

Ecology and behaviour of the ‘road tarantulas’ *Eupalaestrus weijenberghi* and *Acanthoscurria suina* (Araneae, Theraphosidae) from Uruguay

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Abstract

Spatial distribution, burrow morphology, phenology, defensive displays and predation of two theraphosid spiders living in meadows were studied in Uruguay. Exhaustive field studies complemented with laboratory observations were carried out. *Eupalaestrus weijenberghi* occurred throughout the country while *Acanthoscurria suina* occurred only in the southern half. Both species seemed to be the most abundant theraphosid spiders in Uruguay as they live in the dominant landscape of the country. Burrows from both species showed a similar morphological pattern but a terminal narrow tube was found only in *E. weijenberghi*. We observed that *A. suina* always co-occurred with *E. weijenberghi* but this species frequently occurred in the absence of the former. When co-occurring *A. suina* showed an aggregated distribution while *E. weijenberghi* was randomly distributed. A restricted reproductive period was found for both species, mainly between March and April, evidenced by the massive presence of walking adult males and then confirmed by pit-fall traps. Moulting, oviposition and longevity were also studied. Conspicuous species-specific defensive behaviours were displayed by the tarantulas in all cases, when collected. These tarantulas showed spatial co-occurrence and temporal coexistence with the beetle *Diloboderus abderus*, an important pest of grasslands. Tarantula predation on adult beetles was confirmed, these spiders being one of the few beetle predators. Their maximal efficiency in beetle predation could reach 65 000 prey captured per hectare by month. These polyphagous tarantulas seem to be potential agents for the biological control of beetle pests.

Keywords: Ecology, burrow structure, predation, defensive display, tarantula

Introduction

Acanthoscurria suina Pocock, 1903 and *Eupalaestrus weijenberghi* (Thorell 1894) are large-sized spiders living in meadows of the Pampean biogeographic province. These species are nocturnal and dig burrows where they live throughout their life, with the exception of adult males. Walking adult males are usually observed during the reproductive season mainly crossing roads and routes; they also show conspicuous defensive displays when disturbed. Although their taxonomy has been studied (Schiapelli and Gerschman de Pikelin 1964;

Pérez-Miles 1992), their ecology and other biological characteristics are poorly known (Costa and Pérez-Miles 2002). Considering meadows constitute dominant ecosystems in Uruguay (90% of the Uruguayan land area), these tarantulas are probably the most frequent theraphosid species in the country. Meadows are the most important natural resource of the Uruguayan economy, considering that the first productive activity in the country is cattle breeding. *Diloboderus abderus* (Sturm 1826) is an important pest of Uruguayan grasslands (Morey and Alzugaray 1982) because their larvae feed on grass roots. These larvae are subterranean and are therefore protected from predation. We observed that both species of tarantula currently predate on the adult beetles in the field.

In the present research some ecological and biological aspects were studied to estimate the real impact of the predation of these tarantulas on the beetle. The geographic distribution of predators and prey were exhaustively studied throughout Uruguay. The spatial distribution, structure and function of spider burrows, as well as phenology of both tarantulas, were also studied. Behavioural studies of predation and defence were carried out.

Our results led to an estimation of the ecological importance of the tarantulas in meadow dynamics as well as their possible use in the biological regulation of plagues.

Material and methods

This study took place between February 1998 and May 2000. Six thousand kilometres along routes and roads throughout Uruguay were surveyed, stopping each 20 km (south) and 30 km (north) to register the occurrence of tarantulas and beetles (four collectors, 10 min each stop). If tarantula burrows were found, an exhaustive study was done, including excavation of the burrows, drawing, measuring, plaster moulding, expanded polyurethane moulding; collection of prey, moult and cocoon rests; as well as measurement of the volume of extracted soil. Also burrow closing with silk or soil was registered. Temperature and humidity inside and outside of some burrows were measured. The spiders were identified, sexed and sometimes collected.

Additional stops were made when walking or dead theraphosids were observed during trips. In these cases spiders were hand stimulated to study defensive response, and sometimes specimens were measured and weighed.

Density of burrows was measured at five different sites (Figure 1) where the occurrence of tarantulas was frequent. An area was delimited and burrows were carefully counted and excavated to identify the species inhabiting each one. Spatial distribution of burrows was schematized, measuring distances among them; burrow sizes were also registered. An aggregation analysis was performed in Melilla (Montevideo), where both species co-occurred with similar abundance. Field studies of prey captures were performed in Melilla (Montevideo) during the night and were video recorded.

In the laboratory the spiders were maintained in glass jars of 9 cm diameter with soil and water source. They were fed with cockroaches and beetles. Observations of prey capture were done in an arena of 19 cm diameter, with soil. Spiders were weighed weekly, and immediately before and 24 h after feeding, using an electronic scale (readability=0.01 g). Periodical observations of defence behaviour elicited by hand and forceps stimulation were done. Weather data from the meteorological stations of Carrasco and Melilla were provided by the National Office of Meteorology (Uruguay).



Figure 1. Map of Uruguay with the routes and roads surveyed in the study, showing the distribution of *Eupalaestrus weijenberghi* (triangles), and the five sites where density studies were performed (stars). Each triangle represents the occurrence of one or more individuals of the species.

Traps

Pit-fall traps were placed at two sites near Montevideo city (Melilla and Solymar Norte). Both suburban sites have meadows with bushes and a few shrubs. Ten traps of 19 cm diameter and 21 cm height containing 2 litres of preservative solution (10% formaldehyde and detergent) were located at each site. The traps were placed along lines at a distance of 10 m between each one. They were examined and renewed weekly from 16 December 1998 to 28 April 1999. Individuals of the two spider species and of the beetle *D. abderus* were sexed and counted. Other fauna were identified up to order level.

