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Diel movement pattern and microhabitat choice in males and females of a flightless phytophagous bush-cricket (Orthoptera: Tettigonioidea: *Poecilimon veluchianus*)

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Abstract

Males and females of a species typically differ in some characters. Most of these traits are connected to reproduction, e.g. finding mates or laying eggs. However, also basic parts of the behaviour are affected. For example, both males and females move in their habitat, but in some species, they differ in this activity. Here we demonstrate that the increased mobility of females compared to males in the bush-cricket *Poecilimon veluchianus* results from a high female mobility during oviposition in the early night hours. For day resting, females of the nightly active species select the same microhabitats as males, but with different frequencies. About half of the females sit on broadleaved plants (plane), where the other half, but nearly all males, stay on broom, where most animals are at night. The difference may be based on predator avoidance and not on thermal preference.

Zusammenfassung

Männchen und Weibchen einer Art unterscheiden sich normalerweise in bestimmten Merkmalen und Verhaltensweisen. Diese Unterschiede betreffen meistens das Fortpflanzungsverhalten im weitesten Sinn, wie das Auffinden von Paarungspartnern oder die Eiablage. Sie wirken sich jedoch auch auf ganz grundlegende Bereiche des Verhaltens aus. So differieren Männchen und Weibchen mancher Heuschreckenarten in ihrer Mobilität. In dieser Arbeit zeigen wir, dass die beschriebene höhere Mobilität der Weibchen im Vergleich zu den Männchen bei der Laubheuschrecke *Poecilimon veluchianus* im Wesentlichen auf dem Verhalten während einer bestimmten Tageszeit beruht, auf der Eiablage am frühen Abend. Ein anderer quantitativer Unterschied zwischen den Geschlechtern dieser nachtaktiven Art betrifft die Wahl des Tagesruheplatzes. Tagsüber ist etwa die Hälfte der Weibchen auf breitblättrigen Pflanzen (Platanen) anzutreffen, während der andere Teil, wie auch fast alle Männchen, in Ginsterbüschen sitzen. Für diesen Unterschied ist unserer Ansicht nach ein besserer Schutz gegen Fressfeinde und nicht die Wahl eines temperaturbegünstigten Aufenthaltsorts verantwortlich.

Introduction

Like all living organisms, Orthoptera have to successfully manage two tasks, to survive and to reproduce. To do this, males and females of one and the same species differ in many aspects (although they share most of their genes). Both sexes differ often in morphology. If in this case differences are found beyond that of sexual organs, it is called sexual dimorphism (respectively secondary sexual

characteristics). Even more common may be differences in behaviour (sometimes called tertiary sexual characteristics). In bush-crickets, for example, females possess ovipositors and place their eggs at special places in the habitat, whereas males have modified wings and produce species-specific calling songs. Much less, however, is known about sex-specific differences which relate to behavioural traits common to both sexes. There are a few studies of selected species in different groups of animals, but studies in Orthoptera seem to be rare with the notable exceptions of some studies on Tetrigidae species (e.g., AHNESJÖ & FORSMAN 2006, HOCHKIRCH et al. 2007).

Comparatively well-studied concerning sex-specific differences are movement patterns in Orthoptera. Mobility (see INGRISCH & KÖHLER 1998 for the broad usage of this term) on a large scale is important to understand the spreading of species, with interesting cases like flightless females and long-winged males as e.g. in Acrometopini (RAGGE 1960, HEMP et al. 2018) and the Australian *Tympanophora* (RENTZ 2001). On a small scale also sex-specific differences are to be expected, for example, due to phonotactic approaches of females to males whose songs can be heard from distances of more than 1500 m (in Pneumoridae; VAN STAADEN & RÖMER 1997). In general, although there are not very many data (see review for Central Europe in INGRISCH & KÖHLER 1998), sometimes significant differences between the sexes in mobility have been found (e.g., REICH 1990, HELLER 1992, HARTMANN & REICH 1998, LOCK & DURWAEL 1999), but not always (HELLER 1992, KINDVALL 1999, DIEKÖTTER et al. 2005, WEYER et al. 2012). However, movement patterns can be studied on different time scales, mostly concerning distances between observations of an animal on different days or as lifetime activity ranges. In an earlier study (HELLER 1992) we got indications for sex-specific differences in mobility when studied over a three-day interval. To understand the reasons behind this pattern we here measure the displacement of individually marked animals on a finer scale, every four hours.

