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On the life-cycle of *Ameles spallanzania* (Rossi, 1792) (Insecta, Mantodea)

Abstract - the recent find of an *Ameles spallanzania* population in a continental area of northern Italy permitted to redraw the northernmost edge of the distribution of this species and to study its life cycle in extreme climatic conditions. A comparison with collecting records of adult specimens from the Mediterranean area has been performed to put in evidence how this species adapts its life-cycle timings in different latitudes: hatching earlier or using nymphs to overwinter in warmer localities or oothecae in colder ones. Overwintering strategies of *Ameles spallanzania* have been compared with strategies of other genera of mantids that share the same habitat but have different life-cycle strategies and general distribution. Different developing times in mantids seem to be linked to behavioural strategies more than physiological attitudes.

Keywords: *Ameles spallanzania*, Mantodea, life-cycle, ecology.

Riassunto: Sul ciclo vitale di *Ameles spallanzania* (Rossi, 1792) (Insecta, Mantodea).

Il recente ritrovamento di una popolazione di *Ameles spallanzania* in una località continentale del nord Italia ha permesso di ritracciare i confini settentrionali dell'areale di questa specie e di studiarne il ciclo vitale in condizioni climatiche naturali estreme. Una comparazione con i dati di raccolta di individui adulti provenienti dall'area mediterranea è stata condotta per mettere in evidenza come questa specie adegui le fasi del suo ciclo vitale a differenti latitudini: schiusa delle uova precoce o svernamento tramite neanide in località calde o tramite ooteca in quelle più fredde. Le strategie di svernamento di *Ameles spallanzania* sono state comparate con quelle di altri generi di mantide che condividono con lei lo stesso habitat ma hanno differenti strategie di ciclo vitale e distribuzione generale. Tempi di sviluppo differenti sembrano essere legati nelle mantidi a strategie comportamentali più che a predisposizioni fisiologiche.

Parole chiave: *Ameles spallanzania*, Mantodea, ciclo vitale, ecologia.

Introduction

Ameles spallanzania (Rossi, 1792) is a typical mantis of the Mediterranean area distributed from Morocco to Greece and from southern Europe to northern Africa, with a small size (18 mm - 40 mm) and an evident sexual dimorphism (slender full winged males, and stocky brachypterous females, Figg. 1, 2). Despite its well

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studied and discussed taxonomy (Battiston *et al.*, 2010), the ecology of this species is known almost only for few data for a coastal area in southern France (Bernard, 1936), near Frejus (43°25'N, 6° 44'E), where nymphs are reported to hatch in July from the median careen of the ootheca which is laid in September. The hatching process of about 60 nymphs lasts no more than 3 days and the overwintering young nymphs are reported as a rare event for that locality. Korsakoff (1942) reports a detailed analysis on the life cycle of this species in artificial conditions and some considerations in nature. He compared the development of different mantids, observing that in the same breeding conditions some genera, like *Ameles*, *Iris*, *Empusa*, *Blepharopsis*, have very long developing times (260-300 days), caused by a winter diapause that prolongs one nymphal instar, and others, like *Sphodromantis* (and *Mantis*, cited without records) that in same conditions develop in only 86 days, showing a deeper link to a hereditary difference than to environmental conditions.

Usually adults of *A. spallanzania* are observed in many localities of the Mediterranean area from summer to autumn but at the same latitude very different hatching times can be recorded: from late spring to late summer. During October 2003 one of the authors, R. Battiston, observed in central Italy (42° 38'N) a large number of very young nymphs, sharing the same space with a few old adults of the previous generation, and some still active females in northern and cold localities (45°N) at the beginning of November. Extreme life-cycle strategies for a thermophile mantis like *A. spallanzania* as more than one generation per year or overwintering nymphs have been hypothesized but without a clear overview on the ecology of this species. The recent discovery of an isolated population in a continental area of northern Italy, characterized by rather warm temperatures during summer and cold winters



Fig. 1 - *Ameles spallanzania*, adult male / maschio adulto. Photo by / Foto di C. Galliani.

with snow, permitted not only to redraw the northernmost edge of the distribution of this species but also to study the life cycle in extreme conditions and to understand the strategies used to overwinter. A comparison with this data with other historical collectings has been used to put in evidence the way this species adapts its life-cycle strategies at different latitudes.

