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Mating behavior of the mantid *Ameles decolor* (Insecta, Mantodea): courtship and cannibalism

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Abstract

Some observations on the mating behavior of the Mediterranean ground mantis *Ameles decolor* are reported. Sexual cannibalism occurred between female and male; cannibalism occurred between adult males and between adult females. A courtship behavior of the male before mating is described for the first time. Comparisons with other taxa and explanations of courtship occurrence are given.

Keywords

Mantodea, *Ameles decolor*, biology, mating behavior, cannibalism, courtship

Introduction

Ameles decolor (Charpentier, 1825) is a small rather common mantis, typical of arid fields of the Mediterranean basin from Southern and insular Europe to northern Africa (Ehrmann 2002, Battiston & Fontana 2005). Despite its well-known distribution and taxonomy, its biology is practically unknown. Some observations on egg laying and life cycle were made by Bernard (1936) and Chopard (1943); Finot (1883) noted some habitat preferences and Fabre (1897) reported cannibalism but only between female and male during mating.

In general, in some species of the order Mantodea, sexual cannibalism is well studied (Johns & Maxwell 1997; Maxwell 1998, 1999, 2000; Lelito & Brown 2006; Prokop & Vaclav 2005) but very little is known of other behaviors of these insects, even if, as with courtship, they are linked to matings.

Descriptions of courtship display and probably also this behavior's occurrence are very rare in Mantodea. In some species males are observed moving parts of their bodies when approaching the female: "boxing" of the prothoracic legs by *Oxypilus hamatus* Roy (Edmunds 1975), "semaphore" and "stamping" with the metathoracic legs by *Ephestiasula amoena* (Bolivar) (Loxton 1979) and *Acontiothespis multicolor* (Saussure) (Quesnel 1967), "pumping" and "weaving" of the abdomen by *Tenodera aridifolia sinensis* (Saussure)(Liske & Davis 1987); males of *Oligonyx insularis* Bonfils tremble while approaching (Bonfils 1967).

Cannibalism outside matings is reported and often observed in young nymphs of various species of mantids, but its presence is not clear in adults except as anecdotal observations (Prete *et al.* 1999, personal observations). During September 2006, 20 individuals of *A. decolor* were collected in some arid fields in the west of Tolentino (MC, in Central Italy) and caged to verify the presence of cannibalism and to study their mating behavior. An understanding of basic patterns of courtship behavior occurring in a sexually cannibalistic insect like a praying mantis, where the strength of sexual selection is extreme, could help to explain the role and occurrence of this selection in nature.

Materials and methods

Ten adult females and ten adult males were collected by net on the west slopes of Eremo Pistocco (MC), about 14 km west of Tolentino. The 10 females and seven of the males were housed in individual boxes (6 cm × 6 cm × 3 cm) and and fed *ad libitum* with small *Diptera* and *Lepidoptera*. The remaining three males were housed together in one box (15 cm × 12 cm × 11 cm), fed like the other individuals, to evaluate the presence of nonsexual cannibalism between males. Two females were left free to move on a bush of *Rosa* sp. to evaluate the presence of nonsexual cannibalism between females.

In order to study their mating behavior, males and females were then paired on two different kinds of substrates where they were continuously monitored either by an observer or photographed and video-recorded with a Nikon S4 camera at 15 fps.

The first substrate was a completely artificial one: a white wooden table offering no places to hide or adopt any cryptic behavior (mimicry). Tests were run between 11:00 and 16:00, in a room with good daylight illumination coming from a large window about 2 m distant from the mantids and a 12-V lamp situated at a 50-cm distance from them; the temperature was between 24 °C and 26 °C.

The second substrate was a bush of *Rosa* where mantids were set free to move, hide and mimic, left undisturbed in the room without any physical barriers except for the walls of the room itself.

One observer entered the room every 15 min for a few minutes to check the situation and eventually record or photograph particular events, but left the insects undisturbed. None of the mantids turned their head toward this observer, or seemed influenced by his presence during those checks.

