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Mating behavior, morphology and taxonomy of *Pseudoyersinia betancuriae* (Mantodea: Amelidae)

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Abstract
The morphology of the Betancurian Dwarf Mantis *Pseudoyersinia betancuriae* Wiemers 1993 is here presented with a redescription of both male and female, to better understand the taxonomy of this species within the tribe Amelini. The mating behaviour has been studied pairing different males and females in laboratory conditions, recording the occurrence of cannibalism and the presence of a courtship display, here observed and described for the first time. The taxonomy of this species with a peculiar and not well known natural history is described for both its morphology, genetics and ecology.
Keywords: biogeography; cannibalism; conservation; dna barcoding; ethology; praying mantis

Introduction

The Betancurian Dwarf Mantis *Pseudoyersinia betancuriae* Wiemers 1993 is a small species of ground mantis endemic of the Canary Island, described and known to occur on Fuerteventura Island. Its presence in the nearby island of Lanzarote and its islets was uncertain: *Pseudoyersinia subaptera* was the only *Pseudoyersinia* historically listed for Lanzarote (Gangwere et al. 1972, Bland et al. 1996, Becerra et al. 2001), but the real identity of this species (occasionally also reported as *Pseudoyersinia canariensis* Chopard 1942; e.g., Heßler et al. 2008) has been questioned (Wieland et al. 2014). Moreover this species has been proposed for a new subgenus *Canariameles* (Villani 2020), reported as differing from *Ameles ss* in having a "less robust pronotum and different male genitalia" even if the the genitalia of this species were not examined.

Although an accurate taxonomic revision covering both morphological and molecular data, useful to better solve this problematic taxonomy, are still lacking for this genus, especially concerning the Canary Islands, *Pseudoyersinia betancuriae* can be distinguished from all the other species of the area because of its smaller size of the body and tegminae, the lack of ocular crests, a very fine crenulation on the pronotum lateral margins, marked conical compound eyes, and a less broadened abdomen of the female (Wiemers 1993). The few collecting records reported in literature suggest that this species is active at least between February and April (García Becerra et al. 2001) and that it can be found on the herbaceous vegetation or on small bushes like *Salsola* Sturtevant 1921 et al. 2003), reaching up to 600 metres of altitude above the sea level. Very little information is available on *P. betancuriae*. At present, its ecology is almost completely unknown, and the taxonomy needs to be better defined (García Becerra and Oromi 1999, García Becerra et al. 2001, Wieland et al. 2014). Due to the extremely scarce amount of data on this species, its conservation status has been recently assessed as “Data Deficient” (Battiston et al. 2016) and further field-work research has been strongly encouraged to better understand its biology, ecology, and morphological variability.

Although being a popular and iconic animal, the mating behaviour of praying mantises is far to be well known. Beside the renown sexual cannibalism, the male mating behaviour, which includes displays with bending the abdomen, boxing with the fore legs or stomping the mid and hind legs, has been observed and reported for different species from the second half of the last century (i.e. *Acontiothespis multicolor* (Saussure 1870) in: Quesnel 1967 *or Oligonyx insularis* Bonfils 1967 in: Bonfils 1967) till the more recent years (*Hymenopus coronatus* Olivier 1792 in: Rönisch 2021). Mating displays are known in at least 8 of the 29 Mantodea families (more than 27%) and in phylogenetically distant ones: from Metallyticidae Giglio-Tos, 1917 (in: Schwarz 2018) to Eremiaphilidae Saussure, 1869 (in: Govorov 2019), and Mantidae (i.e. *Tenodera sinensis* Saussure 1871 in: Liske and Davis 1987). Mating behavior has been already reported for Amelidae in: Battiston 2008. Mating courtship displays, involving the flexion of legs or abdomen are however known also for other Dictyopterans as

Latiblattella Hebard, 1917 (in: Willis 1970) and this suggests that this strategy, even if readapted in the different groups, has ancient roots.
Understanding these unusual behaviours within the complex mating system of these insects is important to understand a crucial part of their biology that may affect their evolution and even conservation. A deeper knowledge on the ecology of species whose taxonomy is problematic is crucial to better understand their relationships with others. In this perspective peculiar behaviours, especially if related to the sexual selection, may promote local speciation and help taxonomy to validate species separation. For these reasons the biology of *P. betancuriae* is rediscussed here considering both morphology, genetics and ecology, in particular the mating behaviour.
The rearing of some individuals of *P. betancuriae* and their observation in nature allowed to collect interesting, new data on the intraspecific variability of this species and to better describe its mating behaviour.

