Maintenance of polymorphism in the orb weaving spider species *Agalenatea redii* (Araneae, Araneidae)

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Abstract: The maintenance of polymorphism within populations may be the consequence of several elements of species life history such as use of space, activity rhythms, predation, parasitism and reproduction. The present study focuses on the latter aspect using an orb weaving spider, *Agalenatea redii*, which presents five different morphs of the opisthosoma pattern in the adult stage. Over the course of four years, from 2008 to 2011, adult spiders (males, females and pairs) were observed at different sites. In 2011, we also conducted a six-week survey of a single population, observing the number of spiders of each morph and the morph of paired spiders. We collected field data on the spatial and temporal distribution of spiders based on their sex and morph. Using a distance analysis, we compared the field distribution with a simulated one in which pairs were associated at random. The results showed that although there were changes over time and space in the proportions of females of the different morphs, as well as in the proportion of the pair associations, pairing according to morphs probably occurs at random.

Key words: colour pattern, field data, mating, orb weaver

HUXLEY (1955) defined polymorphism as the existence of at least two different phenotypes in a population whose rarest form is too frequent to be solely a consequence of recurrent mutations (GRAY & MCKINNON 2007). Polymorphism can be found in many species such as the mollusc *Cepaea nemoralis* (COOK 2007), the anuran *Bufo canorus* (HOFFMAN & BLOUIN 2000), the spider *Enoplognatha ovata* (HIPPA & OKSALA 1981) and in females of many damselfly species (ROBERTSON 1985, CORDERO 1992, CORDERO et al. 1998, ANDRÉS et al. 2000). The number of morphs can be limited, such as in melanic moths (MAJERUS 1998) or large, as in the meadow spittlebug, *Philaenus spumarius* (HALKKA & HALKKA 1990); a phenomenon called exuberant polymorphism (OXFORD 2009).

Many theories have been put forward to explain the evolution and maintenance of polymorphism. For instance, spatial and temporal habitat heterogeneity has long been known to promote phenotypic and genetic variations (FULLER et al. 2005). BOND & KAMIL (2006) used digital moths preyed upon by real birds to show that the evolution of polymorphism

depended on an interaction between habitat structure and predator pressure. The importance of predation in favouring the rarer morphs has also repeatedly been shown, for example in *Lutianus griseus* (REIGHARD 1908) or in *Cepaea hortensis* (CLARKE 1962). Another factor is linked to differences in reproductive behaviour and mate choice, which maintain polymorphisms (*Cepaea nemoralis*, CAIN & SHEPPARD 1950, 1954; guppies *Poecilia reticulate*, GRAY & MCKINNON 2006) often consisting of morphological variation, for example in colouration (ANDERSSON 1994).

One of the great, persisting issues in ecology and evolution are the numerous cases of polymorphism linked with colour morphs. Indeed, many natural colour polymorphisms have been shown to be caused by non-selective processes such as migration and dispersal (DEARN 1984, KING & LAWSON 1995, REILLO & WISE 1988), or genetic drift and local population bottlenecks (BRAKEFIELD 1990).

Our study was conducted on the spider species *Agalenatea redii*, which presents five different morphs: α, γ, δ, ε and ζ (Fig. 1) in both sexes. The aim of this study was to evaluate over several years the maintenance and stability of the polymorphism in different spider populations using their temporal and spatial distribution. First, a multi-annual study was carried out on different sites to test if polymorphism was maintained across space and time. Afterwards, the study of a breeding season was carried out to determine whether there was a differential emergence of morphs during a season limiting the possibility of morph pairing. Finally, a detailed study of the spatial

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distribution of individuals at a single site was done to test whether aggregation could contribute to an increase in the probability of meeting and reproduction of the different morphs. We calculated the frequency of paired individuals according to morph and sex in the different experiments. We also looked at pair composition (homomorph or heteromorph) and we tested whether or not the frequency of these pairs fitted a random theoretical distribution of spider pairs.

Material and methods

Biological model

Agalenatea redii is an orb-weaving spider, whose geographical distribution extends across the whole of Europe (JONES 1990). This species has an annual biological cycle with post-embryological development spread over the entire year: eggs are protected in cocoons, they are laid at the end of spring and the young spiders remain in the egg sacs at juvenile stages (often sub-adult) during winter. The adults (5.5 to 7 mm for females and 3.5 to 4.5 mm for males, ROBERTS 1996) have a short appearance time that generally starts at the beginning of spring with reproduction, and ends early in the summer when the eggs are laid. This spider is characterized by a polymorphism of the dorsal pattern on the opisthosoma. Five morphs are present in both males and females (α, γ, δ, ε, ζ) (JONES 1990) (Fig. 1).