For both substrates male and female were placed about 20 cm apart. At the beginning of the tests the observer induced both mantids to make a small movement. The subsequent turning of their heads toward each other indicated their mutual awareness. Only one male and one female were paired each time, except for one encounter where, at the end of a successful mating, another male was placed at a 20-cm distance from the couple to observe his strategy in that situation. A total of 8 males were paired with 10 females, using some males in more than one encounter, but always with a different female.

Mantids with prominent eyes such as *A. decolor*, could be expected to see a moving target over 360°, but with a binocular visual

system the forward visual field where the target stimulus produces a consistent reaction (fixation of the target with saccadic movements of the head) is only 50-60° (*Tenodera australasiae*, Prete *et al.* 1999). For this reason two kinds of approach were tested: "frontal", where males approached the female, facing her within a visual field of not more than 80°, *vs* a "lateral" approach where the male came from the other 280°, i.e., from one side or to the rear of the female, completely outside of her normal focus range.

It is important to emphasize that the main aim of the tests was to describe what happens when courtship is displayed during an encounter and not how this behavior occurs in nature.

Results

Cannibalism outside mating.—Cannibalism occurred twice outside mating. One male was captured, cannibalized and completely eaten by another in the box with three males. One female was captured, cannibalized and completely eaten by another female on the rosebush.

Mating behavior.—Sexual cannibalism occurred on both substrates, bush and table, and under different male approach directions. Since cannibalism occurred in different situations, the recorded frequency (16.7% of all encounters) and its relationship to the presence of courtship display, should not be considered as indicative for this species. Two males were able to inseminate females while being cannibalized (Table1). During the approach of the male, in 6 encounters, a complex courtship behavior was observed (Table 1).

Mating behavior can be considered as composed of four kinds of movement: two enacted by the forelegs (Fig. 1), and two by the abdomen (Fig. 2).

The first movement of the legs occurred when the abdomen was still: the fore legs were abducted laterally, perpendicular to the body axis, but never reached full extension (Fig. 1A); they were then oscillated up and down in regards to the body axis in a dorso ventral direction from one to three times alternatively and independently, first one leg, then the other. The frequency of these movements was <1 lateral oscillations per second.

The second foreleg movement (Fig. 1B) was observed only when one of the two different movements of the abdomen was in train: legs were transversely abducted then rotated in a plane perpendicular to the main axis of the body, moving fast together like spokes of a single wheel: when one was rotating upward the other was rotating downward. This second leg movement was faster than the first: from 1 to 3.5 vertical rotations per second.

The observed movements of the abdomen were similar to those reported by Liske & Davies (1987) for *T. aridifolia*: the first probably corresponds to what they called "pumping": the abdomen tip is lifted rhythmically in a dorsoventral plane (Fig. 2A). The second movement is similar to the larger part of what they called "weaving": the abdomen is bent dorsolaterally like the tail of a scorpion, then relaxed (Fig. 2B) Often lifting and bending were alternated during the same approach (Table 2, Fig. 4) and at the same time, tegmina and wings were frequently lifted vertically and rubbed with the tip of the abdomen, producing a barely audible noise (Fig. 3).

The first listed of the leg movements ("lateral oscillation"), was observed in all encounters (100%) and was always performed first. The second leg movement ("rotation") was observed in connection with the bending of the abdomen in two of six encounters (33%) and with the lifting of the abdomen in three of six encounters (50%) (Table 2).

Looking at the amplitude and frequency of the movements, it is possible to recognize two behavioral patterns in the male approach: the first is "shy", hesitant with slow movements of the fore legs (lateral oscillations), sometimes with moderate lifting of the abdomen. The second is "vigorous", with fast movements of fore legs (rotation) and a fuller bending of the abdomen. Of eight males used in these encounters, four performed the "shy" approach, and three the "vigorous".

Courtship behavior was observed on both substrates (table and bush). It was performed by the male only in a range of 2 to 15 cm from the female, and always ended with a flying leap onto her back and copulation, or with the male running away.