Materials and methods

REARING

During December 2018, seven individuals of *P. betancuriae* (five nymphs, one adult female and one adult male) were collected by beating small shrubs and grass in three different localities of Fuerteventura. Three of these individuals (one adult male and two nymphs: a female and a male) were collected near the type locality of this species at the Barranco del Aceituno. Three other specimens (all females: two nymphs and one adult) were collected in La Oliva. Another specimen, an immature female, was collected on the south slope of Calderon Hondo near Las Palmas. Two adult females from the coastal area of Los Cocoteros in Lanzarote were also observed in their habitat and reared.
All specimens were bred in plastic boxes closed on top with a thin net, at room temperature (between 20°C and 30°C), preserving their natural photoperiod and enlightened by indirect sunlight. Adults were housed in individual boxes (10 cm x 10 cm x 13 cm) and fed ad libitum with small Diptera (*Drosophila melanogaster* Meigen, 1830, *Drosophila hydei* Sturtevant, 1921) and Lepidoptera (small Pyralidae and Crambidae). Each specimen was fed at least once every 3 days. Three adults were able to mate several times, and eight oothecae, four for each female, were laid in May 2019 (Fig. 1).
Neanids emerged from these oothecae between one and two months later and reared together in groups of about 10 - 20 individuals, in the same conditions above. Starting from the second instar till the adult stage, the neanids were reared in individual cages and fed only with small Diptera (*Drosophila melanogaster*, *Drosophila hidei*). After at least three months from hatching, 12 mantises reached the adult stage. To ensure that all individuals had reached sexual maturity, experimental mating trials took place at least one month after reaching the adult stage.

MORPHOLOGY

Morphological data were obtained measuring high-resolution pictures of specimens with a Canon 100D camera and a Nikon SMZ2T microscope, then processed on JMicrovision V 1.2.7 software. Discriminative parts of the body and their ratios were considered as in Obertegger et Agabiti (2012): total length of the body (BL) from the vertex to the tip of the terminalia, maximum length of the tegmina (TL), maximum width of the head between the external margins of the eyes (HW), maximum length of the pronotum (PL), maximum width of the pronotum over the supracoxal dilatation (PW), length of the hind femora (HFL), length of the fore femora (FFL), maximum width of the fore femora (FFW). A comparison of average ratios between some representative Amelini species for both male and female specimens, has been done using a typical *Ameles* - *A. spallanzania* (Rossi, 1792), an

intermediate form between *Ameles* and *Pseudoyersinia* like *A. andreae* (Galvagni, 1976), a typical *Pseudoyersinia* - *P. brevipennis* (Yersin, 1860), and *P. maroccana* Battiston et al., 2014 for comparison. Morphometric data for comparison is from Battiston et al., 2018.

MATING

In order to study their mating behaviour, six adult males and six adult females (offsprings of wild-caught individuals, sexually mature and reared as described above) were paired with different combinations on two different kinds of settings/substrates, where they were continuously monitored either by an observer or video-recorded with a Canon SX530HS.

One setting was completely artificial: a table covered with a white paper surface, offering no places to hide or elements to mimic. The tests were run in a room with good illumination coming from a led lamp (warm light) located 50 cm far from the couple and with a room temperature of 20-24°C. The second setting was a small bush of succulents, with portions of bare ground and other small plants (*Thymus* sp.), where mantises were set free to move, hide and mimic, left undisturbed in the room without any physical barriers except for the walls of the room. Observation points for the mating were located in other places of the room about 1 m far from the insects, leaving them undisturbed during the approach.