Different motility in males and females may also easily result in preferences of different microhabitats, as soon as the requirements of the sexes are slightly different. WALTER (1994) showed that the females of the tettigoniid *Platycleis albopunctata* were found at more open areas than the males. In *Tetrix ceperoi,* HOCHKIRCH et al. (2007) observed the opposite; the females spent more time resting and feeding in the vegetation than the males. The authors (HOCHKIRCH et al. 2007) review and discuss the various hypotheses behind this "intersexual niche segregation".

Poecilimon v. veluchianus, the species we studied, is a plant-feeding bush-cricket restricted to Central Greece (LEHMANN 1998, WILLEMSE et al. 2018). This species has served as evolutionary model species (summarized by HELLER 1998) and continues to be extensively studied for speciation and body size evolution (EWELEIT & REINHOLD 2014, EWELEIT et al. 2015), for social aspects of acoustic communication (ANICHINI et al. 2019), predation by acoustic orienting parasitoids (LEHMANN & HELLER 1998) and notably for sperm competition (ACHMANN et al. 1992), and spermatophore evolution (summarized in HELLER 1998, newer work REINHOLD 1999, REINHOLD & RAMM 2013, KOSCHMIEDER et al. 2018). It is not strictly dimorphic in colouration, but males are typically colourful with many black markings, whereas females

are often uniform green (Fig. 1 C, D). There are, however, gradual transitions including changes with age (from green to contrasting) and one can rarely also find green males and strikingly contrastingly coloured females. Similar differences in body colouration (different degrees of melanism) are found in many Barbitistini (see e.g., HARTLEY 1986, KUYUCU et al. 2018) and may depend on population density with males and females probably sometimes having different thresholds. The difference in colouration may be a first but strong clue for different microhabitat choice. Using our observational data, we show that indeed the sexes behave differently although the reasons may differ from other species studied.