Results

Geographic distribution

Two hundred and six individuals of *A. suina* and 414 of *E. weijenberghi* were registered in the field. *E. weijenberghi* occurred throughout the country while *A. suina* occurred only in the southern half of Uruguay (Figures 1, 2). *A. suina* was always found in sympatry with *E. weijenberghi*, and high abundance of both species usually coincided. Both species decreased in frequency drastically in flooded lowlands. The abundance of *E. weijenberghi* decreased also in hilly zones with superficial soil (Cuchilla Grande and Cuchilla de Haedo).

Both species mainly live in meadows but *A. suina* was also found in hilly zones, in burrows excavated under stones. Higher abundances of tarantulas were usually observed in deep soil environments (the most fertile in Uruguay). During the reproductive period, we frequently observed males of both species crossing roads and routes. The beetle *D. abderus*

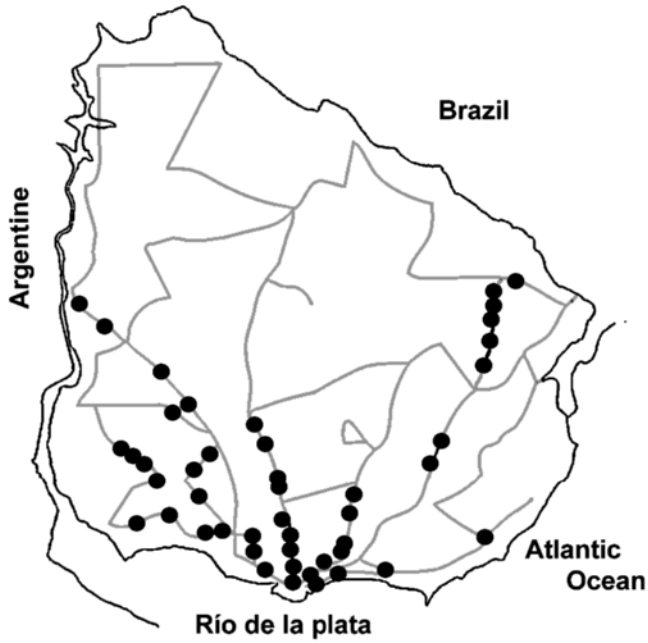


Figure 2. Geographical distribution of *Acanthoscurria suina* in the surveyed areas of Uruguay.

was found throughout the country, including hilly zones and lowlands, and its abundance decreased in the centre and north of Uruguay (Figure 3). Consequently, the distribution of the spiders widely overlaps with the distribution of the beetle.

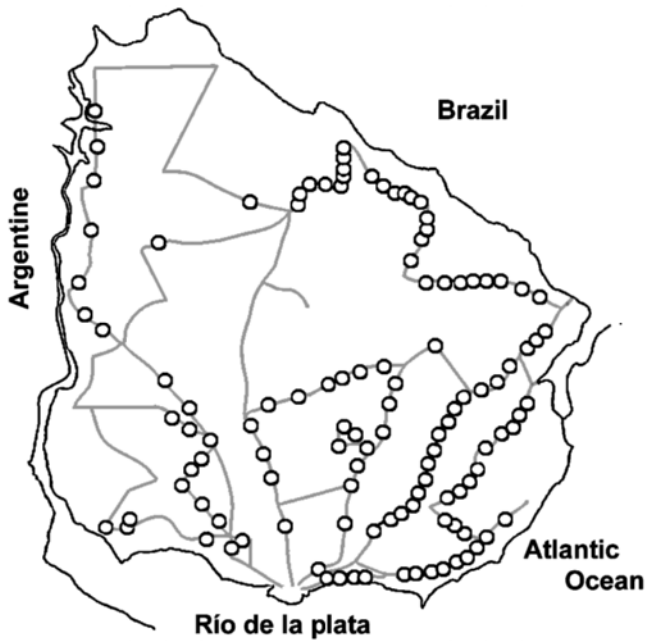


Figure 3. Distribution of the beetle *Diloboderus abderus* in the surveyed areas.

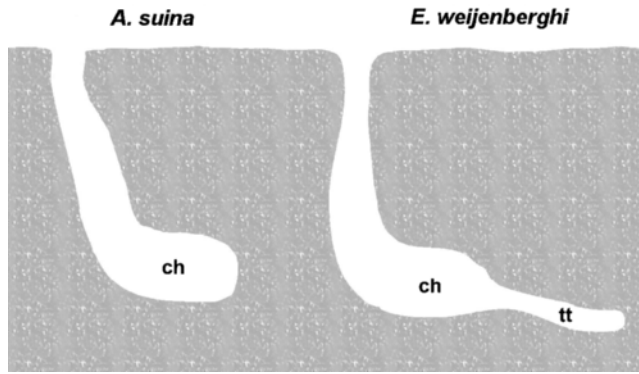


Figure 4. Schematic representation of burrows of *Acanthoscurria suina* and *Eupalaestrus weijenberghi*; ch, chamber; tt, terminal tube (see text).

