

Article

Time till death affects spider mobility and web-building behavior during web construction in an orb-web spider

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Abstract

It is well known that age influences organism mobility. This was demonstrated in vertebrates (such as mammals and birds) but has been less studied in invertebrates with the exception of *Drosophila* and the nematode *Caenorhabditis elegans*. Here we studied the influence of age on the mobility of the orb-weaving spider *Zygiella x-notata* during web construction. The orb-web is a good model because it has a characteristic geometrical structure and video tracking can be used to easily follow the spider's movements during web building. We investigated the influence of age (specifically chronological age, life span, and time till death) on different parameters of spider mobility during the construction of the capture spiral (distance traveled, duration of construction, spider velocity, spider movement, and spider inactivity) with a generalized linear model (GLM) procedure adjusted for the spider mass. The results showed that neither chronological age, nor life span affected the mobility parameters. However, when the time till death decreased, there was a decrease in the distance traveled, the duration of the construction of the capture spiral, and the spider movement. The spider velocity and the time of inactivity were not affected. These results could be correlated with a decrease in the length of the silky thread deposited for the construction of the capture spiral. Spiders with a shorter time till death built smaller web using less silk. Thus, our study suggests strongly that time till death affects spider mobility during web construction but not the chronological age and thus may be a good indicator of senescence.

Key words: ageing, behaviors, orb-web construction, spider mobility, *Zygiella x-notata*.

Ageing in a living organism is generally defined as a progressive degradation of physiological and behavioral functions leading to death (Hamilton 1966; Finch 1990; Kirkwood and Rose 1991; Moya-Larano 2002; Gaillard et al. 2003; Monaghan et al. 2008; Monaco and Silveira 2009; Lliadi and Boulianne 2010; Ricklefs 2010). However, there is another definition of ageing in the context of evolution; ageing is a process then regarded as a decrease in the survival

and reproductive performances of the organisms (Kirkwood and Rose 1991, Partridge and Barton 1993, Bennett and Owens 2002; Gaillard et al. 2004). One of the major effects of ageing on organisms is a decrease in mobility. Studies of the effect of ageing on the behavior and mobility of invertebrates are few (Carey et al. 2006) and they consider the decrease of locomotor activity as a sign of ageing (Glenn et al. 2004; Lliadi and Boulianne 2010). In the *Drosophila* model,

locomotor activity is generally measured by fly displacement in a defined area during a determined period; this spontaneous locomotor activity decreases with age (Ridgel and Ritzmann 2005). This influences the ability of animals to cover long distances for exploring their environment, for searching for food or for avoiding predators (Grotewiel et al. 2005; Ridgel and Ritzmann 2005; Simon et al. 2006; Lliadi and Boulianne 2010). This decrease in locomotor activity also occurs in others invertebrate species (i.e., *Blaberus*, Ridgel and Ritzmann 2005). It was found to be age dependent but was also influenced by the life expectancy (life span); genetically modified flies with a longer life expectancy, showed a reduced mobility deficiency (Helfand and Rogina 2000; Grotewiel et al. 2005; Gargano et al. 2005). This deficiency associated with age was also observed in nematodes (*Caenorhabditis elegans* and *Strongyloides ratti*) even if some of these organisms have a very short life (15 days for *S. ratti*; Gems 2000; Gardner et al. 2004). Ageing may be declined by several variables such as chronological age, life span, or time till death. If the first two had been investigated very often in the study of animal senescence (for review, see, Nussey et al. 2013), the last one received less attention. Only few studies found that actuarial senescence of some prey in a predator-prey system might affect their survival and that their time till death was a best predictor of the individual responses (Carlson et al. 2007, Balbontin and Moller 2015), but nothing is known on the effects of time till death on animal mobility and abilities of displacement in their environment. Indeed, time till death could be a good indicator of senescence and be used in aging studies.