Amplitude of movements of the abdomen increased while approaching the female: the maximum height attained by the tip of the abdomen above the ground was about 4/5 the length of the male (Fig. 3). In **Fig. 4** a plot of measures of abdominal movements recorded during Encounter 4 are reported to summarize a typical sequence of approach for a complete display.

As soon as the male mounted the female, he began characteristic S-bending mating movements of his abdomen similar to those described for *T. aridifolia* (Liske & Davies 1987).

Table. 1 Comparative description of the 12 encounters.

Encounter	Direction of approach*	Substrate	Courtship display	Cannibalism	Pairing
1	frontal	table	yes	no	1♂ + 1♀
2	frontal	table	yes	no	1♂ + 1♀
3	frontal	table	yes	no	1♂ + 1♀
4	frontal	table	yes	no	1♂ + 1♀
5	frontal	table	yes	no	1♂ + 1♀
6	frontal	table	no	yes	1♂ + 1♀
7	lateral	bush	no	no	1♂ + 1♀
8	lateral	bush	no	no	1♂ + 1♀
9	lateral	bush	no	yes	1♂ + 1♀
10	lateral	bush	no	no	1♂ + 1♀
11	lateral	bush	no	no	1♂ + 1♀
12	lateral	bush	yes	no	1♂ + (1♂ + 1♀)

* direction of the final part of the approach which concluded with either the flying leap or runaway of the male. Note that the male was always placed in front of the female, but on occasion the male was able to change this direction.

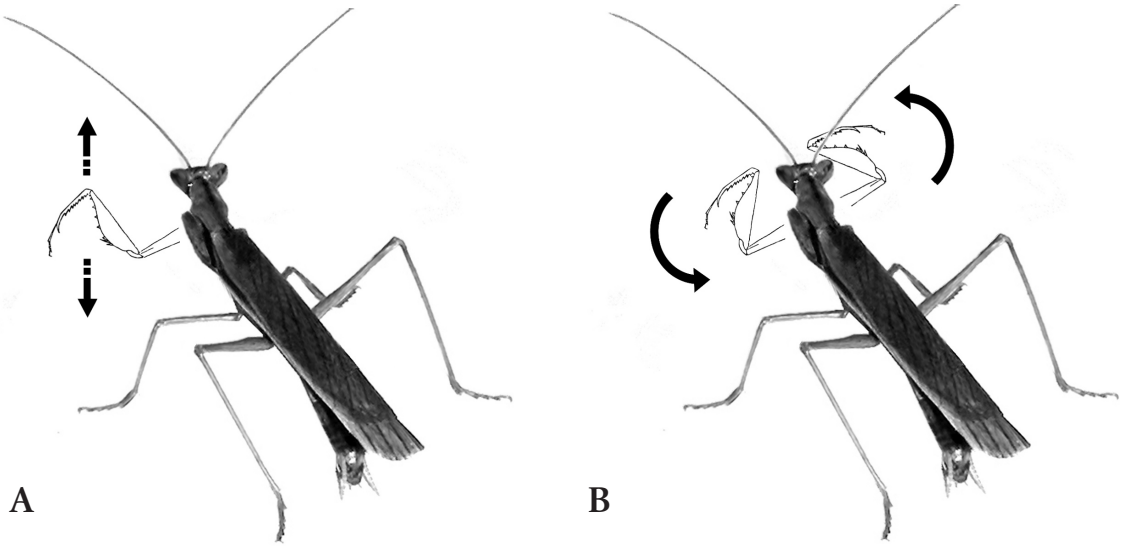

Fig. 1. The two patterns of legs movement in *A. decolor* courtship display: "**lateral oscillations**", on the left, "**rotation**" on the right.