Morphology and structure of burrows

Both species of tarantulas excavate deep tubular burrows in open fields. In *E. weijenberghi* the burrow had a circular entrance, with a curved profile, and was usually covered with a fine mat of silk. The entrance was followed by a vertical tube, continued by a horizontal chamber and then a narrow terminal tube (Figure 4; Table I). The burrow of *A. suina* had a subcircular entrance, usually without silk and with an abrupt profile (step-shaped). The rest of the burrow was similar to that of *E. weijenberghi* but lacked the terminal tube (Figure 4; Table II). The size of *E. weijenberghi* burrows was slightly larger than those of *A. suina*, and deeper.

Sometimes the entrance of the burrow was found closed by silk or soil, mainly in the case of *E. weijenberghi*. Usually, granular soil was found near the burrow entrance of *E. weijenberghi*, at a mean distance of 15.27 cm (SD=5.57; $n=32$), and the volumes of soil removed were up to 80 ml (7 March 1999, Rivera). In *A. suina* volumes of removed soil were up to 50 ml (19 November 1999, Melilla). In the laboratory, *A. suina* frequently closed the burrow entrance with silk and soil at the beginning of winter; *E. weijenberghi* also closed the burrow but in fewer cases. Both species showed the ability to submerge in flooded burrows for several minutes in the field when they were disturbed.

Entrance diameters of the burrows varied widely in both species (Tables I, II). A significant correlation was found between entrance diameter and cephalothorax width:

Table I. Burrow dimensions of *Eupalaestrus weijenberghi* (in cm).

Characteristics	<i>n</i>	Mean	SD	CV (%)	Min	Max
Entrance diameter	41	2.38	0.63	26.47	1.0	4.7
Tunnel diameter	35	2.74	0.66	24.09	1.5	4.0
Tunnel length	38	11.46	4.63	40.40	6.0	19.0
Chamber width	33	4.22	0.97	22.99	2.5	7.0
Chamber length	32	8.69	4.94	56.85	2.5	24
Chamber height	13	4.08	0.81	19.85	3.0	6.0
Terminal tube diameter	23	1.90	0.56	29.47	1.2	3.0
Terminal tube length	26	6.93	4.16	60.03	2.5	18.0
Total burrow length	34	26.10	9.92	38.01	13.0	65.0
Depth	22	18.50	4.54	24.54	11.5	29.0

Table II. Burrow dimension of *Acanthoscurria suina* (in cm).

Characteristics	<i>n</i>	Mean	SD	CV (%)	Min	Max
Entrance diameter	36	2.33	0.47	19.97	1.30	3.65
Tunnel diameter	34	2.75	0.48	17.45	1.80	3.60
Tunnel length	35	9.99	3.25	32.54	5.00	16.00
Chamber width	31	4.04	0.66	16.32	3.00	5.00
Chamber length	31	5.90	1.38	23.30	4.00	10.00
Chamber height	24	3.85	0.84	21.83	2.50	5.00
Total burrow length	34	15.96	5.18	32.44	11.00	27.00
Depth	29	14.03	3.26	23.21	9.50	20.00

$r=0.451$ ($P<0.02$, $n=27$) for *A. suina* and $r=0.613$ ($P<0.001$, $n=37$) for *E. weijenberghi*. From the measurement of cephalothorax width and the study of spermathecae moults, we found juveniles and adults of *A. suina* between 12 and 14 mm of intercoxal width; adult females being from 14 mm. In *E. weijenberghi*, juveniles and adults measured between 13 and 14 mm of intercoxal width, adult females being from 14 mm. Considering the correlation of body size and entrance diameter we estimated that in *E. weijenberghi*, 57% of the burrows ($n=37$) were occupied by adult females or subadult males. In *A. suina*, 67% of the burrows ($n=27$) were occupied by adult females or subadult males.

Differences in temperature and relative humidity were recorded between soil surface and burrow interior; in *E. weijenberghi*, surface temperature averaged 20.84°C (SD=1.68) and inside the burrow the temperature averaged 27.00°C (SD=1.56) (five burrows measured on the 29 February 2000, 21:00 h); in a burrow of *A. suina*, temperatures on the surface and inside the burrow averaged 20.01 and 25.60°C, respectively. In *E. weijenberghi*, the surface relative humidity registered was 86.08% (SD=9.73) and inside the burrow 100% in all cases. In *A. suina*, the surface relative humidity registered was 93.0% and inside the burrow 100%.

Spatial distribution

Tarantula distribution was not homogeneous; in selected sites with high densities quantitative studies were performed. In Flores, Trinidad, we found 30 burrows of *E. weijenberghi* in 300 m² (0.10 individuals per m²), with a minimal distance between entrances of 36 cm. In Canelones, Canelón Grande, we found eight burrows of *E. weijenberghi* and two of *A. suina* in 100 m² (0.10 individuals per m²), with a minimal distance of 71 cm (interspecific). In Canelones, Solymar Norte, we found one burrow of *E. weijenberghi* and six of *A. suina* in 100 m² (0.07 individuals per m²), with a minimal distance of 35 cm (between two individuals of *A. suina*). In Lavallega, Aguas Blancas, we found burrows only of *E. weijenberghi*; 35 in 100 m² and 52 in 80 m² (0.35 and 0.65 individuals per m², respectively), and the minimal distance was 33 cm. In Montevideo, Melilla, we found 21 of *A. suina* and 20 of *E. weijenberghi* in 100 m² (0.41 individuals per m²) and the minimal distance between them was near to 8.0 cm (two individuals of *A. suina*).