Nature abounds with structures built by animals (termite mounds, bird nest, beaver dams, spider webs), which arise from more or less complex building behaviors. The performance of these building behaviors is linked to morphological capacities and coordination of movements (Hansell 2005, 2007). Orb spiders build webs, which result from successive, simple, and reproducible behavioral patterns organized in time (Vollrath 1992), that are easily modeled with simple algorithms (Krink and Vollrath 1998). Thus, web geometry is a representation of the spider's behavioral components and silk manipulation (Vollrath 2000; Foelix 2011). In spiders, the consequences of age-related motor deficits upon behavior have not been clearly defined. Recently, the effects of ageing on web structure were demonstrated in spiders (Anotaux et al. 2012), and webs built by old spiders were smaller, less geometrically regular and presented more anomalies than those built by younger spiders. Thus, ageing appears to alter web structure and construction behavior. However, to have a complete and successful behavioral analysis of web building, a good understanding of both web engineering and spider movement and activity is necessary. Spider behavior during web construction has been very well studied (Vollrath 1988; Vollrath et al. 1997; Heiling and Herberstein 1998; Herberstein and Heiling 1999). Until now, very few studies have investigated age effects in orb spiders (Mayer 1952; Witt et al. 1972). Among the diversity of spider web types, the geometrical analysis of the orb-webs is relatively simple, and has provided important datasets for web-structure description and for the analysis of the behavior expressed during web building (Vollrath 1992; Zschokke and Vollrath 1995; Hesselberg 2010). Currently, using modeling tools and filming techniques as well as movement analysis, the steps during web construction can be recorded and used to infer the rules guiding web building (Gotts and Vollrath 1992; Krink and Vollrath 1997, 1998, 1999).

In the present study, we focused on the orb-web construction of the spider *Zygiella x-notata* to compare the effects of the different variables measuring age (chronological age, life span, and time till death) on spider web-building behavior and to show which is the best indicator of ageing. We expected that age: 1) may influence the

speed of the spider during web building and so affect the duration of web construction and 2) may affect the building capacities of the old spiders and have material effects on web design. Using videos and tracking software, we analyzed spider mobility during web construction at different ages, and in the light of other recent studies, we discuss the effects of age on the spider's web-building behavior.

Material and methods

Spiders and rearing conditions

Zygiella x-notata is a widespread medium-sized orb-web spider (5–7 mm for adult females) in northern Europe, which preferentially lives in the vicinity of human buildings. It constructs an orb-web, which is generally characterized by the presence of a free sector in the upper part, and feeds primarily on flying prey (generally Dipterans). In eastern France, its development cycle is annual: the juveniles leave the egg sacs at the beginning of spring; reproduction starts in summer with mating and females lay eggs in September–October. While males die after reproduction, the majority of females disappear after egg-laying but some of them can survive till the next spring (Roberts 1996; Thévenard et al. 2004; Bel-Venner and Venner 2006). In the adult stage, the life span of females is approximately from 5–7 months (Thévenard et al. 2004). The spiders used in this study hatched in the spring and were captured as sub-adult individuals in August and September, outside human buildings, and reared in the laboratory in plastic boxes (10 × 7 × 2.5 cm) (temperature of the room: 19°C and an hygrometry: 50%). They were sprayed with water and fed once a week with a fly *Lucilia caesar*. They were last fed 4 days before the tests. All the spiders used for the tests moulted in their boxes, became adult in the laboratory, and finally died in the laboratory so their exact age as adult individuals could be recorded. We defined 3 different ages: chronological age, which was the age (in days after adult moult) at which the test was carried out; adult life span, which was the duration (in days) of adult life; and time till death, which was the time (in days) between the test and the death of the spider. This latter value corresponds to the number of days that the spiders survived after the test. All spiders were virgin females. Since spider body mass may influence web-construction characteristics and varies with age (Venner et al. 2003), spiders were weighed before being placed in experimental conditions (balance Sartorius BASIC BA110S, precision 0.1 mg). As the amount of silk deposited for the construction of the web depends on age (Anotaux et al. 2012), we estimated this amount of silk from the length of thread (capture thread length (CTL)) used for building the sticky capture spiral (Venner et al. 2001) from a photograph of the web.

