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On the mating and laying sites of *Uromenus brevicollis* ssp. *insularis* in Corsica (Ensifera, Tettigoniidae)

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Abstract

Mating and laying sites of *Uromenus brevicollis insularis*, a Cyrno-Sardininian micro-endemic species, are described from observations conducted at night in several Corsican localities. *Asphodelus ramosus* was found to be a key host species as both mating and oviposition of this insect take place mainly on the erect dry stems of the plant. Some aspects of the meeting of the sexes are assessed: male stridulation does not appear to play an important role. The females lay their eggs, creating vertical lines in the stem by chewing regularly spaced holes containing nearly 3 eggs per hole. One to three laying lines can be observed on a single stem. *Ferula communis* is frequently used as an alternative laying site when *A. ramosus* is absent or rare, but in this case, the eggs can be attacked by woodpeckers (*Dendrocopos* sp.) or parasitized by Hymenoptera.

Résumé

Les sites d'accouplement et de ponte d'*Uromenus brevicollis insularis*, micro-endémique cyrno-sarde, sont décrits à partir d'observations nocturnes de terrain dans plusieurs localités corses. *Asphodelus ramosus* est une espèce clé dans la mesure où ses tiges sèches dressées sont le lieu principal de ces deux activités de reproduction. Les modalités de la rencontre des sexes sont décrites et il ne semble pas que la stridulation des mâles joue un rôle prépondérant. Les femelles pondent selon des lignes verticales sur la plante en creusant des trous régulièrement espacés, contenant en moyenne près de trois œufs chacun. On peut rencontrer de une à trois rangées de ponte sur une tige. Nous avons pu observer que les pontes déposées dans *Ferula communis*, espèce qui semble être particulièrement recherchée en cas d'absence ou faible densité de l'asphodèle, peuvent subir des attaques de pic (*Dendrocopos* sp.) ou encore d'hyménoptères parasitoïdes, notamment.

Key words

Uromenus brevicollis ssp. *insularis*, Asphodels, mating site, laying site

Introduction

The reproductive biology of Tettigoniidae (Orthoptera) has been actively studied, with a focus on acoustic communication involved in mate pairing (see for example Heller 1988, Robinson 1990, Bailey 1991 and Gerhardt & Huber 2002, reviewed in Gwynne 2001) and on the spermatophylax, transferred by the male and consumed by the female at the end or after copulation; the spermatophylax is interpreted as a nuptial gift or a factor increasing sperm transfer (Gwynne 1995; Vahed 1997, 1998; reviewed in Gwynne 2001). Choice of site for mating and laying has been less investigated because field observations by night are needed. In these conditions, quantitative approaches are facilitated when numerous individuals can be observed in a short period during the night and in a limited area.

According to Gwynne (2001) the probable ancestral oviposition site for the family Tettigoniidae is in soil. This is certainly true for most Spanish and French Bradyporinae (Vahed, pers. comm.), *e.g.*, in *Ephippiger vitium* in Pyrénées-Orientales (France) (Peyerimhoff 1908). Thus it is of particular interest to describe the oviposition habit in plant stems by a species belonging to *Uromenus*, a genus close to *Ephippiger*.

Peyerimhoff (1908) gave a detailed report of the laying of the Algerian subspecies of *U.* (*Bolivarius*) *brevicollis* (Fisher 1853). He described how the female attacks the bark of *Asphodelus aestivus* (Asphodelaceae) with her mandibles, before introducing the ovipositor 2 to 3 times in the same hole. He also noticed that the laying begins at the close of the day.

However, to our knowledge there is no information about the laying habit of the subspecies endemic to Corsica and Sardinia, *Uromenus* (*Bolivarius*) *brevicollis* ssp *insularis* Chopard, 1923. Interestingly, both laying and mating activities of this subspecies take place on erect dry stems of another species of asphodel (*Asphodelus ramosus* L.). This species, blooming in spring, has a single stem per plant, ramified at the top, and is generally found in prairies, fallow lands and erms (a degradation stage of scrub and garrigue in the west Mediterranean area, see Diaz Lifante 1996). There is no trophic interest in the climbing behavior, as all the parts of the plant summit are dried when the insects are in the reproductive season.

