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Authors: Bauer, Norbert, and Kenyeres, Zoltán

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Habitat preference studies of some species of the genus *Isophya* Brunner von Wattenwyl, 1878 (Orthoptera: Phaneropteridae) in the western part of the Carpathian Basin

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Norbert Bauer and Zoltán Kenyeres

[NB] Department of Botany, Hungarian Natural History Museum, 1087 Budapest, Könyves K. krt. 40., Hungary. E-mail: bauer@bot.nhmus.hu
[ZK] * 8300, Tapolca, Deák F. u. 7., Hungary. E-mail: kenyeres@vnet.hu

Abstract

Species of the tettigoniid genus *Isophya* are indicators of biogeographical history and also measures of the state of nature conservation in the Carpathian Basin and in Europe. We surveyed the occurrence and habitat preference of five species (*I. camptoxypha*, *I. costata*, *I. kraussii*, *I. modesta*, *I. modestior*) living in the Transdanubian region (the western part of the Pannonian biogeographical region) to determine the potential for the preservation of the insects and their habitats. Statistical analysis shows the optimal habitats of *I. camptoxypha* are patches of herbaceous plants and lower shrub layers within natural forests dominated by tall or medium-height broad-leafed (mainly dicotyledonous) mesophytic forest species. For *I. camptoxypha* smaller clearings, and the forest ecotones containing the aforementioned plant species are suboptimal, and populations of the insect species occur there at a significantly lower density. Present-day *I. costata* find optimal conditions in highly natural, loess grasslands or mesophytic hayfields and steppe grassland–hayfield transitions rich in plant species. This same *Isophya* species at a lower density can be found in grasslands having suboptimal conditions, but with a similar habitat physiognomy, adjoining the above-mentioned grasslands or developing through their slight degradation. Based on a critical literature review and our own sampling, we also comment on the habitat choice of a further three species (*I. kraussii*, *I. modesta*, *I. modestior*).

Key words

habitat preference, biogeography, Carpathian Basin, Orthoptera, Tettigonioidea, Phaneropteridae, *Isophya camptoxypha*, *I. costata*, *I. kraussii*, *I. modesta*, *I. modestior*

Introduction

We studied habitat preference of five *Isophya*, Brunner von Wattenwyl 1878, species in the Transdanubian region (western part of the Carpathian Basin). The genus, localized in Europe, includes 46 species (Heller *et al.* 1998). Six species occur in Hungary (Nagy 2003, Heller *et al.* 1998, 2004): *Isophya camptoxypha* (Fieber 1853) [syn.: *Isophya brevipennis* Brunner von Wattenwyl 1878 (Heller *et al.* 2004)]; *Isophya costata* Brunner von Wattenwyl 1878; *Isophya kraussii* Brunner von Wattenwyl 1878; *Isophya modesta* (Frivaldszky 1867); *Isophya modestior* Brunner von Wattenwyl 1882 and *Isophya stysi* Cejchan 1957. *Isophya stysi* is known only from the eastern part of the Carpathian Basin.

Isophya spp. have a particular importance in the Carpathian Basin from the perspective of biogeography and conservation. The ranges of the several taxa having restricted distributions and the topographic relationship between individual species, are of key importance in the exploration of zoogeographical processes following the last ice age. Due to the reduction of their natural habitat, these mostly strongly specialised species — those most sensitive in their choice of habitat — have been strongly constrained since the second half of the previous century, and are therefore considered to be indicator species of the state of nature conservation in the region.

These *Isophya* species are characterised by limited mobility and a topographic distribution of isolated populations of low density and close habitat-dependence — partly due to their dicotyledonous plant-feeding preferences (Varga 1999). Within the European range of the genus there are a large number of endemic species having a restricted distribution, particularly in the center of dispersal in the Southern Balkans and Asia Minor (Otte *et al.* 2004, Heller 2004, Çiplak 2004). Hungary and the area within Hungary discussed in the present article — the region west of the Danube — are situated on the edge of the distribution of the taxon (Fig. 1.). Here, as a general biogeographical phenomenon (Varga 1971), the number of detected species is much smaller than in the center of dispersal.

The objective of our research was to survey the occurrence, habitat preferences and sensitivity to habitat changes of the five species living in the Transdanubian region (Fig. 1A, western part of the Pannonian biogeographical region) and to evaluate possibilities for their preservation—several populations being subject to human interference.

I. camptoxypha is an endemic species of the Carpathian Basin, widespread in the Carpathians and Transylvania (Kis 1960, Storozhenko & Gorochov 1992, Fedor 2001, Nagy *et al.* 1998, 1999). It occurs at the edge of the western part of the Carpathian Basin and in the lower mountains of the Eastern Alps (Nagy *et al.* 2003). In Hungary (Fig. 1B) it is known from the Soproni Mts (Nagy *et al.* 2003), Kőszegi Mts (Szövényi & Nagy 1999, Kenyeres & Bauer 2005), Mecsek Mts (Vadkerti *et al.* 2003), Villányi Mts (Nagy A. & Nagy B. 2000) and Őrség (Nagy & Szövényi 1997, Kenyeres & Bauer 2005). The Kőszegi Mountains incorporate the main distribution of this species in Hungary.

I. costata is another species endemic to the Carpathian Basin, relict from the postglacial steppe period, with a disjunct distribution (Varga 1995). Outside the boundaries of Hungary it is known only in the eastern part of Austria (Viennese Basin) (Kaltenbach 1970, Berg *et al.* 1996), and in the Maros valley in Romania (Kis 1960). In Hungary (Fig. 1C) it has several isolated occurrences in the colline region of the Hungarian Middle Range and the Mecsek Mts (Nagy 1981, 1987; Kenyeres *et al.* 2004; Vadkerti *et al.* 2003; Vadkerti 2004), and also in Tolnai-Hegyhát (Kenyeres & Bauer unpub.). Besides this it is known from some populations in the Hungarian Great Plain (Nagy 1984, Nagy & Szövényi 1999, Kenyeres & Bauer unpub. from the Marcal-Basin and Mezőföld). Perhaps its most robust Hungarian populations can be found in the Balaton Uplands and on the southern slopes of the Transdanubian Mountains: our habitat preference examination was also carried out here.