Tests

For one test, spiders were removed from their small boxes and placed into large wooden frames (50 × 50 × 10 cm) closed by glass on 2 sides, where they could build a web. During the tests, we made video recordings ($n = 27$) as the spiders of different ages constructed the capture spiral by placing cameras on tripods (camera Sony HDR-CX550) at frame height. Each spider was used only one time. As in nature, *Z. x-notata* generally builds its webs very early in the morning, when it is still dark, thus, filming was done in the night mode with infrared light (using the night shot of the camera), with the light of the room still turned off. For each round of experiments, 8 spiders were placed in the frames and 2 cameras were used placed in front of the frames. As soon as 2 spiders began web construction,

we began recording. Thus, to be sure that we recorded the very initial stages of the construction, spider behavior in their frames was permanently observed. Once a spider moved into a frame, the recording was started and the deposit of the radii was defined as the first building step; this ensured that a complete record of the construction of the capture spiral was made. When the spider completed the web or if it stopped building and went back to its retreat, the recording was stopped and a new frame was recorded. Thus, to obtain a video of the complete construction of 27 webs, we had to put more than 100 spiders in the frames to follow their web-building behavior. This experiment took 2 months to complete.

Mobility parameters

After recording, videos ($n = 27$) were analyzed using a video-tracking software package that tracks and analyzes the behaviors, movements, and activity of animals: EthoVision XT[®] 7.0 (Noldus Information Technology, Wageningen, The Netherlands). This tracking software is based on the existence of a contrast between the background and the subject (spiders appeared black on a green background): the software recognizes the animal (surface defined in pixels) based on the contrast between it and the background; it detects the animal's center of gravity and assigns its coordinates (x, y). By analyzing 3 images per second, the software associated a time unit (0.33 s) with the position of the spider (coordinates (x, y)). Then, the coordinates of the position of the spider body were plotted and the browser linked automatically to the successive points. An example of the track of a spider's body made with Ethovision is illustrated in Figure 1. The following spider mobility parameters were calculated from the successive positions of the spider:

- Distance traveled: the total distance the spider traveled from the beginning to the completion of the capture spiral (cm); this length

was calculated by adding all the segments between two successive points.

- Velocity: the mean of spider displacement (cm/s) velocities calculated for each unit of displacement.
- Duration of capture spiral construction: the total time the spider took to build the capture spiral (min) from the first deposited unit of the capture spiral until the deposit of the last unit.
- Duration of movements: the time(s) during which the spider was moving during capture spiral construction. The threshold of movement was defined after validation at 0.5 cm/s: above 0.5 cm/s, the spider was regarded as moving; below that 0.5 cm/s, the spider was regarded as motionless. It is the smallest level at which the program is able to perceive a movement. It corresponds to a displacement of the spider of 0.2 mm per picture.
- Duration of inactivity: the time(s) during which the spider was motionless (see above for definition).

Statistical analysis

A total of 27 recorded videos of capture spiral building by adult female spiders of different ages (from 20 to 259 days) were analyzed and used to assess the associations between the 5 spider mobility parameters (distance traveled, velocity, building duration of the capture spiral, duration of movements, duration of inactivity) and 1) chronological age, 2) life span, 3) time till death, and 4) web characteristic as CTL (capture thread length). Series of generalized linear model (GLM) were used where chronological age, life span, time till death, and CTL were the independent variables and all spider mobility parameters were the dependent variables. As CTL could be affected by ageing, all mobility parameters were statistically corrected for CTL, using the CTL as covariable in a linear regression model. These models were adjusted for body mass, collected at each



Figure 1. Photograph of a web built by *Zygiella x-notata*. (A) The web built by a 112-days-old spider (72 days before death). (B) The same web represented by video-tracking software EthoVision XT[®] 7.0. The trail followed by the spider during auxiliary spiral construction is shown in red. Each circle indicates a regular time interval used for the analysis.

test, as a potential confounding factor. Statistical analyzes were performed using R 2.15.0 software. Parametric tests were realized when normality was verified. A Shapiro–Wilk test was applied to determine whether the sample data were likely to derive from a normally distributed population and the homogeneity of variances was done with a Levene’s test. Significance was considered at $P < 0.05$.

Results

General data

Our methodology introduced significant variability into the experiment as the chronological age of the spiders ($CV = 47\%$) (Table 1). This variability appeared to be close to that of time till death ($CV = 69\%$) (Table 1) but not to life span, which was lower ($CV = 29\%$) (Table 1). We observed a large variability in the length of the capture spiral ($CV = 43\%$), which was followed by significant variability in the web-construction characteristics (duration of web building ($CV = 37\%$) and distance traveled ($CV = 46\%$) (Table 1). Only the velocity showed lower variability ($CV = 22\%$) (Table 1). There was no relationship between spider chronological age and mass.