Materials and Methods

The area of the study is located in northern Italy in the Parco Lago Nord inside the Parco del Grugnotorto in the town of Paderno Dugnano, 12 km North of Milan, 45°34'40"N 09°10'47"E, 157 m a.s.l. in a sub-urban plain terrain and entirely surrounded by the suburbs of Milan city that isolate this area from other green ones.

Parco Lago Nord is the result of the reconversion of the old part of a quarry used for sand and gravel extraction and it is possible to recognize in it three different zones: woodland, sportive fishing lake, and a naturalized lake with typical pond-like vegetation as *Phragmites australis* (Cav.) Trin. ex Steud. In the surroundings of the park, parts of the quarry are still active for sand and gravel production.

The population of *A. spallanzania* was observed only near the naturalized lake in a small area of about 60 square meters covered with grass and bushes *Lavan-*



Fig. 2 - *Ameles spallanzania*, adult female / femmina adulta. Photo by / Foto di C. Galliani.

dula augustifolia Mill., a plant where young and adult *Ameles* usually spend their time, and a white building where, on the external walls most of the oothecae were laid. Behind this area, outside the edges of the park, some private semi-urbanized strips of terrain colonized by *Cirsium arvense* (L.) Scop., *Erigeron annuus* (L.), *Artemisia vulgaris* L., *Conyza canadensis* (L.) Cronq., 1943, etc. were present. The presence of few individuals of *Ameles* can be here hypothesised.

Daily temperatures (minimum T°C and maximum T°C of all the day) were obtained by a meteorological climatic station located 15 km SE in Milano Linate at 103 m a. s. l. and in similar ambient conditions.

The main population was checked from October 2008 to November 2009 every 15 days, searching for nymphs, adults or oothecae and recording their presence and developing stage with notes and photographs, that are now in C. Galliani photographic collection. Two males and two females have been collected in the study area and dissected to identify the species using the internal morphology of the genitalia. The hatchings from two different oothecae laid during autumn 2008 were recorded: both of them were laid on a bright wall exposed to SW but one was covered by the roof and never received direct sunlight during the day; the other was exposed to the sunlight for about 6 hours on average from noon to sunset, from the laying to the hatching, located about 15 cm below the other one (Fig. 3).



Fig. 3 - The two oothecae considered laid on a west interception of the south wall of the building. Picture taken on the 22/02/2009 at 12.49 a.m. by C. Galliani.

Fig. 3 - Le due ooteche considerate deposte sull'intersezione ovest del muro a sud dell'edificio. Foto scattata il 22/02/2009 alle 12.49 da C. Galliani.

We estimated that the average daily temperature of the ootheca constantly in the shadow was equal to the average daily temperature recorded by the meteorological station, the average temperature of the partially illuminated one as this average daily temperature increased by half of the difference between the daily maximum and average temperature recorded by the meteorological station. This hypothesis has been confirmed to be a good approximation by occasional direct on-site measures performed by the authors. A two tailed t-Student test was performed to estimate the significance of the difference between these two paired means at significance level of 0.05, using single day measurements data sets from 01/10/2008 to 30/11/2009 (426 days), obtained from the meteorological station.

Three oothecae from specimens of *A. spallanzania* collected in different localities of southern Italy (39-40° N) that overwintered as nymphs, laid within the same week (the last week of June), were housed in the same indoor conditions (between 20-25°C, never exposed to direct artificial light or sun) to evaluate the hatching time in the same conditions.

Historical observations from 2006 to 2008 were also used to have a general idea of the population dynamics in other years.

Historical collecting records were used to evaluate the presence of adult stages in different latitudes and information on the life-cycle of other genera were obtained by literature (Agabiti, 2002; Battiston & Fontana, 2005; Battiston *et al.*, 2010; Chopard, 1943; Cogo & Battiston, 2007), from specimens preserved in private collections of R. Battiston, B. Massa, P. Fontana, and from precise and detailed personal communications (C. Muscarella, E. Stival) using a total of 142 specimens of *A. spallanzania* from 109 different localities from the southernmost to the northernmost edges of distribution of this species.