Dynamics of the population
Multi-annual study

Data from several populations of *Agalenatea redii* studied from 2008 to 2010 at different sites in the area of Nancy (Meurthe-et-Moselle, France, 48°41'N, 6°17'E, 272 m a.s.l.) were compiled. These data enabled us to characterize dynamics of the population according to the sexes, morphs and pairs (by distinguishing homomorph from heteromorph pairs). For these studies, two spiders (one male and one female) were considered as forming a pair when they were both present at the same time on the same stem and less than 3 cm apart, which is the mean distance between a male and a female (there was no direct link with potential fertilization) (personal observations). In 2008 four sites were surveyed (number of spiders; N1 = 207). In 2010 three sites were surveyed (N2 = 399). In 2011 only one site was examined (N3 = 551). Visual hunting was the method employed to spot and identify spiders, while being careful of all the supports (dry stems of vegetation) used by spider. At the beginning of spring the green vegetation had not yet grown and only the dry stems of the previous year remained, which allowed us to search exhaustively for spiders.

Single breeding season study

For this study, we surveyed one site during the reproductive period (from March 28th to May 6th,
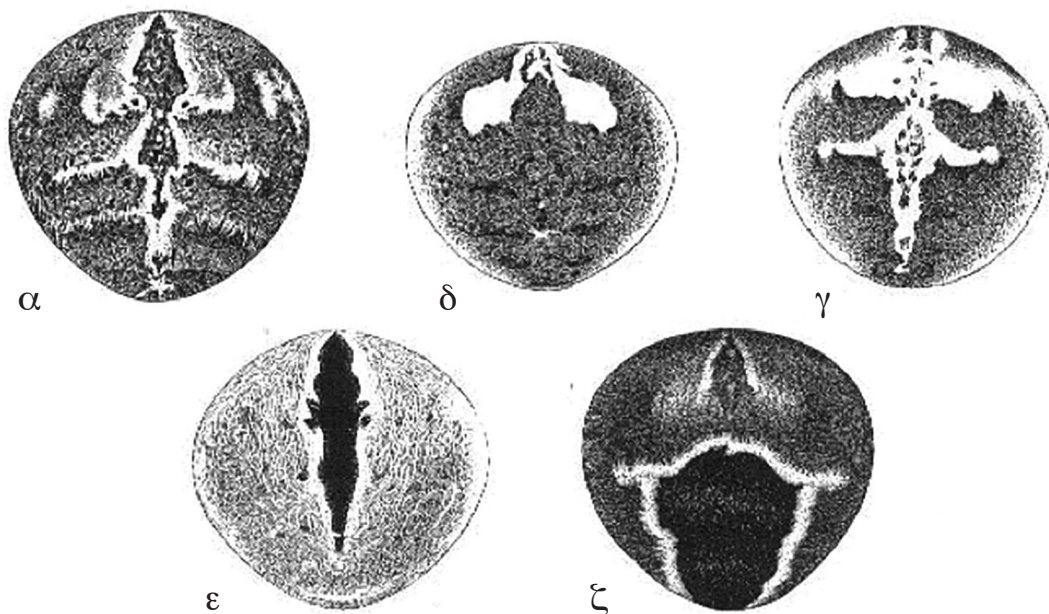

Fig. 1: Schematic representation of morphs observed in the species *Agalenatea redii* (from DÉOM 1996).

2011). Two transects (26 and 28 m, respectively) were performed in the field using a string to mark them. The spiders were located on vegetation in a strip of one meter on either side of the transect lines.

Spatial distribution of the spiders

On the site of the 2011 survey, a positional map of the spiders was constructed on March 22nd for a rectangular area (10 m * 26 m), divided into units of one square meter. Spiders were located and morph and sex were noted. The position of each individual or each pair was entered into the computer to determine the spatial distances between the individuals and the type of distribution. To do this, a dispersion index I (based on the index of FISHER 1922) was calculated based on the map distances:

(1) $I = S^2/X$

(2) $X = S_{(1 \text{ to } s)} x_i/n$,

where x_i is the number of individuals of morph i and s is the number of different morphs in all the n units of the surveyed area,

(3) $S^2 = S_{(1 \text{ to } s)} (x_i - X)^2/n - 1$.