I. kraussii is a species with a Central-European distribution (Ingrisch & Köhler 1998), formerly known as *Isophya pyrenea* (Serville 1839) in the Hungarian literature. Acoustic analyses have shown that it occurs in mountains of moderate height in France: Massif Central, adjacent to the Pyrenées (Ingrisch 1991); it is also known from Germany, Austria, Poland, the Czech Republic, Hungary and Slovenia (Heller 2004).

In Hungary *I. kraussii* (Fig. 1D) has been described as characteristic of forest clearings, semidry grasslands (on deforested areas), and forest ecotones of the Transdanubian Medium Mountains (Rácz 1979, 1992, Kenyeres 2006) and the adjoining Northern Medium Mountains (Nagy *et al.* 1998, 1999, Nagy & Rácz 1996, Rácz 1992, 1998). [The Transdanubian Medium Mountains and the Northern Medium Mountains together make up the Middle Range.] This species has only some isolated island-like occurrences in other Hungarian regions (Kőszegi Mountains: Szövényi & Nagy 1999; Hercseg Hill: Kenyeres & Bauer unpub.).

I. modesta is known from Bulgaria, Romania and also from the territory of the former Yugoslavia (Heller 2004). A large percentage of the occurrence data in Hungary (Fig. 1E) is from the western part of the country: Mecsek Mts (Nagy 1981, Nagy A. & Nagy B. 2000) Villányi Mts (Nagy 1981, Nagy A. & Nagy B. 2000) Somló Hill (Nagy 1981); but the species is also known from some localities in the Northern Mountains (Nagy 1981, Nagy & Rácz 1996, Rácz 1998).

Besides its center of distribution, which includes Bulgaria, Macedonia and the southern parts of Romania, there are isolated occurrences of *I. modestior* in Yugoslavia (Serbia, Kosovo, Voivodina, Montenegro), Italy, Austria and Hungary (Fontana 1998, Nagy *et al.*

A

B

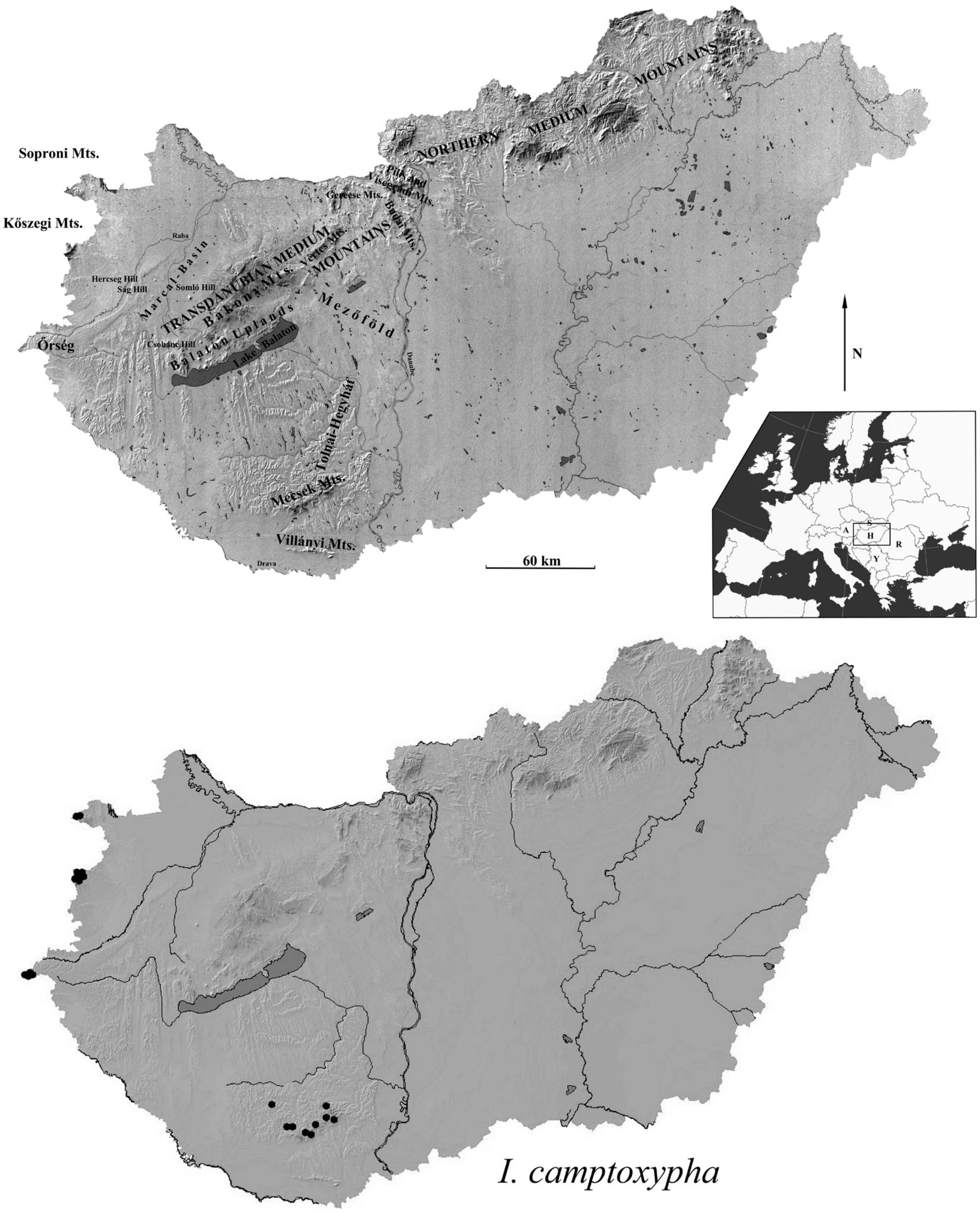


Fig. 1A. Transdanubian region under study. **B.** Distribution of *I. camptoxypha*.

