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Autor(en): **Hertach, Thomas**

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Three species instead of only one: Distribution and ecology of the *Cicadetta montana* species complex (Hemiptera: Cicadoidea) in Switzerland

THOMAS HERTACH

Untere Mühle, 8112 Otelfingen; hertach@gmx.ch

Investigations over the last few years by French, Swiss and especially Slovenian researchers suggested that *Cicadetta montana* is a complex of at least three morphologically similar sister species in Central Europe which are characterized easily by their calling songs. For that reason the biogeography of mountain cicadas has now to be reinvestigated for the whole Palaearctic. Based on 283 recent and acoustically confirmed observations, this is the first study to present detailed distribution maps for an entire country. *Cicadetta montana* s. str. is known from 117 locations, *Cicadetta cerdaniensis* s. l. from 67 and *Cicadetta brevipennis* from at least six sites. The occurrence of *Cicadetta cerdaniensis* s. l. can be definitely confirmed for Switzerland. Also, a critical comment on the very recently described and closely related species *Cicadetta cantilatrix* is provided. *Cicadetta brevipennis* is a new and rare species for Switzerland. Furthermore, the present study offers an approach to the ecological niches of the three sister species. Comparing the two more frequent species, the ecological variables «vegetation type», «altitude» and «substrate» differ significantly. After the acoustic and genetic discrimination, ecological separation is now possible for the first time. Endangerment and protection of the three species are discussed.

Key words: *Cicadetta montana*, *Cicadetta cerdaniensis*, *Cicadetta brevipennis*, *Cicadetta cantilatrix*, species complex, Switzerland, distribution, ecological niche.

INTRODUCTION

Although many species and subspecies of mountain cicadas (*Cicadetta montana* s. l., Scopoli, 1772) have been morphologically described in the 18th and 19th century, most authors later assigned them to a single taxon (e.g. Nast 1972; Schedl 2000). A few years ago, Puissant & Boulard (2000) described the new species *Cicadetta cerdaniensis* as a result of acoustic studies in the French Pyrenees. Hertach (2004) found a similar, but slightly different song structure in the Swiss Jura Mountains whose existence has already been indicated by Artmann (1987). Analysing songs in different countries, Gogala & Trilar (2004) and Gogala (2006) claimed the occurrence of three species in Central Europe. Their third species, *Cicadetta brevipennis*, had been known as *Cicadetta montana* var. *brevipennis* since Fieber (1876). Its song was already described by Boulard (1995) in France, but he assigned it to *C. montana* s. str. The three species can be separated by genetic characters as well (Gogala, Trilar & Simon, personal communication). The morphological discrimination is very difficult due to high intraspecific variability (Gogala, Hertach & Trilar, in preparation). Very recently, Sueur & Puissant (2007a) separated the new species *Cicadetta cantilatrix* from *C. cerdaniensis* based on some acoustical differences, already indicated by Hertach (2004). However, this study calls for a critical discussion of the new species. Therefore, the name *C. cerdaniensis* s. l. is generally used

and includes different song variations, especially the typical *C. cerdaniensis* s. str. and *C. cantilatrix* patterns.

The biogeography of the mountain cicadas needs to be reinvestigated in the whole Palaearctic. Recently, a few acoustically proven observations of the three or four species were published from Germany, Slovenia, Great Britain, Italy (Gogala & Trilar 2004), France (Puissant & Boulard 2000, Puissant 2006, Sueur & Puissant 2007a, 2007b), Spain (Puissant 2001), Austria (Trilar & Holzinger 2004), Macedonia (Gogala *et al.* 2005), Romania (Trilar *et al.* 2006a) and Poland (Trilar *et al.* 2006b). Most of them refer to very few observations. Only about 25 records of *C. montana* s. l. were available in the Swiss Central Fauna Data Bank (CSCF) when starting this study. The single comprehensive study on cicadas in Switzerland is by Pillet (1993), but it is not known if he had proven his observations by acoustical recordings. The habitat requirements of these probably competing sister species have not been described and the ecological niches have not been considered.

MATERIAL AND METHODS

The potential areas could be defined closely, due to their obvious preference for dry and warm habitats with sparse woodland. Making use of vegetation data (Hegg *et al.* 1993), the main potential regions were visited from 2004 to 2006 and have been completed with spot checks in the entire country. This study integrates records of other entomologists if confirmed by the calling songs. The following persons put their data at the author's disposal, some of them after having been briefed: Christian Monnerat (27 records), Bruno Keist (23), Laurent Juillerat (18), Georg Artmann (10), Heinz Bolzern (3) and Sibille Jenni (2).

Although the songs of mountain cicada species have a high frequency (10–18 kHz) and are hardly audible for elderly people, their calling song is still the most effective way to prove their presence. The first recordings of calling songs were performed with very simple equipment (Grundig GW-R50 recorder and SSF-Bat detector). After 2005, the equipment has been replaced by a more effective ultrasonic detector (Petterson D 200) whose microphone was fitted into a Telinga parabola (adapted from Popov *et al.* 1997). Recordings were made with a Marantz PMD 660 and analysed qualitatively with different elementary software.

Some voucher specimens have been collected for morphological studies and are kept in the private collection of the author. All records have been transmitted to the Swiss Central Fauna Data Bank (CSCF).

The number of singing individuals was counted or estimated. In case of unsuitable weather conditions, some sites were visited several times. Ecological variables were registered, e. g. vegetation types following Delarze *et al.* (2000) and Hegg *et al.* (1993), altitude and substrate. In order to interpret and visualise the vegetation types, they were combined to eight classes. The whole data set was analysed on three different levels (Tab. 1).

Comparing the two more frequent species, the ecological variables «altitude», «vegetation type», «substrate» and «activity time» were tested for significance at observation level with the statistical software R2.4.1. Using exact values, the altitude and the adult seasonal pattern were analysed by the Wilcoxon rank sum test with continuity correction. Concerning vegetation types and substrate, chi-square cross table tests were conducted to contrast the frequencies of the observations.

Tab. 1: Ecological variables and their analyses on three levels.

Observation level	An observation refers to a record of one or several individuals of the same species found in a more or less continuous and homogenous habitat at one time.*		
	Variable	**Measurement**	**Note**
	Altitude	Metres above sea level (a.s.l.)	An observation can belong to more than one interval of altitude (0 – 200 m a.s.l., 201 – 400 m a.s.l., etc.) for the histogram.
	Activity period	Date	In order to test statistically, dates were transformed into continuous natural numbers.
	Vegetation type	Eight classes	1. Dry meadow (often *Mesobromion*) with woods (hedges, shrubs, edges of the forest); 2. *Molinio-Pinetum*; 3. Dry Pine forest (*Erico-Pinion, Ononido-Pinion*); 4. *Fraxino orno-Ostryon*; 5. *Quercion pubescentis*; 6. Mesophilous mixed woodland (*Carpinion, Quercion robori-petraeae, Tilion*); 7. Elevated coniferous forest (*Piceion, Laricetum*); 8. Other vegetation types. An observation can belong half to a first and half to a second vegetation type.
	Substrate	Two classes	1. Bedrock (on cliffs and ridges); 2. Other substrates.
Population level	Observations from the same location made at different times were put together as well as locations which are not isolated by insufficient habitats of more than about 0.5 km distance.		
	Variable	**Measurement**	**Note**
	Association	Number	Populations of the three species occur either sympatrically (same region) or syntopically (same location) or allotopically (not same location).
Distribution level	According to the Swiss graticule, data is visualized in a grid of 25 sq km.		
	Variable	**Measurement**	**Note**
	Intensity of the field work	Three classes	1. High = square visited by the author at least two times, once with optimal weather conditions; 2. Low = square visited by the author once or weather conditions several times suboptimal; 3. Unknown = square visited by other entomologists.
	Abundance	Two classes	The maximum number of singing individuals observed for each population in a square was added to get a value for the abundance. 1. High abundance = more than 30 singing individuals (more than 20 singing individuals in case of suboptimal weather conditions); 2. Low abundance = less than 30 singing individuals (less than 20 singing individuals in case of suboptimal weather conditions).

* Numbers of observed individuals are not included for the comparisons at the observation level. Therefore, each observation is assigned the same weight.

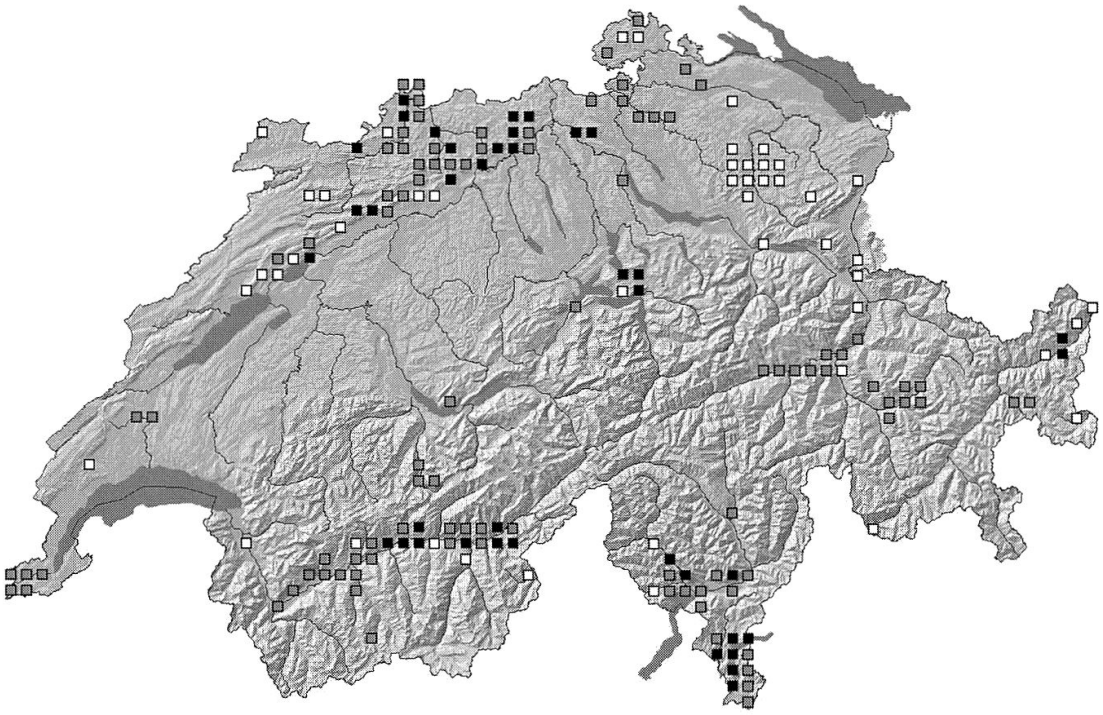

Fig. 1: Map showing intensity of field work (high = black, low = grey, unknown = white).