Table 1. Mean, standard error (SE) and coefficient of variation (CV) of the parameters describing age (chronological age, life span, time till death) and mobility (duration of building, velocity, duration of movements, duration of inactivity, and distance traveled), spider mass, and of the length of the silky thread of the capture spiral (sample size = 27)

Parameters	Mean	Standard error	CV (%)
Chronological age (days)	141	13	47
Life span (days)	213	12	29
Time till death (days)	74	10	69
Duration of web building (min)	19.5	1.4	37
Traveled distance (cm)	272.2	24.8	46
Velocity (cm/s)	0.23	0.01	22
Duration of movements (min)	18.2	1.4	39
Inactivity (s)	77	10	66
Spider mass (mg)	33.8	2	30
Length of spiral thread (cm)	336.7	28.6	43

Table 2. Relationships between spider mobility parameters and chronological age using a GLM adjusted for body mass ($SE =$ Standard error)

Variables	Estimates	SE	<i>t</i>	<i>P</i> level
A. Distance traveled				
Intercept	39.01	80.06	0.49	0.63
Chronological age	-0.08	0.32	0.26	0.79
B. Duration of movements				
Intercept	4.71	4.31	1.09	0.28
Chronological age	-0.006	0.02	0.35	0.73
C. Duration of immobility				
Intercept	17.65	5.92	2.98	6.44e-04
Chronological age	-0.02	0.02	1.02	0.32
D. Velocity				
Intercept	1.96e-01	2.97e-02	6.62	7.60e-07
Chronological age	-7.56e-05	1.20e-04	0.63	0.53
E. Building duration of the capture spiral				
Intercept	5.55 4.43	1.25	0.22	
Chronological age	-0.007 0.02	0.43	0.67	

Influence of chronological age on spider mobility during web construction

The chronological age of adult spiders ($n = 27$) during web construction ranged from 20 to 259 days old, with an average age of 141 days. Once adjusted for spider body mass, none of the spider mobility parameters differed with chronological age (distance traveled: Table 2A; duration of movements: Table 2B; duration of inactivity: Table 2C; velocity: Table 2D; building duration of the capture spiral: Table 2E).

Influence of life span on spider mobility during web construction

The life span of the adult females spiders captured on videos during web construction ranged from 57 to 303 days old, with an average age of 212 days. Life span did not affect spider mobility parameters adjusted for body mass (distance traveled: Table 3A; duration of movements: Table 3B; duration of inactivity: Table 3C; velocity: Table 3D; building duration of the capture spiral: Table 3E).

Influence of time till death on spider mobility during web construction

When adjusted for body mass, some parameters of spider mobility differed with their time till death: the distance traveled, the movement duration, and the building duration decreased when spiders build closer to the date of their death (distance traveled: $R^2 = 0.13$, $P = 0.065$, Figure 2A; duration of movements: $R^2 = 0.22$, $P = 0.013$, Figure 2B; building duration of the capture spiral: $R^2 = 0.22$, $P = 0.012$, Figure 2C). However, the duration of inactivity and spider velocity did not differ with time till death (duration of inactivity: $P = 0.56$, Figure 2D; velocity: $P = 0.70$, Figure 2E).

Age, silk investment, and spider’s mobility

The CTL (adjusted for spider body mass) tended to decrease when time till death of the spider decreased (Table 4A). However, CTL did not correlate with either the spiders’ chronological age (Table 4B), or the lifespan (Table 4C). When adjusted for body mass, the distance traveled by the spiders and the total duration of their movements during capture spiral building increased with CTL (distance traveled: $R^2 = 0.73$, $P < 0.0001$, Figure 3A; duration of movements: $R^2 = 0.77$, $P < 0.0001$, Figure 3B). In the same way, spider velocity and building

Table 3. Relationships between spider mobility parameters and life span using a GLM adjusted for body mass ($SE =$ Standard error)