2003, Heller 2004). In Hungary it is rare — apart from substantial populations in Mecsek and the Villányi Mts (Nagy A. & Nagy B. 2000, Szövényi *et al.* 2001, Vadkerti *et al.* 2003, Vadkerti 2004). It has small populations in the Kőszegi (Szövényi & Nagy 1999) and Vértes Mountains (Szövényi *et al.* 2001) and we detected it in Csobánc Hill (Kenyeres 2006) in the western part of the Balaton Uplands in 2004.

Distributions of the analysed *Isophya* species show a certain biogeographical isolation in the western part of the Carpathian Basin (Fig. 1). From our experience, this detachment can also be observed in the habitat choice of the species.

We attempted to visit as many known and potential habitats as possible for these *Isophya* spp., determining their extent and associated habitat variables (plant coenological samples, measurements of air temperature and relative humidity).

Since the effective protection and preservation of these insects can only be based on accurate knowledge of their choice of habitat, our work has both autoecological and conservation implications.

Methods

Our research extended to the whole Transdanubian region. However, most sampling originates from the northern part of this area — which is richer in potential *Isophya* habitats.

In the course of systematic fieldwork repeated over several years, while keeping the phenology of the species in mind, we recorded information on density, geographical location, habitat and plant association. Plant coenological samples [samplings of the vegetation types were taken in 2 × 2-m quadrats (1–5) at all sites, using the Braun-Blanquet method; cover of the plant species in percentages were recorded], measurements of air temperature and of relative humidity were also made at every site (on the surface and in the air at 10, 20, 30 and 120 cm above the surface).

In the case of two species, *I. costata*, *I. camptoxypha*, the quantity of data allowed statistical processing. Due to the basic differences in habitat of these two species, different sampling methods were

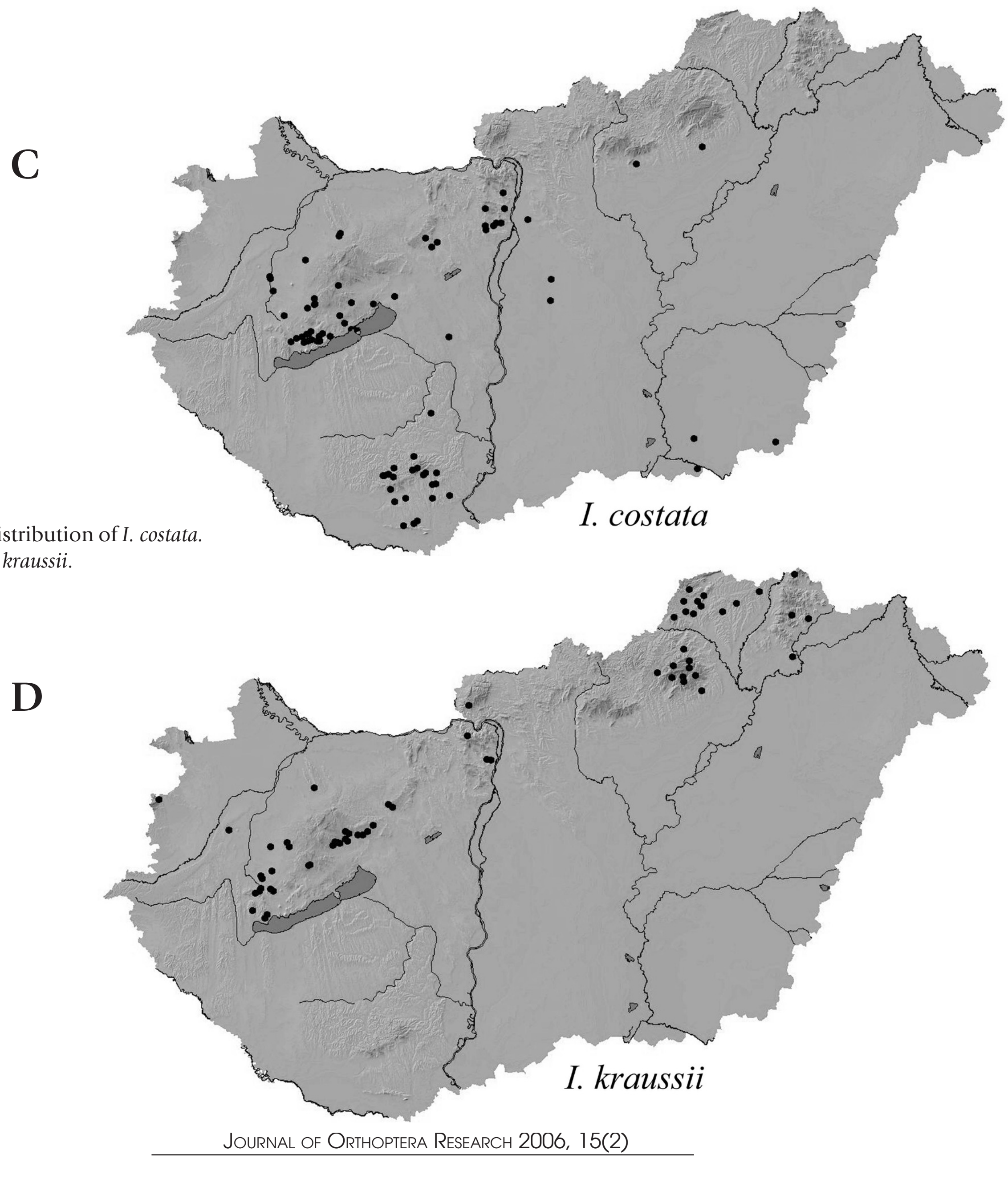
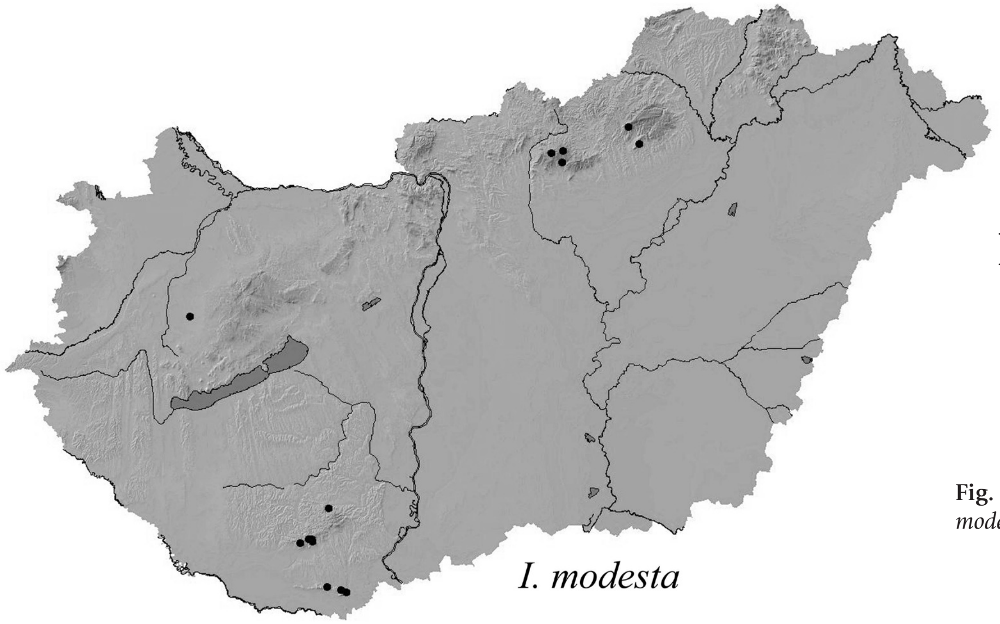