One male and one female were placed in their area at the same time about 20 cm from each other. At the beginning of the tests the observer induced both mantises to make small movements until they turned their heads toward each other, indicating their mutual awareness, then left undisturbed until the complete mating and the occurrence of sexual cannibalism. A total of six male-female pairing was observed; all males were used in more than one encounter (at least two), but always with a different female. Each encounter consisted of one or more attempts of approach by the male (trial). Males and females were left free to interact and move on the substrate. If there were no approaches for more than 30 minutes, the trial was interrupted and considered as “failed”.

All the individuals involved in the mating were sexually mature (all specimens had already completed the last molt since at least one month) when tested and, in order to avoid stress caused by repeated mating, each of them was only engaged once a week at most. The same protocol was applied with the same timing and resting times to all individuals, both male and female. Considering the same pair, there were both cases of mating on the first attempt, as well as cases where mating did not occur even after several attempts, so it was not possible to detect a significant difference given the amount of mating attempts.

MITOCHONDRIAL DNA ANALYSIS

Mitochondrial DNA analysis was carried out on 4 samples: 3 females from the Fuerteventura Island (specimens CI1f, CI1g and CI1h) and 1 female from the Lanzarote Island (specimens CI1j). As a comparison, 2 *A. spallanziana* specimens (1 from Spain and 1 from Italy) have also been analysed.

Total DNA was isolated from a single leg per specimen using the NucleoSpin DNA Insect kit (Macherey/Nagel). A fragment of the mitochondrial gene cytochrome oxidase subunit 1 (*cox1*), corresponding to the DNA barcoding region (Folmer et al. 1994), was PCR amplified using the LC01490 (5′-GGT CAA CAA ATC ATA AAG ATA TTG G-3′)/HC02198 (5′-TAA ACT TCA GGG TGA CCA AAA AAT CA-3′) primer pair. PCR amplifications were performed using the GoTaq DNA polymerase kit (Promega), following the manufacturer’s protocol. Thermal cycling program included: initial denaturation for 5 min at 95 °C; 30 cycles of 30s at 95°C, 45s at 55°C, 30s at 72°C; final extension for 7 min at 72 °C. PCR products were purified using ExoSAP-IT PCR Product Cleanup Reagent (Thermofisher) and both strands were Sanger sequenced at Macrogen Europe Lab. Obtained sequences have been deposited in NCBI Genbank under the accession number: OQ058990-OQ058995 .

Sequence chromatograms check, alignments, genetic divergence and phylogenetic analyses with the maximum likelihood method (substitution model: GTR+G; 1000 bootstrap replicates) were performed using Mega X (Kumar et al. 2018). The homologous *cox1* fragment from a *Mantis religiosa* mitochondrial genome (NCBI Genbank accession number: MZ153073; Luchetti et al. 2021) was used as outgroup sequence.

Results and Discussion

The morphology of *P. betancuriae* (Fig. 2, Tab. 1) reveals a stronger similarity with specimens of the *Ameles* Burmeister 1838 genus than with specimens of the *Pseudoyersinia* Kirby 1904 genus (see. i.e. Agabiti et al. 2010 and Battiston et al. 2010 for single characters comparisons). There is a long and still unresolved debate on the separation of these two genera, which is based on the single character of the wings development: males being macropterous in *Ameles* and micropterous in *Pseudoyersinia* (Battiston et al. 2018, Wieland et al. 2014). This character here also seems not sufficient to group the observed *P. betancuriae* specimens in the genus *Pseudoyersinia*, as traditionally considered (Galvagni 1976). In fact, while the latter genus specimens are usually (but not always, e.g. *A. andreae*) more slender and provided with spines on the apex of the phalloid apophysis (Battiston et al. 2018), observed *P. betancuriae* specimens have a short pronotum and massive limbs, and no trace of spinal processes on the phalloid apophysis (Fig. 3).

