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DIPLOMARBEIT

Titel der Diplomarbeit

**Population Density, Habitat Preferences and Nest
Predation and of the River Warbler (*Locustella fluvi-
atilis*) in the Donau-Auen National Park,
Eastern Austria**

Verfasser

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Zusammenfassung

Populationsdichte, Nestprädation und Habitatpräferenzen des Schlagschwirls (*Locustella fluviatilis*) im Nationalpark Donauauen

Die jahrhundertlange land- und forstwirtschaftlich Nutzung der Donauauen östlich von Wien und zahlreiche flussbauliche Maßnahmen führten zu starken Habitatveränderungen und zur Fragmentierung der Auen. Nichtsdestotrotz stellen die Auwälder Niederösterreichs immer noch eines der wichtigsten Brutgebiete für Schlagschwirle in Österreich und Mitteleuropa dar. Die Ziele dieser Arbeit waren, die Erhebung der aktuellen Brutdichte des Schlagschwirl im Nationalpark Donauauen, ein Quantifizieren der Bedeutung in der Literatur genannter Habitatansprüche und Nahrungspräferenzen für die Schlagschwirlpopulation in Auwäldern östlich von Wien und ein experimentelles Testen inwiefern sich Nestprädation zwischen Schlagschwirlterritorien und zufällig ausgewählten Standorten im Auwald unterscheidet. Unsere Ergebnisse zeigen, dass die Schlagschwirldichte von 1,8–1,9 Brutpaaren/10 ha im Jahr 1983 auf 0,12 Brutpaare/10 ha im Jahr 2009 abnahm. Die publizierten Habitatansprüche des Schlagschwirl stimmen gut mit den Ergebnissen unserer Studie überein. In unserem Untersuchungsgebiet wurden nur Flächen in der Weichholzaue, die eine regelmäßige Überflutung aufweisen, besiedelt. Dort wurden Standorten mit einer hohen Krautschicht und einer hohen Abundanz an Hymenopteren bevorzugt. Das experimentelle Ausbringen von Kunstnestern zeigte ein deutlich niedrigeres Prädationsrisiko in Schlagschwirlrevieren im Vergleich zu den Kontrollflächen auf. Unsere Ergebnisse weisen darauf hin, dass Schlagschwirle bei der Wahl geeigneter Territorien Vegetationsstruktur, Nahrungsverfügbarkeit und kleinräumige Unterschiede des Nestprädationsrisikos berücksichtigen. Der Rückgang des Schlagschwirl in den Donauauen östlich von Wien ist wahrscheinlich auf durch Flussregulierungen verursachte Habitatveränderungen zurückzuführen. Änderungen der Vegetationsstruktur könnten auch Nahrungsverfügbarkeit und Nestprädation beeinflusst haben.

Abstract The floodplain forest system of the Danube east of Vienna has been used for forestry and agriculture for centuries and was affected by several river regulation measures leading to dramatic habitat changes and fragmentation of the floodplain. Nevertheless, the alluvial forests in Lower Austria are still one of the most important breeding areas for the river warbler in Austria and Central Europe. The aims of this study were to assess the present river warbler density in the Donau-Auen National Park; to evaluate the importance of published habitat requirements and food preferences for the river warbler population in the floodplain forest east of Vienna; and to test if nest predation differs between river warbler territories and randomly selected sites in the floodplain. Our results show that the river warbler density decreased over the last few decades from 1.8–1.9 breeding pairs/10ha in 1983 to 0.12 in 2009. Published habitat requirements of the river warbler are in line with the results of our study. At Donau-Auen National Park river warblers only colonize the regularly flooded forest area, where they prefer forest sites with a high herb layer and a high abundance of Hymenoptera. The experimental exposure of artificial nests showed a lower predation risk at river warbler territories compared to control sites. Our results indicate that selection of breeding territories in river warblers is driven by vegetation structure, food availability and spatial differences in nest predation risk. The decline of river warblers in the studied Danube floodplains east of Vienna is – most likely – related to habitat changes due to river regulation measures, which, besides changing vegetation structure, also may have been affected food availability and nest predation risk.

Keywords: alluvial forest, dummy eggs, artificial nests, habitat requirements, ground breeding passerine, food availability

Introduction

The river warbler (*Locustella fluviatilis*) is a widely distributed bird in Central and Eastern Europe and represents a “key species” of river floodplains (Glutz von Blotzheim and Bauer 1994). More than 75% of its global breeding range is in Europe, and the estimated European breeding population is 1.9–4.6 Mio breeding pairs (Birdlife International 2009). In the last decades the species apparently shows a range expansion towards Western Europe. Therefore its status is provisionally evaluated as Secure (Birdlife International 2009; Goffart et al. 2010).

The main breeding habitat of the river warbler, riverine floodplains, belong to one of the most endangered ecosystems worldwide and often represent regional biodiversity hotspots, particularly in human dominated regions like Central Europe (Brinson and Malvarez 2002; Tockner and Stanford 2002). Natural floodplain forest systems are characterized by periodic flooding events of varying intensity typically resulting in a diverse mosaic of habitats (Tockner and Stanford 2002; Tockner et al. 1998). The floodplain forest systems of the rivers Morava and Danube east of Vienna represent the largest remaining near-natural floodplain forests in Central Europe and both are identified as Important Birds Areas (IBAs) (Teufelbauer and Frank 2009; NP Donauauen 2010; Zuna-Kratky 2009). Both IBAs have large breeding populations of river warblers (Teufelbauer and Frank 2009; Zuna-Kratky et al. 2000) which certainly represent the vast majority of breeding pairs in Austria. However, while the species appeared to be still common in floodplain forests along the river Morava in the 1990ies (Austrian part only: 400-600 estimated territories; Zuna-Kratky et al. 2000), it was assumed that it declined significantly during the last decades in the Danube floodplains east of Vienna (Teufelbauer and Frank 2009). The reasons for the decline remain unknown particularly because habitat requirements of the species are only incomplete known or have never been assessed quantitatively.