RESULTS

General characters of the data

Tab. 2 shows the main characters of the field work. During the last four field seasons between May 2003 and August 2006, 180 squares of the Swiss graticule (25 sq km) were visited. The main work concentrated on three different regions (see Fig. 1): the eastern part of the Jura Mountains, the southern Ticino and the Valais. Due to climate and vegetation factors, these are probably the most important regions for mountain cicada species in Switzerland. Best results were obtained under sunny, hot and windless weather conditions.

200 records of species from the *C. montana* complex have been registered by the author. Altogether, distribution maps are based on 283 acoustically proven observations at 166 different locations. Individuals of the mountain cicada group have been found in 111 squares of the mentioned grid.

Cicadetta montana s. str. (Scopoli, 1772)

Distribution

C. montana s. str. (see Fig. 7A, B) is distributed widely in all regions of Switzerland apart from the high Alps and a good portion of the hilly Swiss Plateau (Fig. 2). Most of the observations are based on just a few individuals. Only in the central and upper Valais, high densities are the rule. It is the only species in the Grisons and the Prealps. 57 % of all records refer to *C. montana* s. str. The altitude range is remarkable (Fig. 5A). In the Valais, the most elevated population is estab-

Tab. 2: Main characters of the field data.

	***C. montana* s. str.**	***C. cerdaniensis* s. l.**	***C. brevipennis***	**None**	**Total**
Observations	161	112	10		283
Populations	117	67	6		190
Visited squares (map grid)	80	53	5	69	180

lished at 2010 m (Rosswald), in the Jura Mountains at 1280 m (Weissenstein). Median and average values are around 850 m.

Ecology

C. montana s. str. prefers sparse woodland with pine (*Pinus sylvestris*), especially dry varieties as *Erico-Pinion* and *Ononido-Pinion* (Fig. 4A). *C. montana* s. str. is often concentrated on rocky cliffs and ridges. These habitats are usually split into very small fragments. The range of occupied habitats is fairly wide and can extend to mesophilous forests as *Carpinion*, *Quercion robori-petraeae*, *Tilion* and elevated coniferous forests like *Laricetum* and *Piceion*. In all cases, a sparse structure and a sunny exposition are essential. Ecotone habitats between forests and dry meadows are important, too. Males mostly sing on different tree species (deciduous trees and especially conifers), sometimes high in the treetop. None of the observations refers to a male singing in the herb layer. The first singing specimen was registered on 15 May (2006) and the last on 31 July (2004); maximum activity was in the second half of June (Fig. 6A).

Example of the typical calling song of *C. montana* s. str. is given in Fig. 3.

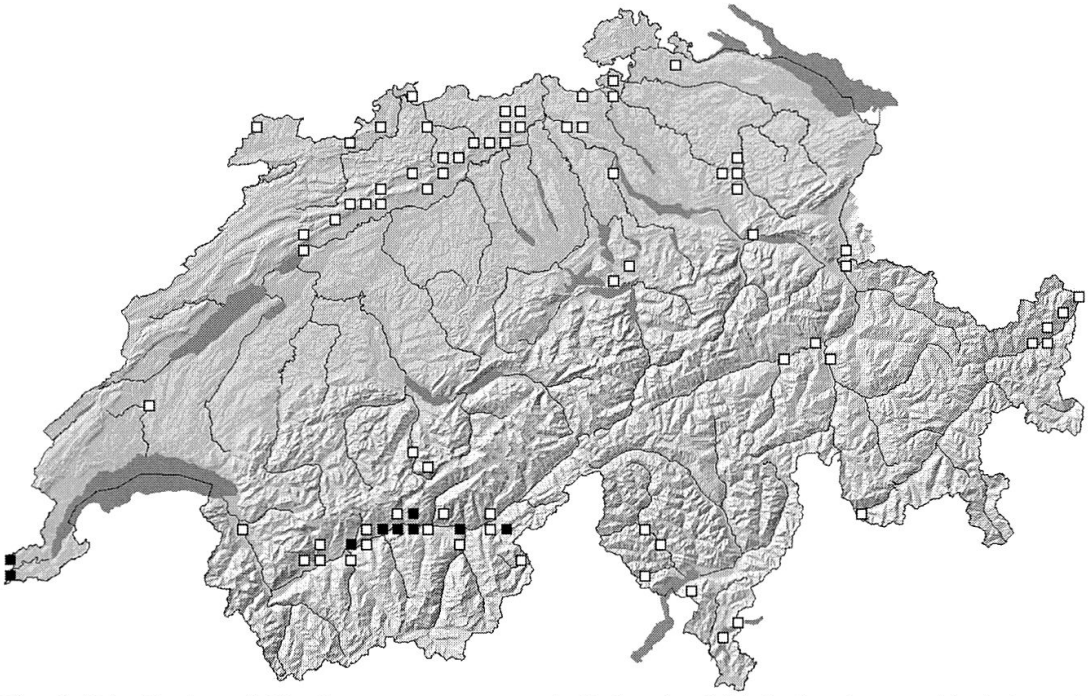

Fig. 2: Distribution of *Cicadetta montana* s. str. in Switzerland (high abundance = black, low abundance = white).

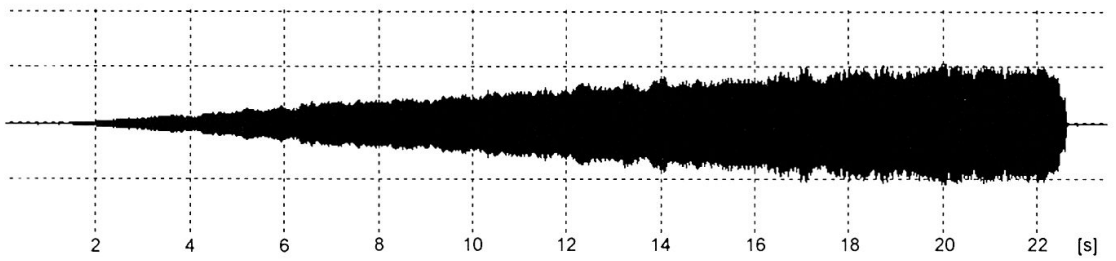

Fig. 3: Oscillogram of the calling song of *Cicadetta montana* s. str. recorded in Zeglingen, Jura Mountains (12 June 2006).

Cicadetta cerdaniensis s. l. Puissant & Boulard, 2000

Distribution

After the first uncertain description (Artmann 1987) and its «rediscovery» in 2003 (Hertach 2004), the occurrence of *C. cerdaniensis* s. l. can now be confirmed definitely for Switzerland (see Fig. 7C, D). Its distribution is split into three separated areas (Fig. 9): Firstly, the species occurs in the Jura Mountains (60 % of all observations) and sporadically in its eastern vicinity, secondly, in the Valais, and thirdly, in the Southern Ticino. In some parts of the eastern Tabular Jura, the western part of the Rhone Valley and the Southern Ticino, *C. cerdaniensis* s. l. has been observed even more frequently than *C. montana* s. str. Sixty-seven populations of *C. cerdaniensis* s. l. are currently known in Switzerland. This species never reaches 1200 m a.s.l., median value is 560 m. 57 % of the observations were made between 400 and 600 m (Fig. 5B).

Ecology

North of the Alps, *C. cerdaniensis* s. l. is clearly specialized on very sparse *Molinio-Pinetum* on marl (e.g. Effingen, Diegten) and variable edges of the forest along extensively used meadows like *Mesobromion* (Fig. 4B). This species normally needs more extended habitats than *C. montana* s. str., but it often has a high population density. In the Valais, a clear affinity exists to *Quercus pubescens*. For that reason *C. cerdaniensis* s. l. was found concentrated in the western part of the Rhone Valley. In the Ticino, sunny and sparse sites with *Fraxino orno-Ostryon* were especially occupied. *C. cerdaniensis* s. l. rarely enters vineyards. Males usually sit on low trees or shrubs, sometimes even in the herb layer when emitting their calling song. The singing period started at the earliest on 7 May (2000) and lasted until 27 July (2006). In June, song activity reached the culmination point (Fig. 6B).