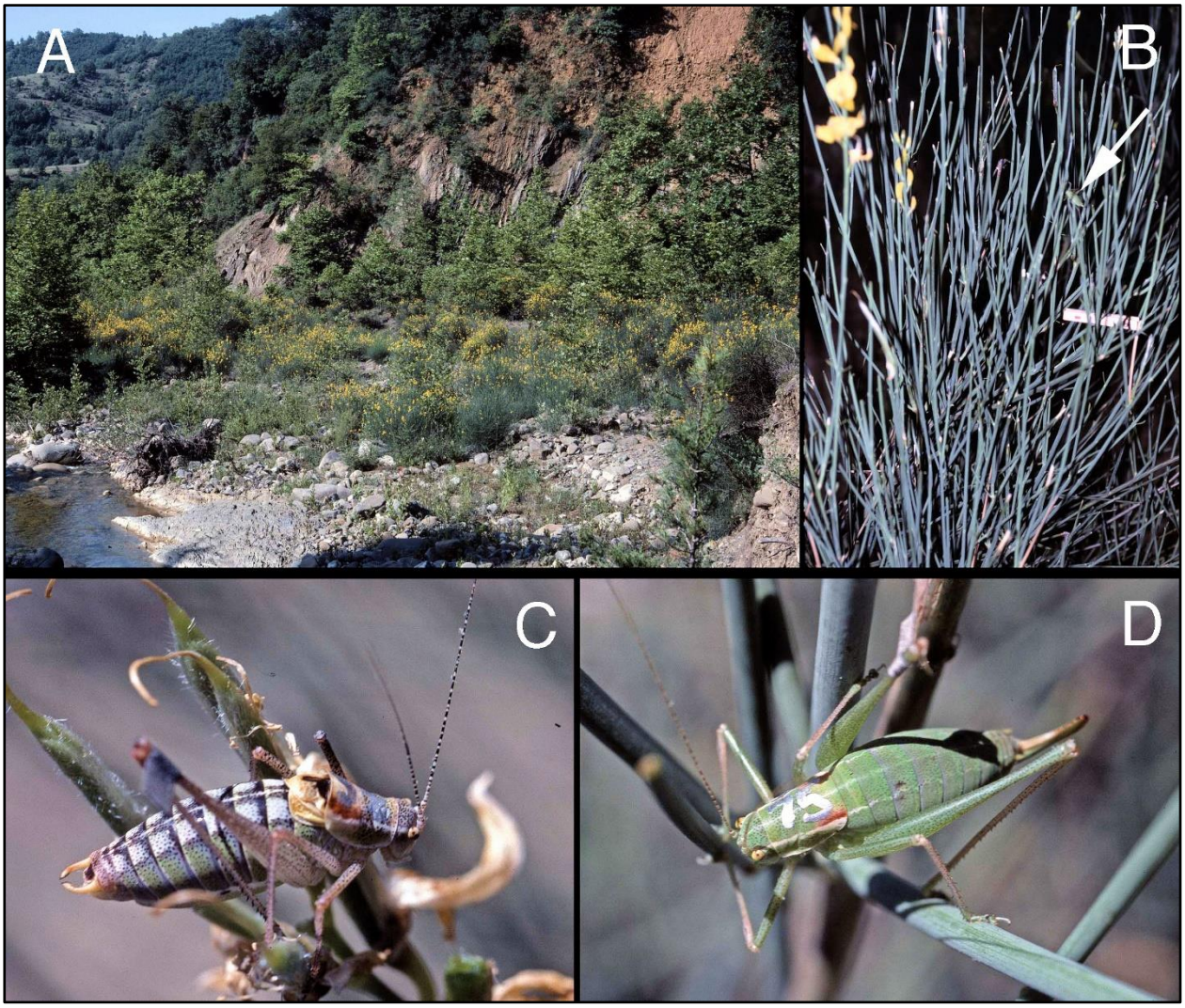

Fig. 1: A: Study area; B: Animal (see arrow) on broom besides clothepeg marked with red reflective tape; C: Contrastingly coloured male; D: Uniform coloured female (both animals marked with silvery numbers on pronotum and tag of reflective tape, see HELLER & HELVERSEN 1990).

Material and Methods

Poecilimon v. veluchianus Ramme, 1930 is a medium sized bush-cricket (mean body mass male 0.66 g, female 0.74 g; HELLER & HELVERSEN 1991, endemic to Central Greece. The study site is located a few km north of the small village of

Vitoli (22º01'E, 38º58'N) near the small town of Makrakomi, Nomos Fthiotis, Greece, at about 330 m a.s.l. The area (about 540 m^2) is situated at the bottom of a small valley, bordered on one side by a creek, on the other side by dense forest or rocks or other areas without vegetation (Fig. 1 A).

15 males (10 on 26th of May, 5 on 3th of June 1989) and 25 females (20 on 21th of May, 5 on 3th of June 1989) were collected in the field, marked individually with a printed cable marker and a tag of reflective tape (details of marking see HELLER & HELVERSEN 1990) and released at the same place where they had been found. During the following days (end of observations 7th June) the animals were regularly observed (for details of the method see HELLER & HELVERSEN 1991) so that their diel behaviour could be described.

To estimate the distance the animals moved during a certain period of the day (typically periods of 4 hours), an animal needs to be observed at least twice. After having detected an animal we placed a wooden clothes-peg marked with reflective tape near to the animal (Fig. 1 B). After having relocated the animal four hours later we estimated the distance between the animal and the clothes-peg using a folding yardstick and - if the animal has moved - replaced the peg for a new estimate. If the animal had been observed twice (in 2-h intervals) within 4 h, the estimated distances were added. In addition, for each observation we noted the substrate an animal was sitting on. We used four categories: the two by far most common plant species (1) *Platanus orientalis* (plane) and (2) *Spartium junceum* (Spanish broom), (3) all other plant species and (4) bare ground.