Fig. 1 (contin.) **C.** Distribution of *I. costata.* **D.** Distribution of *I. kraussii*.



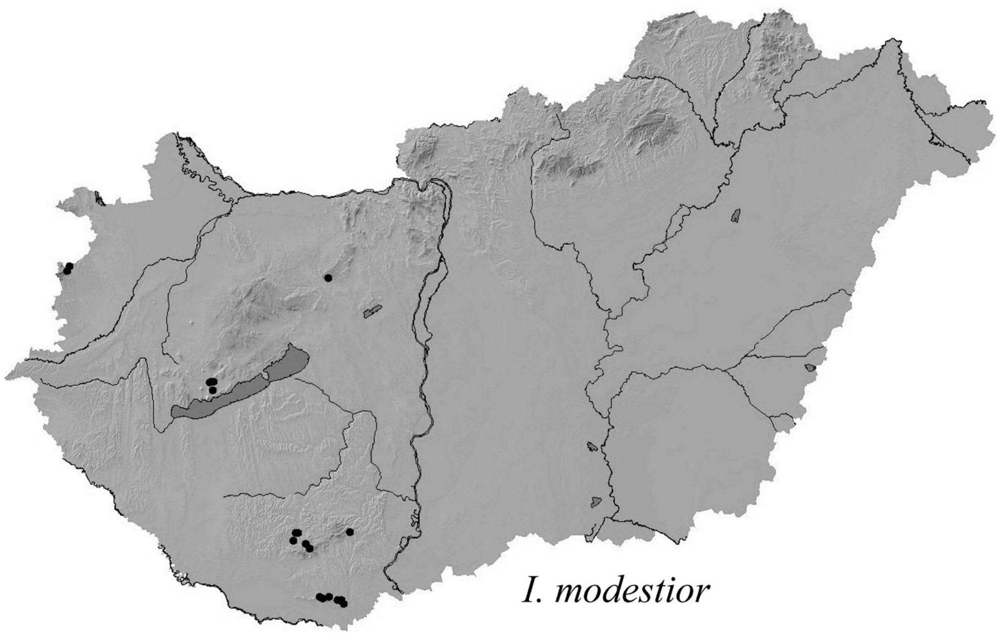


Fig. 1 (contin.) **E.** Distribution of *I. modesta*. **F.** Distribution of *I. modestior*.

necessary in determining the size of the population. In the case of *I. costata*, the deme was determined for a 10 × 10-m, homogeneous quadrat. In the course of visual detecting by line-transect, 10-m long 1-m wide grassland strips were examined and the estimated population of the quadrat calculated by multiplying the number of insects observed by 10.

During the detailed quantitative examination of *I. camptoxypha* — a species found previously mainly in disturbed forest ecotones — it was established that, apart from these secondary habitats, it was most abundant in the richer herb layer under natural forest openings. The choice of habitat of the species was examined in 32 areas. Sampling concerning the size of the located populations was carried out by visual detection, but due to the different habitat and in contrast to the former case, the 5 × 5-m quadrats were sampled pseudorandomly (for 10 min per each sample). During this time each detection of an *I. camptoxypha* individual was recorded as well its sex and what plant it was on at the time of detection. In the case of both species, the connections between the species abundance of *I. camptoxypha* and the habitat parameters were examined with Pearson Product-Moment Correlation analysis (StatSoft 1995).

Nomenclature of the orthopterans follows Heller *et al.* (2004), plant names are after Simon (2000) and plant association after Borhidi (1996).

Results

I. camptoxypha

I. camptoxypha (Figs 2, 3) specimens were collected from patches of herb and lower-shrub layers of natural forests (*Cyclamini purpurascentis-Carpinetum* Csapody *ex* Borhidi et Kevey 1996, *Cyclamini purpurascentis-Fagetum* Soó 1971, *Castaneo-Quercetum* I. Horvat 1938) which were dominated by tall or medium-high broad-leafed (mainly dicotyledonous) mesophytic forest plant species. Such habitats are typically the undergrowth of clearings within forests, developing as

Fig. 2. *Isophya camptoxypha* (male).