A comparison of the main body ratios (Fig. 4) seems to allocate *P. betancuriae* in a unique position in the Amelini tribe, on one side closer to other *Pseudoyersinia* species, like *P. maroccana* for the length of the micropterous tegmina (as expected in males) but, on the other side, more similar to *Ameles*, like *A. spallanzania* for the massive fore femora. The inclusion of this species in the subgenus *Canariameles* Villani 2020 seems here not appropriate. The characterization of this subgenus was indeed based on a marked pubescence on the walking legs, defined descriptively as more pronounced than in other subgenera (i.e. *Ameles* ss) and the prozone of the pronotum clearly longer than wide (generally 1.2-1.6 times longer than wide). The pubescence in the examined specimens was however not appreciably longer, differently pronounced or arranged than the examined *Ameles* considered as ss (*Ameles spallanzania*), both in males and in the females. The prozona in the specimens studied was nearly as long as wide with a ratio (0.96-1.17) outside of the proposed reported range. Therefore, Villani's taxonomy was not used here, pending further verifications and more morphometric data on a larger sample of species, to support the validity of the subgenus.

Though, molecular data clearly point out a net separation of the two latter lineages (Fig. 5), with a 11.1% of genetic divergence between the analysed *P. betancuriae* samples and the two *A. spallanzania* specimens. Moreover, the extent of divergence between specimens of *P. betancuriae* from Lanzarote and Fuerteventura results about 1.2%, suggesting they are from the same species. The presence of *P. betancuriae* in both islands should be considered however cautiously regarding its conservation. In both islands this species was found in extremely scarce numbers and in localised and fragmented populations.

In the present analysis, for the first time, it has been observed that *Pseudoyersinia betancuriae* is able to perform a simple courtship display, made by a fast and alternate stomping of the hind legs (Fig. 6). This display occurred when the male was standing still near the female or, more often, when it was slowly approaching the female and was, in sight, close to her. The male kept all the body motionless, while the hind legs were stomped alternately and independently, with small rocking movements of a few millimetres of amplitude, never reaching full flexion of the femora.

The courtship display was observed in seven out of 54 encounters (13%), and in six cases it resulted in successful approach and mating (Fig. 7). Successful approaches were observed

also in further seven encounters, although in two cases the mating failed. The courtship behaviour was observed in both settings, but more frequently in the artificial one (17%) than in the natural one (8%), and with different direction of approach (43% frontal, 57% lateral). Moreover, this behaviour was observed when the male was close to the female, in a range of 2 to 10 cm. Cannibalism occurred only in 2 encounters, either with or without a courtship display, and both in the "natural" setting (Fig. 7).

Overall, the courtship display does not seem to be a usual behaviour for this species, although if we consider only successful matings, it occurs in 64% of instances. This could suggest a considerable impact of the courtship display on mating, either on the reduction of the cannibalism or just inducing the female to a less aggressive/defensive attitude, more as suggested by the observation in other species or genera (see : i. e: Barry et al. 1987, Schwarz et al. 2017, Govorov 2019). The fact that it has been observed more frequently in the artificial setting and, mostly, when the male can be easily seen by the female may imply it could be a behaviour induced by environmental conditions with few hiding places or distractions for the female.

Generally speaking, these results should be taken carefully, as we must consider that in nature (closer conditions to the "natural" setting) the behaviour may occur with different frequencies. However, our observations indicate that a courtship display is present in the behavioural range of this species, where cannibalism occurs, contrary to common expectations, only rarely. Moreover, since most encounters after this behaviour resulted in successful mating, it is likely that such courtship display may indicate increased chances of a successful mating.

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Tables and figures legends

Table 1. Measures: total length of the body (**BL**) from the vertex to the tip of the terminalia, maximum length of the tegmina (**TL**), maximum width of the head between the external margins of the eyes (**HW**), maximum length of the pronotum (**PL**), maximum width of the pronotum over the supracoxal dilatation (**PW**), length of the hind femora (**HFL**), length of the fore femora (**FFL**), maximum width of the fore femora (**FFW**).

Figure 1. *Pseudoyersinia betancuriae* from Lanzarote. A, Adult female with her just laid ootheca (photo R. Battiston). B, Adult male (photo Joan Escobet).

