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DISPERSAL MECHANISMS OF *STEGODYPHUS* (ERESIDAE): DO THEY BALLOON?

Silk is used by spiders in dispersal in different ways. One method, bridging, is to cast a line into the breeze and, when it catches on a distant object, to climb out on the line to its end. Bridging may also be accomplished by dropping on a line and swinging on it to reach a new site (Barth et al. 1991). A second method is to balloon: when the extruded thread and the spider get enough lift from updrafts (usually thermals or vertical wind-velocity gradients), the spider will be lifted off the substrate and carried through the air (Decae 1986; Eberhard 1987; Greenstone 1990; Suter 1991, 1992; Weyman 1993; Follner & Klarenberg 1995).

Stegodyphus species (Eresidae) have been reported to disperse both by bridging and ballooning. Details of ballooning in *Stegodyphus* were reported by Wickler & Seibt (1986). They observed a gravid female *S. mimosarum*, one of three social species of *Stegodyphus*, ballooning over a distance of 18 m, having started at a height of 2 m. The spider had a body length of 10 mm with an estimated mass of 85–150 mg and was hanging from 3–4 silk threads of 60–80 cm length, i.e., the estimated total silk length was 1.8–3.2 m.

We compare the dispersal methods of bridging and ballooning for *Stegodyphus* in terms of their aerodynamics, consequences and relative importance. With this analysis we evaluate previous interpretations of dispersal of *Stegodyphus* in relation to current knowledge of their ecology and population biology. We use evidence from the literature and our own general observations made during several years of fieldwork with four species of *Stegodyphus*, namely, the social *S. dumicola* Pocock 1898 and *S. mimosarum* Pavesi 1883, and subsocial *S. lineatus* Latreille 1817 and *S. bicolor* (O. Pickard-Cambridge 1869).

We estimated the vertical air velocity required for Wickler & Seibt's (1986) *S. mimosarum* to remain airborne, using Suter's (1991) equation 7:

$$V_{sb} = W \div (11.5 \times L \times W^{0.094} + 1.94 \times W^{0.366})$$

where V_{sb} = vertical air velocity in m/sec acting on the spider's silk and body, W = weight in μN (1 μN ≈ 0.1 mg), L = silk length in m. To apply this equation, we assumed that the physical parameters remain constant beyond the boundaries for which Suter's equation was developed. By substituting the maximum silk length and minimum *S. mimosarum* mass (above), a vertical velocity component of 9.2 m/s was necessary; minimum silk length and maximum spider mass requires 21.6 m/s. A wind of this strength would not have been described as a "barely perceptible breeze" (Wickler & Seibt 1986; p. 628), which may refer to a 0.1–1.0 m/s wind. A horizontal wind of 3 m/s near the ground is the maximum at which thermals, suitable for ballooning, can be maintained (Greenstone 1990; Weyman 1993). For controlled ballooning, we assume a maximum vertical wind component of 3 m/s, following Stull's (1988) description of boundary layer meteorology. If Wickler & Seibt's (1986) *S. mimosarum* experienced vertical winds of 0.1–3 m/s, it would have required 12–655 m of silk to become airborne.

It is possible that the drag line was longer than reported because its distal end can be difficult to see (Eberhard 1987). Furthermore, the above calculation does not take into account that spiders can change the drag on their bodies by several orders of magnitude when changing posture in relation to the direction of air flow (Suter 1992).

Wickler & Seibt's (1986) *S. mimosarum* was at least 3–6 times the maximum mass (25.5 mg) found in 2800 ballooning species investigated by Greenstone et al (1987). It clearly requires extreme conditions for this spider to experience lift. These conditions are well outside the boundaries used in aerodynamic models of spider ballooning (Humphrey 1987; Suter 1991, 1992). Ballooning is the domain of small spiders (Weyman 1993) and over 90% of them are < 1 mg in size (Greenstone et al. 1987). When members of large taxa, such as mygalomorphs, balloon, it is the small spiderlings (< 2.2 mg with an outlier of 5.8 mg) that do so (Coyle et al. 1985).

Social *Stegodyphus* are typically big at first dispersal, as they usually disperse only when adult, or, more rarely, subadult. Dispersing female *S. dumicola* weigh 103–213 mg and males some 23–48 mg (Henschel et al. 1995). By contrast, subsocial *S. lineatus* are 3–8 mg at first dispersal (Schneider 1992), within the size range of some heavy ballooning spiders. Nonetheless, *S. lineatus* have not been recorded ballooning.