Burrow distribution was studied in Melilla where high abundance of both species was found. The sampling plot was divided into: (a) 25 squares of 4 m²; (b) nine squares of 10 m² and (c) four squares of 25 m²; the aggregation index was calculated. In all cases *A. suina* showed an aggregated distribution ($X^2_a=52.32$, $X^2_b=22.24$, $X^2_c=12.33$; $P<0.01$); [1]

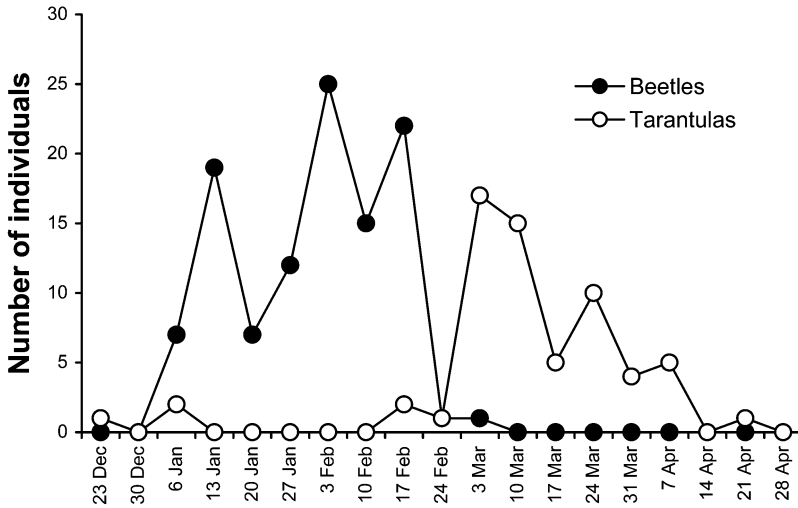


Figure 5. Temporal distribution of beetles and tarantulas captured by pit-fall traps during summer 1998–1999.

conversely *E. weijenberghi* showed random distribution. Analysing the possible influence of the distribution of individuals of one species affecting the distribution of the individuals from the other one, no significant correlations were found ($r = -0.63$, $P = 0.07$).

Phenology

Adult beetles were collected in pit-fall traps: 103 males and six females. They started their activity in the first week of January, maintaining high abundances in traps until the middle of February (Figure 5). Tarantulas collected in traps included 18 *E. weijenberghi* and 45 *A. suina*. They appeared abruptly in the first week of March and decreased in abundance from the first week of April. Abundance profiles through the study period were similar for both species of tarantulas, with a slight numerical dominance of *A. suina* (Figure 6). Males

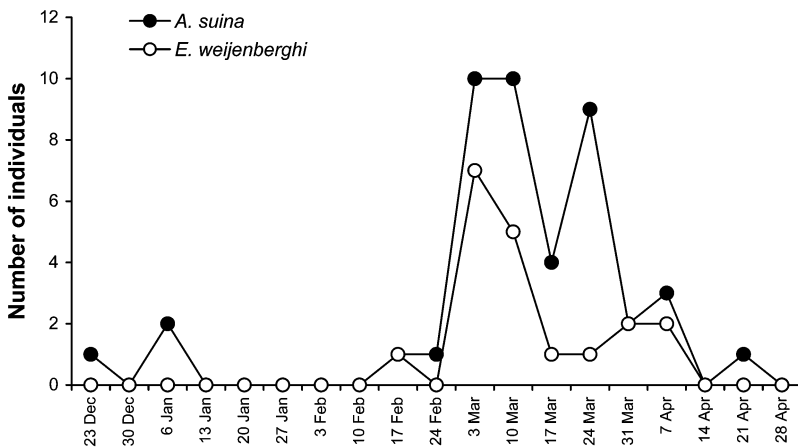


Figure 6. Temporal distribution of tarantulas captured by pit-fall traps.

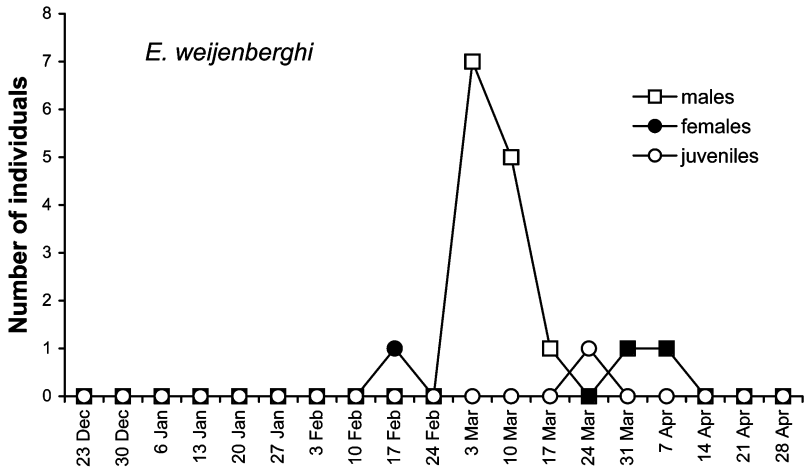


Figure 7. Temporal distribution of males, females and juveniles of *Eupalaestrus weijenberghi* collected in pit-fall traps.

predominated among the captured tarantulas, mainly in *E. weijenberghi* (Figures 7, 8). The occurrence of female *A. suina* in traps was constant from the middle of February (Figure 8). Weather data during the trap capture period are given in Figure 9.

Other fauna captured in traps are given in Table III; woodlice (Isopoda) were not counted because of their rapid decomposition, but were estimated as very abundant. Among the Arthropoda, ants were dominant, and in decreasing order: other spiders, other coleopterans, crickets, dipterans and other arachnids.