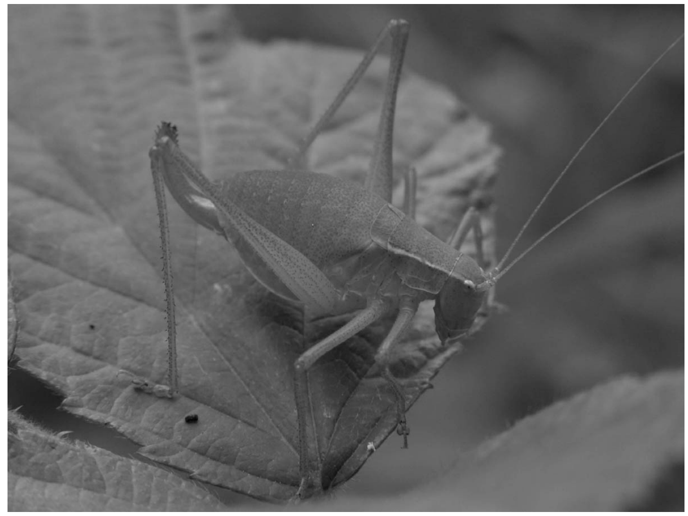


Fig. 3. *Isophya camptoxypha* (female).

a result of spontaneous natural tree-falls or selective forest management. Seventy-two percent of the collected insects were obtained from seven plant taxa (*Rubus fruticosus* agg., *Salvia glutinosa* L., *Aegopodium podagraria* L., *Circaea lutetiana* L., *Urtica dioica* L., *Impatiens parviflora* DC., *Stachys sylvatica* L.).

I. camptoxypha usually achieves high density in natural clearings in forests and forest ecotones significantly covered by the plant species *Salvia glutinosa*, *Aegopodium podagraria*, *Circaea lutetiana*, *Stachys sylvatica etc*. The average density of the examined populations living in the herb layer of the medio-European oak-hornbeam forests was 4.6 specimens per 10-m^2 quadrat. On the other hand, the average density of the populations living in the herb layer of degraded and mixed stands of the medio-European oak-hornbeam forests, of different types of alder forests and of beech forests, was about 1 specimen per 10-m^2 quadrat (Table 1).

A significant positive correlation was found between the density of *I. camptoxypha* and 1) the cover of broad-leafed, mesophytic dicotyledonous plant species [r = 0.37]; 2) the cover of *Aegopodium podagraria* [r = 0.49] 3) the cover of *Stachys sylvatica* [r = 0.49] (Table 2).

Fig. 4. *Isophya costata* (male).

Fig. 5. *Isophya costata* (larva).

I. costata

Today in the western part of the Carpathian Basin *I. costata* occurs under optimal conditions of undisturbed loess grasslands or mesophytic hayfields and steppe grassland-hayfield transitions rich in plant species. Nevertheless, it can also be found at lower densities under suboptimal conditions that adjoin these habitats and arise through their degradation (Kenyeres *et al.* 2004). The population size (average values of the individual numbers per 10-m^2 quadrats) was 56.8 in hayfields and 40.0 in steppe grasslands. The other extremity was found on balks and weedy vegetation patches. In these latter grasslands the population size was around one individual per quadrat (Table 1).

The size of the *I. costata* populations showed a positive correlation with the overall cover of mesophytic [WB (Water Balance) values are 4–6 in Borhidi (1995)] dicotyledonous plant species (r_1 = 0.952, r_2 = 0.993, r_3 = 0.995, r_4 = 0.960, with different sampling methods) (Table 3). Based on this, we can state that the size of the population of *I. costata* (Figs 4, 5) is predicted by the cover value of dicotyledonous species satisfying the nutrition needs of the insect species on the adjoining suitable grassland patches.

Fig. 6. *Isophya kraussii* (male).

Fig. 7. *Isophya modesta* (male).

I. kraussii

This *Isophya* species is originally from forest clearings of xerothermic tomentose oak forests and shrub forests of the submontane (*Orno-Cotinetalia* Jakucs 1960). This habitat is characterised by vegetation types such as xeromesophytic grasslands (*Festuco-Brometea* Br.-Bl. et R.Tx. ex Klika et Hadac 1944), forest steppe and rocky shrublands with mainly low-shrub species (for example *Rosa spinosissima* L., *Rosa gallica* L., *Cotoneaster integerrimus* Medic., *Cotinus coggygria* Scop.).

On the basis of our experience with the other species of the genus, it seems probable that *I. kraussii* also has a most-preferred, optimal habitat (presumably xeromesophytic clearings dominated by *Bromus erectus sl.* which are partly of natural origin, partly the result of human-clearing origin) in which it occurs with its highest density. The species can settle in suitable adjoining habitats but also disperse elsewhere or it can remain and be constrained, establishing populations with low density. (These results were also confirmed by the examination of small, island-like populations living in Somló Hill and in the Kőszegi Mountains.) Populations of *I. kraussii* (Fig. 6) are endangered by occasional forest fires in the xerotherm oak-forest clearing mosaic serving as its habitat. The specimen numbers per 10 × 10-m quadrats ranged between 1 and 4 (Table 1).

I. modesta

We examined two habitats of *I. modesta* (Fig. 7), in Somló Hill on the northeastern edge of its range and in one of the centrally located steppe meadows of the Mecsek Mts. On the plateau of Somló Hill it occurs in the grass — currently maintained by cutting — which can be considered as a semidry, ancestral-clearing (human-deforested) meadow. Besides the growing amount of meadow elements resulting from cutting, a marked presence of the original forest-steppe species (*Nepeta nuda* L., *Centaurea scabiosa* L., *Salvia pratensis* L., *Thalictrum minus* L. *etc.*) is also apparent — the grass mostly resembles the structure of natural semidry steppe-meadows. Similarly, the habitat of the species in the Mecsek Mountains can also be classified as a semidry steppe meadow. Average density of the species in 10 × 10-m quadrats sampled at Somló Hill was 6.50; the individual numbers of the samples ranged between 1 and 12 (Table 1).