On three occasions, one of the authors (JH) observed *S. dumicola* parachuting downwards when his presence disturbed spiders that were casting silken lines, evidently for bridging. The spiders landed several meters away on the ground. Size may explain why airborne *Stegodyphus* drop and land a short distance from the start. Perhaps other observations of ballooning by *S. dumicola* (in the laboratory, S. Kürpick pers. comm.) and by *S. sarasinorum* Karsch (Jambunathan 1905; Jacson & Joseph 1973) also occurred upon disturbance caused by the observers' presence. If escape were not the case, the observation of several *S. sarasinorum* ballooning together on one gossamer (Jacson & Joseph 1973) would be puzzling in view of the weight handicap this imposes on the conditions for remaining airborne.

We have seen *Stegodyphus* casting bridging lines on numerous occasions over distances of several meters. The slightest vertical air movement is sufficient for silken threads to be airborne (Suter 1991). Thus, silken threads easily cross gaps, enabling even large spiders to move on them when the lines snag on objects. Bridging was used by over 88% of the dispersing *S. dumicola* recorded by Henschel (pers. obs.).

The adoption of the tiptoe posture and the location of nests on the windward side of trees were interpreted as indirect indications of aerial dispersal (Wickler & Seibt 1986; Seibt & Wickler 1988). However, we have observed *Stegodyphus* standing tiptoe when casting bridging lines and reaching windward destinations via these bridging lines. This stance and location can therefore not serve as independent evidence of dispersal by ballooning.

Both social and subsocial species of *Stegodyphus* appear to face high risks of predation during dispersal (Ward & Lubin 1993; Henschel pers. obs.). Ballooning must be regarded as a hazardous method of dispersal for such slow-moving spiders that are ungainly off the web. By ballooning, they immediately forgo the possibility of backtracking to the safety of their colony of origin if the new site turns out to be unsuitable, especially if it is occupied by predators such as ants. For this reason, bridging is likely to be safer.

Occasionally, social spiders are carried to new sites by agents beyond their control. Storms translocate spiders, large potential prey escape with spiders attached, mammals and birds pass through webs bearing spiders, and Gabar goshawks carry occupied spider nests onto their own nests (Seibt & Wickler 1988; Henschel et al. 1992a, b; Riechert & Roeloffs 1993). Social spiders may colonize new regions by such fortuitous, hazardous translocations, but the significance at the population level is unknown.

The extreme population subdivision indicated by protein allozyme electrophoresis (Smith & Engel 1994) constitutes additional evidence that *Stegodyphus* have poor powers of dispersal. Colonies of *S. sarasinorum* in India had low frequencies of polymorphic loci with most of the variation occurring between different subpopulations. The known distances of dispersal of *Stegodyphus* during their lifetime are short: 1–26 m for *S. dumicola* (Henschel pers. obs.); 1–83 m for *S. lineatus* (Ward & Lubin 1993). Most *Stegodyphus* disperse no more than a few meters at a time (op. cit.; Schneider 1992). Furthermore, the patchy distribution patterns of webs suggests that most dispersal is over very short range (Wickler 1973; Seibt & Wickler 1988; Schneider 1992; Ward & Lubin 1993; Henschel pers. obs.).

We conclude that there is insufficient evidence to support the impression expressed by authors citing the Wickler & Seibt (1986) report (e. g., Seibt & Wickler 1988; Riechert & Roeloff 1993; Smith & Engel 1994; Avilés 1995) that *Stegodyphus* uses ballooning regularly and therefore is expected to have greater powers of dispersal than other social spiders. Current evidence indicates that *Stegodyphus* are conservative dispersers that normally employ bridging lines to move only short distances from their natal nest. Rarely, spiders may become airborne when they are disturbed and drop while casting bridging lines. They escape and land a short distance away, no further than when bridging.

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LITERATURE CITED

Avilés, L. in press. Causes and consequences of co-operation and permanent-sociality in spiders: a review of non-territorial permanent-social spiders. *In* Social competition and cooperation in insects and arachnids. Vol.2, Evolution of sociality. (B. Crespi & J. Choe, eds.). Princeton Univ. Press, Princeton.

Barth, F. G., S. Komarek, J. A. C. Humphrey & B. Treidler. 1991. Drop and swing dispersal behavior of a tropical wandering spider: experiments and numerical model. J. Comp. Physiol. A, 169:313–322.

Coyle, F. A., M. H. Greenstone, A.-L. Hultsch & C. E. Morgan. 1985. Ballooning mygalomorphs: Estimates of the masses of *Sphodros* and *Unmidia* balllooners (Araneae: Atypidae, Ctenezidae). J. Arachnol., 13:291–296.