The large floodplain ecosystems east of Vienna faced dramatic changes due to human activities such as land use, forest conversion and the resulting fragmentation of floodplain habitats. Some of the biggest impacts on the Danube floodplains were caused by the river regulation measures in the late 19th century. These measures dramatically reduced the natural hydrological dynamic leading to substantial changes in the floodplain ecosystem (Reckendorfer et al. 2006; Schratt-

Ehrendorfer 2000; Zulka 1994). The damming of the majority of sidearms prevented the water flow in many tributary rivers and led to an increasing sedimentation. This caused changes in vegetation cover and habitat structure (Dynesius and Nilsson 1994; Eichelmann 1994) and an invasion of (often neophytic) shrubs and trees in formerly treeless habitats resulting in a dramatic loss of herb dominated areas (Lazowski 1997).

In Austria, the River Warbler is predominately restricted to alluvial lowland forests and its distribution is limited mainly to the eastern part of the country (Dvorak et al. 1993). The small socially monogamous passerine is a long-distance migrant wintering in the southern parts of East Africa (e.g. northern Botswana; Herremans 1994). In its West Palearctic breeding area the species is primarily found from April to August. It only has one brood per season, but there is the possibility for up to three replacement clutches, if clutches gets lost due to disturbance, predation or flooding (Glutz von Blotzheim and Bauer 1994).

The river warbler prefers breeding sites with dense herb cover characterized by a high leaf density in its upper layer and a low leaf density close to the ground. Perhaps this combination provides good visual cover against predators and allows the birds to move unobstructed during foraging close to the ground. Another habitat requirement appears to be trees or shrubs overtopping the herb layer. In Central Europe these demands are best realized in floodplain forests with old stinging nettle stocks or partly in coppices of raspberries (Glutz von Blotzheim and Bauer 1994). The main food of the river warbler consists of adults and larvae of insects and arachnids as well as small snails (Glutz von Blotzheim and Bauer 1994).

Besides assessing the current density of river warbler territories in the Donau-Auen National Park, this study aimed to identify habitat parameters contributing to understand the species' selection of territory sites. Particularly, we analysed to what extent different vegetation characteristics (density of woody vegetation, herb layer height, reed and stinging nettle cover), emphasized as important habitat variables in existing literature (e.g. by del Hoyo et al. 2006; Glutz von Blotzheim and Bauer 1994; Südbeck et al. 2005), and the distance to water bodies contribute to predicting the spatial distribution of territories. We also quantified to what extent food availability affects the choice of nesting sites in the mainly insectivorous river warbler (Glutz von Blotzheim and Bauer 1994). Spatial variation of insect abundance can have a strong influence on the spatial distribution of insectivorous birds in riparian forests (Iwata et

al. 2003). Furthermore, we quantified to what extent differences in nest predation contribute to explaining the selection of territory sites by river warblers. Nest predation can be particularly important for birds breeding on or close to the ground (Söderström et al. 1998).

Material and Methods

Study area and study sites

Mapping of river warbler territories was conducted in a 37 km² area on the left bank of the river Danube in the Lower Austrian part of the Donau-Auen National Park between the border of the state of Vienna and the village Stopfenreuth (Fig. 1). In this stretch of the river, the bedrock of the floodplain forest consists of brash originated from river sedimentation in past glacial and interglacial times. Deposited on the brash are often loess and drifting sands (Teufelbauer and Frank 2009; Thinschmidt 1999).

The entire study area is divided by a flood-protection dam (Fig. 1), which isolates large parts of the former floodplain forest from the natural flood dynamics. The parts facing the river are characterized by flood-tolerant trees (especially poplars and willows), nitrophilous understorey plants (e.g. stinging nettles) and (semi-)aquatic plants like reed. The forests outside the dam have a more homogeneous understorey with a much lower herb layer density and are only flooded by rising groundwater (Lazowski 1997). The floodplain area is covered by 60% forest; the rest is subdivided into open water, brash surface and reed beds. A total of 5–10% of the river facing area is used as meadows for producing hay (Burger and Dogan-Bacher 1999; Manzano 2000).