Results

Ameles spallanzania (Rossi, 1792)

Mantis abjecta (Cyrillo, 1787). Ent. Neapol. 4 (*species inquirenda*).

Mantis spallanzania Rossi, 1792. Mant. Ins., Ross. 1: 102.

Ameles africana Bolivar, 1914. In: Agabiti, 2001-2002; Battiston & Fontana, 2005.

Ameles soror (Serville, 1839). Hist. Ins. Orth. 200.

Ameles spallanzania (Rossi, 1792). In: Finot. 1895. Anns Soc. ent. Fr. 64: 104.

Paralectotypus: 3 males, Zoological Museum of Berlin, Germany.

Locus typicus: Italy?

Distribution: Albania, Algeria, Dalmatia, France, Greece, Italy, Libya, Morocco, Portugal, Spain, Tunisia.

Specimens collected in the study area

1 adult male: Italy: Paderno Dugnano (MI), Parco Lago Nord, 27-IX-2009, leg. C.

Galliani, det. R. Battiston, Museo di Storia Naturale di Milano.

1 adult female: Italy: Paderno Dugnano (MI), Parco Lago Nord, 27-IX-2009, leg.

C. Galliani, det. R. Battiston, Museo di Storia Naturale di Milano.

1 adult male: Italy: Paderno Dugnano (MI), Parco Lago Nord, 27-IX-2009, leg. C.

Galliani, det. R. Battiston, R. Battiston private collection.

1 adult female: Italy: Paderno Dugnano (MI), Parco Lago Nord, 27-IX-2009, leg.

C. Galliani, det. R. Battiston, R. Battiston private collection.

In Parco Lago Nord, *A. spallanzania* starts its life-cycle between September and October, when the oothecae are laid often on hard and dry surfaces exposed to the sun. Last living individual of the 2008 generation (an adult female, Fig. 4c), was observed on the 10th of November. Both of the two oothecae studied were laid between 19th and 24th of October 2008 (Fig. 4a), overwintered and proved to resist to cold temperatures below 0°C (min recorded in January 2009: -9°C), ice and snow.

The first ootheca, the one exposed to the sunlight, hatched at the beginning of June when air temperatures reached a minimum of 15-20°C and a maximum of about 27-32°C (Fig. 4d). The second ootheca hatched one month later in July in a min-max range of 19-32°C (Fig. 4e). In August both adults and nymphs were present and by the end of the month, the last juvenile was observed (Fig. 4f). By the end of the season the last male was observed at the end of September (Fig. 4g) and the last female at the beginning of November (Fig. 4h). Females proved to resist alive to very low temperatures, even for few days (min recorded: 0.8°C) and males to few degrees over 0°C (min recorded: 4°C), but from 2006 to 2009 males always disappeared few weeks before females.