Decae, A. E. 1986. Dispersal: ballooning and other mechanisms. Pp. 348–356, *In* Ecophysiology of spiders. (W. Nentwig, ed.). Springer Verlag, Berlin.

Eberhard, W. G. 1987. How spiders initiate airborne lines. J. Arachnol., 15:1–9.

Follner, K. & A. J. Klarenberg. 1995. Aeronautic behaviour in the wasp-like spider, *Argiope bruennichi* (Scopoli) (Araneae, Argiopidae). Pp. 66–72, *In* Proc. 15th European Colloquium of Arachnol. (V. Ruzicka, ed.). Inst. Entomol., Ceske Budejovice.

Greenstone, M. H. 1990. Meteorological determinants of spider ballooning: the roles of thermals vs. the vertical windspeed gradient in becoming airborne. Oecologia, 84:164–168.

Greenstone, M. H., C. E. Morgan & A.-L. Hultsch. 1987. Ballooning spiders in Missouri, USA, and New South Wales, Australia: family and mass distributions. J. Arachnol., 15:163–170.

Henschel, J. R. in press. Group-living reduces risk of predation in the spider *Stegodyphus dumicola* (Eresidae). Zool. J. Linn. Soc.

Henschel, J. R., Y. D. Lubin & J. Schneider. 1995. Sexual competition in an inbreeding social spider, *Stegodyphus dumicola* (Araneae: Eresidae). Insectes Soc., 42:419–426.

Henschel, J. R., J. M. Mendelsohn & R. E. Simmons. 1992a. Is the association between the Gabar goshawk and social spiders *Stegodyphus* mutualism or theft? Gabar, 6:57–59.

Henschel, J. R., R. E. Simmons & J. M. Mendelsohn. 1992b. Gabar goshawks and social spiders revisited: untangling the web. Gabar, 7:49–50.

Humphrey, J. A. C. 1987. Fluid mechanic constraints on spider ballooning. Oecologia, 73:469–477.

Jacson, C. C. & K. J. Joseph. 1973. Life-history, bionomics and behaviour of the social spider *Stegodyphus sarasinorum* Karsch. Insect Soc., 189–204.

Jambunathan, N. S. 1905. The habitats and life history of a social spider (*Stegodyphus sarasinorum* Karsch). Smithson. Misc. Coll., Washington, 47, 2:265–372.

Riechert, S. E. & R. M. Roeloffs. 1993. Evidence for and consequences of inbreeding in the cooperative spiders. Pp. 283-303, *In* Natural history of inbreeding and outbreeding. (N. Thornhill, ed.). Univ. Chicago Press, Chicago.

Schneider, J. 1992. Die Wurzeln des Soziallebens bei der subsozialen Spinne *Stegodyphus lineatus* (Eresidae). Ph. D. dissertation, Ludwig-Maximillian-Universität, München, Germany, 135 pp.

Seibt, U. & W. Wickler. 1988. Bionomics and social structure of 'Family Spiders' of the genus *Stegodyphus*, with special reference to the African species *S. dumicola* and *S. mimosarum* (Araneida, Eresidae). Verh. naturwiss. Ver. Hamburg, 30:255–303.

Smith, D. R. & M. S. Engel. 1994. Population structure in an Indian cooperative spider, *Stegodyphus sarasinorum* Karsch (Eresidae). J. Arachnol., 22:108–113.

Stull, R. B. 1988. An introduction to boundary layer meteorology. Kluwer Academic Publishers, Dordrecht.

Suter, R. B. 1991. Ballooning in spiders: results of wind tunnel experiments. Ethol., Ecol. & Evol., 3:13–25.

Suter, R. B. 1992. Ballooning: data from spiders in freefall indicate the importance of posture. J. Arachnol., 20:107–113.

Ward, D. & Y. Lubin. 1993. Habitat selection and the life history of a desert spider, *Stegodyphus lineatus* (Eresidae). J. Anim. Ecol., 62:353–363.

Weyman, G. S. 1993. A review of the possible causative factors and significance of ballooning in spiders. Ethol., Ecol. & Evol., 5:279–291.

Wickler, W. 1973. Über Koloniegründung und soziale Bindung von *Stegodyphus mimosarum* Pavesi und anderen sozialen Spinnen. Z. Tierpsychol., 32: 522–531.

Wickler, W. & U. Seibt. 1986. Aerial dispersal by ballooning in adult *Stegodyphus mimosarum*. Naturwiss., 73:628–629.

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