Song variability

The song is very remarkable and structured into three phrases (see Puissant & Boulard 2000). First phrase: very short or even missing first part of double echeme, low agitation phrase; second phrase: increasing to full duration of first part of double echeme, high agitation phrase; third phrase: abrupt change to quick repetition of pulses. There are two qualitatively checked and obvious differences in song patterns between specimens of the Valais and the Jura populations in comparison to

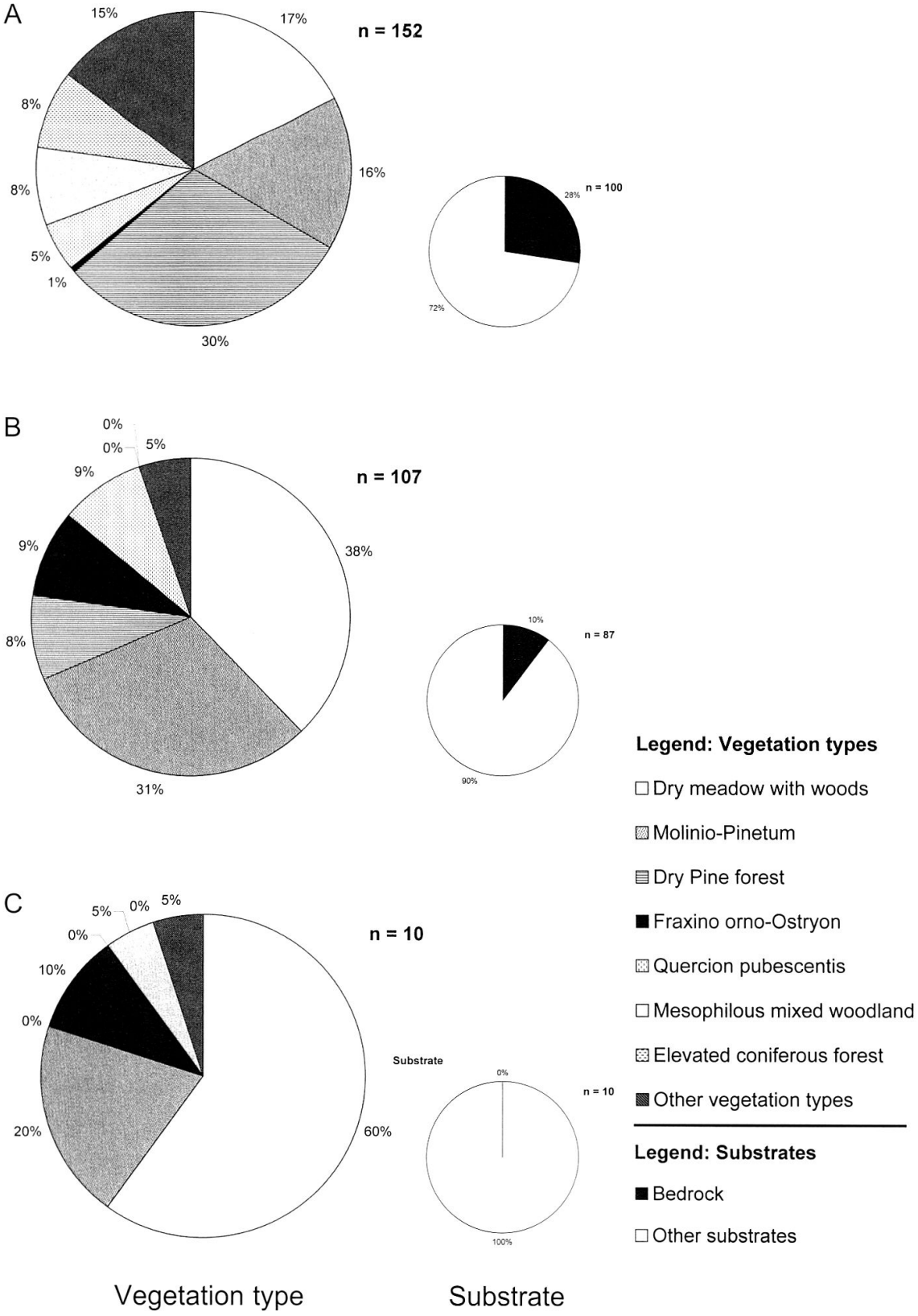

Fig. 4: Vegetation types and substrates concerning the observations done in the *Cicadetta montana* species complex from Switzerland: (A) *C. montana* s. str., (B) *C. cerdaniensis* s. l. and (C) *C. brevipennis*.

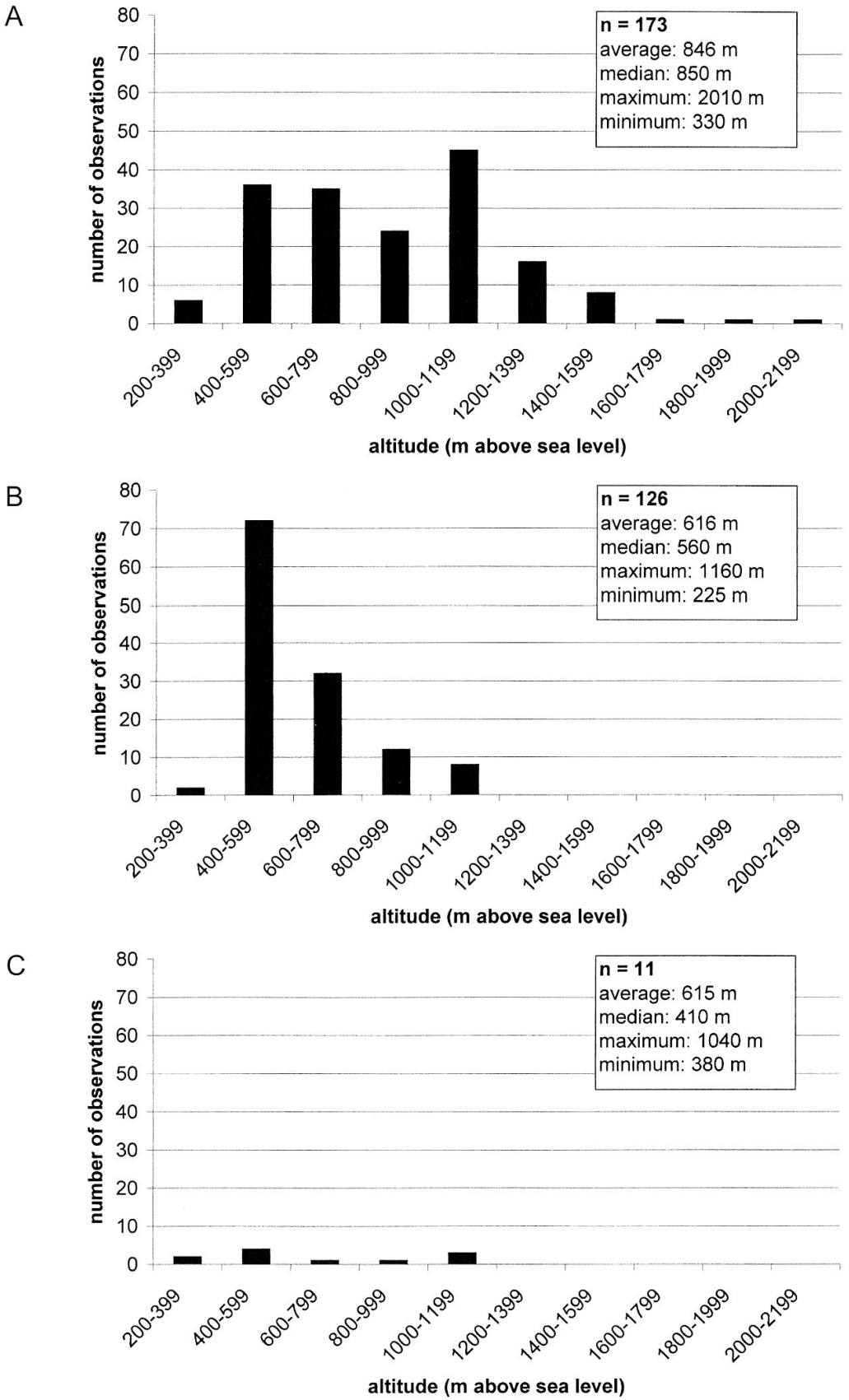

Fig. 5: Altitudes above sea level [m] in the *Cicadetta montana* species complex from Switzerland: (A) *C. montana* s. str., (B) *C. cerdaniensis* s. l. and (C) *C. brevipennis*.