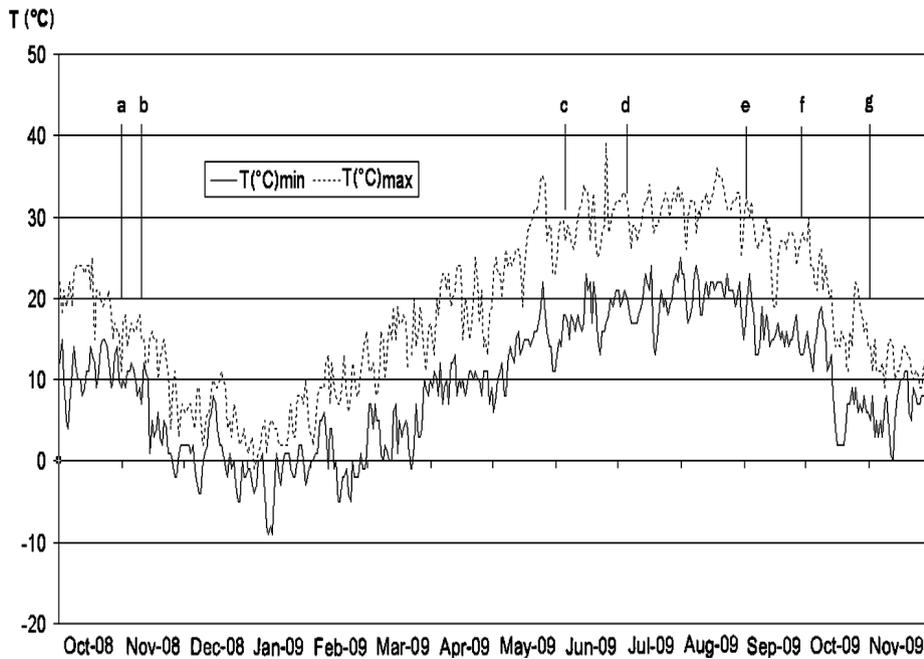


Fig. 4 - Daily temperatures (minimum and maximum) recorded from October 2008 to November 2009 in Milano Linate with mayor events of the population life-cycle. a) oothecae laid; b) last male observed in 2008; c) last female observed in 2008; d) first ootheca hatches; e) second ootheca hatches; f) last juvenile observed in 2009; g) last male observed in 2009; h) last female observed in 2009.

Fig. 4 - Temperature giornaliera (minimo e massimo) registrate da Ottobre 2008 a Novembre 2009 a Milano Linate con i principali eventi del ciclo vitale della popolazione. a) deposizione ooteche; b) ultimo maschio osservato nel 2008; c) ultima femmina osservata nel 2008; d) apertura della prima ooteca; e) apertura della seconda ooteca; f) ultimo giovane osservato nel 2009; g) ultimo maschio osservato nel 2009; h) ultima femmina osservata nel 2009.

Considering the life-cycle in this area with collectings in different latitudes (Fig. 5) we can observe similar trends. Adults have never been collected in the first part of the year and are mostly concentrated in summer. However it is clear that at low latitudes (*i.e.* below 40°N), adults can be observed in nature also in spring and sometimes very early (April). This means that these mantids hatched from the ootheca at least in winter or, since the hatching moment and the following first nymphal stage are very critical for a young mantis because of the climatic parameters (Hurd in Prete *et al.*, 1999), probably just before it, and this supports the hypothesis of overwintering nymphs as a strategy for low latitudes. However, by historical observations previously cited, this strategy seems to be possible even in the northernmost edges of distribution in southern Europe but, in this case, only in coastal areas where temperatures are mitigated by the presence of the sea where yearly minimum temperatures usually rest few degrees over 0°C (northernmost location recorded seem to be Frejus, a locality characterized by a warm Mediterranean climate: Bernard, 1936). Usually over 43° the ootheca overwinters.

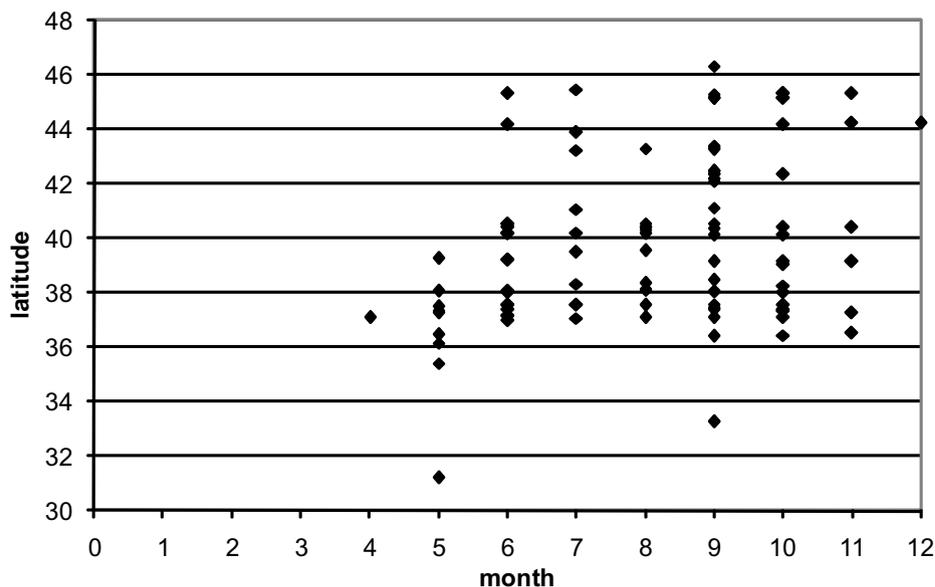


Fig. 5 - Records of single adult specimens (both males and females) represented by the period (month, x axis) and latitude (degrees, y axis) of collecting.

