# Population density, habitat preferences and nest predation of the River Warbler (*Locustella fluviatilis*) in the Donau-Auen National Park, Eastern Austria

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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 resulting in 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 accordance 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 affected food availability and nest predation risk.

**Hoelzl F. & Schulze C.H., 1985: Populationsdichte, Habitatpräferenzen und Nestprädation des Schlagschwirls (*Locustella fluviatilis*) im Nationalpark Donau-Auen, Ostösterreich.**
Die Auwaldbereiche entlang der Donau östlich von Wien sind durch jahrhundertelange forst- und landwirtschaftliche Nutzung und diverse Flußregulierungsmaßnahmen geprägt. Dies führte zu dramatischen Habitatveränderungen und einer zunehmenden Fragmentierung der Überschwemmungsflächen. Trotzdem repäsentieren die letzten verbleibenden Auwälder östlich von Wien noch immer eines der wichtigsten Brutgebiete des Schlagschwirls in Österreich und Mitteleuropa. Ziele dieser Studie waren neben der Erhebung der aktuellen Schlagschwirldichte im Nationalpark Donau-Auen, die Untersuchung der Habitatansprüche, Nahrungspräferenzen sowie die Bedeutung von Nestprädation bei der Wahl der Territorien in den Auwäldern östlich von Wien. Unsere Ergebnisse weisen auf einen deutlichen Bestandsrückgang des Schlagschwirls in den Donau-Auen in den letzten Jahrzehnten von 1,8–1,9 Brutpaaren/10 ha 1983 auf 0,12 2009 hin. Die in der Literatur dokumentierten Habitatansprüche des Schlagschwirls ließen sich durch die Ergebnisse der vorliegenden Studie bestätigen. Im Nationalpark Donau-Auen besiedelt der Schlagschwirl nur regelmäßig überflutete Waldbereiche. Dort werden Standorte mit einer hohen Krautschicht und einer hohen Abundanz an Hymenopteren bevorzugt. Experimente mit ausgebrachten Kunstnestern zeigten ein niedrigeres Risiko der Nestprädation in Schlagschwirl-Territorien im Vergleich zu Kontrollstandorten. Unsere Ergebnisse deuten darauf hin, dass Vegetationsstruktur, Nahrungsverfügbarkeit und räumliche Unterschiede im Nestprädationsrisiko wichtige Faktoren bei der Wahl geeigneter Territorien darstellen. Der Rückgang des Schlagschwirls in den Donauauen östlich von Wien steht sehr wahrscheinlich mit durch Flußregulierungsmaßnahmen ausgelösten Habitatveränderungen in Verbindung, welche nicht nur die Vegetationsstruktur, sondern auch Nahrungsverfügbarkeit und Nestprädationsrisiko verändert haben.

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

## Introduction

The River Warbler (*Locustella fluviatilis*) is a widely distributed bird species in Central and Eastern Europe and represents a "key species" of river floodplains (Glutz v. Blotzheim & Bauer 1991). More than 75% of its global breeding range is in Europe, and the estimated European breeding population comprises 1.9–4.6 Mio breeding pairs (IUCN 2010). During the last decades the species apparently shows a range expansion towards Western Europe. Therefore its status is provisionally evaluated as Secure (Goffart et al. 2010, IUCN 2012).

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 Central European landscapes dominated by land-use systems of low conservation value (Brinson & Malvarez 2002, Tockner & Stanford 2002). Natural floodplain forest ecosystems are characterized by periodic flooding events of varying intensity typically resulting in a mosaic of diverse habitats (Tockner et al. 1998, Tockner & Stanford 2002). The floodplain forest ecosystems 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) (NP Donauauen 2010, Teufelbauer & Frank 2009, Zuna-Kratky 2009). Both IBAs have large breeding populations of River Warblers (Teufelbauer & 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 1990s (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 & Frank 2009). The reasons for that decline remain unknown particularly because habitat requirements of the species are only incompletely 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 during the late 19th century. These measures dramatically reduced the natural hydrological dynamics 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 water flow in many tributary rivers and led to increasing sedimentation. This caused changes in vegetation cover and habitat structure (Dynesius & 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 mostly 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 (Kennerley & Pearson 2010). In its West Palearctic breeding area the species is primarily found from April until August. It only has one brood per season, but there is a possibility for up to three replacement clutches if clutches are lost due to disturbance, predation or flooding (Glutz v. Blotzheim & Bauer 1991).