Statistical analyses were performed using Statgraphics (Statistical Graphics Corporation), Chi-Square Test Calculator (https://www.socscistatistics.com) and SPSS (SPSS for Mac, Version 16.0. Chicago, SPSS Inc.). However, a field protocol was lost containing the assignment of the measurements to individual animals. So, number and quality of tests were restricted.

Results

Diel movement pattern

The species is strictly active during nighttime. During the day most animals remained motionless sitting at the same spot. Movement starts in the early evening. The females left the plants and started to deposit eggs in the ground. This is not only concluded from their walking on the ground (see below) - during this time many animals could be directly observed ovipositing (as in the years before; HELLER & HELVERSEN 1990). During this period (16:00-24:00, but with a strong peak between 20:00 and 22:00) the females moved significantly larger distances than the males (Fig. 2; p from Mann-Whitney-Wilcoxon U tests with all observations considered as independent; ANOVA not possible due to data clumping at zero). The distances of females, which were observed during oviposition (or behaving similarly but proof of observed oviposition lacking), were significantly larger than that of females without such indication (time 16-22:00: median 100 *vs* 0 cm; n = 23 *vs* 59; U-Test; $p < 0.001$). During the rest of the night, no significant differences in motility between the sexes were observed. In the morning the males were slightly more active than the females.

Microhabitat selection

Males and females differed significantly in their resting behaviour (X^2 (3, N=1421) = 7.71, p<0.001; all observations considered as independent), especially during daytime. Here males were found more often on the small-leaved *Spartium* (more than 80%) than on other plants (Fig. 3). However, in males there were no significant differences with time, although the extraordinarily high preference for *Spartium* at night fits well to their behaviour and may become significant if the number of observations would be higher. In females the differences with time were significant (X^2 (15, N=914) =197, p<0.001). During the day they rested on *Spartium* as often as on other plants (mainly on the broad-leaved plane; on both each about 50%). In the early evening (20-22:00) the females were quite often moving around and/or laying eggs on the ground. In late evening (22-24:00) all males and a high percentage of females were found on *Spartium*. Later in the night (0-4:00 in males, 0-8:00 in females) a more or less continuous transition to the daytime pattern was observed. So many animals changed the microhabitat every night and returned to the typical daytime resting place in the morning. The daytime roosting of the females changed also slightly, but significantly with season. During the first two parts of the season (May 21th to 26th and May 27th to June 3rd, 42 resp. 40% of the females were found on plane during the day (8:00-20:00), but during the last days (June 4th to 7th) this percentage increased to 65% (X^2 (1, N=343) =11.90, p<0.01).

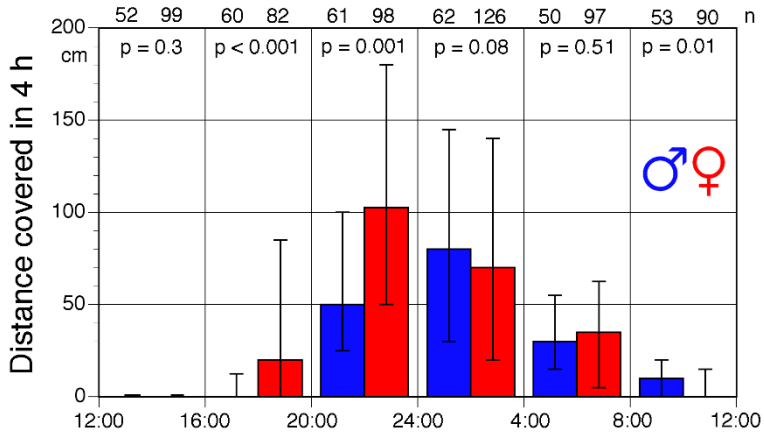

Fig. 2: Distances covered by males and feales within 4 h during the course of a damy (median and inter-quartile ranges; n = number of measurements; p from Mann-Whitney-Wilcoxon U tests).