The aim of this paper is to test if the subspecies present in Corsica shows the same behavior as *U. b. brevicollis* and if the dry stems of other plants could serve as laying sites. In addition, as the matings were also found to occur mainly on asphodel stems, we assessed some factors that determine the meeting of the sexes. Finally, we estimated the risk of damage to the eggs, by bird predation and insect parasitism, when laid in the stems of different plant species.

Material and methods

Mating sites. — Three sites were studied: the beach of San Pellegrino (Penta-Di-Casinca, Haute-Corse, on 19 July 2006, between 9:00 and 9:30 PM), the prairies of Biaggiola (Porto-Vecchio, Corse-du-Sud, on 22 July 2006, between 11:40 and midnight) and the plateau of Maora (Bonifacio, Corse-du-Sud, on 24 July 2006, between 9: 50 and 10:25 PM). A particularity of the San Pellegrino station is

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Fig. 1. A. Mating of *Uromenus brevicollis*. The male, which has produced the spermatophore, is upside down, and hangs under the female, the head of which is oriented upward. B. More detailed view (photos E. Boitier).

that asphodels were spaced over tens of meters, in contrast to the other stations, where the mean distance between stems was rather regular and ranged from 0.70 to 2 m. More than 20 asphodel stems were chosen at random on which to count the males and females, climbing up the stems or waiting for mating at the inflorescence summit. Only insects that had left the plant base and begun to climb or reached the top were counted. No confusion was possible with laying females. On the insect's arrival at the inflorescence its head is oriented upward, but it usually then positions itself with the head downward.

Laying sites and fecundity.— Six females found at the summits of asphodel stems were collected from Baggiola at night and dissected the following morning. Brown mature eggs and yellow immature eggs (size smaller or equal to mature ones) were counted.

Asphodel stems were collected at San Pellegrino (Penta-Di-Casinca, Haute-Corse, on 19 July 2006), at Pertusato (Bonifacio, Corse-du-Sud, on 21 July 2006) and at Biaggiola (Porto-Vecchio, Corse-du-Sud, on 22 July 2006). Two stems found at Pertusato were split lengthwise in order to count the number of eggs laid in each hole. We compared the pattern of laying in 30 stems of asphodels (*A. ramosus*) and the same in ferulas (*Ferula communis*, Apiaceae) from samples taken at Bocca di Sant'Alparte, near the crossroad to Rovani (Coggia, Corse-du-Sud, on 31 July 2006).

Statistics.— If the reproductive individuals climb at random on the stems, we expect the number of stems bearing *i*= 0, 1, 2 or 3 individuals, to follow the Poisson probability distribution

$$p(i) = e^{-m}\, m^i/i!$$

where m is the mean number of insect occurrences per stem. The distribution of the stem numbers bearing *i* individuals under a null hypothesis of random occurrrences is calculated by:

$$\text{No. individuals per stem} = p(i) \times \text{total number of stems.}$$

Various combinations of the numbers of males and females per stem can also be compared to a random distribution. In this case, the expected number of males and females per stem would be:

$$p(i \text{ males}) \times p(j \text{ females}) \times \text{total number of stems.}$$

A Chi-square goodness-of-fit was used to test these distributions.

The chance of a male meeting a female was calculated by taking into account the observed number of individuals climbing (individual i) and the probability of success of each one (proba success i), as follows:

$$\frac{\Sigma \text{ individual i} \times \text{proba success i}}{\Sigma \text{ individual i}}$$

We compared the numbers of eggs per hole between *Asphodel* stems and the number of holes between Asphodel *versus Ferula* stems by ANOVAs with the use of PAST vers. 1.48 (Hammer *et al*. 2001). The means are given with standard deviation.

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Table 1. Distribution of individual numbers per stem. In the case of the San Pellegrino station, the observed and expected numbers of stems corresponding to 2 and 3 males per stem have been pooled to avoid an expected value less than 1.