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 v. Blotzheim & Bauer 1991). The main food of the River Warbler consists of adults and larvae of insects and arachnids as well as small snails (Glutz v. Blotzheim & Bauer 1991).

Besides assessing the current density of River Warbler territories in the Donau-Auen National Park, this study aimed to identify habitat parameters contributing to an understanding of the species' selection of territory sites.

Particularly, we analyzed

– 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 v. Blotzheim & Bauer 1991, Südbeck et al. 2005),

– and the distance to water bodies contribute to predicting the spatial distribution of territories.

– We also quantified to which extent food availability affects the choice of nesting sites in the mainly insectivorous River Warbler (Glutz v. Blotzheim & Bauer 1991). 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 which 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).

# 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 (Tab1). 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. Often loess and drifting sands are deposited on the brash (Teufelbauer & 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. *Urtica dioica*) 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 & Dogan-Bacher 1999, Manzano 2000).

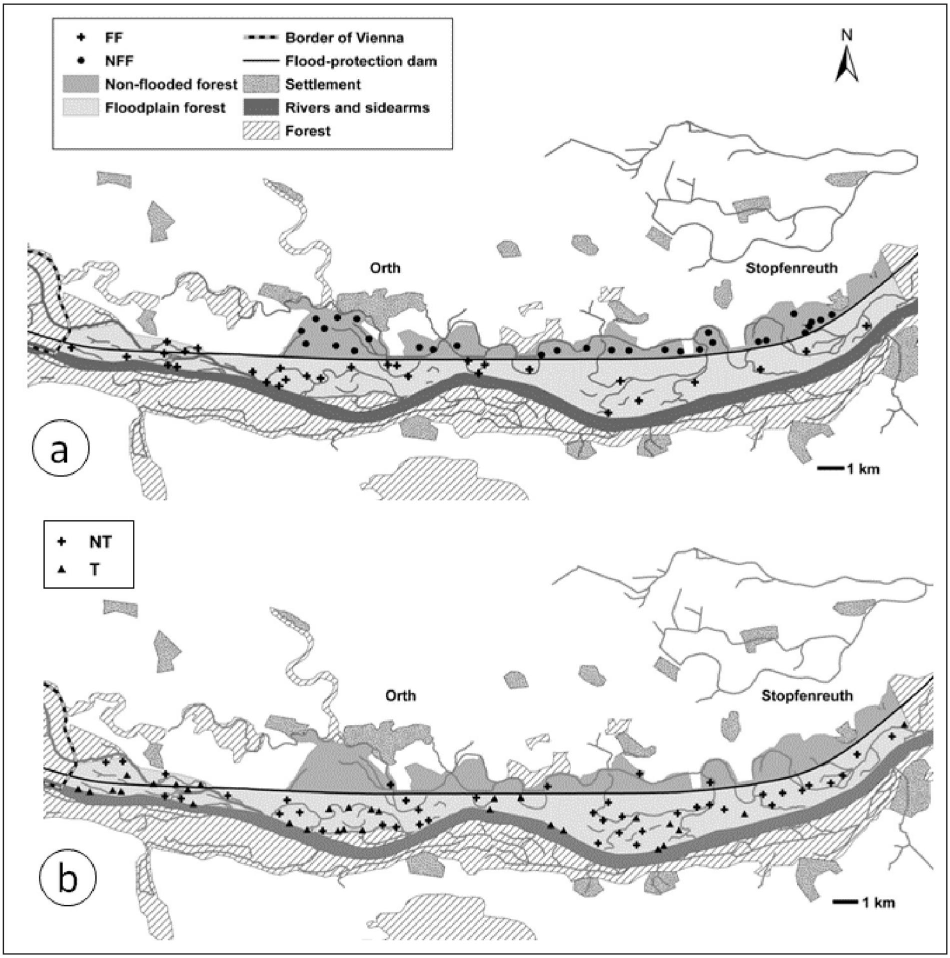


Fig. 1: Maps indicating (a) surveyed non-flooded and flooded forest areas as well as randomly selected study sites in the floodplain (FF) and the non-flooded forest area (NFF) north of the Danube River east of Vienna and (b) identified River Warbler territories (T) and sites, where River Warblers were observed but no territories were established (NT). – Abb.1: Karten mit Anzeige (a) untersuchter nicht-überfluteter und regelmässig überfluteter Waldflächen sowie der zufällig ausgewählten Untersuchungsstandorte im Bereich des regelmäßig überfluteten (FF) und des nicht-überfluteten Auwalds (NFF) nördlich der Donau östlich von Wien und (b) den festgestellten Schlagschwirl-Territorien (T) und Standorten, an denen Schlagschwirle festgestellt, jedoch keine Territorien etabliert wurden (NT).

In 1996 the area was designated as a national park and great parts of the region were also declared as protected areas according to the Ramsar Convention and became a Natura-2000 Site (NP DONAUAUEN 2010, TEUFELBAUER & FRANK 2009).