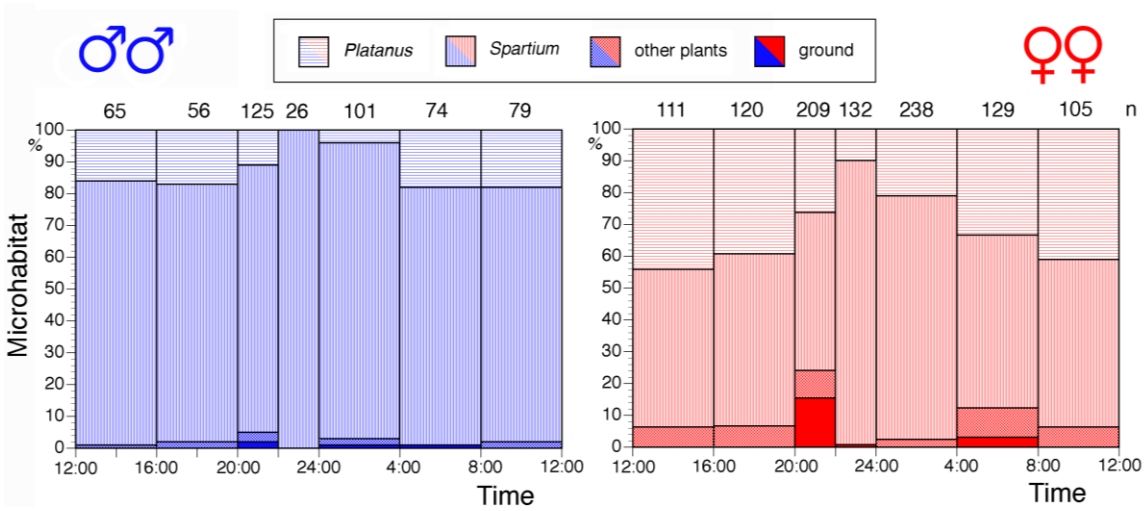

Fig. 3: Microhabitat selection of males and females (measured as substrate the animals were sitting on) during the course of a day (n = number of observations).

Discussion

From the acoustic behaviour, *Poecilimon v. veluchianus* is known to be exclusively active during evening and night (at the study site; HELLER & HELVERSEN 1993, HELLER & REINHOLD 1994; or nearby; ANICHINI et al. 2019). The movement data confirm this activity pattern. Neither males nor females move much during the day (Fig. 2). They rest in bushes and trees mainly in a height of 1-2 m (unpublished data). In the early evening the females become active and a relatively large percentage of them is observed walking on the ground probably looking for oviposition sites. This seems to be a very dangerous phase of their life; according to direct observations many females become prey of lycosid spiders (*Hogna radiata* (Latreille); HELLER & HELVERSEN 1990), scorpions and other predators living on the ground. So, moving long distances may have negative consequences for the fitness of females although for other reasons than found in acridid grasshoppers (SAMIETZ & KÖHLER 2012). They observed a reduction of the number of eggs laid with distance.

Why do the animals oviposit at that dangerous time? Probably they do not have another option and make the best of their bad situation. May be, they can avoid lizards for which it is possibly too dark (and already too cold?) and birds (too dark), but it may be still warm enough for insects to move quickly and to escape predators.

These two factors, to reduce the risk of predation and to live in thermally suitable places (see AHNESJÖ & FORSMAN 2006), may also be most crucial for the selection of microhabitats. Interestingly, males and females of *Poecilimon v. veluchianus* differed significantly in their preferred microhabitats. They differed mainly in their daytime resting positions.

The males started to sing at about 21:00 (HELLER & HELVERSEN 1993), probably soon after many had changed their positions, sometimes involving moving from bush to bush above bare ground. Later, but still before midnight both sexes are found mainly on *Spartium* bushes; all males and more than 90% of the females were located there. At the study site *Spartium* (mainly buds and flowers) is certainly the most preferred food plant, at least as long as the bushes are flowering. However, relatively soon after midnight (before 4:00 in the morning) many females and some males leave the broom bushes and return to the plane bushes and trees and to other plants. A few females even went to the ground before reaching their day roosts. From occasional observations we had the impression that some animals returned to exactly the same spot where they had been in the night before. Such homing behaviour is known from a few other Orthoptera species (BELWOOD 1990, HALE & BAILEY 2004), but the design of our study does not allow safe conclusions.