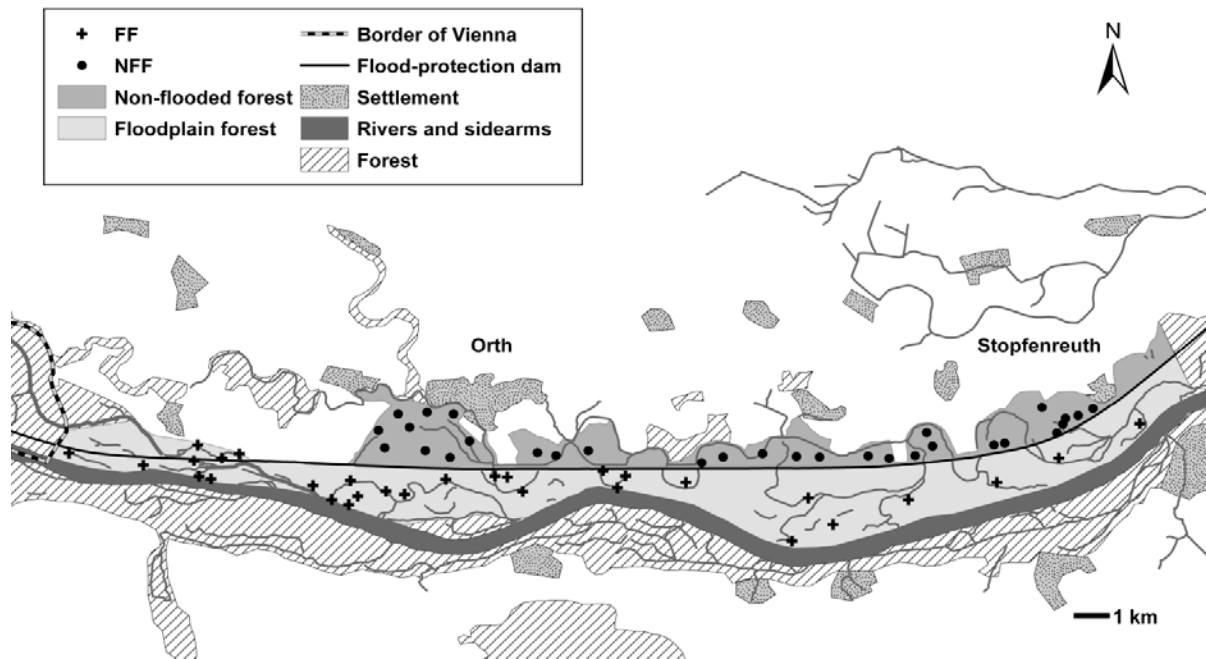


Fig. 1 Map indicating the surveyed non-flooded and flooded forest areas as well as randomly selected study sites in the floodplain (FF) and the non-flooded forest area (NFF) north of the Danube River east of Vienna

In 1996 the area was designated as national park and great parts of the region are also declared as protected areas according to the Ramsar Convention and became a Natura-2000 Site (NP Donauauen 2010; Teufelbauer and Frank 2009).

Bird survey

Between 26 April and 23 June 2009 the total area was surveyed to map breeding territories of the river warbler. At the end of June most of the area between the dam and the river Danube was inaccessible due to flooding. To keep wildlife disturbance to a low level, the high density of forest roads and tracks in the study area was used for territory mapping. Due to its far-reaching song (150–200 m) most likely the vast majority of territories should have been discovered. The complete study area was surveyed three times by bicycle. When a river warbler was located, the distance between the road and the birds was estimated and the position was marked on an aerial map and digitized by the GPS device Garmin GPSmap 60CSx. Surveys took place predominantly between 4:30–11:00 and 16:00–21:00, thereby covering the time periods of highest song activity of the species (Glutz von Blotzheim and Bauer

1994; Südbeck et al. 2005).

Following the recommendations by Südbeck et al. (2005) a breeding territory was defined as a site where a river warbler was recorded twice with at least seven days between the two records. Sites were immediately classified as breeding territories when nest building and feeding activities (adults carrying food or feeding fledglings) were observed (Südbeck et al. 2005). After the territory mapping, the coordinates of identified breeding territories were transferred from the GPS device to the computer with the program Garmin MapSource Version 6.10.2., and charted on a map with the software ArcGIS 9.0 (ESRI). When two or more records were classified as belonging to one territory, the spatial center of the territory was defined by the midpoint of the measured coordinates.

Habitat variables

After the territory mapping five habitat variables were measured or estimated in the field (Variables 1–5 in Table 1) between 16 July and 7 August 2009 at river warbler territories and 30 sites randomly distributed in non-flooded forest (in parts of the study area outside the dam) and 30 in frequently flooded forest (between dam and Danube river) (Fig. 1). The selection of the control sites was generated with ArcGIS 9.0. with the exclusion of inappropriate areas like meadows, waterbodies or reed beds. All habitat measurements or estimates refer to an area within a 10 m radius around the centres of the territories and around randomly selected control points. This small area corresponds to the small size of river warbler territories (Glutz von Blotzheim and Bauer 1994).

Tree density was quantified as the number of trees with a diameter in breast height (dbh) of more than 10 cm. Shrub layer density was estimated in categories (see Table 1). Furthermore, the percentage of reed bed and stinging nettle cover was estimated. Height of herb layer (regardless of reed) was quantified as the mean of measurements at five regularly distributed points per plot (see Fig. 2). The distance to the next water body was calculated with the software ArcGIS 9.0 (ESRI).

Table 1 Measured habitat variables. Variables 1–5 were measured (variables 1 and 3) or estimated (2, 4, and 5) for an area within a radius of 10 m around the center of the randomly selected study sites or river warbler territories. Variable 6 was measured using ArcGIS 9.0 (ESRI)

No.	Habitat variables	Units of measurement
1	Tree density	Number of trees with dbh >10 cm
2	Shrubs	5 categories from (1) no shrubs to (5) very dense shrub layer
3	Height of herb layer	cm
4	Reed cover	%
5	Stinging nettle cover	%
6	Distance to next waterbody	meter

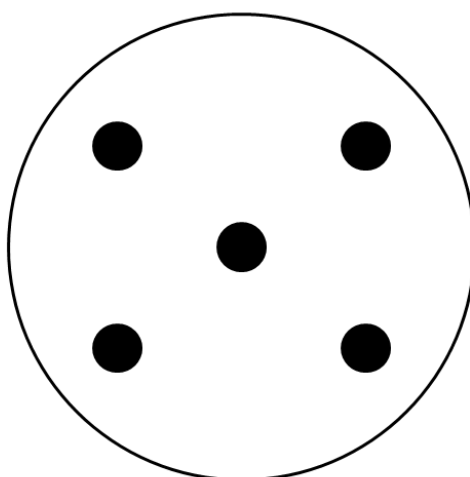


Fig. 2 Schematic illustration showing the 5 points (indicated by black dots) at which height of herb layer was measured at each river warbler territory and at randomly selected sites in flooded and non-flooded forest. Other habitat variables (tree density, shrub density, reed cover and stinging nettle cover) were measured or estimated for the entire area within the black circle ($\varnothing = 20\text{m}$)

Food availability

For determining the food availability, standardized sweep netting in the herb layer was conducted. Sweep net samples consisted of 10 sweeps per plot. The captured arthropods and molluscs were preserved in 90% alcohol for identification and counting in the laboratory. The considered taxonomic groups were Formicidae, other Hymenoptera, Diptera, Hemiptera, Coleoptera, Arachnida and Pulmonata. All groups

represent prey commonly used by river warblers (Glutz von Blotzheim and Bauer 1994). We did not further differentiate between adults and larvae due to the small number of collected larvae.