Fig. 5 - RegISTRAZIONI di singoli individui adulti (sia maschi che femmine) rappresentati nel periodo di raccolta (mesi, asse x) e latitudine (gradi, asse y).

While a population of adult *Ameles* can be active on average from the beginning of the summer to the end of autumn, it appears evident that males disappear almost everywhere earlier than females (Fig. 6, 7), but this seems more evident at higher latitudes.

The three oothecae housed in indoor conditions opened during the same week at the end of July about one month later from the laying day (the last week of June).

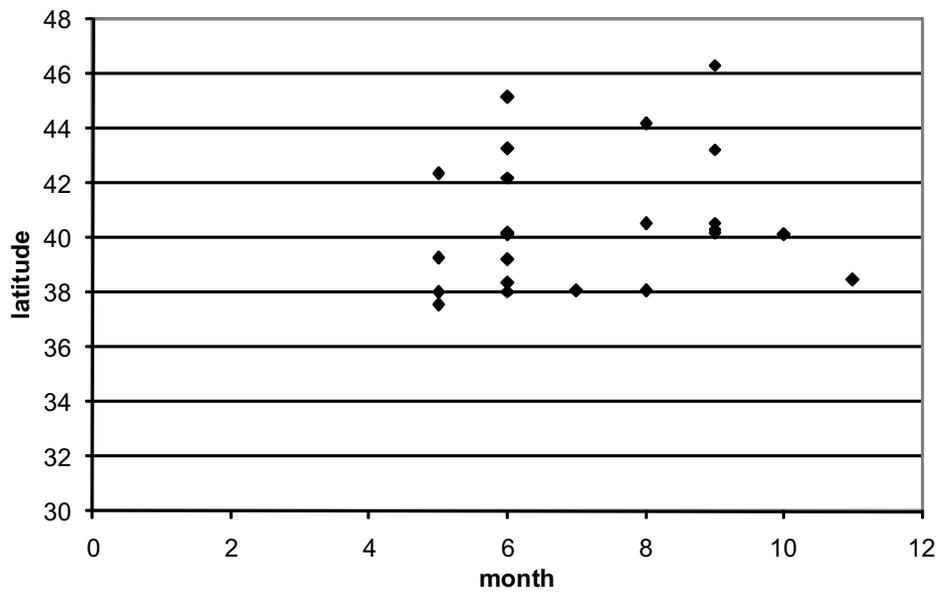


Fig. 6 - Records of single adult specimens (males) represented by the period (month, x axis) and latitude (degrees, y axis) of collecting.

Fig. 6 - RegISTRAZIONI di singoli individui adulti (maschi) rappresentati nel periodo di raccolta (mesi, asse x) e latitudine (gradi, asse y).