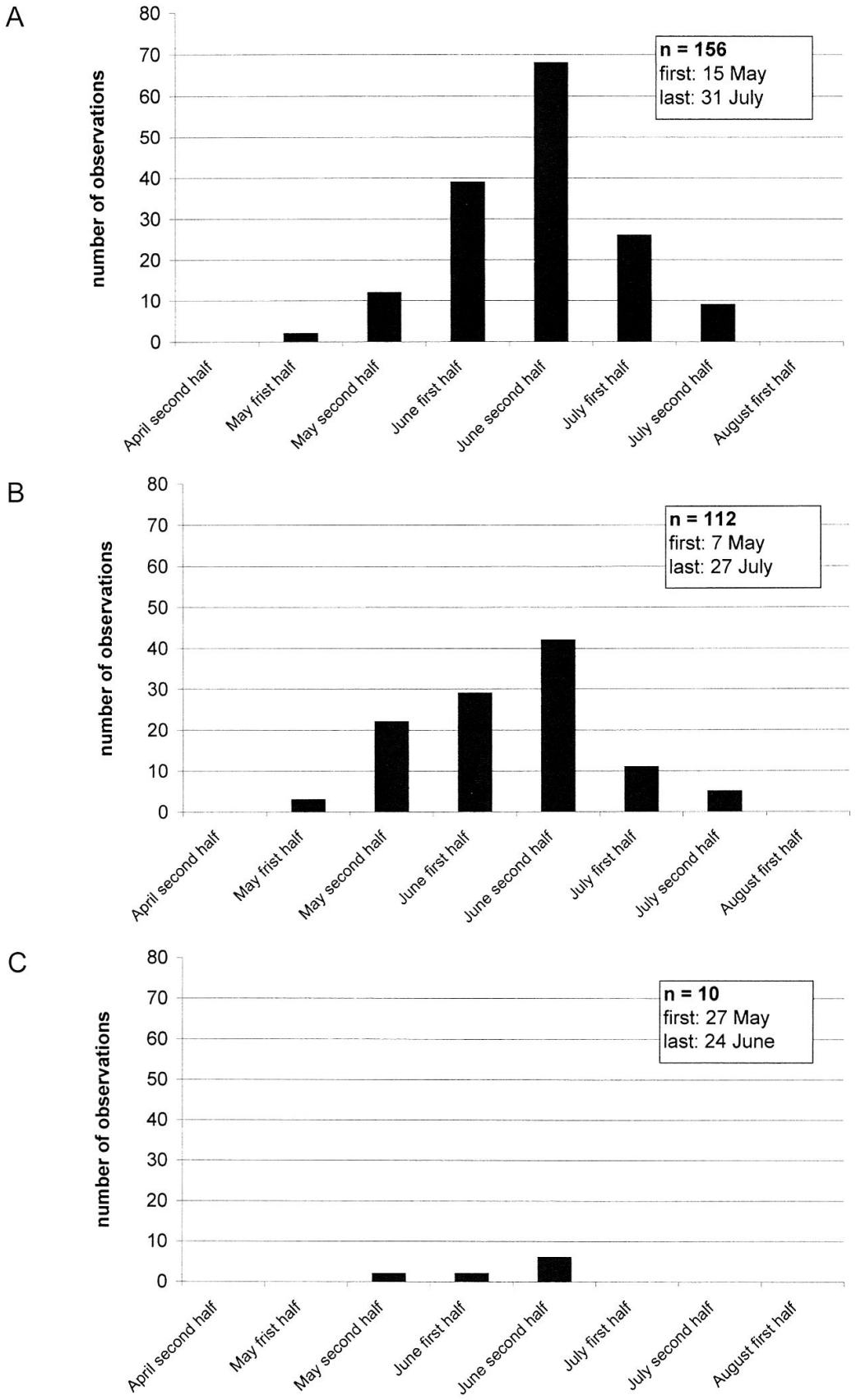

Fig. 6: Adult seasonal patterns in the *Cicadetta montana* species complex from Switzerland: (A) *C. montana* s. str., (B) *C. cerdaniensis* s. l. and (C) *C. brevipennis*.

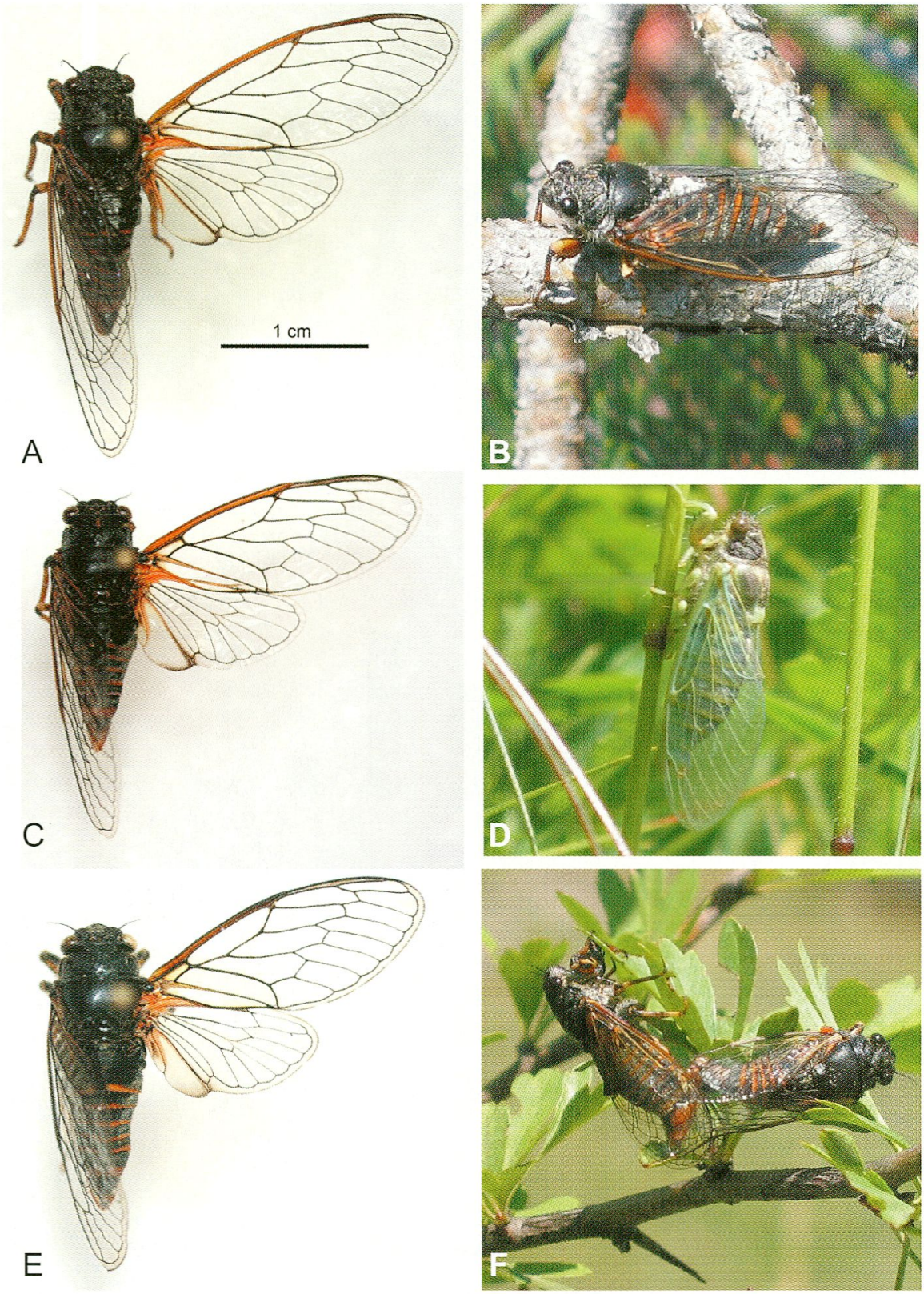

Fig. 7: Voucher specimens and animals in natural habitat of the three species in the *Cicadetta montana* complex: *C. montana* s. str.: (A) Male voucher specimen (Fôret de Finges, Valais, 18 June 2006) and (B) female on *Pinus sylvestris* (Salgesch, Valais, 18 June 2005); *C. cerdaniensis* s. l.: (C) Male voucher specimen (Le Châtelard, Valais, 20 June 2006) and (D) animal directly after metamorphosis (Rothenfluh, Jura Mountains, 7 June 2006); *C. brevipennis*: (E) Male voucher specimen (Monte San Giorgio, Ticino, 27 May 2006) and (F) pair in copulation (Vernier, Geneva region, 24 June 2006).

Fig. 8: Swiss habitats of the three species in *Cicadetta montana* complex: (A) *Erico-Pinion* on limestone at Balmfluechöpfli, Jura Mountains (3 July 2006), habitat of *C. montana* s. str.; (B) subalpine coniferous forest with *Larix decidua*, Rosswald (1800–2050 m a.s.l.), Valais (23 June 2006), most elevated habitat of *C. montana* s. str.; (C) well structured edge of the forest besides extended *Mesobromion*, Rothenfluh, Jura Mountains (7 June 2006) habitat of *C. cerdaniensis* s. l.; (D) mixed habitat with *Ononido-Pinion* and *Quercion pubescentis* at Lintellière, Valais (21 June 2006), syntopic habitat of *C. montana* s. str. and *C. cerdaniensis* s. l.; (E) sparse *Molinio-Pinetum*, Vernier, Geneva region (24 June 2006), habitat of *C. brevipennis*; (F) sparse *Fraxino orno-Ostryon* at Monte San Giorgio, Ticino (5 June 2005), syntopic habitat of *C. brevipennis* and *C. cerdaniensis* s. l.

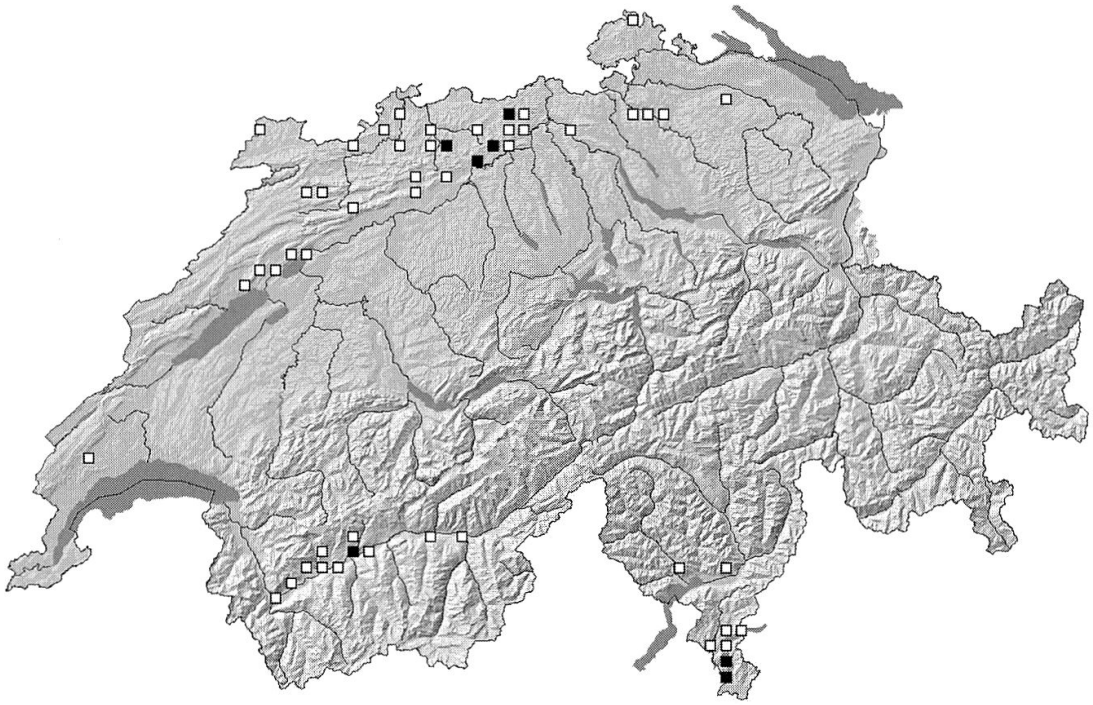

Fig. 9: Distribution of *Cicadetta cerdaniensis* s. l. in Switzerland (high abundance = black, low abundance = white).

the ones of the Ticino (Fig. 10): a) Duration of the low part of double echeme is shorter in the second phrase in the Ticino (Fig. 10B, D) than in the other regions (Fig. 10A, C) while the repetition period is approximately equal. b) Third phrase is regularly emitted in the Ticino (Fig. 10B), but only sporadically shown by males of the other regions (Fig. 10E).