I. modestior

In the course of our examinations, two habitats of this species (Fig. 8) were sampled: 1) on one of the isolated basalt volcanic island-hills of the Balaton Uplands (Csobánc Hill), that from a biogeographic point of view is characterised by very valuable plant and animal species, and 2) in a centrally located steppe-meadow of the Mecsek Mountains, adjoining a forest ecotone where several *Isophya* species occur simultaneously. Festuco-Brometea grasslands of partly shadowy forest clearings, rich in dicotyledonous herbaceous species, seemed to be optimal as the choice of habitat of *I. modestior* too. The habitat found in Csobánc Hill is a cultivated forest-steppe fragment, the grass of an extensive orchard abandoned long ago. Average density of the species in 10 × 10-m quadrats sampled in the Csobánc Hill's steppe-meadows was 6.50; the individual numbers in the samples ranged between 1 and 4. These same parameters were average density 1.20, with individual numbers in the samples ranging between 1 and 2, on cultivated forest-steppe fragments (Table 1).

Fig. 8. *Isophya modestior* (female).

Table 1. Average density [no. of insects per 100 m[2] (10×10-m quadrats)]. Ranges of individuals per quadrat in parens.

Isophya camptoxypha	AD
Herb layer of medio-European oak-hornbeam forests	4.60 (1-7)
Herb layer of medio-European oak-hornbeam forests including beech stands	3.00 (1-5)
Forest edges with tall herb vegetation	1.80 (1-6)
Herb layer of degraded stands of medio-European oak-hornbeam forests	1.30 (1-2)
Diverse alder forests	1.30 (1-2)
Beech forests	1.00 (1-1)
Isophya costata	AD
Hayfields	56.80 (20-70)
Steppe grasslands	40.00 (10–60)
Rush fens	30.00 (20–40)
Semidry grasslands	1.60 (1-3)
Balks	1.30 (1-2)
Weedy vegetation	1.25 (1-2)
Isophya kraussii	AD
Xeromesophytic clearings dominated by *Bromus erectus*	2.14 (1-4)
Forest ecotones	2.62 (1-4)
Isophya modesta	AD
Semidry clearing-meadows (human-deforested)	6.50 (1-12)
Isophya modestior	AD
Steppe-meadows	2.40 (1-4)
Cultivated forest-steppe fragments	1.20 (1-2)

Table 2. For the correlation analyses significant positive correlations (*) were obtained between the species abundance of *I. camptoxypha* (I.ca.-N) and plant cover: (1) the cover of the "fine" plants [dicotyledonous plant species with medium (4-6) WB- value, CofFP]; (2) the cover of *Aegopodium podagraria* (A.p.-C); (3) the cover of *Stachys sylvatica* (S.s.-C). Also significantly correlated was the cover of *Aegopodium podagraria* and *Stachys sylvatica*. [Other abbreviations: R.f.-C: cover of *Rubus fruticosus*; S.g.-C: cover of *Salvia glutinosa*; C.l.-C: cover of *Circaea lutetiana*; U.d.-C: cover of *Urtica dioica*; I.p.-C: the cover of *Impatiens parviflora*.]

	I.ca.-N	CofFP	R.f.-C	S.g.-C	A.p.-C	C.l.-C	U.d.-C	I.p.-C	S.s.-C
I.ca.-N		*0.37	-0.12	0,25	*0.49	-0.02	-0.17	0.19	*0.49
CofFP	*0.37		0.30	0.20	0.32	0.03	0.32	0.18	0.28
R.f.-C	-0.12	0.30		-0.31	-0.12	-0.17	-0.11	-0.04	-0.14
S.g.-C	0.25	0.20	-0.31		0.27	0.01	-0.15	-0.16	0.06
A.p.-C	*0.49	0.32	-0.12	0.27		-0.04	-0.02	-0.04	*0.40
C.l.-C	-0.02	0.03	-0.17	0.01	-0.04		-0.09	-0.10	0.17
U.d.-C	-0.17	0.32	-0.11	-0.15	-0.02	-0.09		-0.06	-0.05
I.p.-C	0.19	0.18	-0.04	-0.16	-0.04	-0.10	-0.06		0.20
S.s.-C	*0.49	0.28	-0.14	0.06	*0.40	0.17	-0.05	0.20	

Marked correlations are significant at $p < 0.05$

Earlier (previously published) information about the habitat choice of the examined species

I. camptoxypha

Previous literature reporting the presence of *I. camptoxypha* makes diverse statements concerning its habitat (Kis 1960, Storozhenko & Gorochov 1992, Nagy & Szövényi 1997, Szövényi & Nagy 1999, Nagy *et al.* 1998, 1999, 2003, Fedor 2001, Vadkerti *et al.* 2003). In effect almost all potential orthopteran habitats are listed as habitats of this species [shrubby vegetation with many weed (ruderal) elements beside roads, clearings, mesophytic grasslands, forest-steppe patches, tall herb stands (altoherbosa vegetation), mountain meadows *etc.*].