Nest predation

For quantifying nest predation artificial nests with artificial clutches were exposed in all breeding territories and control plots. To imitate river warbler eggs, dummy eggs were formed (20 x 15 mm in size) of the polymer clay “Fimo” (© Staedtler) and sprinkled with “9330/5/1 Zinnoberrot 9330-0043” of the trademark Jolly (Fig. 3a). Afterwards the dummy eggs were coated with achromatic and odourless food lacquer (© Euro Sweet, Fessler), which prevents a loss of colour by rain and stabilize the surface of the eggs. The artificial nests were made of small wire baskets filled with hay (Fig. 3b). During the production process of the nests and eggs and during the placement in the study area, the material was only handled with gloves to avoid that predators would be attracted by human smell (Whelan et al 1994). Four dummy eggs were placed per nest. The size of the used artificial eggs and clutches resembled the mean egg size (19.76 x 14.95 mm) and clutch size (4 - 6 eggs) of river warblers (see Glutz von Blotzheim and Bauer 1994).

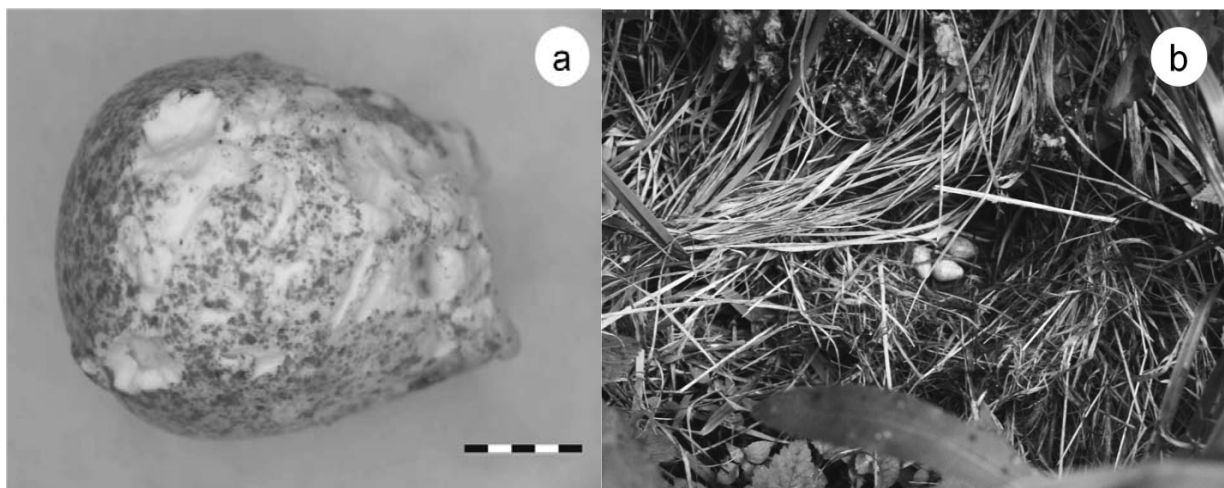


Fig. 3 (a) Dummy egg with bite marks of a rodent (scale bar indicates 5 mm) and (b) artificial nest with dummy eggs exposed in the field

Between 17 and 23 July 2009, one artificial clutch was exposed close to the centre of each river warbler territory and at all randomly selected points for a period of 13 days which corresponds to the species' natural incubation period (Glutz von Blotzheim and

Bauer 1994). All artificial nests were placed on the ground and hidden under dead wood or near tree trunks to imitate the natural nest sites of the mainly ground breeding river warbler (Glutz von Blotzheim and Bauer 1994). Afterwards the nests were controlled for missing and/or damaged dummy eggs indicating predation. We considered a nest as predated whenever the nest or single eggs disappeared or dummy eggs with bite and/or beak marks were found in or near the artificial nests.

Data analysis

All statistical analyses were conducted using the program Statistica 7.1 (Statsoft Inc., Tulsa). Data was tested for normal distribution with Kolmogorow-Smirnow test and – if necessary – adequate data transformation was carried out. To test for differences of variables between river warbler territories (T) and randomly selected floodplain forest sites (FF) and between randomly selected FF sites and non-flooded forest (NFF) sites univariate tests were used. We did not apply Bonferroni correction to avoid that potentially important variables are excluded at this stage of our analyses. River warbler observations which did not indicate a territory were not considered in these analyses. Furthermore, two T sites had to be excluded from our analyses because they were not accessible due to a strong flood.

Subsequently a model selection approach only considering variables significantly differing (according to t, χ^2 or U tests) between T and FF sites was used to identify important habitat structures for river warblers in flooded forest areas. NFF sites were not further considered because this forest type appeared to be not used by river warblers. Generalized linear models (GLMs) with binomial error distribution and logit-link function were calculated including all variables, which proved to be not significant in univariate tests, and all possible subsets. Resulting GLMs were ranked according to their corrected AIC (AICc) values. For the models within 2 AICc values of the model with the lowest AICc, AICc weights were calculated as a relative measure of support for the model. The higher the AICc weight, the higher is the relative likelihood of a model compared to alternative models (Wagenmakers and Farrell 2004).

Results

River warbler abundance and territory density

River warblers were observed at 73 different sites in the alluvial forest (Fig. 4). At 30 of these sites observations indicated occupied territories, which all were located in the floodplain forest. Only at four sites river warblers were observed in non-flooded areas of the national park (Fig. 4), but they did not establish a territory. For the flooded forest area the river warbler density was 0.12 breeding pairs per 10 hectare.