	Observed number of stems	Expected number of stems	Chi²		Observed number of stems	Expected number of stems	Chi²
San Pellegrino							
M=0	13	12.51	0.019	F=0	2	5.48	2.208
M=1	7	7.62	0.050	F=1	11	7.86	1.255
M=2 or 3	3	2.79	0.016	F=2	8	5.64	0.989
				F=3	2	2.67	0.180
	Total = 23		0.085 N.S.		Total = 23		4.632 N.S.
Biaggiola							
M=0	17	19.13	0.236	F=0	10	13.70	1.001
M=1	14	10.43	1.220	F=1	18	12.04	2.946
M=2	2	2.85	0.251	F=2	4	5.29	0.315
				F=3	1	1.55	0.195
	Total = 33		1.707 N.S.		Total = 33		4.458 N.S.

Abbreviations: M=i means i males observed on a stem; F=j means j females observed on a stem.

Results

Mating.— The male hangs under the female and holds onto her ovipositor with his first two pairs of legs (Fig. 1), as described for *U. rugosicollis* (Rigalleau 1936, Vahed 1997). This position is also found in other Ensifera, as in many Tettigoniidae (Chopard 1938).

For the San Pellegrino site, 23 stems were considered and the mean numbers per stem were 0.61 males and 1.43 females. Asphodels (*A. ramosus*) were the only plant species where mating was observed taking place. For the Biaggiola site, among the 33 stems examined, the respective means per stem were 0.54 males and 0.88 females. At this site, mating was observed not only on asphodels but also on several other herbaceous species, characterized by a single erect dry stem: *Dipsacus fullonum* (Dipsacaceae), *Onopordum illyricum*, *Carthamus lanatus*, and *Cirsium vulgare* (Compositae). At other sites *Silybum marianum* (Compositae) was also found to be a suitable substratum for mating.

For each site and for each sex, the distribution appeared to be at random: calculated chi-square were less than threshold values (Table 1). However, it should be pointed out that the female distribution follows the Poisson distribution less closely than that of the male, mainly due to many of the observed stems bearing a single female.

It could be hypothesised that females are present having been attracted by the stridulation of a male. In the case of the San Pellegrino population, we compared the co-occurence distributions of males and females with random distributions from all possible combinations (0 to 3 males × 0 to 3 females). It appears that the presence of j females on a stem is independent of the male number as the calculated Chi square is 7.25 (risk > 40 %). In the case of the Biaggiola population, fewer combinations were found (0 to 2 males × 0 to 3 females). The calculated chi-square is 34.83, so the deviation from the null hypothesis is highly significant (risk = $1.6\ 10^{-6}$), mainly by reason of an excess of stems with an insect of only one sex.

It could be objected that an absence of stems bearing no individual could result from a sampling bias. We simulated several situations where 10, 20, or 30 stems bearing no insect were "forgotten". The chi-square risks obtained were respectively 0.0009, 0.012, and 0.0066, and the deviation from random distribution was then mainly due to an absence of stems with 2 to 3 females and no male.

We can deduce that in the San Pellegrino population, where asphodel stems are rare, the individuals of both sexes climb onto the stems at random, in contrast to the Biaggiola population, where the stem density is high and many individuals climb on a stem and stay alone.

We obtained preliminary observations supporting the hypothesis that females climb slightly later than males: on the Maora plateau (Bonifacio, Corse-du-Sud, on 30 July 2007, at 9:50 PM), a small population showed the following numbers: 3 males and 1 female already at the summit of asphodel stems, and 1 male and 4 females climbing. However, the time available for observations within a night is limited: 10 min later, no individual was seen climbing. The other sites also gave only a short period for workable study.

Fecundity and laying.— The mean number of mature eggs per female was 38.17 ± 19.81 (n=6). The brown mature eggs were approximately 5 mm long × 1.5 mm wide. We also observed between 8 and 13 yellow (immature) eggs per female developing for a future laying.

When a female climbs on a stem, she progresses along a vertical line and behaves in the same way as described for *Uromenus rugosicollis* (Chopard 1951). While she introduces her ovipositor into a hole she has made in the stem, she bites the cuticle ahead with her mandibles to prepare the next hole. As a result, the holes follow each other very regularly and their distance corresponds uniformly to the space between mandibles and the base of ovipositor (figs 2A, B), *i.e.*, about 1.3 cm. If the bark is too tough, she moves farther forward, but generally along the same vertical path. In this way, one can count the number of females that have laid in an asphodel stem and the number of holes made during a single laying session by a female.