A test of threshold significance was performed (at α=5%) and compared to the Chi-square table: X^2 (p=0.05, df=59)=77.93 and X^2 (p=0.95, df=59)=42.34). Two conditions were then checked: $I*(\text{number of units (n)} -1) > X^2$ if the distribution is aggregative and $I*(\text{number of units (n)} -1) < X^2$ if the distribution is uniform. The type of distribution can provide a clue to the pairing. If the distribution is uniform it means that pairing is random, but if the distribution is aggregative it suggests that pairing may not be due to chance.

Statistical analysis

The relationship between the various morph proportions for males, females and pairs were analyzed based on the 2008/2010/2011 data. The temporal follow up of a 2011 population was evaluated using a Monte Carlo method (METROPOLIS & ULAM 1949) specifically programmed for this study. The null hypothesis was: at each period and every location, the male morph is independent of his female partner's morph. The statistical test employed looks like the Chi-square test of independence. It differs from the latter in the following points. The theoretical frequency ($f_{\text{th } x,y,z,t}$) of male morph x and female morph y pairs, at location z and period t was estimated with the product of the entire male frequency (paired or alone)

of morph x among the males at location z and period t and the frequency of all females (paired or alone) of morph y among the females at location z and period t. The theoretical number ($N_{\text{th } x,y,z,t}$) of morph x and y pairs, at location z and period t, was estimated by the product of their frequency ($f_{\text{th } x,y,z,t}$) and the total number of pairs at location z and period t.

According to this calculation, the theoretical number is the null hypothesis and $N_{\text{obs } x,y,z,t}$ is the number of male morph x and female morph y pairs among the males at location z and period t. The test was done using a distance calculation with two methods: the first by calculating the square distance:

(1) $sq = \sum_{x,y,z,t} (N_{\text{obs } x,y,z} - N_{\text{th } x,y,z,t})^2$

and the second by calculating the absolute value of distance:

(2) $ad = \sum_{x,y,z,t} |N_{\text{obs } x,y,z} - N_{\text{th } x,y,z,t}|$.

One hundred thousands simulations were carried out on each distance. For each simulation in every location z, at every period t, the males and females of location z and period t mated randomly. We calculated the number N of simulations in which the distance
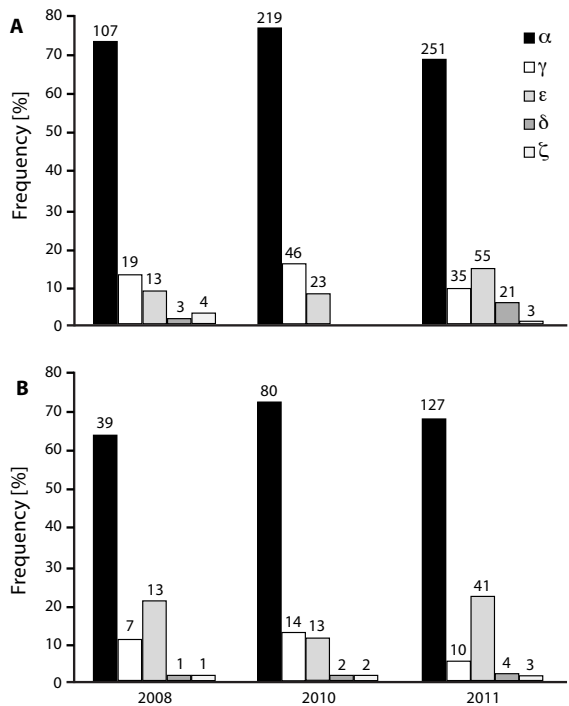

