 3 m·s^{-1}, or even 6 m·s^{-1}, is expected to compromise dispersal, as showed under laboratory conditions [15,21,23,35,36,38]. High temperatures and precipitation are also likely to negatively affect dispersal by modification of air currents; the important influence of these factors increases as conditions become more extreme [15,19,21–23,39]. Here, we aim at increasing the knowledge on the determinants of spider ballooning in an agricultural landscape by conducting field experiments utilizing a 12-m high suction trap [24] and testing several hypotheses related to the timing of ballooning events. First, we expect the existence of several ballooning peaks during the course of a year, including a main one in the summer [33]. Considering the life cycle of most spider species [40], we also predict that dispersal phenology will differ between adults and immature individuals [33]. The predominant disperser is expected to be Linyphiidae because it is the most diversified and abundant family in temperate regions of the Northern Hemisphere [11,19] and because linyphiids are particularly abundant in meadows and agroecosystems [8,11,13,14,26,27,29]. Finally, we expect a difference between adults, juveniles and sex ratio abundances among families [22], because of differences in mean weight between life history stages and sex.

2. Methods

2.1. Study site and sampling design

A Rothamsted Insect Survey suction trap was employed to study spider dispersal in Brittany, western France (48°6′44.82″N 1°46′51.16″O) in an agricultural landscape consisting of crops, hedgerows, woody areas and human infrastructures (e.g., buildings, roads). The 30-cm-diameter trap, with a maximum power of inhalation of 40 m^3·h^{-1}, was placed at a height of 12.2 m. Samples were collected daily over the course of three years (from 1st January