Figure 2. *Pseudoyersinia betancuriae*, habitus of adult specimens from Fuerteventura. A, Male. B, Female. Scale bar: 5 mm.

Figure 3. *Pseudoyersinia betancuriae*, disarticulated male genital complex, specimens from Fuerteventura. A, B, phallomere in dorsal view: A, right; B, left. C, Phallomere in ventral view. D, Outlines of the ventral phallomere. E, Phalloid apophysis of a second individual. Scale bar: 1 mm.

Figure 4. Comparison of some of the most discriminative average ratios of *Pseudoyersinia betancuriae* (red) and other representative Amelini species.

Figure 5. Maximum likelihood tree (-lnL=2441.31) built on *cox1* sequences. *Pseudoyersinia betancuriae* specimen ID and collection locality have been indicated. Numbers at nodes represent bootstrap support. The bar below represents the number of substitutions/sites.

Figure 6. Lateral approach of the male of *Pseudoyersinia betancuriae* (foreground) toward the female (background) during the mating tests, with a graphical representation of the stamping movement of the hind leg.

Figure 7. *Pseudoyersinia betancuriae*, strategies of approach of the male and their relative frequencies (p): without or with courtship and the direction of approach.

Supplemental Material:

Table 2. Mating behaviour tests of *P. bentacuriae*. Encounter: code-number of each encounter (e.g. A1: A= male individual code, 1= trial number); Approach: direction of the approach of the male; Setting: blank table (artificial) or plant bush (natural); Courtship: presence of courtship display; Cannibalism: presence of cannibalism; Pairings: codename of each paired individual; Duration: duration of the mating; Mating success: successful transfer of the male spermatophore into the female.

Video recording of the male courtship: MP4 0:10s

	MALES	**FEMALES**				
MEASURES	MEAN	MIN	MAX	MEAN	MIN	MAX
BL	17.39	14.17	19.54	19.46	16.91	23.37
TL	2.49	1.63	2.88	1.89	1.59	2.50
HW	3.30	2.89	3.65	4.17	3.88	4.83
PL	4.05	3.77	4.34	4.38	4.12	5.13
PW	2.00	1.75	2.19	2.38	2.16	2.78
HFL	6.30	5.53	6.96	6.94	5.47	8.30
FFL	4.03	3.77	4.31	4.55	4.23	4.98
FFW	1.20	1.12	1.31	1.37	1.26	1.62
RATIOS	**MEAN**	**MIN**	**MAX**	**MEAN**	**MIN**	**MAX**
PL/PW	2.01	1.80	2.22	1.88	1.76	2.22
BL/PL	4.28	3.75	4.50	4.26	3.33	4.67
FFL/FFW	3.32	2.89	3.48	3.33	2.82	3.74
HFL/HW	2.02	1.64	2.41	1.55	1.32	1.72