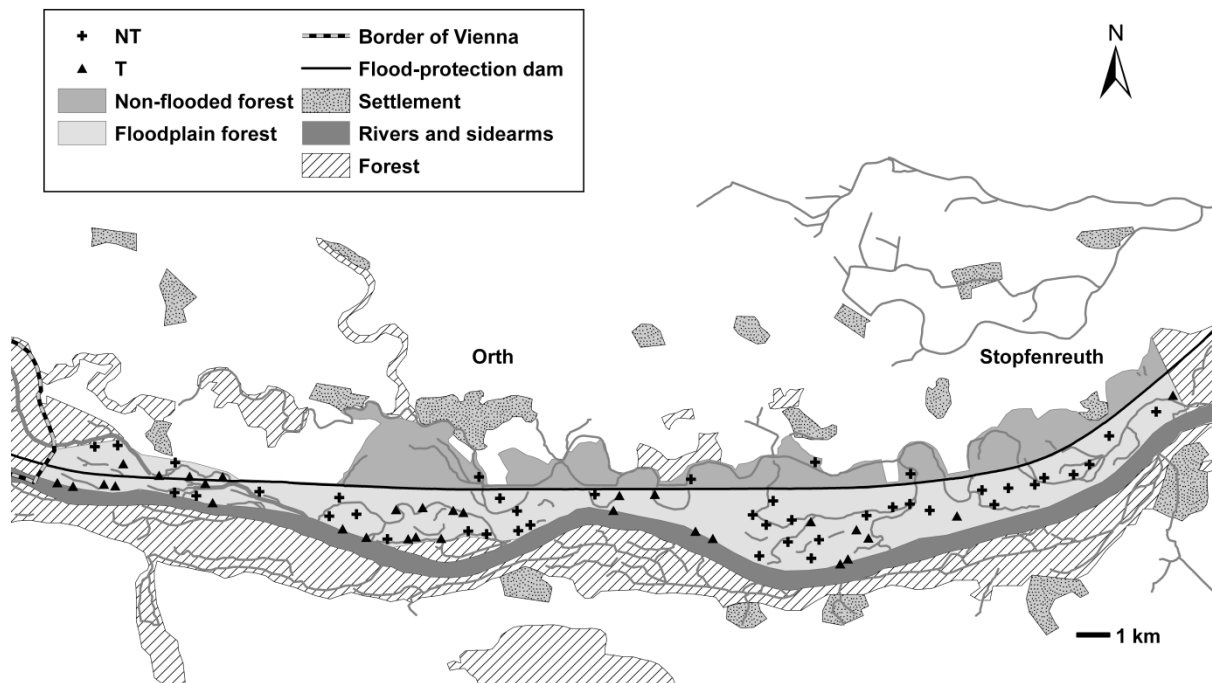


Fig. 4 Map indicating identified river warbler territories (T) and sites, where river warbler were observed but no territories were established (NT)

Effects of habitat variables

Shrub density was significantly higher at FF than NFF sites, but in the regularly flooded forest areas river warbler territories were found at sites with a significantly lower shrub density than at randomly selected FF sites (Table 2, Fig. 5b). Herb layer height was significantly higher at FF sites than at NFF sites. In the flooded forest an even higher herb layer height was found at T than FF sites (Table 2, Fig. 5c).

Stinging nettle cover was significantly higher at T sites than at FF sites, and significantly higher at FF sites than at NFF sites (Table 2, Fig. 5e). The other three habitat variables (number of trees, reed cover and distance to next water body) showed significant differences between NFF and FF sites but no differences between FF and T sites (Table 2, Fig. 5).

Table 2 Results of univariate tests for differences of habitat variables between flooded (FF) and non-flooded alluvial forest sites (NFF), and between FF sites and river warbler territories (T). The variables number of trees and distance to next waterbody were log (x+1) transformed before analysis. Significant differences are printed bold. See also Fig. 5

Variable	Test	NFF vs. FF sites	FF vs. T sites
Number of trees	t-test	$t = -4.24, p < 0.001$	$t = -1.02, p = 0.311$
Shrubs	U-test	$U = 281.5, p = 0.013$	$U = 258, p = 0.012$
Height of herb layer	t-test	$t = 8.27, p < 0.001$	$t = 2.32, p = 0.024$
Reed cover	U-test	$U = 195, p < 0.001$	$U = 366, p = 0.401$
Stinging nettle cover	U-test	$U = 87, p < 0.001$	$U = 288.5, p = 0.041$
Distance to next waterbody	t-test	$t = -4.96, p < 0.001$	$t = -0.55, p = 0.583$