Fig. 2: Changes in the proportion of female (A) and male (B) morphs (from the left to right: morphs (α, γ, δ, ε, ζ) according to the year of observation (number of captured spiders on the graph).
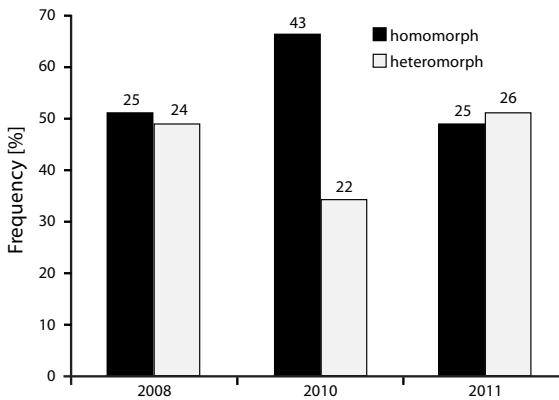
Fig. 3: Frequencies of homomorph and heteromorph pairs (%) observed over the period 2008–2011 (number of spider pairs on the graph).
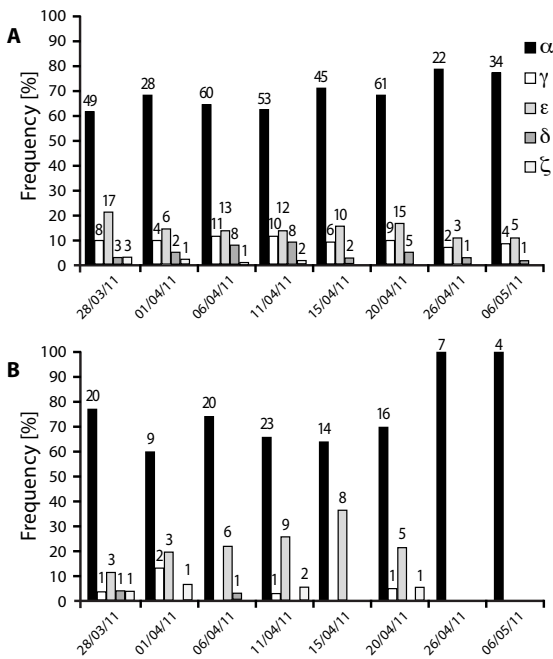

Fig. 4: Changes over time in the proportion of female (A) and male (B) morphs (number of spiders on the graph) during a reproductive season survey in 2011.

between the random distribution of the simulation and the theoretical distribution was greater than the distance between the real distributions observed in the wild and the theoretical distribution. The test's level of significance was then N/100000. The different frequencies were compared with a Chi-square test.

Results
Multi-annual study
Ratio of males and females of different morphs

The distribution of morphs over the years appeared to be the same for the males (Chi-square test, X^2=9.66; df=8; p=0.29) but not for the females, which varied every year (Chi-square test, X^2=41.14; df=8; p<0.01). Indeed the ratio of morphs amongst females fluctuated between 2008–2010 (Chi-square test, X^2=14.57; df=4; p<0.01), 2010 –2011 (Chi-square test, X^2=32.17; df=4; p<0.01), and 2008–2011 (Chi-square test, X^2=10.28; df=4; p<0.05) (Fig. 2).

Proportion of heteromorph and homomorph pairs of spiders

Over the three years (from 2008 to 2010), the division between homomorph and heteromorph pairs did not differ (Chi-square test, X^2=4.22; df=2; p=0.12) (Fig. 3). Furthermore, the Monte Carlo simulations showed that there was no significant difference from a random association of the two morphs, based on their frequencies in the population (N=100000 runs, square distance (sq): p=0.61; absolute distance (ad): p=0.72).

Single breeding season study
Proportion of males and females of different morphs

The ratios of morphs among the females did not vary according to the observation dates (Chi-square test, X^2=19.34; df=28; p=0.89). The same pattern was witnessed among the males (Chi-square test, X^2=22.56; df=28; p=0.75) (Fig. 4).

Proportion of heteromorph and homomorph pairs of spiders

The distribution of the heteromorph and homomorph pairs was independent of the date, and thus of

Tab. 1: Results of the simulations by date for the pairs observed on field transects and according to the proportion of each morph in each pair.

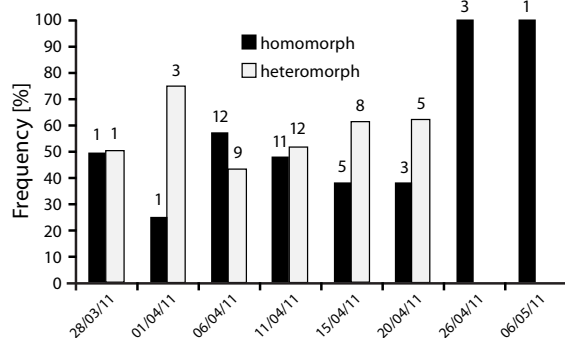| probability	Date of observation in 2011					
	28/03	01/04	06/04	11/04	15/04	20/04
square distance (sq)	0.36	0.48	0.57	0.81	0.094	0.11
absolute distance (ad)	0.36	0.34	0.37	0.72	0.32	0.14

Fig. 5: Proportion of homomorph and heteromorph pairs (%) observed in 2011 with the number of spiders on the graph.

the time within the reproductive period (Chi-square test, X^2=6.65; df=7; p=0.51) (Fig. 5). Moreover, the simulation showed that the observed pair distribution according to the proportion of spiders did not diverge from a random distribution for all dates (N=100000 runs, square distance (sq): p=0.44; absolute distance (ad): p=0.28) or for each observation dates (p>0.05) (Tab. 1).