A mean number of 2.91 and 2.50 eggs per hole was found in two stems collected at Pertusato. We verified their homogeneity (ANOVA, $Fr_{1,39} = 1.39$, $p > 0.20$). Taken together, a hole corresponds to a mean of 2.73 ± 1.12 eggs.

Of the 20 stems collected at Pertusato, Casaglione and San Pellegrino, one to three laying lines were observed per stem (a mean of 1.71 ± 0.85). Among 30 laying lines studied, we counted 13.77 ± 6.3 holes per line, resulting in 37.61 ± 17.21 eggs per laying session;

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Fig. 2. A. Holes dug by female *Uromenus brevicollis insularis* in a dry stem of *Asphodelus ramosus*. The space between the successive holes is about 1.3 cm. B. Female *U. b. insularis* introducing her ovipositor and at the same time digging the next hole with her mandibles (photos E. Boitier).

this is close to the number recorded in the abdomen of dissected females. The maximum number of holes dug during an oviposition bout was 26, corresponding to about 71 eggs. Again, there is a good match with the maximum observed in the female collected at Ponte-Leccia. Asphodels thus play a major role in the reproduction biology of *U. b. insularis* since we recorded a mean number of 64 ± 32 eggs per stem at the sites where the insect is present.

However, other plant species can be used as laying sites, whether the asphodel is present or not. At San Pellegrino for example, we found a few egg-bearing stems of the introduced reed *Cortaderia selloana* (Schultes & Schultes *fil.*) Ascherson & Graebner, which was abundant at this site. At the Coggia locality, *Ferula communis* was also a laying site for the insect. Among 30 stems of asphodels and of ferulas chosen at random, there was a mean number of holes per stem of 7.9 and 15.47 respectively, showing a strong preference for ferula (ANOVA, $Fr_{1,58} = 5.55$, $p = 0.022$). However, ferula bark is tougher, perhaps explaining the more irregularly spaced holes on these hosts.

Predation and parasitism of eggs.— At Coggia, 2 to 3 ferulas of 30 sampled, showed attack traces from woodpeckers (*Dendrocopos* sp.) as evidenced by claw and beak marks at the level of holes previously dug by *U. brevicollis ssp. insularis* (Fig. 3). This tall Apiaceae has sufficiently rigid stems to sustain a bird's weight. No observation of this kind was ever made on asphodel stems in all the study sites on Corsica.

At the same Coggia site, minute Scelionidae (Hymenopterans) were observed at the entrance of holes dug by *U. b. insularis* on ferula stems (Fig. 4), but never on asphodel stems. We hypothesize that the hole made by the bushcricket on the more rigid ferula stem remains more open, which would facilitate the access of the parasitoid. Peyerimhoff (1908) reported the species *Catoteleia peyerimhoffi* Kieffer, belonging to the subfamily Scelioninae, parasiting the eggs of *U. brevicollis brevicollis* in Algeria.

Discussion

A clear preference for certain mating and oviposition sites by *U. b. insularis* makes quantitative studies very easy in the field, despite their nocturnal activity. In contrast, reproductive biology studies of numerous other nocturnal Tettigoniidae species need to be conducted with lab-reared individuals, as for *Meconema* (Vahed 1996) or *Leptophyes* (Vahed & Gilbert 1997).

When a male is climbing, he has little chance of finding a female at the summit of the stem, since the males are likely the first. This complies with their quite random distribution on stems. What,

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Fig. 3. Traces of attack on *Uromenus brevicollis insularis* laying sites by a woodpecker (photo D. Petit).



Fig. 4. Two females of a parasitoid scelionid wasp inspecting holes before laying in the eggs of *U. brevicollis ssp. insularis* (photo E. Boitier).

therefore, is the chance that a given male will meet a female on a given night? If the observed numbers are taken into account, there is about a 91% chance of meeting on a given night at the San Pellegrino site and 52 % at the Biaggiola site. If the reproductive season lasts approximately 10 d, a male therefore has a high probability of mating.