Table 1

Figure 1

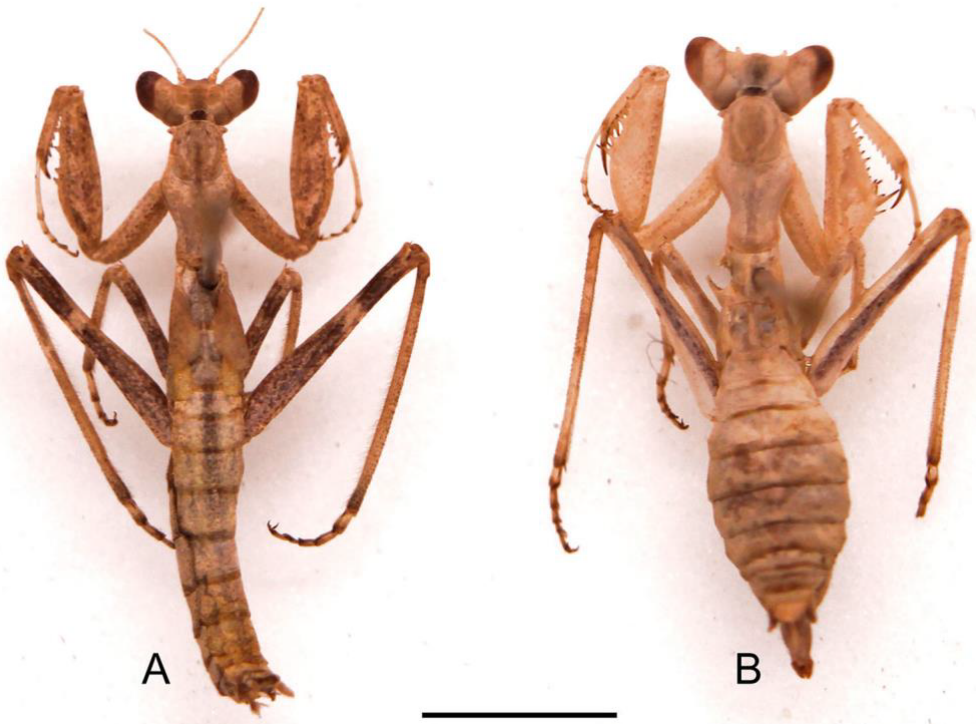

Figure 2

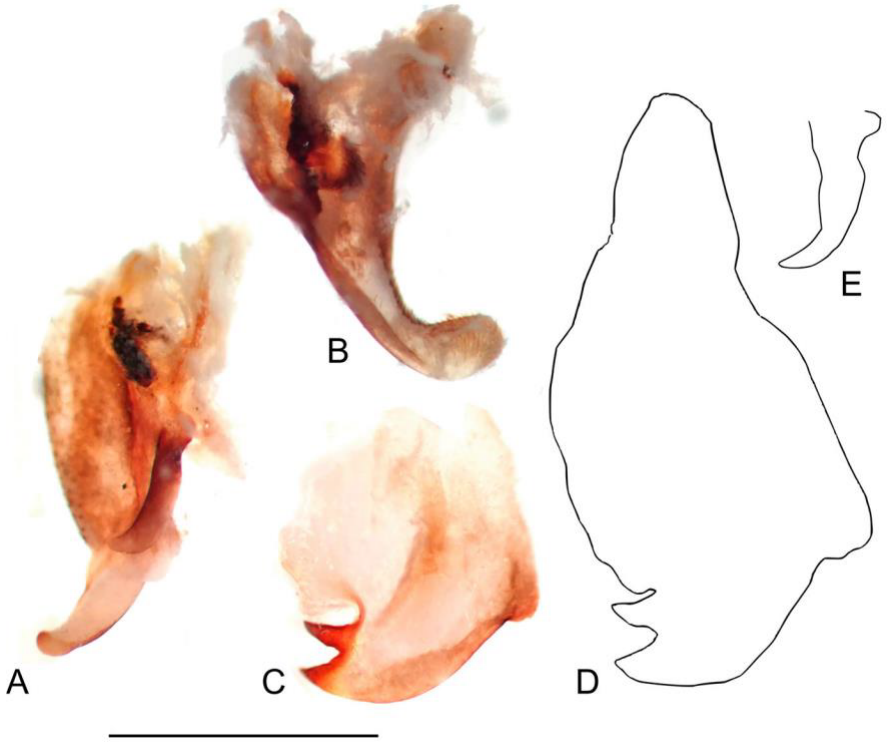

Figure 3

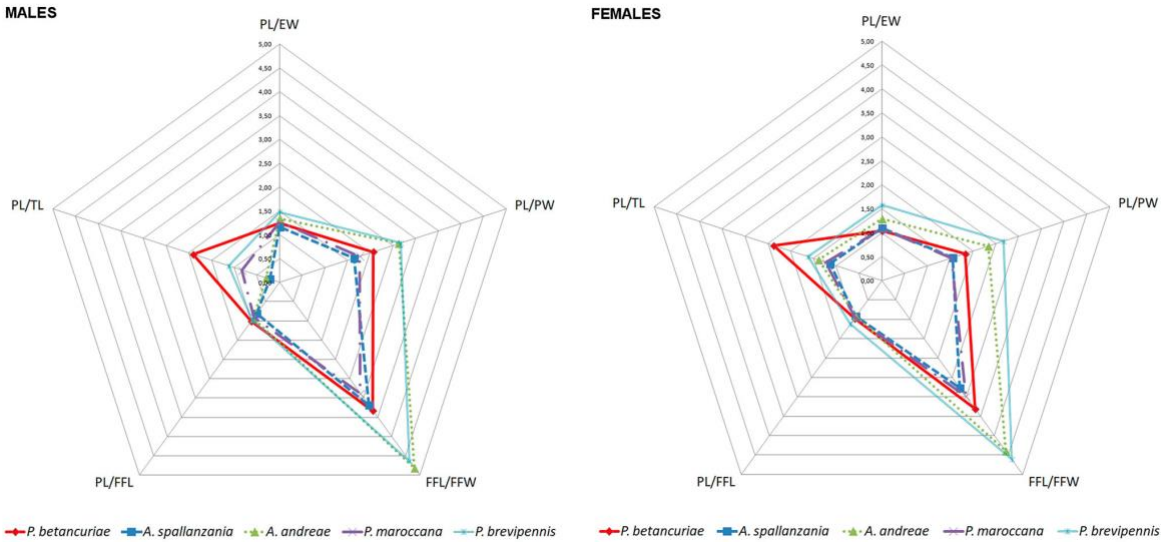
MALES
PL/EW
PL/PW
FFL/FFW
PL/FFL
PL/TL
FEMALES
PL/EW
PL/PW
FFL/FFW
PL/FFL
PL/TL
P. betancuriae
A. spallanzania
A. andreae
P. maroccana