## Bird survey

Between April 26 and June 23 2009 the total area was surveyed for mapping 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. In order to avoid wildlife disturbance, the high-density network of forest roads and tracks in the study area was used for territory mapping. Due to its far-reaching song (150–200 m) the vast majority of territories was most probably discovered. The complete study area was surveyed three times by bicycle. When a River Warbler was located, the distance between the road and the bird 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 v. Blotzheim & Bauer 1991, 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 copulation (N = 3 territories), nest building (N = 14 territories) or feeding activities (adults carrying food or feeding fledglings; N = 7 territories) 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 using the programm 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 Tab. 1) between 16 July and 7 August 2009 at 28 of the 30 identified River Warbler territories (2 territories not accessible due to flooding) 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. 1a). 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 v. Blotzheim & Bauer 1991).

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 Tab. 1). Furthermore, the percentage of reed bed and *Urtica dioica* cover was estimated. Height of herb

Tab. 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). – Tab. 1: Erhobene Habitatvariablen. Variablen 1–5 wurden gemessen (Variablen 1 und 3) oder geschätzt (2, 4 und 5) für eine Fläche innerhalb eines Radius von 10 m um das Zentrum von zufällig ausgewählten Untersuchungsstandorten oder Schlagschwirl-Territorien. Variable 6 wurde mittels ArcGIS 9.0 (ESRI) ermittelt.

| **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 | Urtica dioica cover | % |
| 6 | Distance to next waterbody | Meter |

layer (regardless of reed) was quantified as the mean of measurements at five regularly distributed points per plot. The distance to the next water body was calculated with the software ArcGIS 9.0 (ESRI).

## Food availability

For determining 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 v. Blotzheim & Bauer 1991). 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. 2a). Afterwards the dummy eggs were coated with achromatic and odourless food lacquer (© Euro Sweet, Fessler), which prevents a loss of colour by rain and stabilizes the surface of the eggs. The artificial nests were made of small wire baskets filled with hay (Fig. 2b). 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 an attraction of predators 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 v. Blotzheim & Bauer 1991).

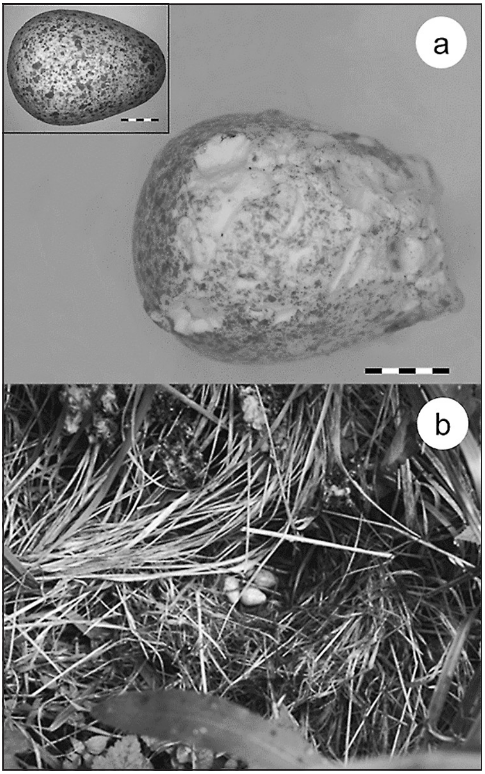


Fig. 2: (a) Dummy egg with bite marks of a rodent (scale bar indicates 5 mm) and original artificial egg without damages (inlet), and (b) artificial nest with dummy eggs exposed in the field. – Abb. 2: (a) Eiattrappe mit Bißmarken eines Nagers (Maßstabsbalken zeigt 5 mm) und unbeschädigtes Kunstei (kleines Bild), sowie (b) im Freiland exponiertes Kunstnest mit Ei-Attrappen.