I. costata

The previous literature also contains significant contradictions concerning the choice of habitat of *I. costata*. According to Berg *et al.* (1996), in Austria the insect can find optimal conditions from the tall, continental semidry grasslands (*Festuco-Brometea*) to the class of tall-grass meadows and hayfields (*Molinio-Arrhenetheretea*). In Hungary published accounts embrace loess grasslands, the cut sides of banks, hayfields, steppe meadows, moist grasslands, clearings in oak forests *etc.* Most occurrences take place in regions characterized as potential steppe and forest-steppe vegetation (*e.g.*, the Balaton Uplands, the Southern-Bakony, Mezőföld, margins of the Mecsek

Table 3. Significant positive correlations (*) were shown between the species abundance of *I. costata* and the cover of mesophytic dicotyledonous plant species. 1: Species abundance of *I. c.* based on visual detection by line-transect (data were collected by morning examinations); 2: Species abundance of *I. c.* based on visual detection by line-transect (data were collected by evening examinations); 3: Species abundance of *I. c.* (average); 4: Species abundance of *I. c.* based on sweep-netting (data were collected by morning examinations); 5: Species abundance of *I. c.* based on sweep-netting (data were collected by evening examinations). — I: cover of mesophytic plant species; II: cover of nonmesophytic plant species; III: percentage of mesophytic plant species; IV: percentage of nonmesophytic plant species; V: percentage of mesophytic monocotyledonous plant species; VI: percentage of mesophytic dicotyledonous plant species; VII: percentage of nonmesophytic monocotyledonous plant species; VIII: percentage of nonmesophytic dicotyledonous plant species.

	I	II	III	IV	V	VI	VII	VIII
1	*0.979	*-0.975	*0.969	*-0.969	0.947	*0.952	*-0.976	-0.276
2	0.830	-0.805	0.797	-0.797	0.751	*0.993	-0.833	-0.025
3	0.920	-0.904	0.897	-0.897	0.862	*0.995	-0.920	-0.146
4	0.725	-0.687	0.683	-0.683	0.629	*0.960	-0.725	0.069
5	0.888	-0.922	0.874	-0.874	0.838	0.940	*-0.960	0.002

Mts., southern slopes of the Northern Mts.). But, if habitats suitable for colonization are present, isolated occurrences with low density can be found in the Viennese Basin as far as the Pannonian climate boundary (Berg *et al.* 1996).

Due to its phenological features (larvae in early April, adults in May), in order to preserve this animal it is essential to prevent fires within the parched grass of early spring, to avoid mowing before egg laying and treading/travel of various origins.

I. kraussii

Earlier this xero-mesophytic species (Chladek 1995, Varga 1997) was detected in the distinctive tall-grass fields of semidry grasslands (on deforested areas), clearings, forest edges and grasslands of extensive orchards (Nagy & Rácz 1996, Nagy *et al.* 1999, Szövényi & Nagy 1999). Bönsel (2003) gives a more accurate description of its habitat, according to which, *I. kraussii* lives in the tall grass fields of forest ecotones and semidry grasslands.

I. modesta

To date shrubby steppe patches, karst shrubforest clearings and mesophytic grasslands have been named as the habitat of one of Hungary's rarest *Isophya* species (Nagy 1981, Nagy & Rácz 1996, Vadkerti *et al.* 2003).

I. modestior

Previously many things have been indicated as this species' habitat from the steppe through the karst shrubforest mixed with rocky grasslands, to degraded tall herb vegetation (Szövényi & Nagy 1999, Nagy A. & Nagy B. 2000, Szövényi *et al.* 2001). Its Austrian occurrences are known from steppe-meadows (Nagy *et al.* 2003). Locations in the Balkan center of dispersal of *I. modestior* are connected mountains with a height of 1000-2000m above sea level [Macedonia: Šar-Mts, Crna-Mts; Bulgaria: Vitosa-Mts; Serbia and Montenegro: Rtanj-Mts, Suva-Mts (Ramme 1951, Hubenov *et al.* 1998)]. Its habitats in Austria and Northern Italy are also characterized by the plant types of high mountains, which fulfill the needs of a thermophytic species (Ingrisch & Köhler 1998). Its occurrences on the eastern edge of the Alps are associated with xeromesophytic steppe-grassland patches (Nagy *et al.* 2003). This view gains support from the fact that *I. stysi*, the vicariant sibling species (Varga 2002) of *I. modestior*, living in the eastern part of the Carpathian Basin, is a typically montane insect, which does not occur under 400 to 500 m above sea level (Nagy *et al.* 1998).

Discussion

Inconsistencies in earlier publications concerning the choice of habitat of *Isophya* species have called attention to the fact that anthropogenic deterioration and transformation of habitats makes the recognition of habitat preferences difficult. Studies specifically targeting this issue have become urgent for the preservation of species.

Based on the earlier papers and our own statistical results, it can be stated that *I. costata* was formerly a species typical of loess grasslands, rich in dicotyledonous plant species, as well as other closed-steppe meadows of the colline region. However, due to the fact that natural grasslands tend to be decreased in extent owing to human activities, *I. costata* adapted to anthropogenic hayfields, which contain dicotyledonous plant species in suitable numbers to cater to its nutritional needs; this was true especially in places where these hayfields occasionally adjoin the remaining stands of steppe grassland. Based on our study of the size of populations of the species, these transitory grasslands, which are particularly rich in plant species, are optimal. The frequency of hayfields in Hungary has significantly exceeded that of natural steppe grasslands for a long time and by now this habitat has become the ideal habitat of *I. costata*.

In other types of grasslands adjoining mesophytic hayfields which contain dicotyledonous plant species, there occur smaller populations of *I. costata*. In parts of the species' area where, following the disappearance and constraining of former loess grasslands, hayfields with a similar structure and vegetation rich in mesophytic dicotyledonous plant species did not develop (were not re-sown, were regularly cut, or kept weedless), *I. costata* has disappeared. This is how isolated populations of the species having low density have developed far from each other.

By contrast the optimal habitats of *I. camptoxypha* are patches of herbaceous and lower-shrub layers of natural forests, dominated by tall or medium-high broadleafed (mainly dicotyledonous) mesophytic forest plant species. The systemic form (stable stem and leaf structure) of these plant species, satisfies both *I. camptoxypha*'s nutritional needs and the habitat-structural requirements of these relatively big and heavy insects for locomotion. Like *I. costata*, this

Table 4. Habitat preferences of the examined species.

