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„Ecological Analysis of a Declining Population of the Penduline Tit *(Remiz pendulinus)* at Morava River in Eastern Austria"

verfasst von / submitted by

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Abstract (deutsch)

Der auffällige Rückgang einer bekannten Beutelmeisenpopulation in den March-Thaya Auen im Nordosten Österreichs wurde in dieser Arbeit mittels historischer Funddaten (1969-2018, entlang ca. 130 km Flussstrecke) und selbstständiger Feldbegehungen (2018, entlang ca. 45 km habitatreicher Flussstrecke) erstmals detailliert quantitativ analysiert. Außerdem wurden mögliche Gründe für den Rückgang untersucht: Mittels einer GIS-Analyse rezenter Biotopkartierungen wurde die Habitatstruktur von stark und weniger stark frequentierten Habitaten verglichen; eine Zeitreihe von vier Pegelstellen entlang Thaya, March und Donau wurde auf veränderte Wasserstände zur Brutzeit hin untersucht; und eine Zeitreihe der Temperatur- und Niederschlags- Monatsmittel einer zentral gelegenen Messstelle genutzt, um klimatische Muster zu entdecken.

Seit Mitte der 1990er Jahre konnte ein Rückgang um 81 – 87 % der Beutelmeisen-Meldungen im gesamten Untersuchungsgebiet beobachtet werden. Im Frühjahr 2018 konnten im Begehungsgebiet 3 gesicherte und 5 mögliche Bruten, sowie 13 – 20 Individuen nachgewiesen werden, ein Großteil der Vorkommen befand sich auf slovakischer Seite des Gebietes. Gute Bruthabitate wiesen einen höheren Anteil an Wiesen- und Weideflächen, flachgründiger Gewässer und naturnaher Weichholzauen auf als schlechte Bruthabitate. An drei Pegelstellen konnten sinkende Wasserstände und an allen vier Pegelstellen eine Zunahme von Niedrigwasserständen beobachtet werden. Es konnte eine Temperaturzunahme zur Brutzeit beobachtet werden, jedoch kein Trend bezüglich der Niederschlagsmenge. Großräumige klimatologische Studien weisen jedoch auf eine Zunahme von Extremniederschlagsereignissen im Osten Österreichs hin.

Die sinkenden Wasserstände deuten auf eine Abnahme wichtiger dynamischer Prozesse in dem Augebiet hin; einsetzende Sukzession führt vermutlich bereits zu Habitatsveränderungen die sich negativ auf die Beutelmeise auswirken. Tendentiell zunehmende Extremniederschläge sowie großräumige Populationsdynamiken könnten weitere bedeutende Einflussfaktoren sein. In jüngster Zeit vorgenommene Flussrenaturierungen an Teilen von Donau, March und Thaya sind ein Schritt in die richtige Richtung, um natürliche Dynamiken wiederherzustellen und strukturreiche Habitate für die Beutelmeise und andere typische Arten der Aulandschaft zu sichern.

Schlagworte: *Remiz pendulinus, Beutelmeise, Population, Rückgang, Österreich, March, Ökologie, Habitatsstruktur, Wasserstand, Sukzession, Niederschlag*

Abstract (english)

In this work, the apparent decline of a well-known population of Penduline Tits in the Morava-Thaya floodplains in north-eastern Austria was analysed in detail using historical data (1969-2018, ca. 130 km of river flow length) and own field surveys (2018, ca. 45 km of river flow length). Additionally, possible reasons for the decline were investigated: By means of a GIS analysis of recent biotope mappings, the habitat structure of heavily and less heavily frequented habitats was compared; a time series of four water level recording stations along Thaya, Morava and Danube river was examined to look for changes in water levels during the breeding season; and a time series of the monthly temperature and precipitation averages from a centrally located measuring point were used to discover climatic patterns.

Since the mid-1990s, a 81 – 87 % decrease in Penduline Tit reports could be observed for the entire study area. In spring of 2018, 3 certain and 5 possible broods as well as 13-20 individuals could be detected in the field survey area; a large part of the occurrences were on the Slovakian side of the area. Good breeding habitats had a higher proportion of meadow and pasture areas, shallow waters and near-natural softwood riparian forest than poor breeding habitats. Falling water levels could be observed at three gauging points and an increase in low waters at all four gauging points. An increase in temperature during the breeding season could be observed, but no trend with regard to the amount of precipitation. Large-scale climatological studies, however, suggest an increase in extreme precipitation events in eastern Austria.