Between July 17 and 23 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 v.

Blotzheim & Bauer 1991). 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 v. Blotzheim & Bauer 1991). 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. The experiments with artificial nests were carried out rather late in the breeding season to avoid serious disturbance in River Warbler territories. However, we doubt that this affects the outcome of our nest predation experiment because the abundance of relevant predators (e.g. corvids, rodents, snakes) should not drastically change between June and July.

### 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 be excluded at this stage of our analyses. River Warbler observations which did not indicate a territory were not considered in these analyses. Furthermore, two of the 30 T sites had to be excluded from our analyses because they were not accessible due to a strong flooding.

Subsequently a model selection approach only considering variables significantly differing (according to t, $Chi^2$ 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 not to be 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 the relative likelihood of a model compared to alternative models (Wagenmakers & Farrell 2004).

## Results

### River Warbler abundance and territory density

River Warblers were observed at 73 different sites in the alluvial forest (Fig. 1b). 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. 1b), but they did not establish a territory. For the flooded forest area the River Warbler density was 0.12 breeding pairs per 10 hectare.

### 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 (Tab. 2, Fig. 3b). 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 (Tab. 2, Fig. 3c). *Urtica dioica* cover was significantly higher at T sites than at FF sites, and significantly higher at FF sites than at NFF sites (Tab. 2, Fig. 3e). 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 (Tab. 2, Fig. 3).

Tab. 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. 4. – Tab. 2: Ergebnisse univariater Tests auf Unterschiede von Habitatvariablen zwischen regelmäßig überfluteten (FF) und nichtüberfluteten Auwaldbereichen (NFF), sowie zwischen FF-Standorten und Schlagschwirl-Territorien (T). Die Variablen Anzahl Bäume und Abstand zum nächstgelegenen Gewässer wurden log (x+1)-transformiert. Signifikante Unterschiede sind durch Fettdruck hervorgehoben. Vergleiche auch Abb. 4.

| **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 |
| *Urtica dioica* 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 |

## Food availability

The abundance of ants was significantly higher at T than at FF sites, but did not differ between FF and NFF sites (Tab. 3, Fig. 4a). A similar pattern was found for the abundance of other Hymenoptera (Tab. 3, Fig. 4b). The abundance of Diptera, Hemiptera, Coleoptera, Arachnida and Pulmonata showed neither significant differences between NFF and FF sites nor between FF and T sites (Tab. 3).

Tab. 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 Formicidae), 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. 5. – Tab. 3: Ergebnisse univariater Tests auf Unterschiede in der Nahrungsverfügbarkeit zwischen regelmäßig überfluteten (FF) und nichtüberfluteten Auwaldbereichen (NFF), sowie zwischen FF-Standorten und Schlagschwirl-Territorien (T). Die Variablen Anzahl anderer Hymenopteren (ohne Formicidae), Anzahl Diptera, Anzahl Hemiptera and Anzahl Arachnida wurden log (x+1)-transformiert. Signifikante Unterschiede sind durch Fettdruck hervorgehoben. Vergleiche auch Abb. 5.