P. brevipennis

Figure 4

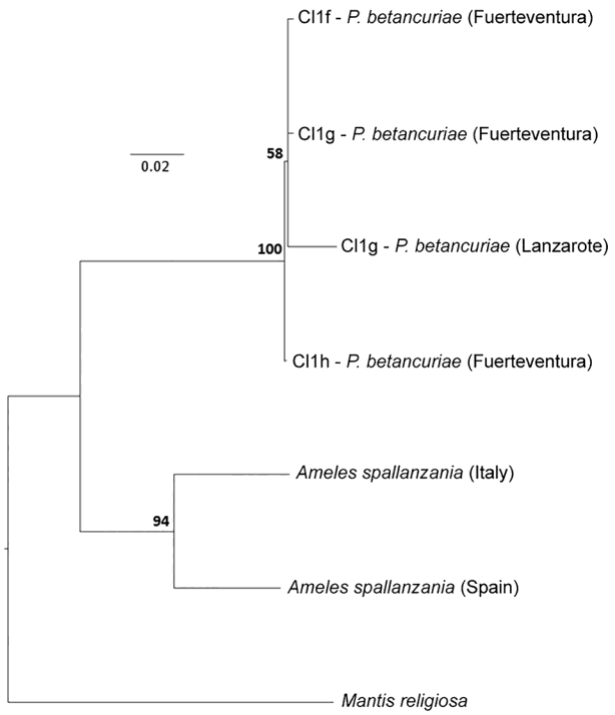
Cl1f - P. betancuriae (Fuerteventura)
Cl1g - P. betancuriae (Fuerteventura)
0.02
58
100
Cl1g - P. betancuriae (Lanzarote)
Cl1h - P. betancuriae (Fuerteventura)
Ameles spallanzania (Italy)
94
Ameles spallanzania (Spain)
Mantis religiosa