Field studies throughout the country showed that male tarantulas were active during the same period that they were found in traps. One hundred and sixty-eight males of *A. suina* were observed walking or recently dead between 27 February and 3 May; and 153 males of

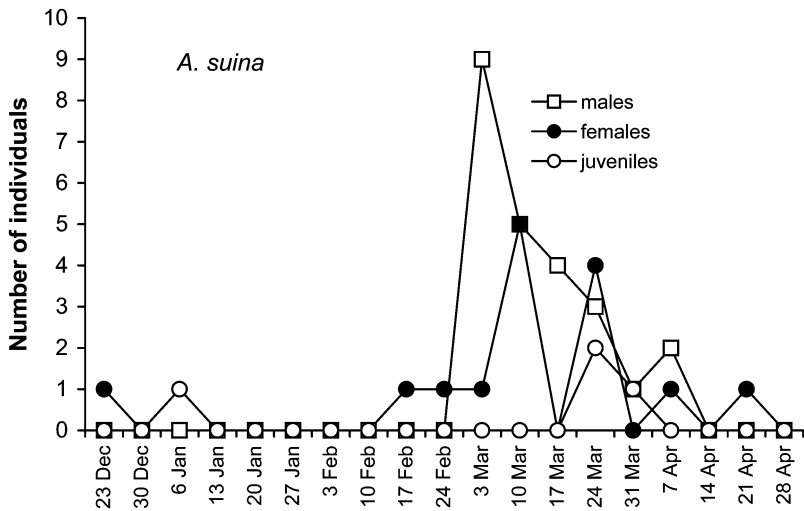


Figure 8. Temporal distribution of males, females and juveniles of *Acanthoscurria suina* collected in pit-fall traps.

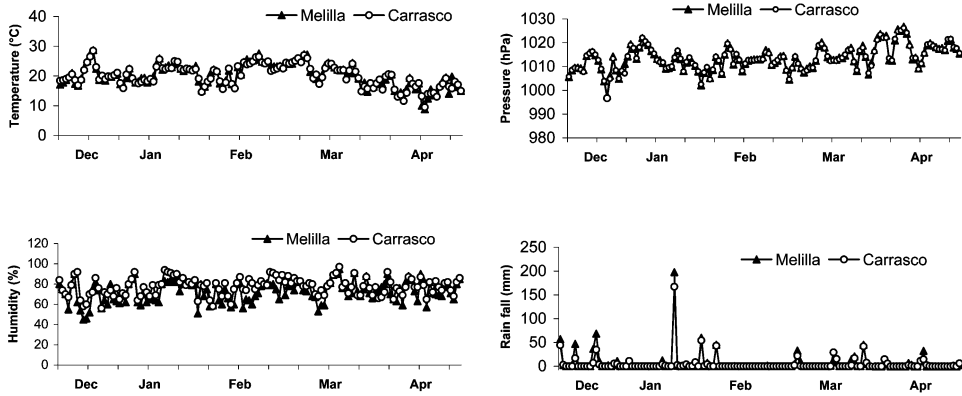


Figure 9. Temperature, atmospheric pressure, relative humidity and rainfall during the trap capture period in the two sites studied (Melilla and Carrasco).

E. weijenberghi between 10 February and 7 May (considering extreme dates from 1998 to 2000). On 26 February 1999, a recently moulted male was observed in the chamber of a burrow with remains of a silk capsule covering this chamber, and also remains of a dense white silk mat that characterizes the sperm web. No male tarantulas were found outside of the mentioned period. The males found at the end of the sexual period were few and showed clear signs of ageing (abdomen without urticating hairs, extreme thinness, motion difficulties and general body deterioration). Numerous males walking were observed on cloudy days with high temperature, with gentle wind or no wind, high relative humidity and usually coinciding with gentle or moderate rain (low atmospheric pressure). Walking male frequency usually increased some hours after the rain had stopped. Few females and juveniles were observed in the open field during March and April, and these were usually *A. suina*.

In the field, we found open egg-sacs with remains of moults, near the entrance of the burrows of *A. suina* and *E. weijenberghi*, from 15 February on. The number of moults varied between 56 and 250 in six egg-sacs observed. From the 15 February on, recently moulted females of both species were found. In the laboratory, four females of *E. weijenberghi* made egg-sacs on 14, 19 November and 10, 12 December, and the juveniles emerged on 27 January and 7, 9, 21 February, respectively. The three former females moulted on 4, 12, 18 March, respectively. Two females of *A. suina* made egg-sacs in the laboratory on 6 and 18 December; the first abandoned it on 5 January and from the second one the spiderlings emerged on 25 February and moulted on 27 February. The mothers then moulted on 7 February and 18 March, respectively.

Females of both species continued moulting annually after adulthood. In the laboratory, the distribution of moults of adult females and last moults of males are given in Figures 10, 11. In *E. weijenberghi*, a peak of female moulting was observed in February while in *A. suina* the peak was found in December. The adult period of males of *E. weijenberghi* in the laboratory was 158.1 days (SD=88.9; range=15–372; $n=60$). In *A. suina* the adult period was: 127.9 days (SD=61.9; range=19–322; $n=57$). Both periods showed significant differences with the non-paired t -test ($t=2.14$, $P<0.05$).

Nine females of *E. weijenberghi* and five of *A. suina* were collected as adults and stayed alive in the laboratory 4.5 years after their capture, showing no signs of deterioration.

Table III. Co-occurrent fauna collected in pit-fall traps (isopods, tarantulas, *Diloboderus abderus* and groups with frequencies less than 10 individuals were omitted).