The falling water levels indicate a decrease of important dynamic processes in the floodplain; the onset of succession probably already leads to habitat changes that have a negative effect on Penduline Tit population. The trend towards increasing extreme precipitation events, as well as large-scale population dynamics, could be further major factors. Recent river renaturations on parts of Danube, Morava and Thaya are a step in the right direction to restore natural water dynamics and to secure richly structured habitats for the Penduline Tit and other typical floodplain species.

Keywords: *remiz pendulinus, penduline tit, population, decline, austria, morava, ecology, habitat structure, water level, succession, precipitation*

Introduction

The Eurasian Penduline Tit *(Remiz pendulinus)* is a small passerine bird of open floodplain forests and similar habitats throughout Europe, Turkey and Azerbaijan (Flade 2020). Its pronounced westward expansion during the second half of the 20th century, together with its complex mating system and elaborate pendulous nest, led to keen interest in this species (species' ecology summarized by e.g. Glutz von Blotzheim & Bauer 1993 and Schönfeld 1994). It is a short-distance migrant in its northern and western territory and generally occurs west of the Ural Mountains. It commonly is divided into four subspecies, of which *R. pendulinus pendulinus* is the one occurring in most of Europe (Madge 2020). In the beginning of the 20th century, the main area of distribution was east of ~14° eastern longitude and ranged between 35° and 55° northern latitude (Schönfeld 1994). During the second half of the century, expansion towards central, north and southwestern Europe happened in several episodes, with southwestern Europe also becoming established as new wintering area (Flade et al. 1986, Valera et al. 1990, Glutz von Blotzheim & Bauer 1993, Schönfeld 1994, Flade 2020). The species' range size peaked during the late 1980ies, populations have been declining since in some parts of western Europe, though a stable population remains in Spain, and new breeding areas have been gained in non-Atlantic climates of northern Europe, even above 60° northern latitude (Bauer et al 2005, Brichetti & Grattini 2010, Keller et al 2020).

The Penduline Tit is generally dependant on wetlands, while being thermophile and susceptible to cold and wet conditions (Flade et al. 1986, Glutz von Blotzheim & Bauer 1993, Schönfeld 1994). This is reflected in the current distribution pattern of the species, showing that it clearly avoids moist Atlantic climates and is restricted to elevations well below ~700m above sea level (Keller et al. 2020). It is a characteristic species of semi-open and structurally rich floodplain and riparian areas with a high number of forest margins and ecotones (Glutz von Blotzheim & Bauer 1993). Therefore, it colonizes dynamic riparian forests, lakes, ponds, marshes, and other associated habitats. However, it was also recorded breeding in transition biotopes as found in former stone and gravel pits, or lignite opencast mines when habitat requirements are met. According to an analysis of around 300 literature sources, the percentage frequency of different landscape elements used for breeding by Penduline Tits is as follows: 25% opencast mines, 23% fluvial valleys, 23% marshes and 29% lakes (Schönfeld 1994).

In eastern Austria, the species has been breeding regularly in the last centuries. Records in the floodplains of the Vienna basin date back to mid 18th century. In the second half of the 19th century, a persistent decrease can partly be ascribed to a flourishing trade with nests and clutches, but populations did not vanish. In the mid of the 20th century, a marked increase in local populations already heralded the approaching European wide expansion (Glutz von Blotzheim & Bauer 1993). From then on, until the 1990ies, the Penduline Tit was a regular and relatively abundant breeder (though with fluctuations) not only in the floodplains of Danube, Morava, Leitha and around Lake Neusiedl, but to a lesser extent also along smaller streams or at ponds of eastern Austria well away from the big floodplains (Glutz von Blotzheim & Bauer 1993). The current Austrian Penduline Tit population is estimated to lay between 300 and 1000 breeding pairs, but a population decline can be observed in recent years, which led to the change of the species' status from "least concern" to "vulnerable" (Dvorak et al. 2017).

The Morava-Thaya river region, the study area of this work, is located east and northeast of the Vienna basin, forming a connected system with the floodplains of Danube. It is classified as important bird area, and 15,086 hectares are part of the European "Natura 2000" network (European Commission 2008, BirdLife International 2021). The Penduline Tit population in the area, still high during the 1990ies (Zuna-Kratky et al. 2000), has been decreasing since then. Recent visits even suggest the total absence in some river sections known to be densely colonized back in the 90ies (Thomas Zuna-Kratky, pers. comm.), but exact numbers are yet unknown – as much as the reasons for the decline.

