

REVIEW OF DISPERSAL IN SPIDERS: MODES, FATE AND IMPLICATIONS

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ABSTRACT

Spiders thrive in a hostile world as a successful group of organisms. One of the reasons for this has been speculated to be their ability to colonize almost every terrestrial habitat. Successful colonization is a result of persistent dispersal. Spiders have evolved two modes of dispersal – cursorial and aerial. Spiders adopt any or a combination of these two depending on developmental stage, body mass, membership of certain guilds, habitat structure and certain other environmental conditions. Both these modes have been found to be successful in carefully manipulated experimental setups as well as indirect observational records. However, contradictory results regarding relative success of each have been reported. Spider dispersal is an important landscape-scale process especially in agrarian landscapes. It has implications for the natural pest control and maintenance of natural habitats. Here, we review important studies on modes, fate and implications of spider dispersal to facilitate formulation of further studies.

Keywords: spider, colonization, ballooning, cyclic dispersal, metapopulation

Colonialist Spiders:

A number of well-known facts amply establish that spiders are successful colonizers. Spiders (Araneae) are a group of highly diversified organisms with the world's third largest count of species (Platnick, 2013). They are generalist predators and have the world's most abundant taxon – Insecta – as their prime food (Maloney, *et al.* 2003). They can be found in almost all terrestrial habitats in natural settings. In fact, they can be found in most anthropogenic habitats too (Wise, 1993). Most spider species occur as high-density populations in diverse communities. With all these properties, they have been hailed as an ideal group for studying metacommunity dynamics (Schmidt, *et al.* 2007) one major process in which is colonization. Indeed, spiders are true colonialists. But spiders, like most other organisms, live in a hostile world (Helsdingen, 2011). And colonization is fraught with numerous challenges as we know in the context of humans-

‘...Send forth the best you breed
Go bind your sons to exile...
...Go mark them with your living
And mark them with your dead...’

– Rudyard Kipling, *The White Man's Burden*, 1899

Colonization is the establishment of a species in new area. Community of organisms at any given locality is built up by niche relations, habitat diversity, ecological equivalency and mass effects (Shmida & Wilson, 1985). Mass effect is immigration and establishment of some individuals of a species in an area previously unoccupied by that species (Shmida & Wilson, 1985). Immigration is the result of dispersal and has been conceived as a response to a forcing event causing ‘changes in the quality, size, density and connectivity of suitable habitat patches’ (Jackson & Sax, 2010). Successful colonization requires a well developed dispersal capacity (Bullock *et al.* 2002).

Thus, dispersal is the key to colonization. And dispersal has certainly gained central position in ecological studies (Bullock *et al.* 2002).

Dispersal

All animals possess the defining ability to move (Biewener, 2003) especially from place to place. Movements are inspired by motives of self-preservation by avoiding mortality from various factors, acquisition of essential resources and avoidance of competition in doing so (Fahrig, 2007). Animals perform several types of movements to accomplish these tasks. These types vary by organism’s size, life history traits, power of movement, geographical range, and habitat. Considering these parameters, Hugh Dingle (Dingle, 1996) has classified movements into three broad categories - station keeping, ranging and migratory movements. The station keeping movements are contained within home range of an individual; ranging movements are in pursuance of an alternate home range; and migratory movements extend beyond the ambit of home range. Dingle argues that migration is distinct from ranging in behavioural and physiological aspects and response of organism to the environment. He includes the conventional concept of dispersal in ranging movements. He calls it a population level phenomenon in which a group of individuals breaks up progressively increasing distance between them. The individuals explore resources while on move and make decision to stop and settle. The more popular connotation of this type of movement is natal dispersal wherein the juveniles move away from their natal home range to establish their own home range.

Although Dingle (1996) has advised to use the term dispersal strictly in the context of natal or breeding dispersal and to use ranging, instead, for exploratory beyond-home-range movements, most spider studies do not distinguish between dispersal and ranging. Hence, we would continue calling all movements across landscape as dispersal in this review.

Nevertheless, dispersal invariably involves travel across landscape. But landscapes are inherently heterogeneous comprising of several types of habitats arranged in patches. Some patches correspond to the suitable habitat while others unfavorable. Dispersing individuals face the problem of covering the distance

between suitable patches (Opdam, 1991). And anthropogenic fragmentation of habitats has increased these distances substantially.

Dispersal is at the base of two major ecological theories - metapopulation dynamics and metacommunity dynamics. Metapopulation Dynamics was initially propounded by Richard Levins in 1969 in the context of demographics of agricultural pests. It subsequently outgrew the original context and assumed a central place in ecological paradigms. On the other hand, metacommunity dynamics emerged from the realization of inadequacy of metapopulation dynamics (Wilson, 1992). It has attained unprecedented levels of popularity amongst ecologists. This is clear from the enthusiastic reviews received by the book ‘Metacommunities: Spatial Dynamics and Ecological Communities’ (Holyoak *et al.* 2005) (e.g. Gaston 2006). It is also evident from the way a comprehensive review (Leibold *et al.* 2004) got cited in over 1000 papers in just 8 years!