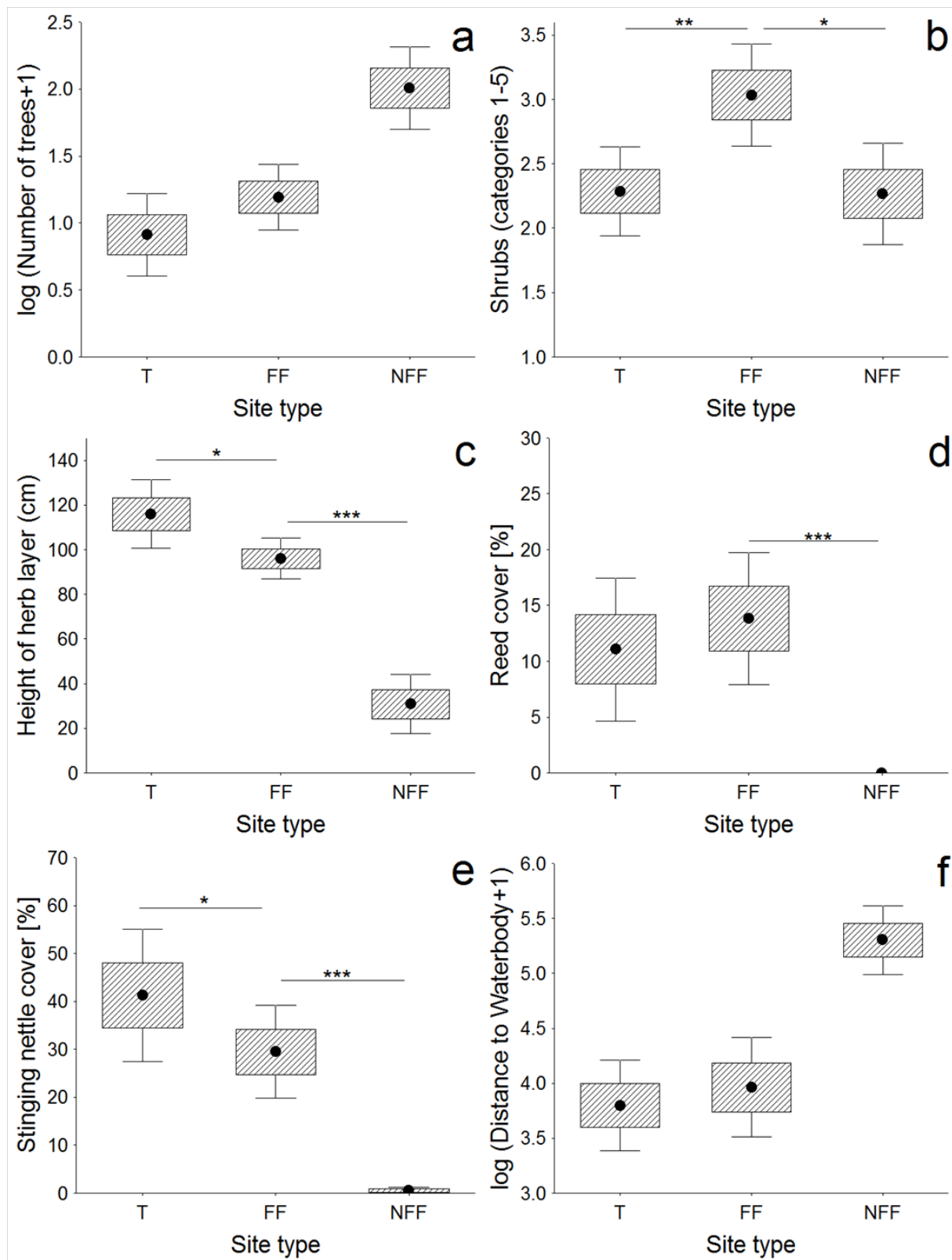


Fig. 5 Mean (a) tree number, (b) shrub density, (c) height of herb layer, (d) reed cover, (e) stinging nettle cover and (f) distance to next waterbody \pm SE (box) and 95% CI (whiskers) at river warbler territories (T), and randomly selected sites in regularly flooded (FF) and non-flooded forest (NFF). Asterisks indicate significant differences (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) between T and FF sites and FF and NFF sites, respectively (for details compare Table 2)

Food availability

The abundance of ants was significantly higher at T than at FF sites, but did not differ between FF and NFF sites (Table 3, Fig. 6a). A similar pattern was found for the abundance of other Hymenoptera (Table 3, Fig. 6b). The abundance of Diptera, Hemiptera, Coleoptera, Arachnida and Pulmonata showed neither significant differences between NFF and FF sites nor between FF and T sites (Table 3).

Table 3 Results of univariate tests for differences of food availability between regularly flooded (FF) and non-flooded alluvial forest sites (NFF), and FF sites and river warbler territories (T). The variables number of other Hymenoptera (excluding ants), number of Diptera, number of Hemiptera and number of Arachnida were log (x+1) transformed before analysis. Significant differences are printed bold. See also Fig. 6

Variable	Test	NFF vs. FF sites	FF vs. T sites
Number of Formicidae	U-Test	$U = 391, p = 0.383$	$U = 245, p = 0.007$
Number of other Hymenoptera	t-Test	$t = -0.41, p = 0.682$	$t = 2.71, p = 0.009$
Number of Diptera	t-Test	$t = -0.97, p = 0.333$	$t = -0.61, p = 0.548$
Number of Hemiptera	t-Test	$t = 4.31, p < 0.001$	$t = -0.32, p = 0.754$
Number of Coleoptera	U-Test	$U = 419, p = 0.635$	$U = 32, p = 0.416$
Number of Arachnida	t-Test	$t = -1.66, p = 0.103$	$t = 1.64, p = 0.106$
Number of Pulmonata	U-Test	$U = 444, p = 0.923$	$U = 32, p = 0.120$