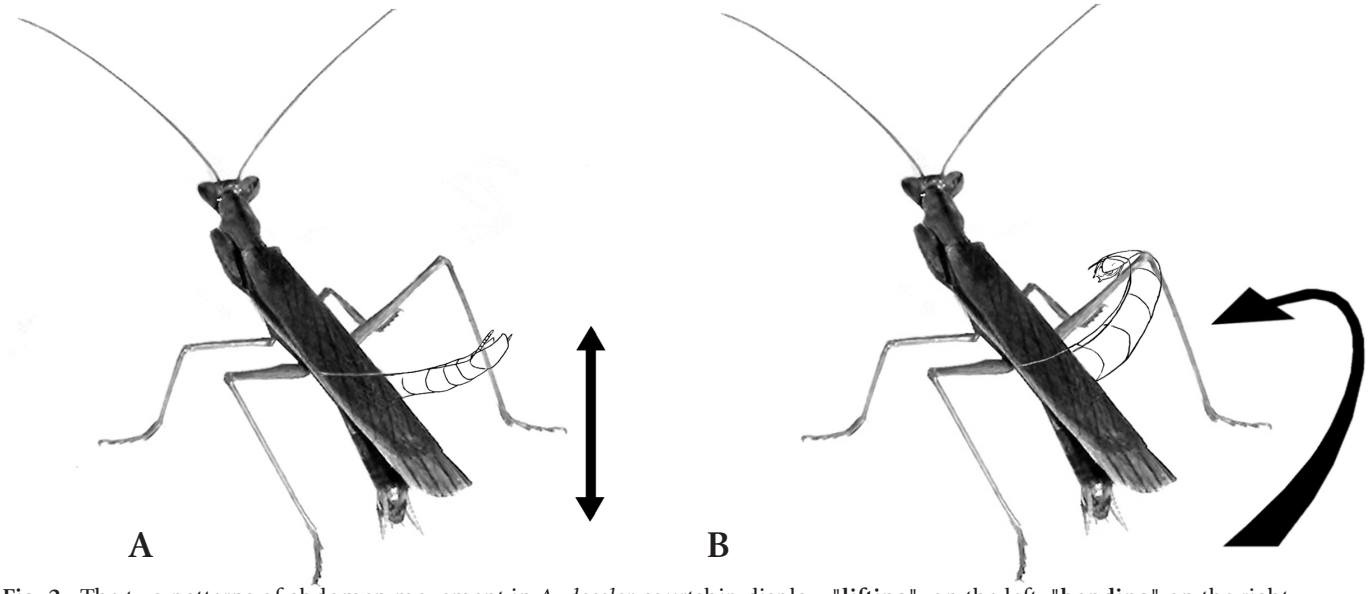

Fig. 2. The two patterns of abdomen movement in *A. decolor* courtship display: "**lifting**", on the left, "**bending**" on the right.

Discussion

Comparing courtship behavior of *A. decolor* with the limited information on the courting of other species in the order Mantodea: courtship in this species appears as one of the most complex. It combines the basic pattern of abdominal movements seen in *Tenodera aridifolia sinensis* with a lateral "boxing" of prothoracic legs, similar to the spacing-out observed in *O. hamatus.* Stamping movements of the metathoracic legs were also sometimes observed in *A. decolor*, but it was not possible to relate them within a precise pattern of courtship behavior and they should be considered occasional movements.

Similar limb and abdomen movements are observed in other species as parts of deimatic (startle) displays and where a courtship determined by context is not known. For example in *M. religiosa* it occurs when the insect, in danger from a predator or often from a conspecific aggressive female, responds by spreading the fore legs laterally and bending the abdomen dorsally against the spread hindwings producing an hissing sound (Prete *et al.* 1999). In *A. decolor* this was observed only once in a mating context, performed by a female. The result, even if not related to mating, is similar to that described for courtship: it occurs in a situation of high stress, and suggests a common root for both courtship and deimatic movements, which could be differentiated and specialized in specific pat-

Table 2. Summary of different components displayed during the six encounters where courtship was observed.