Variables	Estimates	SE	<i>t</i>	<i>P</i> level
A. Distance traveled				
Intercept	-45.57	94.3	0.48	0.63
Life span	0.41	0.34	1.21	0.24
B. Duration of movements				
Intercept	-0.34	5.06	0.07	0.94
Life span	0.02	0.02	1.32	0.2
C. Duration of immobility				
Intercept	15.25	7.32	2.08	0.05
Life span	-0.00	0.03	0.03	0.98
D. Velocity				
Intercept	0.18	0.04	5.14	2.90E-05
Life span	1.14e-03	1.31E-04	0.09	0.93
E. Building duration of the capture spiral				
Intercept	0.56	5.24	0.11	0.91
Life span	0.023	0.02	1.21	0.24

Table 4. Relationships between the length of the CTL and the age of the spider (time till death, chronological age and life span) using a GLM adjusted for body mass (*SE* = Standard error)

Variables	Estimates	SE	t	P level
A. Time till death				
Intercept	56.35	86.72	0.65	0.52
CTL	0.87	0.47	1.88	0.07
Body mass	6.34	2.39	2.67	0.01
B. Chronological age				
Intercept	118.08	98.3	1.20	0.24
CTL	-0.17	0.40	0.43	0.67
Body mass	7.18	2.56	2.80	<0.01
C. Life span				
Intercept	62.48	118.98	0.52	0.60
CTL	0.20	0.43	0.48	0.64
Body mass	6.81	2.55	2.67	0.01

duration increased with CTL (velocity: $R^2 = 0.26$, $P = 0.02$, Figure 3C; building duration of the capture spiral: $R^2 = 0.76$, $P < 0.0001$, Figure 3D). In contrast, there was no relationship between the duration of spider inactivity and CTL (duration of inactivity: $P = 0.19$, Figure 3E).

Discussion

This study investigated the effect of age on spider mobility during web building in the adult orb-web spider *Z. x-notata*. We examined a series of spider mobility parameters that were possibly differentially affected by age. Our results showed that neither the chronological age (adult age in days at the date of the test) nor life span, which is an indication of the individual longevity, had an influence of these mobility parameters during web construction by the spiders. We also observed that spiders did not change their locomotor behavior during web construction. However, some of the mobility parameters did decrease with time till death (at the date of the