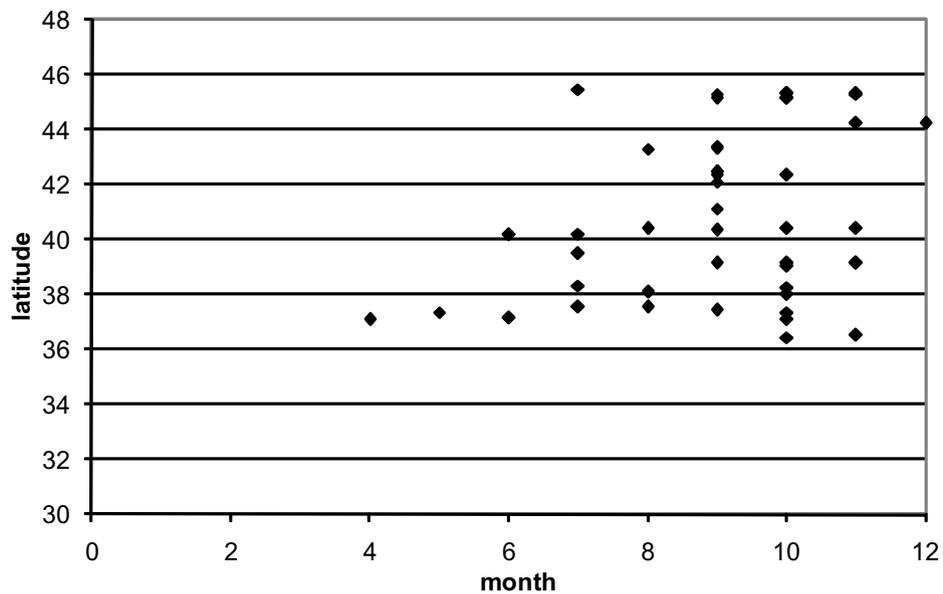


Fig. 7 - Records of single adult specimens (females) represented by the period (month, x axis) and latitude (degrees, y axis) of collecting.

Fig. 7 - RegISTRAZIONI di singoli individui adulti (femmine) rappresentati nel periodo di raccolta (mesi, asse x) e latitudine (gradi, asse y).

Discussion

These data permit to trace out some conclusions on the life-cycle of *A. spallanzania* and this appears interesting if compared with other mantids that usually share the same habitat.

From the data of Parco Lago Nord the hatching time of the ootheca seems to be quite flexible. The two oothecae considered hatched with a delay of about one month one from the other, and this is a remarkable difference if compared to the few days necessary to the hatching of the three oothecae we housed in the same indoor conditions. This points out that the different duration on the life-cycle probably depends on environmental conditions. The minimum time needed by the eggs to develop is quite short and can be in optimal conditions no more than 2 weeks (Korsakoff, 1942), which is the same time observed for other mantids (*i.e.* *Empusa pennata* in Battiston *et al.*, 2010) and the prolonged time of several months observed in northern Italy is probably due to a long pause that interrupts the developing, the winter diapause. The difference of the temperatures of the two sites has been estimated as 2.5°C as a mean of the period considered from laying to hatching, a difference significative in t-Test ($P=1,8E-155$ with 425 d.f.) even if much smaller than the mean of the daily excursion, as the difference from maximum and minimum temperature recorded, which was about 9°C on average during the year.

Looking at the average earlier development at warmer latitudes, temperature seems really to be the key factor for hatching in *A. spallanzania*.

It is interesting to notice that this temperature of activation seems to be linked more to a daily maximum and maybe to an absolute value than to a high daily mean maintained for several days. In Parco Lago Nord a very high maximum of temperature was recorded just before the first ootheca hatching (max= 35°C, avg= 28°C), and a fast increasing of daily means. This was not enough for the second one in the shadow that hatched one month later just after another very high maximum (max= 39°C, avg= 25°C) but after a quite linear situation for the daily means. These 4°C of difference are a bit more than the 2.5°C of the two different oothecae locations and this could have been enough to fill this lack of heating and activate the second hatching, while the two means remained about on the same levels (Fig. 8). Of course further investigations should be considered to confirm this by a statistical point of view.

Other mantids usually share the same habitat of *A. spallanzania* but as observed by Korsakoff (1942) in indoor rearing, have different strategies to overwinter and developing times.

Mantis religiosa (Linnaeus, 1758), the most common one in nature that at least in Europe we often observed in the same localities together with *A. spallanzania* (even in this study area) and by historical and original collecting records seems to have here a less variable strategy in almost all the latitudes here considered (36°-46°N): hatches in spring, reaches the adult stage between July and August and dies in October; overwintering occurs always by the ootheca. In Parco Lago Nord and in Colli Euganei (45°15'N 11°38'E) both on the northernmost continental edge of *A. spallanzania* distribution, the life-cycle of these two species is delayed by about one month: *M. religiosa* closes its life-cycle on average one month earlier than *A. spallanzania*. However also *M. religiosa* seems to have a sort of moderate plasticity in its developing timings: during summer 2009 and 2010 in central and southern Italy we observed three different developing nymphal stages in the same day and in the same locality, probably the result of

