

Temporally diphasic dispersal in siblings of a wolf spider: a game of Russian roulette?

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Introduction

Following a period of dormancy or aestivation the reactivation of siblings of both animals and plants may be differential in timing. In plants this is common and caused by heterogeneity of germination requirements within seed populations produced by a single individual (Koller, 1969). Such heterogeneity effectively prevents the entire seed population germinating to an appropriate cue (e.g. rainfall), which is, however, too ephemeral to permit seedling establishment. I report here on temporally diphasic behaviour of an active stage, namely the dispersal of siblings in the European Tarantula, *Lycosa tarentula* (L.).

Methods

Twelve adult female *L. tarentula* were collected in early August from burrows in karst country adjacent to the Cetina River hydroelectric scheme, 30 km east of Drniš, Republic of Croatia, Yugoslavia. All had egg sacs or produced them within a few days. They were transported to England on August 25, 1978 and housed in burrows in buckets of soil and provided with an incandescent bulb on a 12:12 light-dark cycle to serve as a heat source for basking. Under such conditions lycosids maintain their body and egg sac temperatures similar to those in the field (Humphreys, 1978). Adult lycosids will not initiate burrows but will accept and modify one made in the soil with a stick.

Spiderlings from the initial dispersal were collected and reared for some time in the laboratory, where the temperature fluctuated between about 6 and 20°C.

They were housed individually in batches of 25 in the separate compartments of culture dishes. Five of these batches were provided with water but no food.

No counts were made of the spiderlings remaining on the females after, what turned out to be, the first dispersal. Hence the proportions dispersing in each phase are estimates. They are given to show that a substantial number of spiderlings were retained on the females over winter.

Results

Young of the 12 females which produced egg sacs in early August moved to the backs of their mothers between 25 August and 19 September and the empty egg sacs were discarded. The spiderlings started to disperse from their mothers' backs on 13 September and stopped dispersing on 23 October. All the spiderlings dispersed from 3 of the females but between about 25% and 60% of the spiderlings remained on the other 9 females. These spiderlings remained over winter on the backs of their mothers (including one which died on 15 January), and then dispersed between 22 January and 5 March (Fig. 1).

I observed no evidence of feeding by the mother of those young retained over winter and up to about 20% of these were dead at the time of the secondary dispersal. Young which dispersed in the autumn were unable to survive the winter without food, even with access to water. Late dispersers were not inactive, since heating the female laterally with a focused microscope lamp caused the spiderlings to move, within a few seconds, to the shaded side.

Discussion

The data suggest that at least the diphasic dispersal, if not the timing of the second phase, was not an artefact of laboratory housing. The period between emergence from the egg sac and initial dispersal (16 to 19 days), together with autumn dispersal, is consistent with many other lycosids. Despite warmer than natural conditions in the laboratory, which should tend to accelerate processes, the synchrony of the second phase of dispersal is striking. Late winter mortality in females which bred the previous year is consistent with *Geolycosa godeffroyi* (Koch), its ecological homologue in southern Australia (Humphreys, 1976). Fabre's astute

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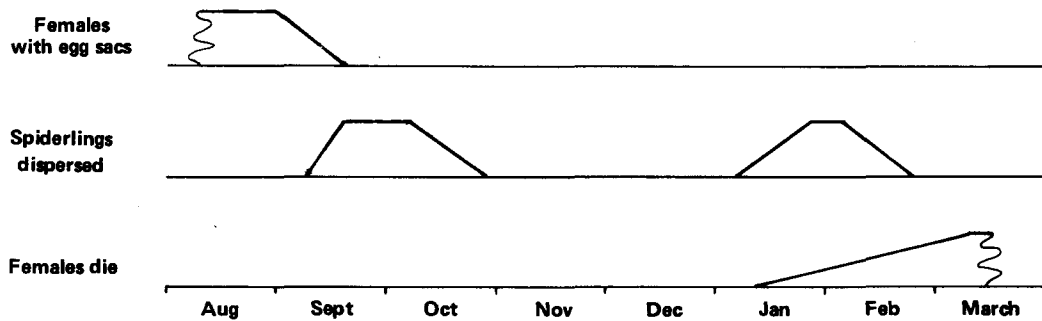