The decrease of a species' population can be caused by either a reduced rate of reproduction and/or an increased mortality. The biggest negative driver of reproduction rate in Penduline Tits is the desertion of nests by both parents. This happens to around one third of all clutches – and can make up between 40% (Upper Main Valley, Germany) and 75% (Lake Neusiedl, Austria) of all losses (Glutz von Blotzheim & Bauer 1993). Reasons for this behaviour can be related to the species' complex mating system. The pendulous nests, found to be the main factor determining male attractiveness to females (Schleicher 1993), are well insulated and offer good protection from predators – allowing for long foraging trips, and for only one partner to take care of the young. This arguably facilitated the evolution of ambisexual polygamy as mating system in Penduline Tits, where always at least one of the partners deserts the nest and re-mates. This system allows males and females to choose between different mating strategies, thereby increasing individual breeding success – at the cost of a high uncertainty of a successful outcome (Persson & Öhrström 1985, Persson & Öhrström 1989, Franz 1989 and 1991, Schönfeld 1994). However, this flexible pair bonding system is an inherent part of Penduline Tit biology and present in all populations. Hence, other factors must be responsible for the local decline.

Bad weather and prolonged rainfall are reported to be a severe threat to Penduline Tit broods (Glutz von Blotzheim & Bauer 1993, Schönfeld 1994). In the Upper Main Valley, an area with high yearly amounts of precipitation and relatively cold climate, 24% of all losses were due to bad weather, compared to only 9% at Lake Neusiedl with its warm Pannonian climate (Franz 1989, Haupt & Todte 1992). This supports the hypothesis that for the Penduline Tit, being a thermophile species, warm temperatures are seen as a positive factor for population development (Flade et al. 1986, Glutz von Blotzheim & Bauer 1993).

Recent climate change has been found to affect populations of many bird species across the world (Stephens et al. 2016), an example being its influence on species richness of birds in a Spanish wetland also housing Penduline Tits (Peiro 2018). Given the topicality of the climate crisis, and the fact that climatic parameters like precipitation and temperature are very likely to have an effect on Penduline Tit abundance, these two parameters shall be investigated in this study.

Besides climate change, as with most species, habitat loss most likely poses the greatest threat to survival of the Penduline Tit (Bauer et al 2005). Over the last centuries, the species has lost big parts of its natural habitat in Europe due to river regulations, drainage of wetlands and subsequent transformation to arable land and forests, facilitated by agricultural mechanisation and intensification. As consequence, about two-thirds of the European wetlands that existed 100 years ago have been lost (European Commission 1995, Owen 2007). But anthropogenic land transformations during the last century also created suitable transition habitats for the species, for example at different types of opencast mines, enabling or at least supporting the strong Europe-wide expansion during that time (Flade et al. 1986, Schönfeld 1994). However, habitat loss at a larger spatial scale can still play an important role in Penduline Tit population dynamics (see discussion in this work and Flade et al. 1986), although the majority of wetland-transformations in Europe already happened long before the recent population decline. This also counts for the river Morava (Lapin 2010). Nevertheless, that decreasing habitat quality is responsible for the population decline is still very likely since other bird species utilizing similar habitats show negative population trends in our study area as well, namely the Lesser Spotted Woodpecker (*Dendrocopos minor*) and the Garden Warbler (*Sylvia borin*) (Teufelbauer & Zuna-Kratky 2006). Because the Lesser Spotted Woodpecker is a non-migrating species, reasons for the decline, at least partly, need to be explained by local factors.

Therefore, this study aims to relate temporal changes in Penduline Tit occurrences across the Thaya-Morava region to spatial changes in the extent of various landscape elements. Additionally, long-term changes of water levels of the three rivers shaping the region (Thaya, Morava, Danube) will be analysed. River water levels provide information about the hydrological regime being active in their floodplains and thereby can act as a very rough proxy of amount and type of vegetation cover (De Jager et al 2016). Vegetation succession remaining increasingly undisturbed due to a declining hydrological connectivity of floodplains could negatively influence Penduline Tit abundance in the long run (see discussion in this work; Bauer et al. 2005). Siltation and ongoing degradation of natural floodplain area meanders started after river regulation measures were implemented in the last century at Morava (1936-1964) and Thaya (1979-1984). As result, 35 meanders were cut-off from the main river, inundation areas shrunk by two thirds and water dynamics in the riparian and alluvial floodplains were reduced (Schwarz 2003, Strohmaier & Egger 2011).