Species	Mentioned habitats in earlier papers	Optimal habitat type(s) with optimal conditions as reported here	Secondary habitats with suboptimal conditions as reported here
I. camptoxypha	- shrubby vegetation with weed elements beside roads - clearings - mesophytic grasslands - forest-steppe patches - tall herb stands - mountain meadows	- natural clearings (forest openings) of mesophytic forests and forest ecotones	- forest edge with shrubby vegetation - forest edge with tall herb vegetation
I. costata	- semidry grasslands - loess grasslands - cut sides of banks - steppe meadows - moist grasslands - clearings in oak forests	- pannonian undisturbed loess grasslands - pannonian undisturbed steppe grasslands	- hayfields (particularly with extensive land use)* - rush fens - weedy vegetation patches (generally near the optimal habitats)
I. kraussii	- semidry grasslands - clearings - forest edges - grasslands of extensive orchards - tall-grassy fields of forest ecotones	- natural forest clearings of the xerotherm tomentose oak forests, and edge-shrubs and shrub forests of colline and submontane regions	- many different adjoining habitats near the main habitats
I. modesta	- shrubby steppe patches - karst shrub forests - clearings - mesophytic grasslands	- semidry steppe meadows	- clearing-meadows created in deforested areas by human agency
I. modestior	- karst shrub forest mixed with rocky grasslands - degraded tall-herb vegetation - steppe meadows - xeromesophytic steppe grasslands	- shrubby forest-steppe vegetation, natural forest clearings of the forest-steppe forests in the pannonian colline and the submontane region	- cultivated forest-steppe fragments - forest clearings

* Secondary, anthropogenic habitat type with optimal conditions for *I. costata*, by now this habitat has become the optimal habitat of the species.

species can access grasslands adjoining its major habitat where, in accordance with the suboptimal circumstances, populations are characterized by low density. Because of this, this montane species, that has been viewed as an endemism of the Carpathians, occurs in Hungary only in areas having a close population genetic connection with populations of neighboring high mountains.

With modern forest management, in addition to the smaller number of natural clearings within forests, forest ecotones have gained a larger significance due to the fragmentation of forest areas. From similar ecological conditions, a plant structure partly created by the same plant taxa, develops in this habitat type (forest edge with shrubby vegetation, forest edge with tall herb vegetation); consequently the discussed tettigoniid species can also find suitable circumstances.

However, contrary to previous publications (for example Szövényi *et al.* 2001), this does not mean that these are the characteristic habitats of the species: it only calls attention to errors involved in conclusions drawn on the basis of superficial examination. If the cover value of other plant species (for example *Rubus fruticosus*) in fulfilling the needs of *I. camptoxypha* is high in its secondary habitats, the insects are also present with a high density. However, if the broadleafed, edible plant species are present with only a very small total cover, or superdominant stands of invasive species (for example *Solidago gigantea* Ait.) become pervasive, *I. camptoxypha* is constrained and finally disappears. Based on these insights, it is markedly important from the point of view of preserving the species, to maintain forest patches of natural structure and dynamics — a consequence of which will be the extra light provided by the removal of trees — resulting in the appearance of patches rich in dicotyledonous plant species.

Based on the distribution of *I. kraussii* (Heller 2004) and our results, it can be stated that the Hungarian Middle Range is situated in the southeastern edge of the area of the Central European species (Ingrisch & Köhler 1998). Our results confirm Samietz's (1995) statements (examinations were carried out in Thüringen): *I. kraussii* is a species characteristic of the semidry grasslands which occur below the southern slopes of the hills. Naturally, the colonization of other types of habitat (*e.g.*, shrubs in forest ecotones) can also be observed.

The least samples are available to assist in determining habitat choice of the two rarest species: *I. modesta*, *I. modestior*. On the basis of our few samples and earlier data, we suppose that *I. modesta*, similarly to *I. costata*, whose occurrenceis characteristic of plains and hilly areas and the forest steppe zones of mountains, is a species of steppe grasslands rich in dicotyledonous plant species (Kis 1960, Rácz 1998). Following the diminishing of its major habitat, however, *I. modesta* could not colonize secondary hayfields with abundant dicotyledonous plants as successfully as *I. costata*. Based on the currently available data concerning the choice of habitat of *I. modestior*, it cannot yet be ascertained whether the species has grassland or forest-ecotone preferences.

The differences experienced in choice of habitat by *Isophya* spp., species which are relatively limited in their mobility, may have played a significant role in a speciation of the genus characterized by rapid evolution (Çiplak 2004). Concerning dispersal and speciation, three habitats occurring close to each other — grassland, forest ecotone (with shrubby character) and forest clearings — were probably important. Choices made between these heterogenous habitats, differing in their plant species composition, led to segregation of incipient species. (Table 4). Beyond this, the results show a separation also in terms of distribution in different altitude zones: *I. costata* is a plains-colline, *I. kraussii* a submontane species, *I. camptoxypha* a mountainous species.

The isolation of species linked to identical habitat-types can presumably be traced back to climatic oscillation and the forest-grassland dynamics related to it and, since the appearance of man, to the habitat preferences established owing to human disturbances.

Conclusions

Based on our examinations and the distribution of the species we conclude:

1. In the western part of the Carpathian Basin the optimal habitat of *I. camptoxypha* are patches of herbaceous and lower-shrub layers of natural forests, dominated by tall or medium-high broad leafed (mainly dicotyledonous) mesophytic forest plant species.

2. Earlier (before human alteration of nature) the loess grasslands and the steppe grasslands, rich in dicotyledonous plant species, may well have been the optimal habitat of *I. costata*. Today in the western part of the Carpathian Basin this species occurs under optimal conditions of undisturbed loess grasslands or mesophytic hayfields and steppe grassland-hayfield transitions rich in dicotyledonous plant species (the most robust populations are in hayfields). It can also be found at lower densities under suboptimal conditions adjoining these habitats and arising through their degradation.

3. The optimal habitat of *I. kraussii* in the examined area is presumably the xeromesophytic clearings dominated by *Bromus erectus sens. lat.* which are partly of natural, partly of clearing origin.

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