Strictly applying the recently adapted nomenclature and the original descriptions, the Ticino populations fit well but not completely with *C. cerdaniensis* s. str. (Fig. 10B, D). The populations from the Valais and the Jura Mountains normally sing similar to the new *C. cantilatrix* description (Fig. 10A, C). Since their song exceptionally consists of three phrases as in *C. cerdaniensis* s. str., one can assign this taxon at best to *C.* conf. *cantilatrix*.

Cicadetta brevipennis Fieber, 1876

Distribution

C. brevipennis is a new and very rare species for the Swiss fauna (see Fig. 7E, F). It was first found at two adjoining locations in the very south of the Ticino in 2005 (Monte San Giorgio) and 2006 (Poncione d'Arzo). Many visits in the surrounding regions did not yield this species. Controlling known populations of *C. montana* s. l. in the Geneva region in 2006, two turned out to belong to *C. brevipennis*. In total, six populations of this species are known now. The two distribution areas in Switzerland are separated completely and situated at the periphery of the country (Fig. 11). Habitats in the Ticino range from 700 to 1080 m, the ones in the Geneva region from 380 to 410 m (Fig. 5C).

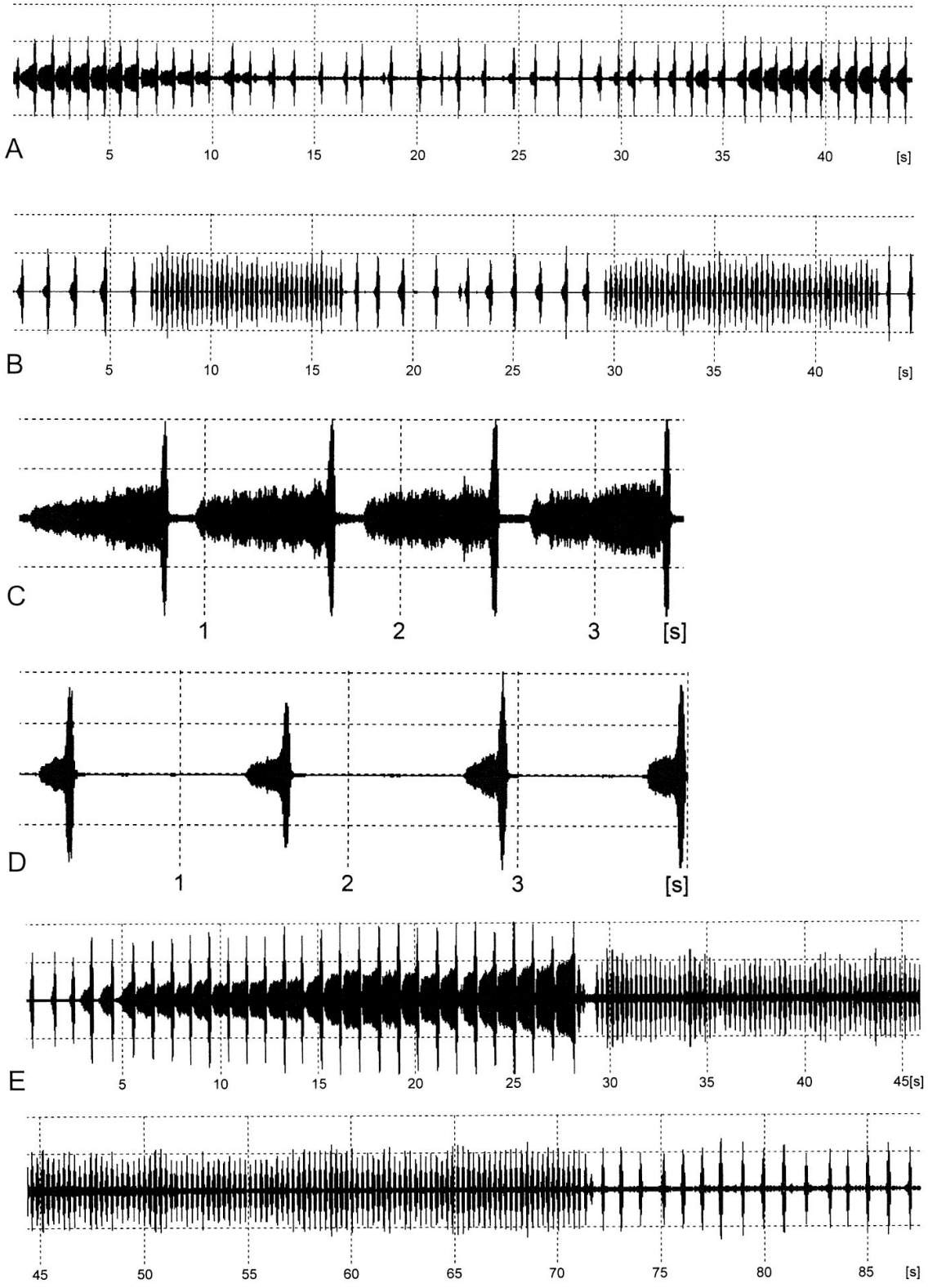

Fig. 10: Oscillograms of the songs of *Cicadetta cerdaniensis* s. l.: (A) characteristic song patterns (phrases 2, 1, 2) emitted north of the Alps and in the Valais, recorded in Saillon, Valais (26 June 2006); (B) characteristic song patterns (phrases 2, 3, 2, 3, 1) registered in the Ticino, recorded at Monte San Giorgio (11 July 2004); (C) detailed sequence of phrase 2 of song A; (D) detailed sequence of phrase 2 of song B; (E) sporadically registered song patterns from the Jura mountains with three phrases (phrases 1, 2, 3, 1), continuous recording (90 seconds) from Kienberg SO (24 June 2004).

Fig. 11: Distribution of *Cicadetta brevipennis* in Switzerland (high abundance = black, low abundance = white).

Ecology

The main habitat in the Ticino is characterized by a very sparse *Fraxino orno-Ostryon* with *Quercus pubescens*. *C. brevipennis* occurs syntopically with *C. cerdaniensis* s. l. there. Males often sing even in the herb layer or on low shrubs. There is a high density at Monte San Giorgio. The Geneva populations prefer sparse pine forests and dry meadows with shrubs and trees (Fig. 4C). The first record in spring refers to 27 May (2006), the last singing specimen was registered on 24 June (2006) (Fig. 6C). The complete adult seasonal pattern is unknown.

The calling song of *C. brevipennis* is shown in Fig. 12.

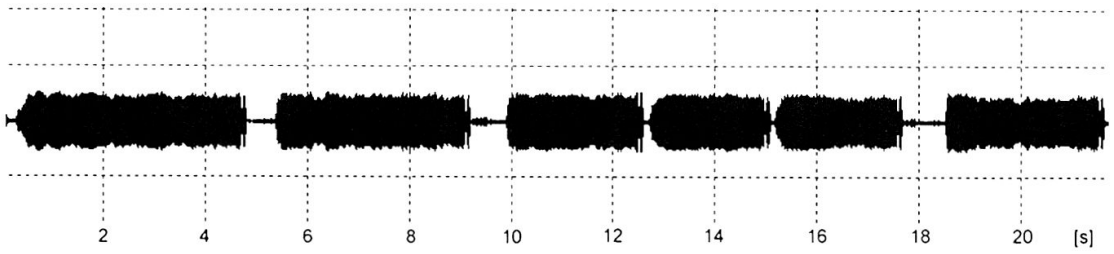

Fig. 12: Oscillogram of the calling song of *Cicadetta brevipennis* recorded at Monte San Giorgio, Ticino (5 June 2005).

Associations

The associations between the three closely related species are shown in Fig. 13. A remarkable part of locations is occupied by two syntopic sister species (14.6 %). Syntopically occurring populations with *C. montana* s. str. have been detected in all three distribution areas of *C. cerdaniensis* s. l. At both sites in the Ticino where *C. brevipennis* is present, coexistence with *C. cerdaniensis* s. l. has been observed. In the Vallon d'Allondon (Geneva region), *C. brevipennis* is mixed with the *C. montana* s. str. population, which seems to be unusual. There is no location where all three species live syntopically, but in the Southern Ticino occurrence of the three species has been registered in the same region.

In the Southern Ticino, *C. cerdaniensis* s. l. has been observed in association with the bigger cicadas *Cicada orni* Linné, 1758 and *Lyristes plebejus* (Scopoli, 1763). In the Valais, both species of the *C. montana* complex can occur syntopically with the other currently registered cicadas *Cicada orni*, *Tibicina quadrisignata* (Hagen, 1855) and *Tibicina steveni* (Krynicki, 1837).