	December			January			February			March			April			Total				
	23	30	6	13	20	27	3	10	17	24	3	10	17	24	31		7	14	21	28
Coleopterans	16	15	22	16	28	23	37	43	28	20	17	12	17	28	39	33	28	29	62	514
Cockroaches	9	6	8	9	3	1	5	1	2	0	2	1	0	0	2	2	0	0	2	53
Crickets	22	17	18	15	32	13	15	4	14	7	2	13	17	26	49	95	57	34	63	513
Acridids	11	13	11	12	6	17	17	21	18	18	20	10	10	20	13	8	11	2	6	244
Phasmids and mantids	1	0	3	3	0	0	1	2	3	2	1	1	1	0	0	0	0	0	0	18
Ants	97	114	136	76	61	62	121	117	119	128	87	102	99	103	111	133	111	82	127	1986
Bees	0	2	2	0	1	0	0	0	2	1	0	0	1	1	0	1	1	0	0	12
Wasps	0	1	0	0	0	1	2	2	2	2	1	0	2	1	1	2	1	0	1	19
Hemipterans	5	7	13	3	0	2	2	1	0	0	0	0	0	0	0	0	0	1	0	35
Dipterans	8	16	8	6	22	15	12	21	8	65	42	16	18	12	49	21	43	69	32	483
Larvae	5	3	2	2	0	0	4	6	17	8	3	2	1	1	1	15	5	3	33	111
Other spiders	94	115	121	101	69	29	41	63	58	38	31	34	17	46	63	63	82	49	96	1213
Scorpions	3	2	0	0	0	0	1	0	1	5	0	1	0	0	0	0	0	0	0	13
Other arachnids	8	13	18	23	15	2	2	0	5	24	19	42	43	15	27	27	24	26	34	369
Other invertebrates	4	10	6	8	14	6	18	23	6	13	13	15	10	7	17	8	5	20	7	210
Amphibians	7	6	6	3	7	13	6	4	3	2	11	8	6	16	7	3	2	3	1	114
Lizards	8	7	5	3	3	1	2	0	0	0	0	0	0	0	0	0	0	0	1	30
Rodents	5	4	5	4	8	5	3	4	6	11	8	5	9	17	10	20	14	29	19	186
Other vertebrates	1	0	4	1	0	1	3	1	0	0	2	1	0	0	0	0	3	0	0	13

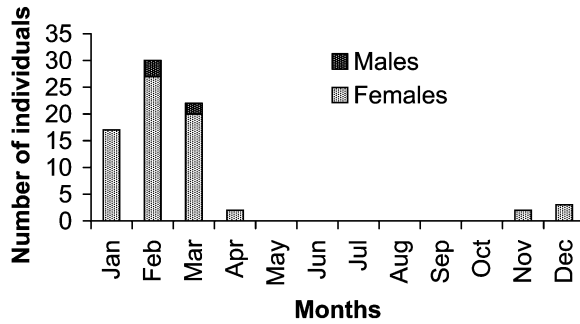


Figure 10. Temporal distribution of moults of adult *Eupalaestrus weijeberghi* under laboratory conditions.

Predation

In January and February we observed remains of *D. abderus* and other prey surrounding tarantula burrows at a distance between 5 and 40 cm from the entrance. During nocturnal observations in the field, tarantulas remained at the entrance of their burrows. Of 10 individuals of *E. weijeberghi* to which an adult *D. abderus* was offered near to the entrance of the burrow, nine were captured. The tarantula detected the prey up to a distance of 12 cm. Adult beetles were offered to two *A. suina* and both were captured. Both species of tarantula emerged from the burrow, put their anterior legs and palps on the prey, rotated it and bit it ventrally, they then dragged the prey back to the burrow. Frequently, beetles tried to resist being dragged into the burrow by extending their legs, but the tarantulas finally succeeded. Two individuals of *D. abderus* were offered to two *Plesiopelma longisternale* (Schiapelli and Gerschman 1964) (Theraphosidae) in their burrows (Melilla); they tried unsuccessfully to capture them.

In laboratory experiments, *D. abderus* were offered as prey to 81 *E. weijeberghi* and 70 *A. suina* without burrows. *E. weijeberghi* captured in 29.6% of the cases and *A. suina* in 44.3%. The spiders showed a pattern of capture similar to that observed in the field. Exceptionally, spiders bit the head or the articulations of the thorax with head or abdomen. There were frequent changes of the bite site to more caudal parts, avoiding horn and leg movements of the prey, which remained hanging. Spiders raised the body, extending their legs and lifting the prey from the substratum. Prey bitten by *E. weijeberghi* stopped moving after 45.3 min (SD=35.4; n=16); while prey bitten by *A. suina* stopped moving after 49.2 min (SD=21.9; n=25). At this point the spider laid silk on the substratum, deposited the prey on it and wrapped it with silk; the spider then took up the prey again and

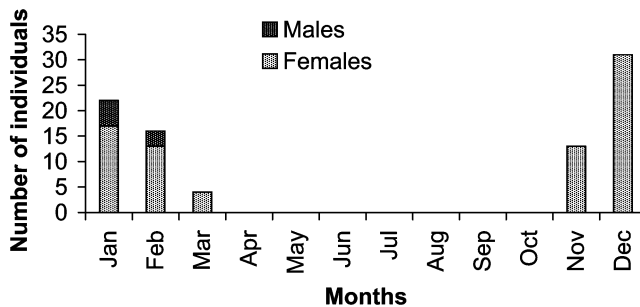


Figure 11. Temporal distribution of moults of adult *Acanthoscurria suina* under laboratory conditions.

continued feeding. During feeding the spiders did not walk. The duration of ingestion was 2.8 h (SD=1.0; $n=6$) in *A. suina* and 5.2 h (SD=1.6; $n=11$) in *E. weijenberghi*. Only the head and thorax cuticle of the prey remained intact.