| **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 |

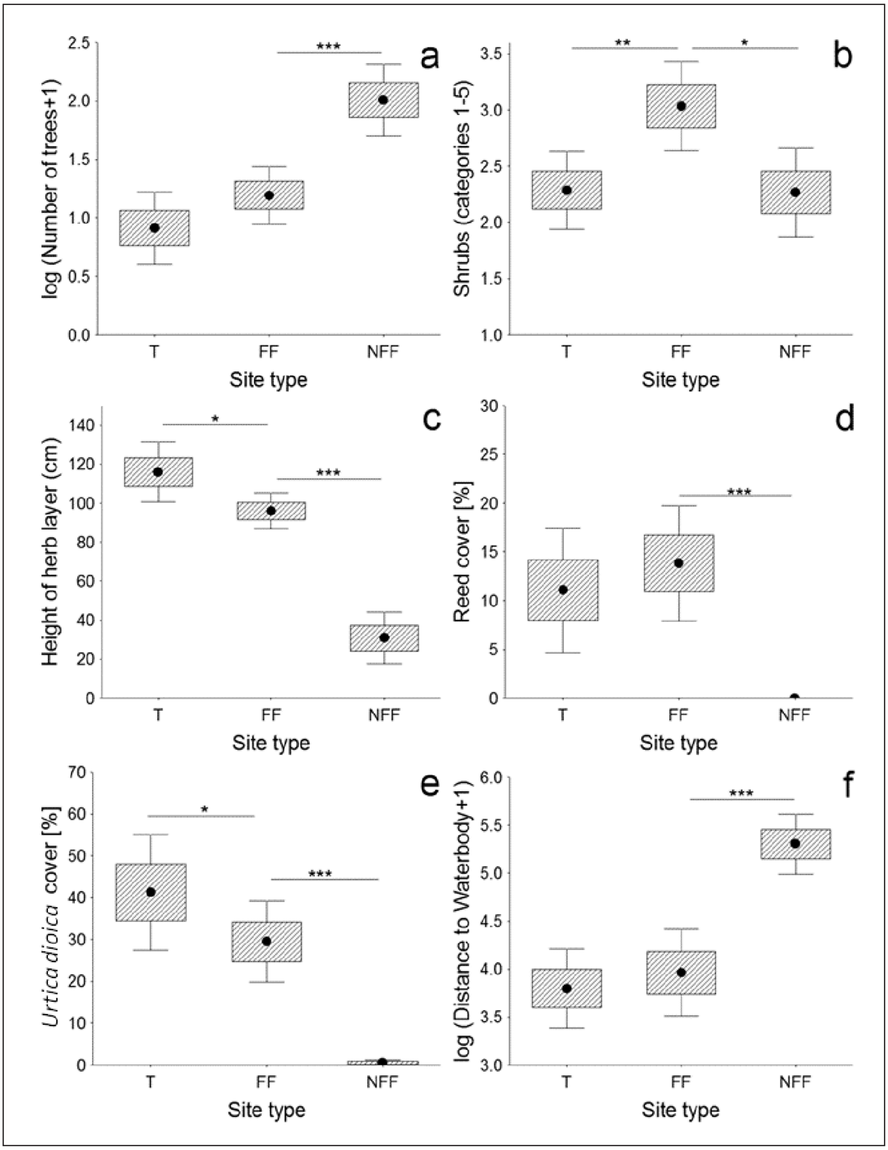


Fig. 3: Mean (a) tree number, (b) shrub density, (c) height of herb layer, (d) reed cover, (e) stinging nettle cover and (f) distance to next waterbody ± SE (box) and 95% CI (whiskers) at River Warbler territories (T), and randomly selected sites in regularly flooded (FF) and non-flooded forest (NFF). 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 Tab. 2). – Abb. 3: Durchschnittliche (a) Anzahl an Bäumen, (b) Strauchdichte, (c) Krautschichthöhe, (d) Schilfdeckung, (e) *Urtica-dioica*-Deckung und (f) Entfernung zum nächstgelegenen Gewässer ± Standardfehler (Box) und 95% Konfidenzintervall (Streuungslinien) in Schlagschwirl-Territorien (T) sowie an zufällig ausgewählten Standorten in Bereich des regelmäßig überfluteten (FF) und des nicht überfluteten Auwaldes (NFF). Sternchen zeigen signifikante Unterschiede (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) zwischen T- und FF-Standorten bzw. zwischen FF- und NFF-Standorten an (für Details siehe Tab. 2).