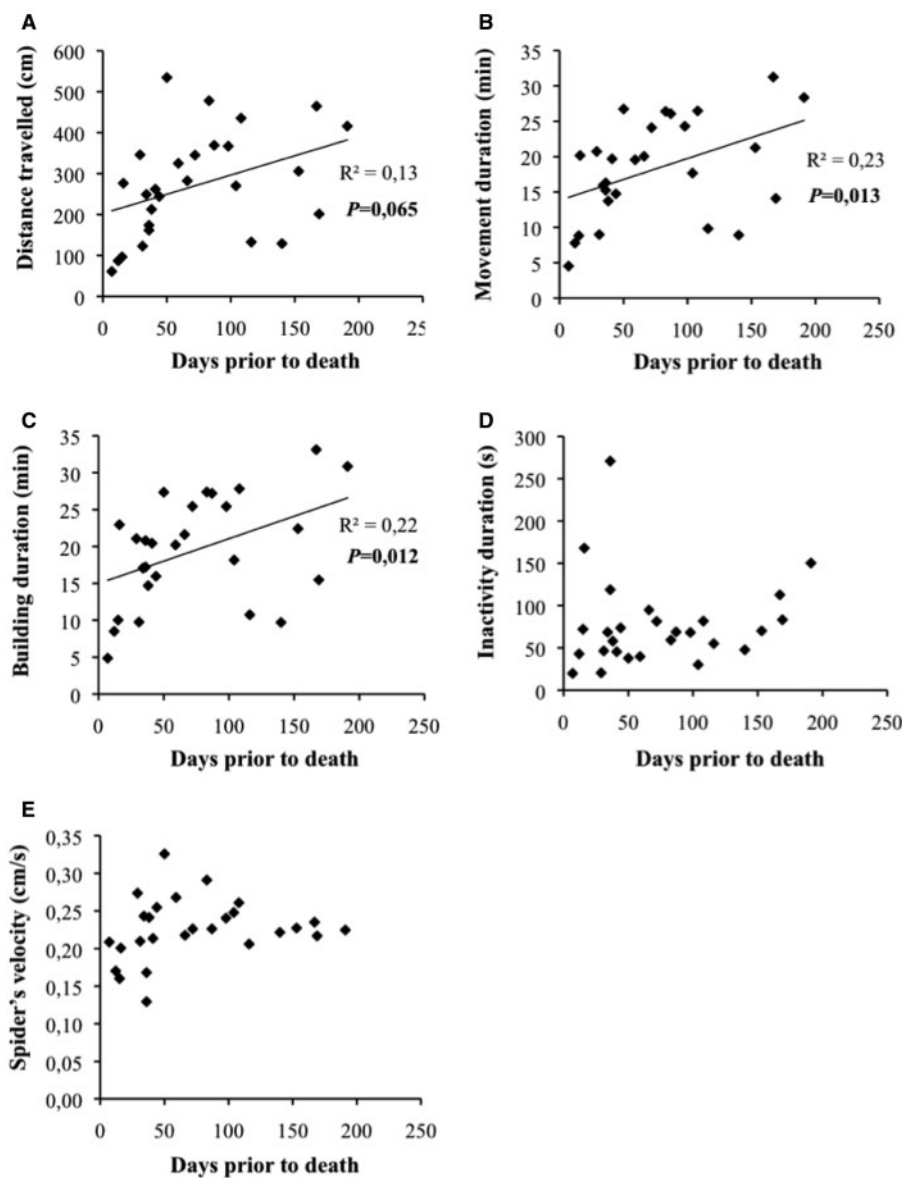


Figure 2. Spider mobility parameters associated with time till death (number of days prior to death). Results of GLM analysis adjusted for the spider mass and corrected for CTL.

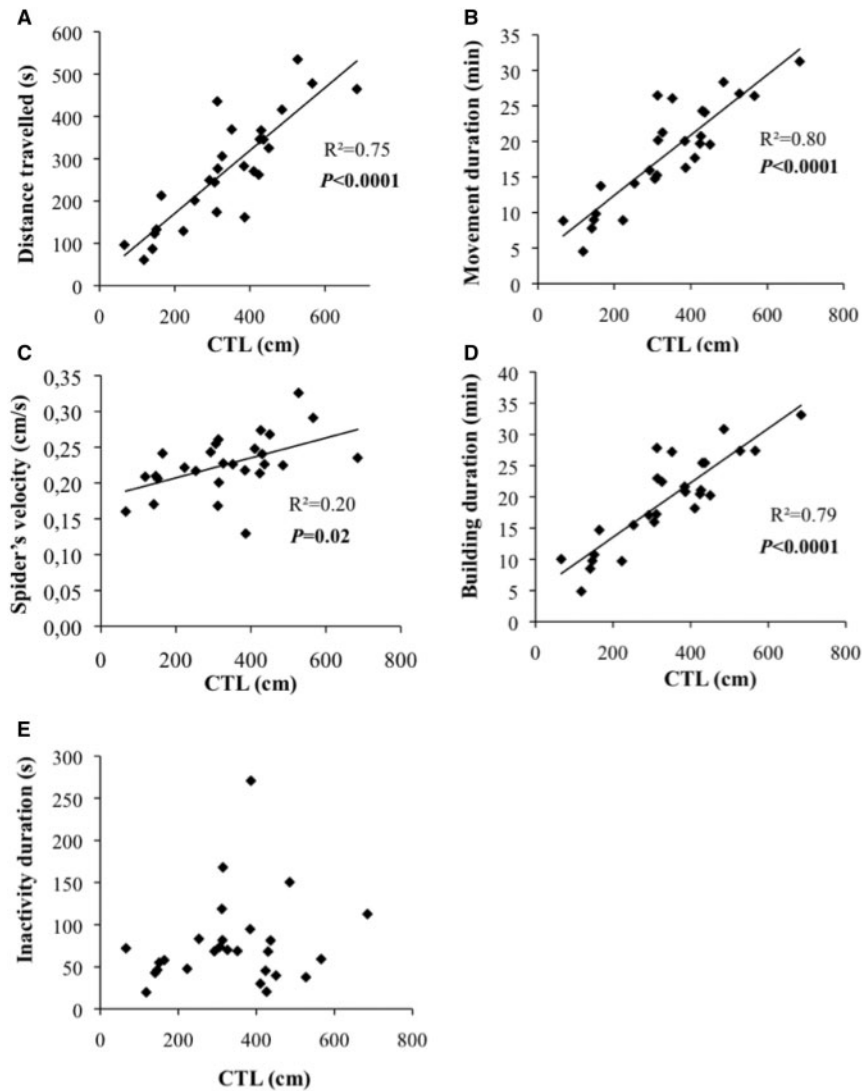


Figure 3. Spider mobility parameters associated with CTL. Results of GLM analysis adjusted for spider mass.

construction) with the exception of the velocity, which did not change. In a complementary analysis, we showed that most of our parameters of spider mobility (except the duration of inactivity) were linked to the size of the web.