In March, the mean weight of female *A. suina* was 4.60 g (SD=1.10; $n=101$) and that of female *E. weijenberghi* was 5.98 g (SD=1.81; $n=182$). The weight increment of *A. suina* was 0.32 g (SD=0.26; $n=29$) and of *E. weijenberghi* 0.18 g (SD=0.12; $n=24$) for each beetle ingested. Weight loss per day in *E. weijenberghi* was 0.032 g (SD=0.043) and in *A. suina* 0.043 g (SD=0.049), equivalent to a monthly loss of 1.0 g in *E. weijenberghi* and 1.3 g in *A. suina*. The individual mean weight of beetles offered was 0.902 g (SD=0.238; $n=105$). To maintain its weight *A. suina* must eat four beetles per month and *E. weijenberghi* must eat 5.5 beetles per month.

Defensive behaviours

At first disturbance made by the observer in the field, both tarantula species displayed different conspicuous and stereotyped defensive responses. These displays were in response to several stimuli: visual, tactile and vibrations on the substratum. *A. suina* raised the cephalothorax, anterior legs and palps beyond the vertical, exposing red ventral hairs; at that moment the spider opened the fangs, releasing poison droplets in some cases (Figure 12). The display of the spider was orientated towards the observer and frequently the spider increased the body angle when the observer approached it. The display was powered by vigorous movements of anterior legs, forwards and downwards. Rarely, the spider tried to bite during this defensive display. Conversely, *E. weijenberghi* raised the abdomen and sometimes legs IV vertically, and extended the spinnerets (Figure 13). Both species could maintain (freeze) this posture for several minutes.

In the field, all 206 *A. suina* and 414 *E. weijenberghi* (males, females and juveniles) performed these defensive displays. In the laboratory, *A. suina* retained the ability to display defensive responses while *E. weijenberghi* progressively lost the ability during captivity, a greater stimulation being necessary to provoke the defensive display.

These tarantulas also display other defensive behaviours such as rapid escape, release of urticating hairs and immobility with flexed legs (freezing). In cases where urticating hair



Figure 12. Defensive threat display of a male *Acanthoscurria suina* (photograph: Marcelo Casacuberta).



Figure 13. Defensive threat display of a female *Eupalaestrus weijenberghi*.

emission was observed, this behaviour occurred after the described defensive display if stimulation continued. In *E. weijenberghi* we observed that the defensive display was frequently combined with escape or urticating hair emission.

Discussion

Distribution, burrows and enemies

Our results showed that the beetle *D. abderus* as well as the tarantula *E. weijenberghi* are widely distributed in the whole country, while the other tarantula *A. suina* is not present in the northern region of Uruguay. The tarantulas and the beetle co-occurred in meadows, which constitute 90% of the surface of the country (Evia and Gudynas 2000). Other invertebrate predators are not frequent in this environment. The wide geographic and ecological overlap of the predators and the prey allow intensive trophic interactions during summer. The high density of burrows, especially at some sites, suggests a reduced territorial area for hunting. But burrows also represent a constraint for sexual encounters; in courtship male tarantulas have developed chemical reception and vibratory communication, and females also have developed vibratory signals which facilitate the encounter with the male (Mignone et al. 2001; Costa and Pérez-Miles 2002). Prentice (1992) first reported a similar behaviour in females of *Aphonopelma* spp.

The protection function of the burrow in open areas is increased by closing the entrance with silk and/or soil when tarantulas are most vulnerable (during moulting and egg-sac care period); this could also avoid attack from parasites. The burrow chamber could be interpreted as a diurnal living place for the spiders, considering that their main activity is performed at night. The chamber allows the spiders to turn, to moult, to construct the egg-sac, to perform first sperm induction and probably to complete the ingestion of prey. Remains of prey, exuviae and egg-sac covers are taken far away from the burrow, as is usual in sedentary animals. The chamber is not used for copulation, which takes place at the entrance of the burrow (Mignone et al. 2001; Costa and Pérez-Miles 2002).

E. weijenberghi burrows also have a narrow terminal tube which serves to protect the spider against predators, especially against *Pepsis* wasps (Costa et al. 2002). This is the only Uruguayan tarantula species which makes this terminal tube, which could reflect a strong

selective pressure on this spider by the wasp and other possible predators. *Acanthoscurria suina*, lacking that terminal tube, is vulnerable to wasp attack. The strict co-occurrence of *A. suina* with *E. weijenberghi* could help the former to decrease the probability of being found by the wasp. In hilly zones *A. suina* occurs also mixed with other theraphosid species such as *Plesiopelma longisternale* and *Grammostola mollicoma* (Ausserer 1875). The spatial and temporal overlapping of active males of both species would also contribute to predator saturation. In agreement with the suggested predation pressure of the wasp, we found more females and large juveniles of *A. suina* than *E. weijenberghi* in traps and walking in the same period that wasps occur. This suggests that the main defensive tactic of the first species against the wasp is to escape from the burrow (Costa et al. unpublished). The observed occlusion of burrow entrance with silk and soil could not be interpreted as a defence against the wasp because we observed that the wasp can easily perforate the seal. Occlusion is probably useful for maintaining microclimatic conditions inside the burrow.