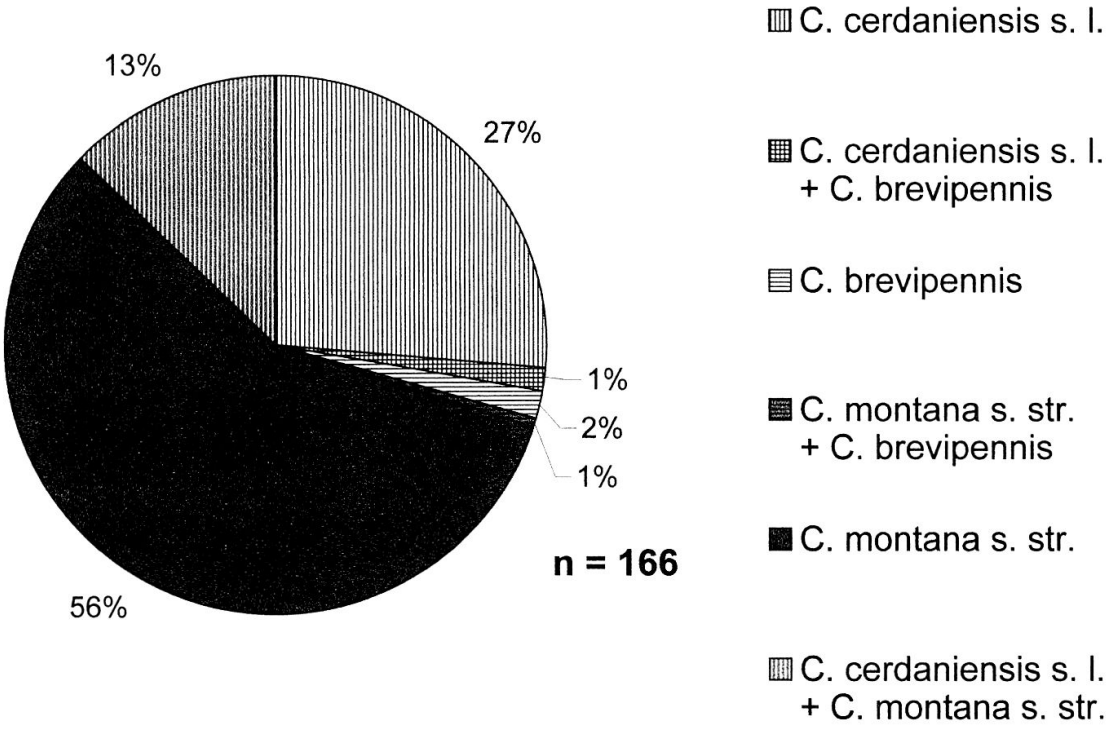

Fig. 13: Associations between the three species of the *Cicadetta montana* complex in Switzerland: Syntopic and allotopic occurrence of the populations.

Niche segregation

Comparing the ecological requirements of *C. montana* s. str. and *C. cerdaniensis* s. l., some aspects are tested about evidence with chi-square cross table test and Wilcoxon rank sum test (Tab. 3). *C. brevipennis* could not be included because of its rare occurrence.

The general selection of the vegetation types differs significantly between *C. montana* s. str. and *C. cerdaniensis* s. l. ($\chi^2 = 65.33$, $p < 0.001$). Even the number of the observations of each single vegetation type varies significantly, except for

Tab. 3: Ecological variables in *Cicadetta montana* s. str. versus *Cicadetta cerdaniensis* s. l.: (A) Habitats were tested by chi-square cross table tests, (B) altitude and seasonal pattern by Wilcoxon rank sum tests.

(A) Habitats	**Dominant species**	χ^2	**p**
Global test over all vegetation types		65.3	< 0.001
Dry meadows with woods	*cerdaniensis*	13.6	< 0.001
Molinio-Pinetum	*cerdaniensis*	8.3	0.004
Dry pine forests	*montana*	17.9	< 0.001
Fraxino orno-Ostryon	*cerdaniensis*	10.9	< 0.001
Quercion pubescentis		1.5	0.214
Mesophilous mixed woodland	*montana*	9.2	0.002
Elevated coniferous forests	*montana*	8.9	0.003
Other vegetation types	*montana*	6.1	0.014
Bedrock as substrate over all vegetation types	*montana*	8.7	0.003

(B) Altitude and adult seasonal pattern	**Dominant species**	**W**	**p**
Higher altitude [metres a.s.l.]	*montana*	13101	< 0.001
Previous singing period [date]	*cerdaniensis*	10012	0.010

the *Quercion pubescentis*. With regard to the main habitats, *C. montana* s. str. prefers dry pine forests ($\chi^2 = 17.93$, $p < 0.001$) whereas *C. cerdaniensis* s. l. dominates clearly in the *Molinio-Pinetum* ($\chi^2 = 8.29$, $p = 0.004$) and in the dry meadows with woods ($\chi^2 = 13.65$, $p < 0.001$). The choice of bedrock as substrate is also evident ($\chi^2 = 8.72$, $p = 0.003$).

The locations of *C. montana* s. str. are significantly more elevated than the ones of *C. cerdaniensis* s. l. ($W = 13101$, $p < 0.001$). Concluding from a Wilcoxon rank sum test, there is a seasonal niche segregation in the singing period between *C. montana* s. str. and *C. cerdaniensis* s. l. ($W = 10012$, $p = 0.010$).

DISCUSSION

Taxonomy

This work supports the suggestion of Gogala & Trilar (2004) to divide the former species *C. montana* s. l. in Central Europe into at least three different species. The song patterns of the three species are clearly different even without the help of analysing methods. In addition to the acoustic (Gogala & Trilar 2004) and genetic (Gogala, Trilar & Simon, personal communication) discrimination, *C. cerdaniensis* s. l. and *C. montana* s. str. can be segregated according to ecological variables.

There are at least two small differences between the typical song patterns of *C. cerdaniensis* s. l. from the Ticino versus the ones from the Jura Mountains and the Valais. Hertach (2004) already mentioned the possibility of two very closely related taxa. Sueur & Puissant (2007a) suggested to divide them and described the very new species *C. cantilatrix*. As long as sound material of only few populations has been analysed, the new species has to be interpreted with caution. Comparing the original descriptions, both typical Swiss song patterns show intermediate elements. The main diagnostic parameters do not seem to be constant enough. In the author's opinion, the existence of a complicated dialect system or of clinal spatial changes is as likely as the existence of a second valid species. Several very closely related taxa (species or subspecies) are also possible. However, more systematic records of the songs all over Europe and genetic analyses are needed to understand the differences definitely. If the current nomenclature remains valid, the description of the song repertoire of *C. cantilatrix* has to be completed.

The names *C. brevipennis* and *C. cerdaniensis* should be used carefully. The first name was created by Fieber (1876) to divide *C. montana* s. l. into two varieties, following slight morphological differences: *C. montana* var. *longipennis* and *C. montana* var. *brevipennis*. *C. montana* var. *longipennis* fits well with *C. montana* s. str. (Gogala & Trilar 2004). *C. montana* var. *brevipennis* sensu Fieber could actually also be a synonym of *C. cerdaniensis* (or the proposed new species), because *C. brevipennis* sensu Gogala & Trilar (2004) and *C. cerdaniensis* s. l. can not be distinguished morphologically until now. Puissant & Boulard (2000) and Gogala & Trilar (2004) did not expect that *C. cerdaniensis* s. l. would be as widely distributed as has been documented in the last three years. Furthermore, there exists another recently used name, probably a synonym for one of the three species: *Cicadetta petryi* Schumacher, 1924. Investigations at the loci typici may help to solve these problems and confirm the valid names. At least, Nickel (2003) indicated that the locus typicus of *C. petryi* in Thuringia (Germany) has been occupied recently only by *C. montana* s. str.

Distribution

The present study gives a good overview of the spatial distribution of the three mountain cicada species in Switzerland. It is surprising that the second and third species were not discovered earlier, since the Swiss fauna is generally well explored. The patterns of distribution differ, but are typical for the Swiss fauna. The distribution of *C. brevipennis* and *C. montana* s. str. for example matches well with that of several grasshoppers (Baur *et al.* 2006), although these insects do not prefer the same habitats.

The inventory is not complete, but most of the omitted regions are unsuited due to climate or land use. The largest lack of data is expected in the Grisons (lower parts of the Rhine Valley), in the western part of the Jura Mountains and in some valleys with distinct influence of foehn (warm south wind). In the Grisons, a few locations of *C. montana* s. str. are known, but the presence of other species cannot be completely excluded, especially in the xerothermic surroundings of Chur. Furthermore, it will be interesting to explore in more detail the area north-east of Geneva. It is possible that the distribution areas of *C. cerdaniensis* s. l. and *C. brevipennis* overlap there, as is the case in the Southern Ticino, or the two species may substitute each other.

The wide distribution of *C. cerdaniensis* s. l. is probably the most unexpected finding of this work. Worldwide unidentified until 2000 and discovered in Switzerland by chance first in 2003, 67 populations are known for this small country. This number surpasses the worldwide populations currently published by far. It is likely that this species is autochthonous and simply has been missed before. In all three distribution areas in Switzerland, *C. cerdaniensis* s. l. is nearly as abundant as *C. montana* s. str., or is even the most frequent species.

Perhaps *C. brevipennis* is the most frequent species in the Geneva region. This species is probably completely missing in the Jura Mountains, in the Prealps and in the big valleys of the Alps as well as in the central and eastern part of the Swiss Plateau. *C. brevipennis* is considered to be rare in the Southern Ticino.