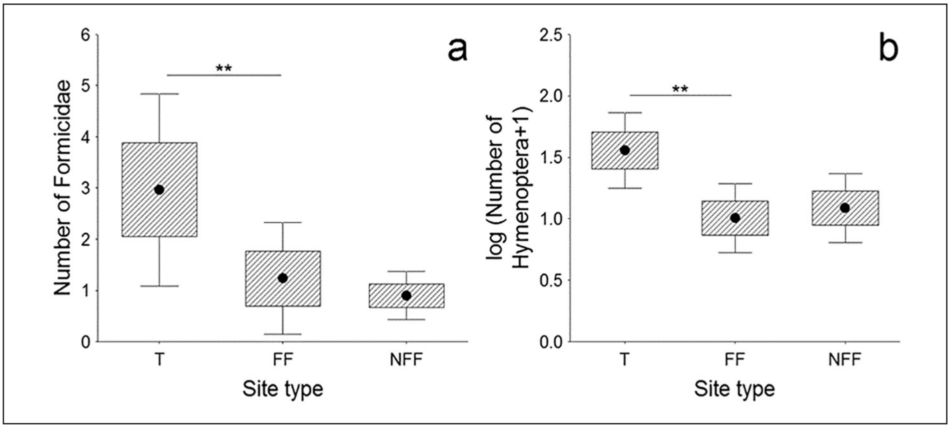


Fig. 4: Mean abundance of (a) Formicidae and (b) other Hymenoptera ± SE (box) and 95% CI (whiskers) recorded in River Warbler territories (T) and randomly selected sites in regularly flooded (FF) and non-flooded forest (NFF). Asterisks indicate significant differences (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) between T and FF sites and FF and NFF sites, respectively (for details compare Table 3). – Abb. 4: Durchschnittliche Abundanz an (a) Formicidae und (b) anderen Hymenopteren ± Standardfehler (Box) und 95% Konfidenzintervall (Streuungslinien) in Schlagschwirl-Territorien (T) sowie an zufällig ausgewählten Standorten in Bereich des regelmäßig überfluteten (FF) und des nicht überfluteten Auwaldes (NFF). Sternchen zeigen signifikante Unterschiede (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) zwischen T- und FF-Standorten bzw. zwischen FF- und NFF-Standorten an (für Details siehe Tabelle 3).

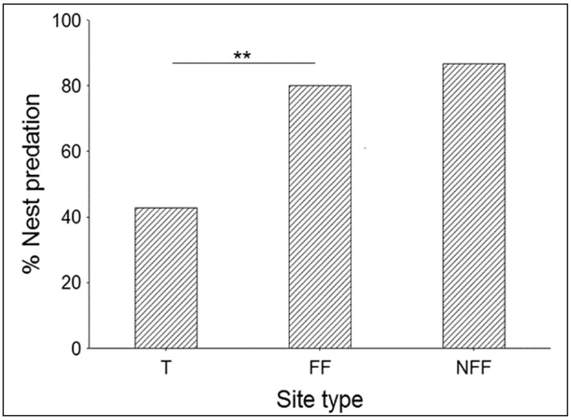


Fig. 5: Percentage of predated artificial nests in River Warbler territories (T), and at randomly selected sites in regularly flooded (FF) and non-flooded forest (NFF). The two asterisks indicate significant effects at a level of $p < 0.01$ ($Chi^2$ tests testing for differences between T and FF and FF and NFF sites, respectively). – Abb. 5.: Prozentsatz prädierter Kunstnester in Schlagschwirl-Territories (T) und an Zufallspunkten in regelmäßig überschwemmten (FF) und nicht überschwemmten Auwaldbereichen (NFF). Zwei Sternchen zeigen einen signifikanten Effekt von $p < 0.01$ an ($Chi^2$-Test auf Unterschiede zwischen T- und FF-Standorten bzw. FF- und NFF-Standorten).

## Nest predation

A total of 42.9% of the artificial nests (12 of 28) exposed at T sites were 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 (Fig. 5). 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 (Fig. 5).