Encounter	fore leg movements		abdomen movements	
	lateral oscillation	rotation	lifting	bending
1	X			
2	X	X	X	
3	X			
4	X	X	X	X
5	X			
12	X	X	X	X

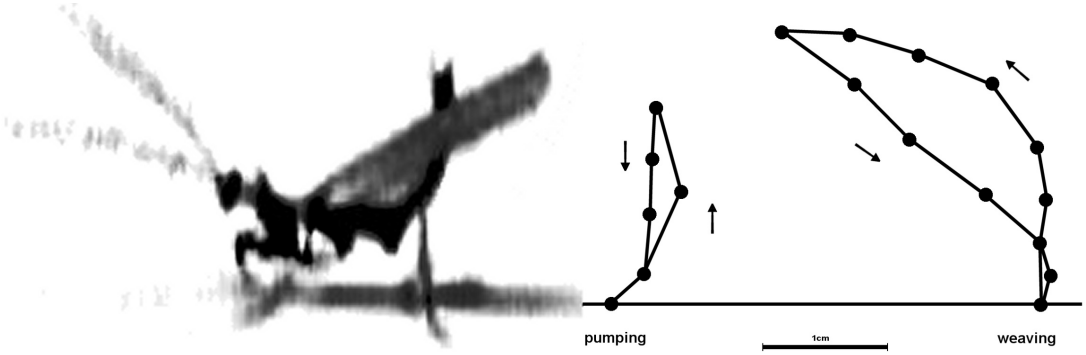

Fig. 3 *A. decolor* during courtship display: components of the male abdominal flexion display, determined by the tracing of the position of the tip of abdomen in single video frames (15 fps), during lifting (left) or bending (right). Note the antennae of the male are oscillating very fast (blurring) during the display.

terns secondarily. With different aims, both deimatic and courtship displays seem to produce the same effect: they enlarge the visual presence of the insect, and lower aggressiveness in a protagonist by discouraging attack upon a potentially difficult and dangerous prey.

If this is true for the "vigorous" approach (fast rotation of fore legs and wide bending of the abdomen), a different effect comes from the "shy" approach, where the body is still or slowly moving towards the female and the weak and slow lateral oscillation of the fore legs is the converse of startling (deimatic). This approach could be compared to the other asymmetrical displays like the "boxing", "semaphore" and "stamping" cited for other species of mantids, where the legs are moved slowly and alternatively.

In Prete *et al.*, 1999 it is reported that a mantis recognizes an object that moves slowly as more distant than another that moves quickly; and if the object is a prey, preference is given to the near as probably the easiest to catch. This could also give an explanation of the "shy" approach: if the male moves a leg very slowly, perhaps the female identifies it as a far and not very interesting prey. Alternatively, the moving of an appendage distally, outside the main shape of the insect, could keep the attention of the predator away from the body and vital organs.

Both episodes of cannibalism outside mating began without anyone in the room, the insects thus undisturbed. Since quantity and quality of prey consumption were regular, these behaviors could be the result of stress caused by housing; but the observations show at least that the presence of cannibalism unlinked to sex is within the behavioral range of adult *A. decolor*.

Sexual cannibalism never occurred when courtship was displayed. This suggests that courtship reduces the possibility of the male being killed by the female, but the presence of artificial conditions should not be forgotten.

Liske & Davis (1987) suggest a heavy influence of artificial conditions, those that usually occur in experimental situations, in promoting cannibalism. This is because the display occurs mostly when the female is looking at the male, a situation that might be enhanced by the absence of hiding places or distractions introduced by human observers. Even with the re-creation of natural conditions in mind, a bush with hiding places, standard illumination, reduced presence of observers, *etc.*, it is difficult to achieve the conditions of a natural encounter between two mantids while carefully observing them. Of course the present study may be affected by such problems.