The altitude range is remarkable for all three species (Fig. 5). Especially *C. montana* s. str. was found several times above 1500 m, which means that this species almost reaches the natural alpine treeline. Pillet (1993) never observed *C. montana* s. l. above 1500 m. Rosswald (see Fig. 8B) at 2010 m is perhaps the most elevated site ever registered for cicadas in Central Europe. The altitude of the sites constitutes a first important factor of the niche segregation between *C. cerdaniensis* s. l. and *C. montana* s. str. in Switzerland (Tab. 3). The locus typicus of *C. cerdaniensis* s. str. from the Pyrenees is situated higher (1350 m) than all Swiss populations (Puissant & Boulard 2000).

From an international view point, the spatial distribution of the sister species in Switzerland matches well with the other records from Europe (Gogala & Trilar 2004; Trilar & Holzinger 2004; Gogala *et al.* 2005; Trilar *et al.* 2006a, 2006b; Sueur & Puissant 2007a, 2007b). All three species are distributed widely from Eastern to Western Europe. The range from north to south is wide in *C. montana* s. str. (South England to Macedonia) and *C. cerdaniensis* s. l. (Poland and France to Macedonia). It is quite possible that *C. brevipennis* is more limited to the south. Nickel (2003) described a song rarely registered in Germany without publishing any acoustical data that would fit *C. brevipennis*. A record of *C. brevipennis* from Germany (Gogala & Trilar 2004) must be considered as uncertain (Gogala, personal communication). Therefore, one can conclude that the French, Swiss and Austrian populations mark the northern borderline of the confirmed distribution.

If *C. cerdaniensis* s. l. turns out to represent two valid species, the Jura and Valais populations would probably belong to the new species *C. cantilatrix*, whereas the Ticino populations may be assigned to *C. cerdaniensis* s. str. For that reason, *C. cerdaniensis* s. str. would not be limited to the Pyrenees.

Tab. 4: Very specific vegetation types occupied by the three species in the different regions.

Region	***C. montana* s. str.**	***C. cerdaniensis* s. l.**	***C. brevipennis***
Jura Mountains and eastern Swiss Plateau	Sparse woodland on bedrock (cliffs and ridges), especially with *Erica-Pinion*	a) Sparse *Molinio-Pinetum* b) Dry meadow (*Mesobromion*) with woods	
Valais	Dry pine forest	*Quercion pubescentis*	
Southern Ticino	Sparse woodland on bedrock (cliffs and ridges)	*Fraxino orno-Ostryon*	Very sparse *Fraxino orno-Ostryon*
Geneva region	Mesophilous forest		a) Sparse *Molinio-Pinetum* b) Dry meadow with woods
Other regions	Dry pine forest		

Ecology

Habitat requirements

Studies of habitat requirements in sister species systems are of high interest. There is an obvious affinity in all three mountain cicada species from Switzerland for warm and dry climate. Favourite habitats are sun exposed and consist of sparse woodland with a distinct herb layer or well structured ecotones between dry meadows and woodland (Fig. 4). While *C. montana* s. str. can occur also in mesophilous habitats or climb over 2000 m altitude, *C. cerdaniensis* s. l. is clearly limited to the warmest locations with traditional land use or to special plant communities. In spite of its rareness, *C. brevipennis* does not seem extremely demanding with respect to the vegetation type, at least in the Geneva region. Probably, climate factors limit its spatial distribution. Therefore, *C. montana* s. str. is the most euryoecious species, *C. cerdaniensis* s. l. the most stenoecious.

In spite of the same main habitat preferences, *C. cerdaniensis* s. l. and *C. montana* s. str. show remarkable differences in the selection of vegetation types (Tab. 3): The number of the observations varies in seven of eight types significantly between the two species. *C. cerdaniensis* s. l. dominates in dry meadows with woods, periodically wet *Molinio-Pinetum* and *Fraxino orno-Ostryon*, whereas *C. montana* s. str. prefers dry pine forest, mesophilous mixed woodland, elevated coniferous forest and other vegetation types. The two pine forest types are a nice example of niche segregation. Furthermore, *C. montana* s. str. is somehow specialised on sparse woodland on bedrock which is remarkable considering the subterraneous life of the larvae (Fig. 4, Tab. 3).

Analysing the occurrence of the three species more in detail, the regional differences in habitat selection seem to be even broader than the national. This may be explained with competition between those closely related species. Each species

has obviously occupied its specific regional vegetation type in order to reduce competition between sympatric species (Tab. 4).

In the Tabular Jura, *C. montana* s. str. seems to be often displaced by *C. cerdaniensis* s. l. in the typical *Molinio-Pinetum* on marl (e.g. Effigen, Küttigen, Diegten). *C. cerdaniensis* s. l. reaches a high density in this vegetation type while *C. montana* s. str. is missing or present with low population sizes. Due to the ability of *C. montana* s. str. to occupy very small and isolated habitats, a coexistence of the two species in the western part of the Jura Mountains seems possible. *C. montana* s. str. occurs more often at rocky and dry locations such as ridges with limestone (*Erico-Pinion*) in the Folded Jura (see Fig. 8A). With regard to vegetation type, *C. brevipennis* seems to replace *C. cerdaniensis* s. l. in the Geneva region. In the Valais, the spatial dispersion can be best explained by the local distribution of *Quercus pubescens* (*C. cerdaniensis* s. l.) and *Pinus sylvestris* (*C. montana* s. str.).

Contrary to the author's expectations, unstable slopes or dry parts of floodplains are usually not occupied by mountain cicada species, although the vegetation structure (plant succession) seems optimal. Probably, the natural incidents in these sites prevent a regularly successful development of the larvae which spend at least two years in the soil. In comparison with cut grassland systems, pastured habitats seem to be abandoned.

These results on habitat requirements can hardly be compared to other studies. Either all recent authors do not provide comprehensive ecological data or their conclusions are limited due to taxonomical problems.

Sympatric and syntopic occurrence

In spite of competition factors, there are several regions with sympatric occurrence and even a remarkable amount of locations with syntopic appearance of two species (Fig. 13). All pairs of sympatric and syntopic occurrence can be observed. Sympatric populations were also mentioned by Gogala & Trilar (2004) and Sueur & Puissant (2007a). Based on observations during the field work, it is possible to present a preliminary model about the habitat partitioning in syntopic systems (Fig. 14).

Fig. 14 shows that in syntopic systems of the sister species a dependence on vegetation structure seems to be decisive in the three illustrated regions. *C. montana* s. str. occupies the highest vegetation, *C. brevipennis* the lowest, *C. cerdaniensis* s. l. is intermediate. The varying vegetation structures, demonstrated in a circle, can also be interpreted as a process of plant succession. In the Jura Mountains, males of *C. montana* s. str. not only prefer higher vegetation, they also sing higher up in the trees than does *C. cerdaniensis* s. l. There is another fact pointing to vertical niche segregation: Males of *C. montana* s. str. have never been observed in the herb layer when singing, males of *C. cerdaniensis* s. l. rarely, males of *C. brevipennis* often. Gogala & Trilar (2004) mentioned similar observations for *C. montana* s. str. and *C. brevipennis*. The behaviour in syntopic systems seems to be influenced by interspecific competition. Sueur & Puissant (2002) gave comparable examples on the genus *Tibicina* in France. In the Valais, syntopic populations can be particularly observed when dry Pine forest and *Quercion pubescentis* overlap (see Fig. 8D).

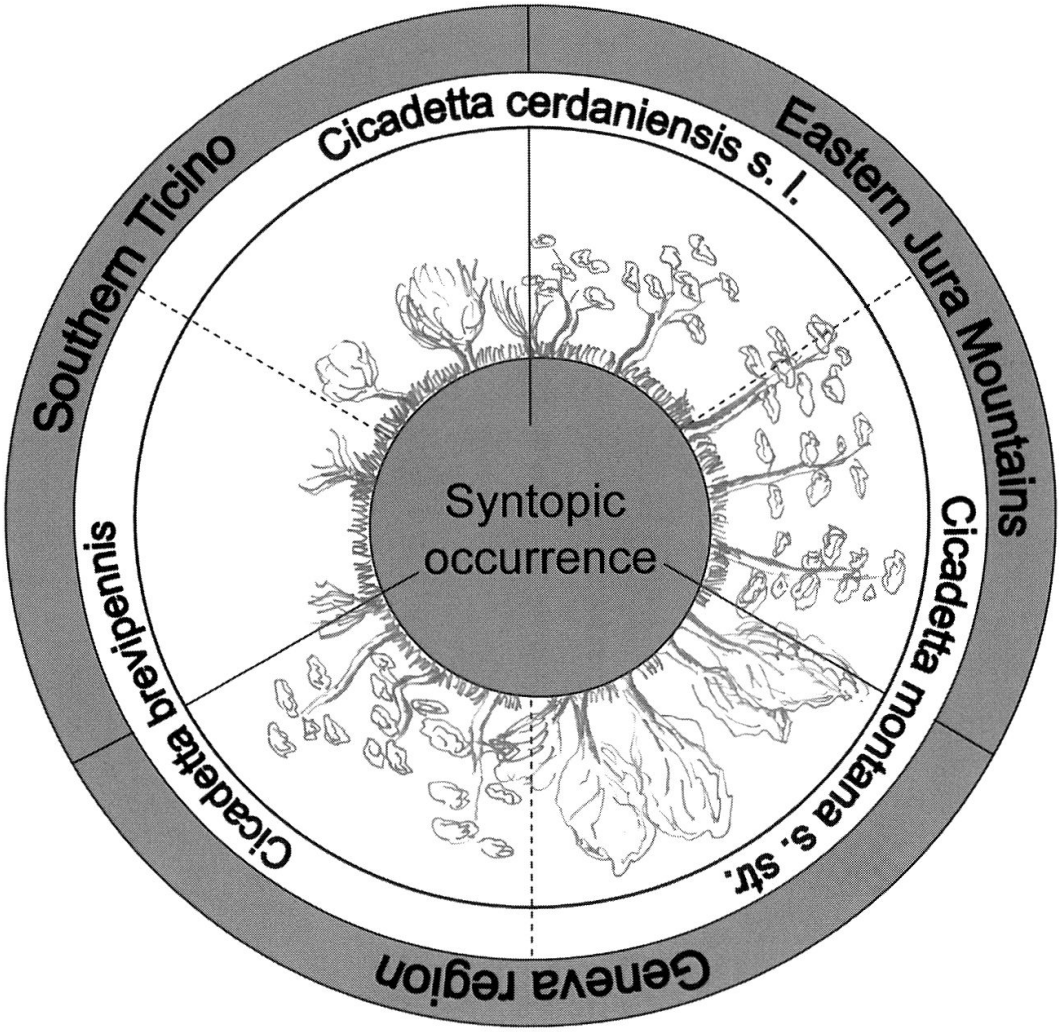

Fig. 14: Preliminary approach of the niche segregation in syntopic population systems: Three sister species pairs in dependence of the vegetation structure and the region.