More physically, and simply put, metapopulations or metacommunities are nothing but occupied patches in a landscape. Metapopulation dynamics is run by architecture of populations and density-dependence in addition to dispersal (Hanski, 1991). Similarly, metacommunity dynamics is run by patch dynamic, species sorting, and niche partitioning in addition to dispersal (Leibold and Miller, 2004). Lower dispersal success is often connected with decline in population in fragmented habitats (Schumaker, 1996). Thus, dispersal remains the key mechanism behind the occupancy of a habitat patch by a species.

Dispersal is a prime process in landscape ecology and its parameters – especially the scale – depend on the heterogeneity of landscape as well as the organism concerned (Turner, 1989). It is triggered by resource- and density-dependent factors working at population levels. Samu *et al.* (1999) have advised to study spiders at 3 scales of spatial hierarchy – micro-habitat, habitat and landscape. For spiders, landscape composition at the scale of 500 m radial area has been found to be appropriate (Clough *et al.* 2005, Schmidt *et al.* 2005).

Scale of dispersal, however, varies with species and must be parameterized to get correct interpretation of the colonization process. In her review, Turner (1989) has also emphasized that in landscape ecological studies, all landscape scales must be organism-centric. Wiens (1989) had opined that different types of species of birds would be affected differently by the fragmentation of habitat. On one hand, habitat generalists and edge lovers can be benefitted by a certain degree of fragmentation. On the other, for habitat specific species, the area between habitat patches acts as a barrier or sink ((Opdam, 1991). Another factor is the ability and tendency of the species to cover distances. Mobility categories of butterflies like sedentary, intermediate, and wide ranging have been identified (Thomas, 2000). Similar categories based on habitat preferences and mobility can be construed in spiders too. Different species, albeit related, showed differential colonization

abilities in the studies of Marshall *et al.* (2000). In habitat specialist spiders, the propensity for dispersal was found to be declining with increasing fragmentation of habitat (Bonte *et al.* 2003).

Studying Dispersal

Advances in telemetry have made real-time tracking of dispersing individuals and their fate. But this technology is restricted in its application to vertebrates only. Arthropod dispersal has been traditionally interpreted indirectly from the monitoring of populations and communities in target habitats. Even capturing dispersing individuals, marking them and releasing back have been attempted. In spiders, several studies have used indirect evidence of dispersal and mark-recapture set ups. Still, there have been very few studies which focused exclusively on dispersal in spiders (e.g. Bishop & Riechert 1990, Blandenier & Fürst 1998; Nicholls *et al.* 2001; Schneider *et al.* 2001; Bonte *et al.* 2003, 2004, 2006; Reynolds *et al.* 2007, Hibbert & Buddle, 2008).

Dispersal has also been extensively modeled. One way is to model the dispersal success rate of organisms through spatially explicit demographic models. Spatially explicit models are either grid based or patch based. Numerous models exist (Vuilleumier & Metzger 2006). But they all are inefficient and unrealistic in the absence of life history data of the target species (Schumaker, 1996). Each approach has its own advantages and disadvantages over and above the loss of complexity of animal behavior. The other way is to predict dispersal success on the basis of indices of fragmentation pattern in the landscape. These are supposed to estimate the habitat connectivity. They have been continuously under scrutiny (Schumaker, 1996). Schumaker showed that of several landscape indices, only those that combined patch area and perimeter were able to predict dispersal success adequately. Even less attempts have been made to model dispersion in spiders.

Colonization and Dispersal in Spiders

Spider colonization takes place through two processes – natal dispersal and cyclic dispersal. In natal dispersal, young spiderlings move away from their mother’s habitat patch and get established elsewhere. However, there has been evidence of natal dispersal being performed by adults especially those of social spiders of the genus *Stegodyphus* (Schneider *et al.* 2001).

The cyclic dispersal results into what is known as ‘cyclic colonization’ in which the spiders colonize a resource-rich habitat for a certain period of year and then return to their original habitat (Wissinger, 1997). Again, in this case the individuals involved could be spiderlings and adults both and the colonization is short-term.

Deprived of wings, spiders disperse relying on their legs and their extraordinary ability to generate silk. Thus, there are two modes of dispersal in spiders – ground and aerial. Aerial dispersal takes place by a mechanism of ballooning. It is known to carry spiders to heights of 5 km above ground and upto 300 km across landscape (Ehmann, 1994). It has been considered a passive mode of dispersal dependent on air currents, wind direction, and body mass and wherein the spider has no control on the flight direction (Thomas and Jepson 1999, Compton 2002). It was seen as a means of dispersal of small young spiders post their emergence from eggsacs. Tiptoeing is a prelude to the ballooning. A tiptoeing spider stands on raised legs and points abdomen upwards (Schneider *et al.*, 2001). In this position, it releases several strands of silk.