Further factors potentially influencing Penduline Tit abundance are food availability, predation and human disturbance. All three would be interesting to investigate for the Morava-Thaya floodplains, but this would go beyond the constraints of this work. While predation and food availability during breeding period are generally not considered being a major factor shaping Penduline Tit populations (Hoi & Darolová 1996), human disturbance and post-fledging food availability are deemed important (Flade et al 1986, Glutz von Blotzheim & Bauer 1993, Schönfeld 1994, Bauer et al 2005,).

This study aims to quantify and document the decrease of the Penduline Tit in eastern Austria between 1970 and 2018. Additionally, the potential influence of habitat structure as well as climate variables and river water levels on its occurrence will be analysed and discussed.

The following hypotheses are made:

(1) The Penduline Tit population of the March-Thaya region is decreasing.

(2) Historical or recent spatio-temporal differences in Penduline Tit densities across the study area are related to changes in landscape composition.

(3) Due to climate change, increasing temperatures are expected. Additionally, assuming a negative impact of precipitation on Penduline Tit abundance, increasing precipitation due to climate change is expected as well.

(4) River water levels are sinking, and flooding events are decreasing.

Methods

Study Site

The study area is located around 50km east and north-east of Vienna, at the borders to Czech Republic and Slovakia (Figure 1). In the north-east, the river Thaya constitutes the Austrian-Czechian border until north of Hohenau, where it enters into the Morava river flowing south along the Austrian-Slovakian border. Five kilometres north-east of Hainburg, the Morava river then issues into the Danube.

Influenced by the Pannonian climate of the Great Hungarian Plain, the floodplains of Morava and Thaya, and adjacent areas, belong to the driest and warmest regions in Austria (Bobek et al. 1971) – with the floodplains being periodically flooded during spring. This spatial and temporal proximity between dry and wet conditions results in a high biological diversity: In total, 444 endangered species and 53 endangered habitat types occur in these floodplains (Strohmeier & Egger 2011).

At its lower stretch in Austria, the Morava is a slow flowing lowland river (0.18‰ slope, Graf et al. 2010). Together with the lower stretch of Thaya River, it is characterized by fine-grained sediments, originally ample meanders, and flooding events early in the year (March + April) due to snowmelt in the catchment area, the Central Bohemian Uplands. In the lowest part of the Morava, roughly south of the town Marchegg, backwater flooding occur during early summer, due to often high water levels of the Danube during that time causing a water backlog. The floodplains of the Danube east of Vienna (designated as national park) form a connected river system with the floodplains of Morava and Thaya in the study area.