Adult seasonal pattern

All three species seem to reach their maximal activity in June (Fig. 6). The seasonal niche segregation of *C. montana* s. str. and *C. cerdaniensis* s. l. with respect to singing period has to be interpreted carefully, taking into consideration the almost equally extreme and median values (Tab. 3). Further studies have to prove if there is really a slight allochrony.

It is also possible that *C. brevipennis* starts and finishes its activity period even earlier than *C. cerdaniensis* s. l. At least, it seems that the proportions of singing individuals change clearly from May to July in the largest syntopic populations of *C. brevipennis* and *C. cerdaniensis* s. l. at Monte San Giorgio. Allochrony in sister species relations was described for other European cicadas of the genus *Tibicina* by Sueur & Puissant (2002).

Comparing the observations over three years, it seems that the population sizes fluctuate highly, probably dependent on weather conditions before metamorphosis.

The wet and cool months of April and May might have caused a very low activity in 2005.

Endangerment and protection

None of the three species is quite frequent in any regions, except for *C. montana* s. str. in the central Valais. There is no suitable habitat elsewhere covering a continuous area of several square kilometres. The situation shown for the Jura Mountains is much more typical for Switzerland: Small habitats with a favourable climate in combination with suitable vegetation structures are isolated and scattered over the landscape. Some of them are clearly smaller than one hectare. A sufficient genetic contact between the populations is given for this well-flying insect group, as long as the different habitats are interconnected. Several sites have already been protected by law or contracts, because they represent a high biodiversity with many thermophilous organisms, especially in the Jura Mountains.

Cicadas are attractive and, therefore, suitable as flagship species in nature protection programs. Regions around Geneva or in the Jura Mountains have so far not been known for their responsibility toward cicada populations.

After analysing the preferences in habitat selection, one can point out the following endangerments for Swiss populations:

a) decreased level of incoming light in sparse woodland
b) abandonment of traditional land use or fertilisation in dry meadows near forests
c) cutting of solitary trees and shrubs, hedges or woods in dry meadows
d) destruction of well structured forest edges
e) probable: pasturing of sparse woodland and dry meadows

Currently it is rather difficult to assess the level of endangerment for the three cicada species because of three facts: Firstly, the impact of good years (2004, 2006) versus bad years (2005) on the population size is presently unknown. Secondly, there is a lack in knowledge concerning the international distribution and abundance. Therefore, one can hardly estimate the responsibility of Switzerland for their protection. Thirdly, the taxonomical problems with *C. cerdaniensis* s. l. may influence the assessments. Nevertheless, the following conclusions are reached:

a) *C. cerdaniensis* s. l. is the most stenoecious species in Switzerland and prefers endangered habitats like dry meadows and sparse *Molinio-Pinetum* which normally need a continuous and costly cultivation. Therefore, it is the most endangered species. This fact would be accentuated if division into two taxa can be proven.
b) *C. montana* s. str. is the most abundant species. Many habitats are not endangered seriously or/and have developed naturally. *C. montana* s. str. is the less endangered species in Switzerland.
c) *C. brevipennis* is very rare in Switzerland and only distributed peripherally. The international responsibility of Switzerland is probably low.
d) All three species must be considered as critically endangered in the Southern Ticino. A remarkable decrease of suitable habitats has obviously taken place in the last century because of the abandonment of agricultural land use and the expansion of settlement areas there.

In order to support the three mountain cicada species, it is suggested to thin out forests on poor soil (especially pine forests) and to improve the structure of forest edges near dry meadows. The sites should to be warm and sunny.

CONCLUSIONS

Based on this study, the following conclusions can be drawn:

a) All three established species of the *C. montana* complex known from Central Europe were recorded in Switzerland. Taking the work of Pillet (1993) into account, a total of seven cicada species are now known for Switzerland.
b) Intermediate song structures between *C. cerdaniensis* s. str. and recently described *C. cantilatrix* exist. Therefore, a complicated dialect pattern or clinal spatial changes in song patterns seem to be as likely as a new valid species.
c) For the first time, comprehensive data on distribution, abundance and ecology of the sister species is published for an entire country.
d) *C. montana* s. str. is the most euryoecious, *C. cerdaniensis* s. l. the most stenoecious and endangered species in Switzerland. *C. brevipennis* occurs only peripherally.
e) For the first time, this work allows to separate *C. cerdaniensis* s. l. from *C. montana* s. str. according to ecological variables. An explicit niche segregation is assumed for vegetation types, altitude and substrate.
f) The following additional factors are supposed to cause an isolation of the competing three sister species: the vertical position of singing males (especially in syntopic populations) and a slightly allochronic singing period.

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ZUSAMMENFASSUNG

Noch gegen Ende des 20. Jahrhunderts vertraten die meisten Taxonomen die Auffassung, dass alle Bergzikaden (*Cicadetta montana* s. l.) Mitteleuropas einer Art angehören. Das Studium der nahe an der hörbaren Grenze befindlichen Gesänge zeigte jedoch in den letzten paar Jahren, dass es sich um mindestens drei Arten handeln muss.
In der zentralen Datenbank des «Centre Suisse de Carthographie de la Faune» (CSCF) waren zu Beginn dieser Studie lediglich zwei Dutzend Funddaten der Sammelart aus der Schweiz verfügbar. Für verschiedene europäische Länder liegen mittlerweile einzelne Beobachtungsdaten der neu getrennten Arten vor. Erstmals werden in dieser Studie basierend auf 283 aktuellen, gesangsbestimmten Beobachtungen (200 eigene und 83 Fremdbeobachtungen) Verbreitungskarten für ein ganzes Land publiziert.
Trotz der noch vorhandenen Bearbeitungslücken zeichnen sich drei sehr charakterische Verbreitungsbilder ab: *C. montana* s. str. besiedelt ausser den Hochalpen und Grossteilen des Mittellandes sämtliche Regionen der Schweiz, allerdings oft in kleinen isolierten Populationen. *C. cerdaniensis* s. l., welche hiermit für die Schweiz definitiv bestätigt wird, kommt primär am Jurasüdfuss, im Tafeljura, Rhonetal und Südtessin vor. Die bis 2003 übersehene Art konnte erstaunlicherweise in den letzten vier Jahren an 67 Standorten nachgewiesen werden und ist somit nicht ausserordentlich selten, weist jedoch

die engsten ökologischen Ansprüche auf. Von *C. cerdaniensis* s. str. wurde kürzlich anhand von Gesangsmustern die neue Art *C. cantilatrix* abgetrennt. Weil in der Schweiz intermediäre Gesänge festgestellt werden konnten, scheint ein europaweites kompliziertes Gefüge an Dialekten oder ein Gradient im Gesangsmuster mindestens so wahrscheinlich, wie die Existenz von zwei «guten» Arten. Genetische Untersuchungen und umfangreiche Gesangsanalysen sollten europaweit durchgeführt werden, um die Problematik zu klären. *C. brevipennis* schliesslich wurde im Jahr 2005 im südlichsten Tessin erstmals für die Schweiz belegt, 2006 folgten mehrere Nachweise im Kanton Genf. Diese Art ist in der Schweiz wohl klimatisch limitiert.

Alle Arten sind auf gut besonnte, warme Trockenlebensräume mit lichter Bestockung (vorwiegend Föhren-, Flaumeichen und Hopfenbuchenwälder) oder Oekotonbereiche zu Magerwiesen angewiesen, wobei *C. montana* s. str. bis in mesophile Vegetationstypen vordringen kann. Zwischen *C. montana* s. str. und *C. cerdaniensis* s. l. lassen sich hoch signifikante Unterschiede in der ökologischen Nischenbesetzung bei den Variablen «Höhenverteilung», «Vegetationstyp» und «Substrat» ausmachen. Damit gelingt erstmals nach der akustischen und genetischen Differenzierung auch eine ökologische Auftrennung zwischen den Zwillingsarten. Im Weiteren werden zwischen den drei Arten Unterschiede in der ökologischen Nische bezüglich vertikaler Höhe der singenden Männchen und jahreszeitlichem Auftreten vermutet.

Die Singzikadenfauna der Schweiz umfasst hiermit statt der bislang angenommenen fünf, mindestens sieben Arten. Angesichts des guten Untersuchungsgrades der Schweizer Fauna und der Gesangsaktivität der Gruppe ist dies eine höchst erstaunliche Entwicklung, welche auch auf den praktischen Naturschutz Auswirkungen haben könnte.

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