Why do some animals - mainly females - leave the broom bushes, search and choose another microhabitat, day by day? At a first glance this behaviour seems to be quite similar to that of *Tetrix ceperoi* (HOCHKIRCH et al. 2007). In this species (as in *T. undulata*; AHNESJÖ & FORSMAN 2006) the authors studied the behaviour during the activity period of their species (11:00-17:00) only and wrote: "Males were found at brighter locations and more often on bare ground than females. [ ] In contrast, females spent more time resting and feeding in the vegetation" and concluded "Females should invest more time in gaining nutrients and energy for

egg production and survival, whereas males should spend more time with searching for mates." In *Poecilimon veluchianus* females sit much longer than males on broad-leaved *Platanus*, while males are more frequently found on *Spartium,* which has much less leave area. We assume that the females choose *Platanus* for feeding during daytime, and the males look for females in the slack broom. However, *Platanus* leaves have some special properties. In young age (beginning of summer) they are covered by star hairs, probably as a kind of feeding protection. These hairs are well-known for enforcing "Platanenhusten" (plane cough) in humans (https://de.wikipedia.org/wiki/Platanen; own experiences). In addition, after leaf fall the leaves are not attacked by aquatic shredders, even after they have lost the hairs (MALICKY 1989), although they are eaten by specialists like the monophagous moth *Phyllonorycter platani* (ELLIS 2019). We have never seen *Poecilimon veluchianus* feeding on the leaves and in captivity the animals strictly refuse to eat them. So, feeding is certainly not a reason to choose *Platanus*.

The feeding situation may even become more complicated when taking the mating behaviour into account. About 20% of all females mate per night and receive a spermatophore with a large proteinaceous spermatophylax from the male (26% of his body weight; HELLER & HELVERSEN 1991, HELLER et al. 1998, MCCARTNEY et al. 2008). He has to regain his weight as fast as possible by feeding, while she does not feed on plants after mating but uses the spermatophore as a fast uptake gift (LEHMANN & LEHMANN 2016 for *P. ampliatus*). In the related and similarly sized species *Isophya kraussii* one spermatophore covers all energy requirements of a female for one to two days (VOIGT et al. 2005). Many females of *P. v. veluchianus* remate after 2 days (HELLER & HELVERSEN 1991, REINHOLD & HELVERSEN 1997) so spermatophores have to be considered as important resource for them while males have to rely on plant materials.

Both microhabitats may differ in temperature and/or humidity. Unfortunately, we lack direct data. However, based on measurements in other species (e.g., KUYUCU et al. 2018), positions on plane leaves might be cooler and moister than on *Spartium* where there is little shade during the day. If the animals would like to be warm during the day they should sit on broom. But even in the northern Sweden overheating seems to be the larger problem: "black females had the highest degree of microhabitat selectivity and spent more time on relatively cold moist moss" (AHNESJÖ & FORSMAN 2006). So, in hot Greece the *Poecilimon* males with larger black patches than females should choose shady places or at least more shady ones than the green females. If there would be too less sun, the females should prefer broom from thermoregulatory reasons. Our data do not support either of these predictions.

So, the other factor, to reduce the risk of predation, comes in focus. The defence against visually hunting predators like birds and lizards is certainly very important as it can be concluded from the high mortality of up to 50% per three days (HELLER & HELVERSEN 1990) and again found for moving males (LEHMANN & HELLER 1998). The contrastingly coloured males may be harder to see in the sun-shade-pattern of *Spartium* than on the green *Platanus* leaves. And for the uniform green females the opposite might be true. In intraspecific communication of *P. v. veluchianus* visual signals are not crucial. For the acoustically signalling males, approached by

the females at night, neither (active) sight nor (passive) visibility may be important at all. However, to be the first on broom when the females arrive in the evening could be an additional advantage for males remaining on the hot place without shade. This would be a factor working even if male and females would not differ in colouration and had the same thermal requirements. Broom could also be considered as rendezvous place where the females find males for mating guided by their songs and leave them again later.

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