In contrast, when a female climbs onto a stem, she has only a 41 % chance of meeting a male during a night at San Pellegrino and 32 % at Biaggiola. These differences are due to a strong deviation from a balanced sex ratio, to the advantage of the females. This deviation could be related to a sexual refractory period, certainly longer in males than in females (Chopard 1938). In *Steropleurus stali* for example, the refractory period for females is around 4.8 d (Bateman 1997, Vahed 1998).

It is very unlikely that stridulation of males at the summit of the stem plays a role in attracting females, because in the Biaggiola population we observed a high degree of stems bearing one female and no male. Calling songs were heard in bushes surrounding the asphodels, suggesting that an aggregation of males takes place in the vicinity of mating sites. The bushes may represent an environment safer from predation for the production of calling songs (Alexander *et al.* 1995), but this needs to be tested. As the meeting of the sexes seems to occur at random, there is a temporal and spatial separation between calling and mating, as in some Gryllidae (Zuk & Simmons 1995).

Peyerhimhoff (1908) also mentioned *Ferula* sp. as a suitable plant for *U. b. brevicollis* in Algeria, but found in addition another Apiaceae, *Thapsia villosa*, and a Compositae, *Cirsium scabrum*. To our knowledge, the plant species used by the subspecies *U. b. ibericus* Schroeter & Pfau, 1987 (in Spain) and *U. b. trimacriae* La Greca 1967 (in Sicilia) have not been identified.

Interestingly, *U. rugosicollis* (Serville, 1838), a species close to *U. brevicollis*, has a related oviposition behavior, digging regular holes in dry stems (Chopard 1951), but this is uncommon in Bradyporinae which usually lay in soil. In contrast, many Tettigoniinae in Europe lay their eggs in the pith of stems, *e.g.*, *Metrioptera roeseli*, *Pholidoptera griseoaptera*, *Platycleis albopunctata* or *P. tessellata* (Ingrisch & Köhler 1998, Gwynne 2001). This behavior likely evolved independently in the different genera, but this should be tested with a robust cladogram of the subfamily.

The number of plant species suitable for the shelter of eggs is limited, as the bark must not be too tough and the pith must be spongy: dry stems of asphodel perfectly fill both requirements. Moreover, asphodels appear to afford good protection of eggs against predation and parasitism, as long as the stem is erect. It would be interesting to examine the situation in spring, when the

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Table 2. Distribution of males and females per stem. Each column corresponds to the number of stems bearing 0 to 2-3 females; the fist line refers to the cases where no male occurred and the second one when there was at least one male.

San Pellegrino					
	M/F	0	1	2	3
Observed	0	1	7	5	0
number of stems	1+2+3	1	4	3	2
	M/F	0	1	2	3
Expected	0	2.98	4.28	3.07	1.47
number of stems	1+2+3	2.48	3.56	2.55	1.22
Chi² test	7.25 N.S.				

Biaggiola				
	M/F	0	1	2+3
Observed	0	0	17	0
number of stems	1+2	10	1	5
	M/F	0	1	2+3
Expected	0	7.94	6.98	3.97
number of stems	1+2	5.51	4.85	2.75
Chi² test	34.83	$p=1.6\times10^{-6}$		

young instars leave the holes to reach the ground. The success of hatching in asphodels and ferulas remains to be compared.

Conclusions

The plant *A. ramosus* appears to play a key role in this insect's reproduction, as mating and laying activities take place mainly on its dry stems during July. We recorded other plant species where matings occurred: all were herbaceous, erect, and nonbushy, with a principal axis higher than 30 cm, e.g., *Dipsacus* (Dipsacaceae) and different thistles (Compositae). Given the relatively high pasture pressure in the scrub and garrigue formations in Corsica, asphodel, an indicator of the ultimate degradation stage of these habitats (Braun-Blanquet, 1964), is a very widespread species that favors the high incidence of *U. b. insularis* populations.

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References

Alexander R.D., Marshall D.C., Cooley J.R. 1997. Evolutionary perspectives on insect mating, pp 4-31. In: Crespi B.J., Choe J.C., (Eds) the Evolution of Mating Systems in Insects and Arachnids. Cambridge Univ. Press.