Bishop & Riechert (1990) found that spider families arriving in their garden plots via cursorial mode and via ballooning were significantly different. They also observed that nearly 50% of all immigrant species arrived from far-away areas via aerial dispersal. Ehmann (1994) manipulated the access of cursorial and ballooning spiders to individual shrubs. He found that control shrubs received over 75% of their individuals via ballooning. But the mode of dispersal did not influence the guild structure in any treatment. It is therefore commonly assumed that the ballooning is used by spiders for natal dispersal as it is usually long distance dispersal (LDD) and walking is used for cyclic dispersal as it is usually short distance dispersal (SDD).

Buddle and Rypstra (2003) trapped emigrating spiders in pit-fall traps in a two-species system of wolf spiders in soybean fields. They found that one species showed very high propensity to emigrate from low-quality habitat showing its specialization on high-quality habitat. The other species showed generalist behaviour. This goes on to show that exclusively cursorial spiders exhibit variable tendencies of dispersal.

Hibbert and Buddle (2008) conducted studies in cornfields and adjacent natural forest in Canada. They used circular aluminium enclosures that allowed only ballooning spiders or both ballooning and cursorial spiders. They found that cursorial mode of dispersal significantly contributed to the colonization of spiders in cornfields. Their other observation was that several spider species were common to both habitats indicating that the natural forest could play an important role in maintaining spider populations in cornfields.

Bishop (1990) reviewed the earlier studies of ballooning and concluded that initiation of ballooning and maintenance of flight were two different aspects influenced by different factors. To fill the gap in information on flight maintenance, she sticky-trapped ballooning spiders at different heights above ground. She found that there was seasonal variation in both the height of ballooning and ballooning taxa. She also found that ballooning took place from just above canopy i.e. 22 m to

even 44 m. She recorded the importance of less fluctuation in wind velocity for successful flight maintenance.

Dr. James Bell of Cardiff University, UK and his colleagues have extensively studied ballooning behavior in spiders and other arthropods and its evolutionary consequences (Reynolds, *et al.* 2007). They have found that the silken dragline is only of as much importance as to launch the spider into the air current. Thereafter, the distance travelled by the spider is determined by the meteorological conditions rather than the properties of the dragline. And that ballooning spiders initiate ballooning at appropriate meteorological conditions that would maximize the dispersal distance. Ballooning was found to be a major mode of dispersal for certain spiders in high-Arctic glacial ecosystems (Coulson *et al.* 2003).

Schneider *et al.* (2001) studied ballooning in adult *Stegodyphus dumicola* spiders. They reported, for the first time, ballooning on multiple – tens to hundreds - strands. They concluded that use of multiple strands of silk to balloon can help even large-sized adults in dispersing to remote locations.

Most spider dispersal and colonization studies have been conducted in agricultural habitats and their surrounding landscape context. One of the limitations of biocontrol by spiders in croplands is that they fail to colonize the crop in advance to the pests. Most studies have targeted at altering the in-field-habitat structure to facilitate colonization by dispersing spiders. Similarly, few studies have also looked at the adjacent non-crop habitats and their role in colonization.

Contrary to the results of Bishop & Riechert (1990), Schmidt *et al.* (2007) have showed that the non-crop habitat is important for colonization of most spiders in wheat-fields. At the same time, some spiders specializing in arable habitats were not influenced by non-crop habitats.

Presence of refuge vegetation does influence the colonization by generalist predators. But the zone of this influence of colonization was found to be very limited. In addition, effect of corridors of refuge vegetation running through extensive monocultures has also been studied. Clara Nicholls and her colleagues (2001) undertook such a study in Northern California in two vineyard blocks of 2.5 ha each and surrounded by riparian vegetation on one side. They used the experiment like presence of a vegetation corridor bisecting one of these vineyards. They tested if this corridor was a ‘consistent, abundant and well-dispersed source of food and habitat’ for the natural predators to act as a source population for colonization in the vineyard and whether it also acted as a ‘conduit for the dispersion of natural enemies’. They estimated populations of pests of grapes along with their generalist predators.

Their main finding was that the population and, hence, the pest control potential of natural enemies was amplified by the corridor in addition to the riparian vegetation edge. They did find lower incidence of pests in the area of influence of the corridor i.e. the pest populations increased gradually away from the corridor. Interestingly, among the complex of arthropod natural enemies they recorded, the second most abundant predators were Thomisid spiders!

Concluding Remarks

Spiders are capable of both local, short distance ground dispersal and distant, long distance aerial dispersal. Both these propensities play a major role in their colonization of unoccupied habitats. Colonization itself can be permanent or cyclic. While aerial dispersal is influenced by meteorological conditions, ground dispersal is affected by habitat configuration. The landscape architecture in terms of habitat-matrix compositions, juxtapositions and corridors determine the success of dispersal events. An understanding of these landscape level phenomena is especially important in heterogenous landscapes for conservation of spider diversity. It is also important to apply spiders as potential biocontrol agents in agroecosystems. It also certainly has implications for maintenance of natural habitats in predominantly anthropogenic landscapes.

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