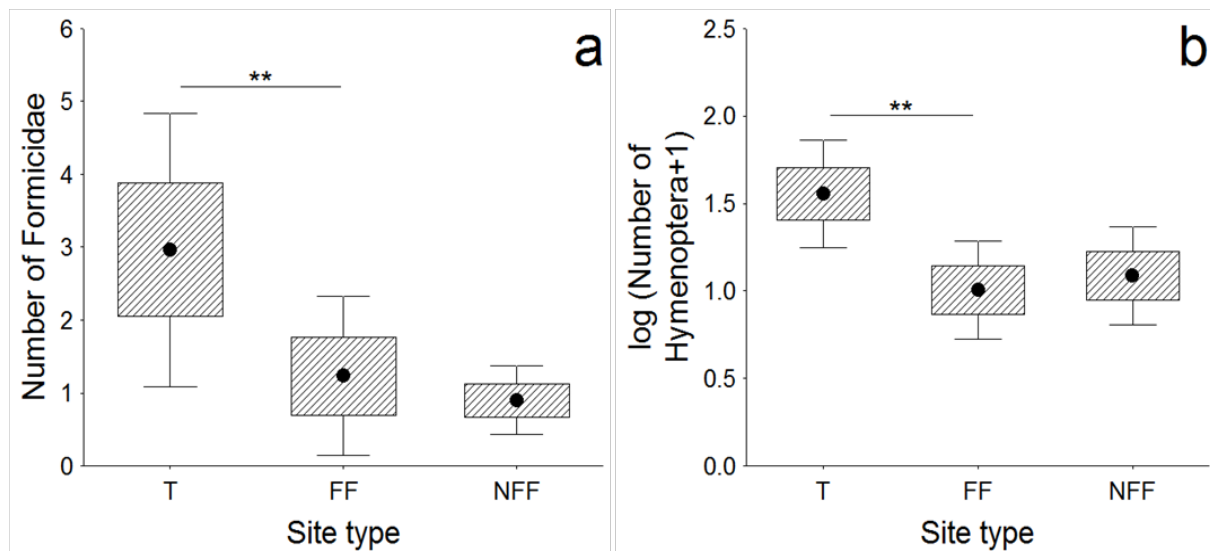


Fig. 6 Mean abundance of (a) ants (Formicidae) and (b) other Hymenoptera \pm SE (box) and 95% CI (whiskers) recorded in River Warbler territories (T) and randomly selected sites in regularly flooded (FF) and non-flooded forest (NFF). Asterisks indicate significant differences (** $p < 0.01$) between T and FF sites and FF and NFF sites, respectively (for details compare Table 3).

Nest predation

A total of 42.9% of the artificial nests (12 of 28) exposed at T sites have been predated compared to 80.0% (24 of 30) at FF sites. The proportion of predated nests was significantly higher at FF sites than T sites (Chi² test: $\chi^2 = 6.92$, $p = 0.009$) (Fig. 7). At NFF sites 86.7% (26 of 30) of the artificial nests were predated. The small difference in nest predation between FF and NFF sites did not achieve a significant level (Chi² test: $\chi^2 = 0.10$, $p = 0.750$).

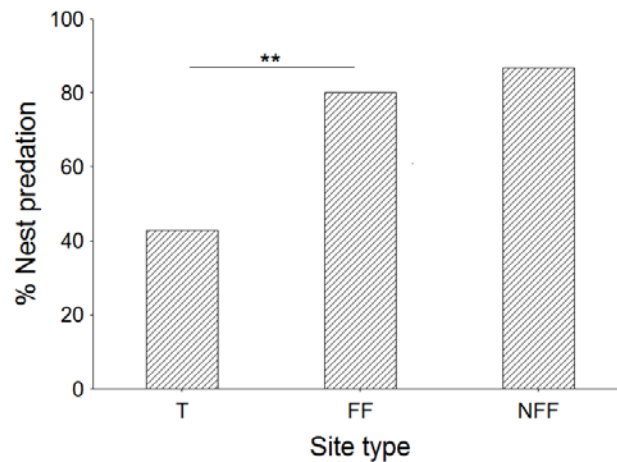


Fig. 7 Proportion of predated nests in river warbler territories (T), and at randomly selected sites in regularly flooded (FF) and non-flooded forest (NFF). The two asterisks indicate significant effects at a level of $p < 0.01$ (Chi² tests testing for differences between T and FF and FF and NFF sites, respectively)

Identification of important habitat variables using a model selection approach

GLMs including vegetation structure variables (shrub density, herb layer height and stinging nettle cover), food availability variables (abundance of ants, abundance of other Hymenoptera) and nest predation and all possible subsets were calculated to evaluate differences between T and FF sites. All considered variables proved to differ significantly between T and FF sites in univariate tests (Table 2 and 3; for nest predation see main text above). Only the variables nest predation, abundance of Hymenoptera (excluding ants) and shrub density were included in the five best models and represented the only variables with a significant contribution according to Wald statistics (Table 4 and 5).

Table 4 Summary of Akaike model selection evaluating effects of three vegetation structure variables (shrub density, herb layer height, stinging nettle cover), two food availability variables (ant abundance, other Hymenoptera abundance) and nest predation on the occurrence of the river warbler (all models within 2 AICc values of the model with the lowest AIC values presented). Variables with a significant contribution according to Wald statistics (Table 5) are printed bold

Variables	AICc	AICc weight	<i>p</i>
Nest predation, other Hymenoptera, shrubs , herb layer , stinging nettle	57.8	0.24	<0.001
Nest predation, other Hymenoptera, shrubs , herb layer	58.6	0.16	<0.001
Nest predation, other Hymenoptera, shrubs , herb layer, ants	58.8	0.14	<0.001
Nest predation, other Hymenoptera, shrubs , herb layer, ants, stinging nettle	59.0	0.13	<0.001
Nest predation, other Hymenoptera, shrubs , stinging nettle	59.6	0.10	<0.001

Table 5 Wald statistics from univariate analyses of predictors in GLMs testing for effects of seven variables on the occurrence of river warblers (see Table 4). Variables with a significant effect are printed bold

Variables	Wald statistics	<i>p</i>
Shrubs	4.73	0.030
Height of herb layer	2.73	0.098
Stinging nettle	2.24	0.134
Number of Formicidae	1.26	0.262
Number of Hymenoptera	6.02	0.014
Nest predation	10.15	0.001