Bailey W. J. 1991. Acoustic behaviour of insects. Chapman and Hall, London.

Bateman P. 1997. Operational sex ratio, female competition and mate choice in the ephippigerine bushcricket *Steropleurus stali* Bolivar. Journal of Orthoptera Research 6: 101-104.

Braun-Blanquet J. 1964. Planzensoziologie Grundzuge der Vegetationskunde. 3ème éd. Springer,Vienne-New- York, 865 pp.

Chopard L. 1938. La biologie des Orthoptères. Encyclopédie Entomologique. Lechevalier ed., Paris, 540 pp.

Chopard L. 1951. Orthoptéroïdes, Faune de France 56. Lechevalier ed., Paris, 359 pp.

Diaz Lifante Z. 1996. Revisión del género *Asphodelus* L. (Asphodelaceae) en el Mediterráneo Occidental. Boissiera, Genève 52: 189 p.

Gerhardt H. C., Huber F. 2002. Acoustic Communication in Insects and Anurans. Common Problems and Diverse Solutions. The University of Chicago Press. Chicago and London. 531 pp.

Gwynne D.T. 1995. The evolution of edible sperm sacs and other forms of courtship feeding in cricket, katydids and their kins. In: Crespi B.J., Choe J.C., (Eds) the Evolution of Mating Systems in Insects and Arachnids. Cambridge Univ. Press. .

Gwynne D.T. 2001. Katydids and Bush-crickets, Reproductive Behavior and Evolution of the Tettigoniidae. Cornell University Press, New York.

Hammer Ø., Harper D.A.T., Ryan P.D. 2001. PAST: Palaeontological Statistics software package for education and data analysis. Palaeontologica electronica 4(1): 9 pp., http://folk.uio.no/ohammer/past

Heller K.G. 1988. Ökologie in Forschung und Anwendung. Verlag (Josef Margraf), Weikersheim: 1-174.

Ingrish, S., Köhler, G. 1998. Die Heuschrecken Mittleuropas. Wesrarp Wissenschaften, Die Neue Brehm-Bücherei 629, Mageburg, Germany.

Peyerimhoff (De) P. 1908. Sur l'éclosion et la ponte d'*Ephippiger confusus* Finot (Orthoptères). Annales de la Société entomologique de France: 505-516.

Rigalleau L. 1936. Observations sur les Ephippigères. Revue de Zoologie Agricole et Appliquée 35: 113-182.

Robinson D. 1990. Acoustic communication between the sexes in bushcrickets. In: Bailey W.J., Rentz D.C.F. (Eds), The Tettigoniidae, Biology, Systematics and Evolution, Crawford House Press, Bathurst (Australia): 112-129.

Vahed K. 1996. Prolonged copulation in oak bushcrickets (Tettigoniidae: Meconematinae: *Meconema thalassinum* and *M. meridionale*). Journal of Orthoptera Research 5: 199-204.

Vahed K. 1997. Copulation and spermatophores in the Ephippigerinae (Orthoptera: Tettigoniidae): prolonged copulation is associated with a smaller nuptial gift in *Uromenus rugosicollis* Serville. Journal of Orthoptera Research 6: 83-89.

Vahed K. 1998. The function of nuptial feeding in insects: a review of empirical studies. Biological Reviews 73: 43-78.

Vahed K., Gilbert F. S. 1997. No effect of nuptial gift consumption on female reproductive output in the bushcricket *Leptophyes laticauda* Friv. Ecological Entomology, 22: 479-482.

Vahed K. 1998. Sperm precedence and the potential of the nuptial gift to function as paternal investment in the Tettigoniid *Steropleurus stali* Bolivar (Orthoptera: tettigoniidae: Ephippigerinae). Journal of Orthoptera Research 7: 223-226.

Zuk M., Simmons L.W. 1995. Reproductive strategies of the crickets (Orthoptera, Gryllidae). In: Crespi B.J., Choe J.C., (Eds) the Evolution of Mating Systems in Insects and Arachnids. Cambridge Univ. Press.

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