Figure 5

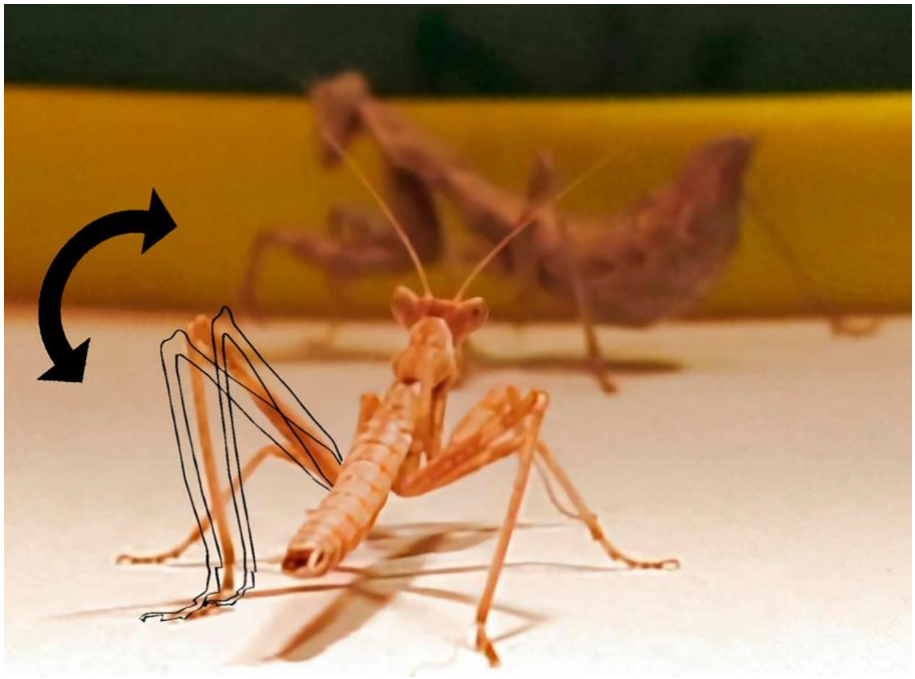

Figure 6

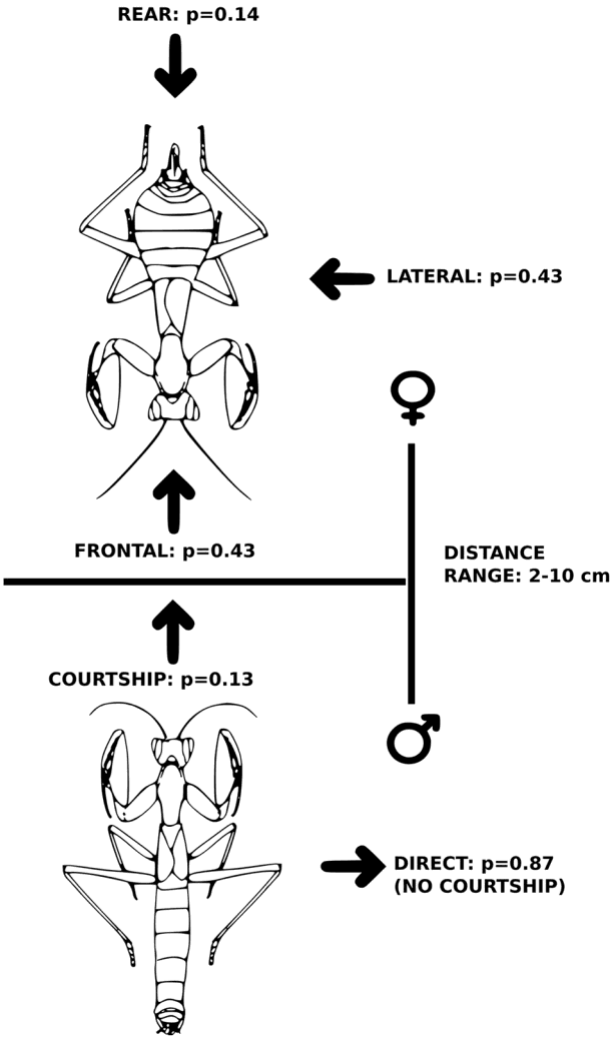
REAR: p=0.14
LATERAL: p=0.43
FRONTAL: p=0.43
DISTANCE
RANGE: 2-10 cm
COURTSHIP: p=0.13
DIRECT: p=0.87
(NO COURTSHIP)

Figure 7