Behavior of old animals or age-specific behavioral patterns have been characterized in detail in relatively few animal species (Bateson 2002; Carey et al. 2006), and mostly declines in age-related behavior in vertebrates and invertebrates concern mobility (Grotewiel et al. 2005). In our experiments, it was, therefore, surprising that chronological age or life span did not affect mobility parameters. In invertebrates, age is known to modify mobility; it can decrease the locomotor activity of cockroaches (Ridgel et al. 2003), *Drosophila* (LeBourg and Minois 1999), or nematodes (Gems 2000, Gardner et al. 2004, Collins et al. 2008). It can also affect the exploratory behavior of the fly (*Drosophila melanogaster*) (Cook-Wiens and Grotewiel 2002, Grotewiel et al. 2005, Jones and Grotewiel 2011). So it is evident that even in short-lived animals, such as *Drosophila*, age directly affects locomotor activity. There is only one case in spiders, where the author showed that in 2-year-old females there was a decrease in the foraging activity of *Lycosa tarantula* (Moya-Lorano 2002); this is a wandering spider without a web, which

searches actively for its prey, so a decrease in foraging activity is directly linked to a decrease in locomotion. We did not find such a phenomenon in *Zygiella*, because in the experiment we used only virgin spiders without distinction between short- and long-lived individuals as in the previous study. Our global analysis of all the individuals may have hidden this difference but, our sample was not sufficient to divide it into 2 groups and the age of the spiders was continuous without a clear separation between older and younger individuals. The most interesting result here is that time till death has a clear effect on the locomotor capacities of the spiders. It seems that when spiders approach death, some behaviors are modified. It is known in invertebrates. In the fruit fly, *Ceratitis capitata*, a few days before dying, adult males exhibited a particular behavior (“supine”), which increased their mortality risk. The authors suggested that flies undergo a period of declining health and that morbidity is a natural stage of senescence (Papadopoulos et al. 2002; Carey et al. 2006). In the same way, we can suggest that spider health declines with age and that this is associated with a decline in spider mobility when webs were constructed close to the spider’s death. This decline in locomotor activity results in the presence of anomalies in the final web (Anotaux et al. 2012). This suggests that it is a general disease,

which affects not only the locomotor ability but also coordination of movements, which are necessary to build an orb-web (i.e., we showed that an error in the position of the spider body during the laying of the thread between 2 radii in the capture spiral may lead to an anomaly in the final web (Toscani et al. 2012)).

The changes in mobility parameters with time till death are also linked to the capture area and the investment in silk, the aim of which is prey capture. We showed that there was a significant decrease in this investment; spiders closer to their death invested less in their web and thus in their opportunity to catch prey. This result is consistent with that previously found in this species (Anotaux et al. 2012). In general, several authors noted that, in invertebrates, there was a decrease in foraging activity with age (Tofilsky 2000; Moya-Larona 2002) correlated with a decrease in the quantity of food ingested (Tofilsky 2000, Arundell et al. 2006). The spiders used in this experiment were adult virgin females and therefore had no specific energetic needs for reproduction. This was not the case for the study on *Lycosa* (*L. tarantula*) in which spiders were reproductive females (Moya-Larona 2002). Although the decrease in foraging effort we observed here, could be explained only by a decrease in the size of the geometrical structure of the web.

It could also be an indicator of a more generalized decline in spider physiological conditions. This interpretation is supported by the observation that the spider velocity decreased with the length of the capture thread; but we did not find a direct relationship between velocity and time till death. This highlights that there is a direct link between locomotor activity and time till death. Our results have thus provided new insights into our understanding of morbidity dynamics and senescence processes in invertebrate organisms. Moreover, the method used had highlighted the importance of time till death as a good indicator of senescence in invertebrate species.

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