## Identification of important habitat variables using a model selection approach

GLMs including vegetation structure variables (shrub density, herb layer height and *Urtica dioica* cover), food availability variables (abundance of Formicidae, abundance of other Hymenop-

Tab. 4: Summary of Akaike model selection evaluating effects of three vegetation structure variables (shrub density, herb layer height, *Urtica dioica* cover), two food availability variables (Formicidae 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 AICc values presented). Variables with a significant contribution according to Wald statistics (Tab. 5) are printed bold. – Tab. 4: Zusammenfassung der Akaike-Modelselektion zur Einschätzung der Auswirkungen der drei Vegetationstruktur-Variablen (Strauchdichte, Krautschichthöhe, *Urtica-dioica*-Deckung), der zwei Nahrungsverfügbarkeit-Variablen (Abundanz Formicidae, Abundanz anderer Hymenoptera) und der Nestprädation auf das Auftreten des Schlagschwirls (alle Modelle, welche einen AICc-Wert aufweisen, der im Vergleich zum niedrigesten AIC-Wert des besten Modells nicht um eine Differenz von >2 abweicht, sind angegeben). Variablen mit einem signifikanten Effekt, beurteilt anhand der Wald-Statistik (vgl. Tab. 5), sind durch Fettdruck hervorgehoben.

| **Variables** | **AICc** | **AICc weight** | p |
|---|---|---|---|
| **Nest predation**, **other Hymenoptera**, **shrubs**, herb layer, Urtica dioica | 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, Formicidae | 58.8 | 0.14 | <0.001 |
| **Nest predation**, **other Hymenoptera**, **shrubs**, herb layer, Formicidae, Urtica dioica | 59.0 | 0.13 | <0.001 |
| **Nest predation**, **other Hymenoptera**, **shrubs**, Urtica dioica | 59.6 | 0.10 | <0.001 |

tera) 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 (Tab. 2 and 3; for nest predation see main text above). Only the variables nest predation, abundance of Hymenoptera (excluding Formicidae) and shrub density were included in the five best models and represented the only variables with a significant contribution according to Wald statistics (Tab. 4 and 5).

Tab. 5: Forest-statistics of univariate analyses of seven predictors used in generalized linear models testing for effects on the occurrence of River Warblers (see Table 4). Variables with a significant effect are printed bold. – Tab. 5: Wald-Statistik für univariate Analysen von sieben Prädiktorvariablen, die in allgemeinen linearen Modellen zur Einschätzung der Auswirkungen auf das Auftreten des Schlagschwirls verwendet wurden (vgl. Tabelle 4). Variablen mit einem signifikanten Effekt sind durch Fettdruck hervorgehoben.

| **Variables** | **Wald statistics** | ***P*** |
|---|---|---|
| **Shrubs** | **4.73** | **0.030** |
| Height of herb layer | 2.73 | 0.098 |
| *Urtica dioica* | 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). Even if the applied definition of a territory may have been less strict than in our study the documented territory density is still remarkable. Even 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 & 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 v. Blotzheim & Bauer 1991). 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 & Frank 2009).

## 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 *Urtica dioica* cover. The importance of these habitat parameters was already emphasized before (Glutz v. Blotzheim & Bauer 1991). 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 remained significant even after applying a Bonferroni correction. Both taxonomic groups are mentioned as prey of the River Warbler (Glutz v. Blotzheim & Bauer 1991). 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 *Urtica dioica* cover compared to the control sites. Vegetation cover and density can affect the probability and frequency of visual nest detection, 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 (Arnold 2002, Luiselli & Angelici 1996). 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 built 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 usually only remove the nest contents 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 rummage for food in the ground and might find the nests by chance. 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

As the population of the River Warbler in Europe appears to be stable (Sanderson et al. 2006), the species' decline in the Danube alluvial forests east of Vienna is most likely caused by a regional loss of suitable habitats due to the change of the entire forest ecosystem. This may not only have resulted in changed vegetation structure of the Danube floodplains but also in changed food availability and predation risk. Main drivers for these changes in the floodplain system are most likely the dramatically reduced hydrological dynamics. Further, it remains to be studied to what extent invasive neophytes such as *Solidago canadensis*, *S. gigantea* and *Impatiens glandulifera* contribute to the population decline of the River Warbler in Danube floodplain forests. These invasive herbs are capable of reducing the *Urtica dioica* cover (Gruntman et al. 2014, Rak & Bergmann 2013, Schmidt 1981), an important habitat requisite of River Warbler territories. To achieve a more detailed understanding of factors with 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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