Spatial distribution of spiders at a site

The spatial distribution of all individuals (males and females all morphs together) in the sample site appeared aggregative (I*(n-1)=85.7). The same was true for the spatial distribution of the males (I*(n-1)=91.7) although that of the females appears to be random (I*(n-1)=71.7).

Discussion

This study carried out a spatio-temporal description of polymorphism in the orb weaving spider, *Agalenatea redii*. The first result was that morphs were not equally probable within a population. Indeed one morph (a) predominated in both males and females. The second result revealed that morph distribution was stable over time for males and females, at least during one reproductive season. The difference of distribution between the female morphs observed during these three years could be due to the absence in 2010 of particular low frequency morphs. This information supported, however, the idea of the maintenance of polymorphism in this species.

The comparisons of field data on morph frequencies with random morph associations showed that pair distributions depending on available morphs did not differ from field distributions either during a reproductive period (2011) or over several years

(from 2008 to 2010). A similar result was found for the damselflies *Ischnura graellsii* (CORDERO 1992), *Ceriagrion tenellum* (ANDRÉS et al. 2002), and for *Ischnura ramburi* (ROBERTSON 1985), where it was observed that males mated with females at random.

In *Agalenatea redii*, males remained with sub-adult or adult females before mating and also some days after (personal observations), as in *Zygiella x-notata* (BEL-VENNER & VENNER 2006). Our study of male distribution (all morphs together) showed an aggregative distribution. This male distribution could reflect the presence of a female signal (pheromones, dragline cues) used to locate them. However, if the encounters were at random, these signals would not be specific to morphs.

Several hypotheses have been proposed in the literature to explain the maintenance of polymorphism in different species. It could be genetic, such as in the spiders *Enoplognatha ovata* (OXFORD 1983, 2009) or *Pityohyphantes phrygianus* (GUNNARSSON 1987). In this case the preservation of morphs that showed a low frequency in the population could be due to an effect of genetic drift (OXFORD 2005). This did not seem to be the case in *Agalenatea redii*, because different morphs were maintained over time and space.

Non-selective processes, such as dispersal and migration (FORD 1975, KIMURA 1983), may cause polymorphism. Our study was conducted on different populations separated by several km from each other. They were not isolated populations. There was a continuum between the different populations, so exchange of individuals between study populations by emigration/immigration processes was possible. However, there is no reason to expect that morphs have different dispersal properties, and so differential emigration is not likely to explain the maintenance of polymorphism in *Agalenatea redii*.

Another hypothesis is the preference for a male morph as in the ladybird *Harmonia axyridis* where females show a male morph preference in relation to the season (UENO et al. 1998). Therefore, polymorphism would be the consequences of directional sexual selection that would change with time. In our case the frequencies of the morphs remained stable over the reproductive season, which makes this hypothesis unlikely.

Polymorphism may be part of an alternative reproductive strategy. For example, one morph may be less attractive – but more competitive – than another (KINGSTON et al. 2003). FINCKE (1994) suggested the hypothesis that polymorphism could be maintained by

a mechanism of negative frequency-dependent selection and this was tested by FITZPATRICK et al. (2007). This hypothesis implies that the rarer morphs have a higher phenotypic aptitude by avoiding, for example, the costs of a long copulation (VAN GOSSUM et al. 1999). In other words, a less prevailing morph can be less appealing, but more reproductively competitive and consequently have higher reproductive success (COOK et al. 1994, KINGSTON et al. 2003), and polymorphism in a population can be stable only if all the present morphs support equal selective advantages (FINCKE 1994, BIZE & ROULIN 2007).

To conclude, our results did not allow us to elucidate mechanisms by which polymorphism is maintained in *Agalenatea redii* populations and hypotheses remain to be tested. Thus, we have to study the behaviour and performance of the males of different morphs based on their pairing with homomorph or heteromorph females.

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