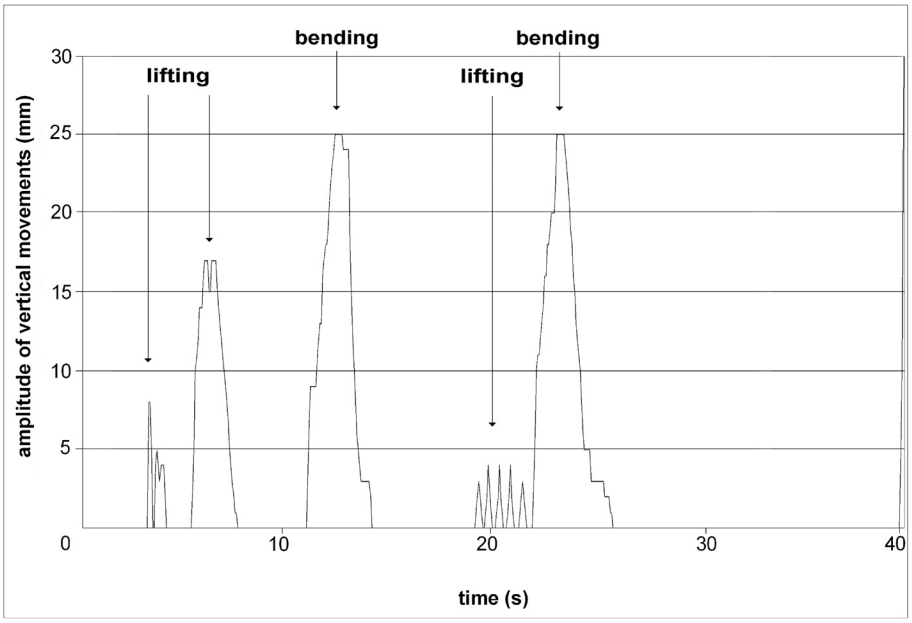

Fig. 4 Progressive amplitude (y axis) of male abdominal movements during a courtship sequence, related to the duration of the approach to the female (x axis) culminating in the flying leap (at 40s). Amplitude of movements was obtained by measuring the distance of abdomen tip from the ground each 0.067s.

It is interesting to notice that courtship behavior really seems to occur when a stress factor (natural or artificial) is added to the encounter: five of six displays were performed in frontal encounters on the artificial substrate, where the female's attention was clearly focused on the male.

During the sixth encounter, in the rosebush, a male approached a female from the rear, probably unseen, but another male was already mounting her. A mounted male creates a stress full situation for the pair. She seems to accept his presence so long as he does not present a disturbing factor or pose potential threat (he is in a good position to harm her). He in turn, evaluating her stress levels, adjusts his position and may try to calm her by tapping his antennae on hers. At any moment she could turn, grab and eat him. A second male that approaches this couple must deal with two stressed and very primed insects. His goal may be displacement of his rival while trying to not disturb the cannibalistic female. The interaction between males is thus damped by the danger presented by the female.

In this particular test the uncoupled male gave his display, jumped on the couple, tried for some minutes to displace the other male with some timid leg slashes, then renounced, jumped off and ran away. I observed in *M. religiosa* a male that successfully displaced a coupled one and successfully inseminated the female. It is not a very common situation, but it occurs.

The similarity of these complex movements between such taxonomically and geographically distant species of mantids as *A. decolor* (Subfamily: *Amelinae*, Mediterranean basin) and *T. aridifolia sinensis* (Subfamily: *Mantinae*, easternmost part of Asia and North America), seems to suggest that this behavior is quite old – present in a common ancestor. Of course this might also be explained as convergence, but using the same stuctures to signal in the same way would seem an improbable result of separate evolution.

Considering it in a broader context, it is interesting to compare this behavior with the courtship display performed by some sexually cannibalistic spiders. The jumping spider *Habronattus dossenus* for example, while approaching the female, uses seismic and visual signals to decrease the possibility of being cannibalized (Elias *et al.* 2005). This strategy is not very far from that observed in *A. decolor*: while a moderate tapping on the floor communicates to the female spider the presence of a nonprey target at long range in a first, shy approach, the sudden spreading wide of the colored forelegs, at short range, enlarges the visual shape of the male and discourages the attack of the female. The use of an approach that gradually increases the power of its signals could be a convergence to an optimal strategy that calibrates the messages with the receptivity of the receiver. We might also remember that the correct execution of a multimodal or, in general, a complex courtship display that exploits different signals or parts of the body, is also a good proof of the high quality of the male (Elias *et al.* 2005, Leitão *et al.* 2006), probably the most important message sent to the female.

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