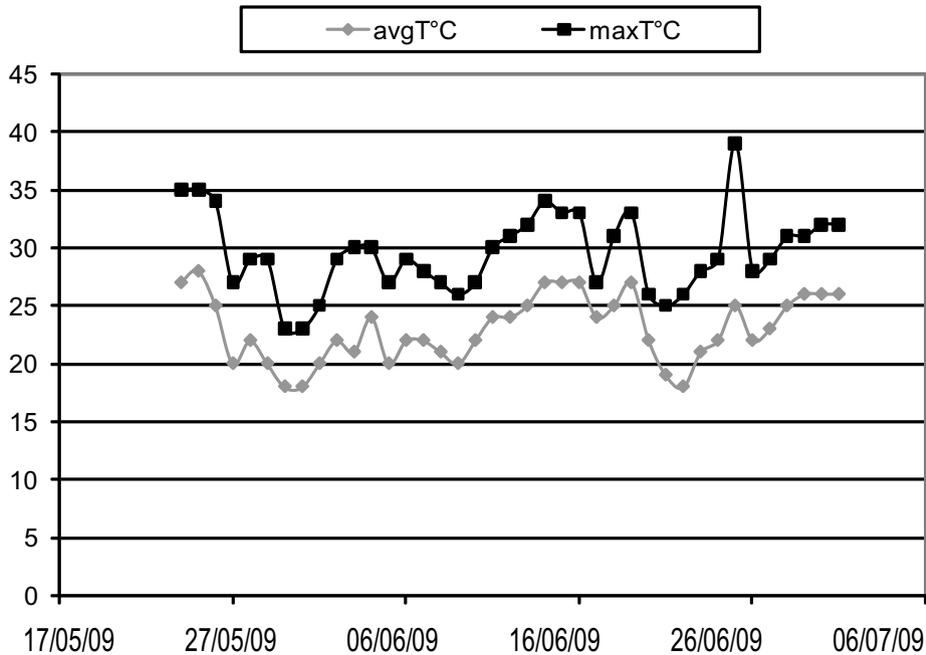


Fig. 8 - Comparison of the daily maximum and average temperatures recorded in the period of hatching of the two oothecae of *A. spallanzania* in Parco Lago Nord (day of the year, x axis; temperature °C, y axis).

Fig. 8 - Comparazione delle temperature massime e medie registrate nel periodo di schiusa delle due ooteche di *A. spallanzania* nel Parco Lago Nord. (giorno dell'anno, asse x; temperatura °C, asse y).

three different hatching moments. It is interesting to notice that while *A. spallanzania* seems to resist better than *M. religiosa* to the first cold temperatures of the autumn, *M. religiosa* reaches much more colder latitudes (50°N) over all its distribution range. The efficiency of *M. religiosa*, by this point of view seems not to be linked to its direct resistance to cold temperatures but to other ecological strategies where probably the life-cycle concentrated in the warmer season, other than the bigger size, plays an important role.

The genus *Empusa* Illiger, 1798 even if not so common, can be often observed together in the same localities with *M. religiosa* and *A. spallanzania* and by historical and original collecting records have opposite strategies: hatches in Summer, nymphs overwinter, adult stage reached in late spring and last individuals found by the beginning of the next Summer. Plasticity in this species, from collecting records, seems to be extremely reduced in all latitudes here considered and in its distribution, generally more southern, and reaches the same north latitude of *A. spallanzania* only in warm coastal localities, but her life-cycle is actually not well known.

A. spallanzania apparently shows more adaptable strategies of its sisters using the ootheca to overwinter in cold latitudes like *M. religiosa* or nymphs in warmer ones like *Empusa*, well adapted to live in the Mediterranean area but not so extreme to reach the northernmost lands like *M. religiosa* or the southern as *Empusa* that is known to live from 46°N to 25°S.

A genetic attitude for a specific strategy that leads different species sharing the same habitat to different life-cycles, is here confirmed. However this attitude seems to be confined in the choice of the laying time of the ootheca and not to the physiological duration of developing, that is linked to environmental conditions.

However a sort of plasticity in adapting these strategies to different latitudes and temperatures seems also to be an ancestral character of the order of Mantodea.

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