The size of the burrow entrance seems to be a good estimator of spider size and development. In the field, large burrows were more numerous than small ones, which could evidence the predominance of adults over juveniles in natural populations. Taking into account the numerous offspring in both species of tarantulas, we may conclude that an early mortality of juveniles takes place. This assumption, combined with the long life of adult females, could explain adult predominance. Conversely, large sizes in these species could restrict competition with other spiders and in general other predators in meadows. This strategy seems to be the rule in theraphosids, and is usually related to stable environments.

Phenology and reproduction

The abrupt peak of adult beetle occurrence immediately before the sexual activity period of the tarantulas could contribute an additional food source, facilitating spider moulting. Efficient predation by these spiders on adult beetles was evidenced both in the field and under laboratory conditions. With this additional food source females would recover from the cost of oviposition and a long period of egg-sac care; after this they would moult, removing old sperm by spermathecae moulting. At this time, penultimate males with increased food would reach adulthood and leave their burrows to seek the females. We have some evidence that males could perform their first sperm induction before leaving their burrows.

Walking males occur abundantly during March and April; this seems to be synchronized with meteorological conditions such as cloudy days, high temperature and low atmospheric pressure ('heavy days'). Male occurrence coincided with moderate rainfall. It is remarkable that walking males are also diurnal. Males of both species are relatively larger than females, contradicting the usual trend in spiders. Large size and especially long legs could favour male locomotion in open fields during this season. Large-sized males could also be a strategy to reduce predation, in combination with their conspicuous defensive behaviours (Pérez-Miles et al. 1999).

Considering that adult males live for only a short period while adult females live several years, sex ratio is strongly biased towards females. As females can mate several times, the copulations are brief and populations have high density, we conclude that males must copulate intensively (numerous mates in a brief period). Male competition would then be limited to female encounter, and consequently direct male–male conflict seems to be infrequent and we never observed it. Adult males do not feed, or feed poorly, under natural

conditions but make a great effort in walking and mating. Consequently, males are scarce and show body deterioration, or die, in April. A similar observation was made by Janowsky-Bell and Horner (1999) in *Aphonopelma hentzi* (Girard 1852). In the laboratory where males are confined in small containers and are fed, they may live more than twice as long as males under natural conditions.

Summarizing, the reproductive strategies for both species would be as follows: females store sperm for about 7–9 months; oviposition takes place mainly in November, caring for the egg-sac lasts about 2.5 months. Coincidentally, an *Acanthoscurria suina* with egg-sac was observed in the field on 7 December (C. Toscano-Gadea, personal observation 2002). Spiderlings would emerge mainly in February, females and penultimate males would then moult, and the mating period would take place (end of February and beginning of March). Laboratory conditions probably affected the moulting periods more in the case of *A. suina* than in *E. weijenberghi*, while the egg-sac care period remained unchanged for both species.

Predation

Field and laboratory data confirm that both species efficiently capture the beetle. That is not the case with *P. longisternale*, which is slightly smaller. Tarantula and prey populations overlap in spatial and temporal dimensions. The predators can detect the beetle by vibrations transmitted by the soil and vegetation. Tarantulas are capable of preying on other prey but this beetle seems to be an additional food source contributing to spider nutrition in a key reproductive period.

The weight loss of a confined female was 1.15 g per month. To maintain their weight, and considering prey yield, the spider could eat four to five beetles per month. Under natural conditions weight loss must be higher due to the energy costs of locomotion, burrowing and other activities in larger areas. Considering a moderate increment of spider weight, a potential consumption of 10 beetles per month seems plausible. In Uruguay, meadows seriously damaged by the beetle larvae showed densities of 700 000 larvae per hectare (Morey and Alzugaray 1982). In a scenario with the highest density of tarantulas and a unique prey, a potential consumption of 65 000 beetles per hectare per month is also plausible.

Threat displays

The initial defensive display of both tarantula species seems to be directed to large predators with good vision, considering the conspicuous characteristics of the displays as well as the warning colours exposed by the spiders. In the field, the main potential predators are birds such as crested caracara (*Polyborus plancus*), chimango caracara (*Milvago chimango*), burrowing owls (*Speotyto cunicularia grallaria* and *S. partridge*), greater rhea (*Rhea americana*), Southern screamer (*Chauna torquata*), red-legged seriema (*Cariama cristata*), Southern lapwing (*Vanellus chilensis*) or guira cuckoo (*Guira guira*); mammals such as skunk (*Conepatus chinga*) and ferret (*Galictis cuja*); and large toads and lizards such as the black tegu (*Tupinambis merianae*). The *A. suina* threat, although involving display of chelicerae, is considered a ritualized behaviour because we never observed real attempts to bite. The occurrence of poison drops on the chelicerae during this display could also represent a chemical advertisement, mainly for mammals.

Defensive displays of both species look similar but involve opposite body regions (Figures 12, 13). This fact suggests that these behaviours are independent acquisitions of the

species. These behaviours are frequent in the theraphosids; front threat is widespread in the family and other spiders while abdominal display (sometimes related with urticating hair emission) is usual in New World Theraphosidae and probably a synapomorphy of Aviculariinae + Theraphosinae (Pérez-Miles et al. 1996).

Tarantulas, when discovered, perform these defensive displays instead of escaping probably because in open areas it is difficult to find shelter for hiding. The posterior occurrence of urticating hair emission in relation to visual defensive displays could be due to its major costs (hairs are lost and are not recovered until the next moult).

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