Fig. 1: The timing of egg-sac production, dispersal of young from mother's back, and female mortality of 12 *Lycosa tarentula*. The bars are scaled to show the intensity of the activity within each period.

observations on *Lycosa narbonnensis* Walck., in a similar climate, support over-winter retention of spiderlings; "in January and February . . . I always find her at home", (i.e. in the burrow), "still carrying her family. This vehicular upbringing lasts five or six months at least, without interruption . . . I do not see them grow larger" (Fabre, 1912). I have maintained many species of lycosid in the laboratory under similar conditions and have never seen live young remain on the mother for protracted periods. The mother seems uninvolved with the timing of dispersal, since the young did not disperse immediately from the female which died.

The inability of first dispersers to survive the winter without food suggests the possibility of metabolic as well as behavioural differences between early and late dispersers.

Sex differences in the timing of juvenile dispersal occur in non-siblings of *Trichosurus caninus* (Ogilby) (Marsupialia: Phalangeridae) (Barnett, How & Humphreys, 1982) but temporally polyphasic dispersal of siblings of the active stage of an animal does not seem to have been reported. It is worth considering how this diphasic dispersal may enhance fitness, since this mixed strategy must have an advantage over either autumn or spring dispersal alone.

Western Yugoslavia has summer drought followed by cold winters, both of which vary widely in severity from year to year (Furlan, 1977). Under such conditions a mixed strategy of dispersal can offer advantages which I will illustrate using data from *Geolycosa godeffroyi*. Burrows of the two species are similar in structure and depth (L. Dufour, cited in

Fabre, 1912; my unpublished observations, and Humphreys, 1973, 1975). Availability of soil moisture to the spider during drought is directly related to burrow depth (Humphreys, 1975) which, in turn, is directly related to spider size (Humphreys, 1973). Deep burrows protect the spiders from lethally cold ambient temperature (Humphreys, 1975, 1978). In mild winters spiders dispersing in the autumn grow several instars by the spring (Humphreys, 1973, 1976).

Using these observations a chart can be drawn (Table 1) of the probable advantages of mixed dispersal. Autumn dispersal followed by a mild winter and summer should be advantageous as it shortens the potential generation time (Cole, 1954; Levins, 1969) and, because wolf spiders are cannibalistic (Edgar, 1969; Hallander, 1970; Humphreys, 1973), spring dispersers, due to their smaller size, may become the prey of autumn dispersers. A mild winter

Seasonal conditions		Dispersal type	
Winter cold	Summer drought	Autumn	Spring
mild	mild	+	-
mild	severe	+	-
severe	mild	-	+
severe	severe	-	+?

Table 1: Schema showing the proposed relative fitness of autumn and spring dispersal in *Lycosa tarentula* with changes in the severity of winter cold and summer drought.

+ = advantaged, - = disadvantaged.

followed by severe drought would be advantageous for autumn dispersers because of shorter generation time and because they would have deeper burrows during the drought and hence greater availability of soil water. Severe winter followed by a mild summer should favour spring dispersers as they would be protected from freezing in the deep burrow of the mother. If both seasons were severe, spring dispersers may be at an advantage because they can occupy the deep burrows of the recently dead adults. If this is the case, Table 1 can be reduced to a 2 x 2 table in which the severity of the winter determines whether autumn or spring dispersal is advantageous. However, in *G. godeffroyi* favourable burrowing sites are limited and some burrows in which breeding occurs are occupied by successive generations (my unpublished observations). Young spiders could not retain these in opposition to one-year-olds, hence no clear advantage befalls either dispersal category.

All things being equal, autumn dispersers will be at an advantage owing to their reduced generation time (by probably 5 months in 2 to 3 years; Humphreys, 1976). For autumn and spring dispersal to coexist in the population some factor, which I consider to be components of weather, must cause them to be equally fit in the long term (Maynard Smith, 1974, 1976). Because weather is non-responsive this cannot be considered a classical game (ibid.) but rather a game of Russian roulette with the two dispersal types pitted against the probability of lethal weather conditions in the future.

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