Discussion

Population density

For calculating the density of a species, it is possible to consider the total survey area (crude density) or only the suitable habitat (ecological density) (Gaston et al. 1999). Due to difficulties in delimiting suitable habitat and better comparability to other studies, we decided to use the crude density to estimate the density of river warbler territories. The only exception is that we excluded the non-flooded forest because of the complete absence of river warbler territories in these areas. The density of 0.12 breeding pairs per ha (bp/10 ha) found by our study is similar to river warbler densities reported from other areas such as a floodplain forest of the river Inn in Upper Austria (0.13 bp/10ha; Schuster 2006) or the Białowieża Forest in Poland (0.2 bp/10ha in the time period 1995–1999; Wesołowski et al. 2002). A slightly higher density of river warbler territories (0.5/10ha in 2007) was recorded from the border zone of the Oostvaardersplassen Netherlands (Bijlsma 2008). The highest density of river warbler territories was reported from regularly flooded forests (with a dense herb layer) in the Morava floodplains (Lower Austria) where in 1978 and 1979 47 and 69 territories, respectively, were found in a study area of 46.5 ha corresponding to 10-15 territories/10 ha (Zuna-Kratky et al. 2000). Although when the used definition of a territory may have been less strict than in our study the documented territory density is still remarkable. Still until recently territory densities of up to 3-5 bp/10 ha were frequently found in the Morava floodplains (Zuna-Kratky et al. 2000).

In the alluvial forests of the Donau-Auen National Park a declining river warbler density since the 1980s was assumed (Teufelbauer and Frank 2009), which is supported by our data. The current density of 0.12 bp/10 ha (this study) is much lower than the population density of 1.8–1.9 bp/10ha estimated for the Danube region east of Vienna in 1983 (Glutz von Blotzheim and Bauer 1994). Apparently, it is a general process in the Danube floodplains east of Vienna that bird species (such as the river warbler) typical for forests shaped by regular flooding events are decreasing. This is most likely caused by the loss of the formerly high hydrological dynamics and the associated transfer of former floodplain forests to forests of late successional stages. As consequence, bird assemblages typical for forest frequently

disturbed by flooding are increasingly replaced by bird assemblages typical for hardwood forests (Eichelmann 1994; Teufelbauer and Frank 2009). An additional loss of suitable habitats can be caused by neophytes, which are immigrating especially into dynamic habitats such as floodplain areas (Essl and Rabitsch 2002). In alluvial areas, perennial shrubs are the vegetation type under the strongest pressure of water accompanying neophytes. Highly competitive species like *Impatiens glandulifera* can overgrow autochthonous species like stinging nettle already in spring (Rak and Bergmann 2006). Such changes of the understorey vegetation cover of floodplain forests may decrease their suitability as breeding habitat for the river warbler.

Habitat variables and food availability

In the Donau-Auen National Park the river warbler is only breeding in the parts of the alluvial forest with annual flooding. Furthermore, our results confirm that the river warbler prefers nesting sites with a moderate shrub density, a high herb layer and a dense stinging nettle cover. The importance of these habitat parameters was already emphasized before (Glutz von Blotzheim and Bauer 1994). The variables tree density, reed cover and distance to the next water body did not have any detectable effect on the selection of nesting sites.

Differences between T and FF sites in the availability of arthropods potentially used as food by river warblers were only found for Formicidae and other Hymenoptera. Both groups were more abundant in river warbler territories than at randomly selected FF sites. These differences would have been even remained significant after applying a Bonferroni correction. Both taxonomic groups are mentioned as prey of the river warbler (Glutz von Blotzheim and Bauer 1994). The abundance of other Hymenoptera (excluding ants) was also indicated as an important variable for the establishment of territories by our model selection approach. Other studies emphasized Diptera, Hemiptera and Lepidoptera as the most important food source (e.g. Inosemzew 1963; Mackowicz 1989). To confirm the importance of Hymenoptera as food source for the river warbler in our study area, an analysis of the prey used by river warblers in the studied Danube floodplains would be an important precondition.

Nest predation

Nest predation did not differ between forest types but was significantly lower in river warbler territories than at FF control sites, indicating that predation risk may be an important factor driving the choice of nesting sites in river warblers. The lower risk of predation in river warbler territories could be caused by the higher herb layer and stinging nettle cover compared to the control sites. Vegetation cover and density can affect the probability of how many nests can be visually detected especially by avian predators (Filliater et al. 1994).

The identification of nest predators was difficult because most of the dummy eggs from predated nests were missing and only a few eggs showed distinguishable beak marks of birds or bite marks of rodents. Also snakes were identified as predators on our artificial nests because they regurgitated the dummy eggs in or near the nests. In the Danube region east of Vienna Aesculapian snake (*Zamenis longissimus*) is a common species (own observation) known as nest predator on passerines (Luiselli and Angelici 1996; Arnold 2002). Jays and ground-foraging mammals, which also occur in our study area (own observation), can be particularly important predators of ground nests (Angelstam 1986; Söderström et al. 1998) as build by river warblers.

In our study 40% of the predated nests vanished as a whole, but jays, other corvids, and the majority of the mammalian predators are usually only removing the nest content and not the whole nest (Andrén 1992; Angelstam 1986; Schaefer 2004). One reason for the large number of missing nests could be the high abundance of wild boars (*Sus scrofa*) in our study area (own observation). They are rummaging for food in the ground and might find the nests by random. These findings are in line with results of other studies reporting that wild boars have an impact on ground breeding birds (Gimenez-Anaya et al. 2008; Henry 1969).

Conclusions

The decline of the river warbler in the Danube alluvial forests east of Vienna is caused most likely by a loss of suitable habitats due to the change of the entire forest ecosystem. This may not only have changed vegetation structure but also food availability and predation risk. Main drivers for these changes in the floodplain system are the dramatically reduced hydrological dynamics and – to a minor extent – the invasion of neophytic plants. To achieve a more detailed understanding of factors having a negative impact on key species of floodplain areas such the river warbler, a comparison with the population in the nearby Morava floodplains, which did not suffer such a dramatic decline during the last decades (Zuna-Kratky et al. 2000), may be helpful.

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