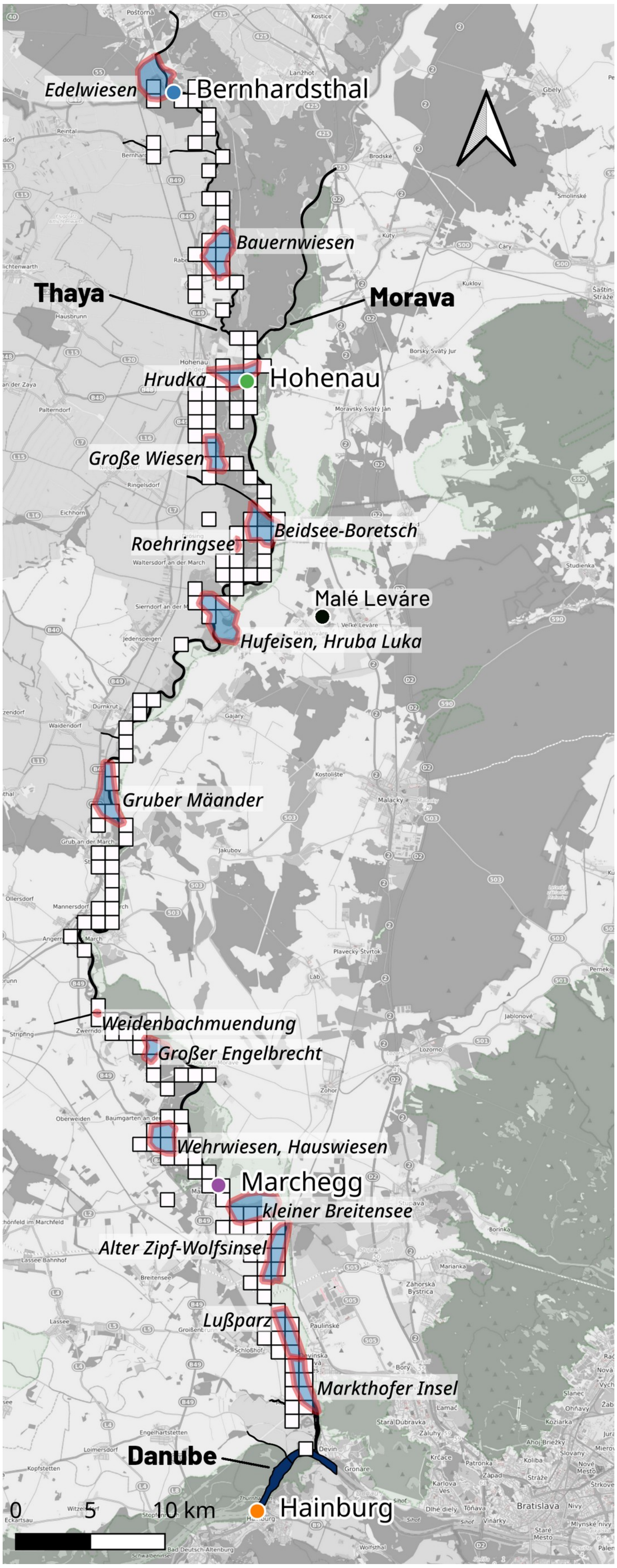


Figure 1. Overview of the study area. White squares (n=177) symbolize all sextants where Penduline Tits occurred between 1969-2018 (Austria only), river length from northernmost to southernmost sextant is approximately 130km. Blue areas with red borders mark survey sites during spring 2018, river length of all survey sites adds up to around 45km. The four coloured dots represent water-level recording stations (LRS). Austria is west of Thaya and Morava; Slovakia is east of Morava; in the north, Czech Republic extents between Thaya and Morava; in the south, Morava issues into Danube river.

Survey Data (2018)

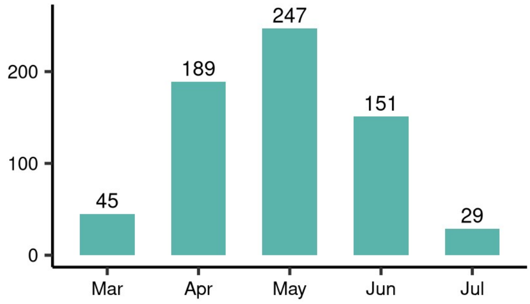
Between 4th April and 11th June 2018 on 42 days, a total of 112 hours were spent searching for Penduline Tits at the survey areas depicted in Figure 1. Note that some of the sites extended to the Slovakian territory of the Morava floodplains. If this data from the Slovakian area are additionally considered, this is explicitly noted in the results section. Each survey area was visited at least twice. Penduline Tits were detected mainly by slowly walking the area and listening for calls. Occasionally, a recorded call was played by a Bluetooth speaker to increase detection-range. Sites where nests were found were revisited one to three times. Areas, where calls occurred repeatedly were considered to have at least one individual present. Occurrences/calls up to ~1km around known nests were not considered as "new" individuals.

Presence Data (1969-2018)

Presence-only data (documented encounters of Penduline Tit individuals) in the study area was obtained for the period 1969–2018 from various sources: avifaunistic database of BirdLife Austria and historical and more recent survey data collected by Thomas Zuna-Kratky and Michael Dvorak. Figure 2 shows the cumulative number of encounters per month in the study area between 1969-2018 (note: only Austria). For all analyses, only Penduline Tits observed in March-July were considered, to include mainly non-migrating individuals (Zuna-Kratky et al 2000, Südbeck et al 2005).

The spatial resolution of findings was generally lower for older data (mostly, precision was at a level of sextants) and better for newer data (mostly, exact localization via GPS-device). To achieve comparability, sextants were used as area of reference for the whole set of presence-data of Penduline Tits. A sextant is defined as 1/6th of the area of 1x1 arcminute. In Austria, this equals to squares with side lengths between 616m and 640m. For some analyses, data was pooled for five-year periods or periods of other length. Graphical illustration of all recorded Penduline Tit encounters during 1-year periods can be found in the results section in figure 7.

Figure 2. Number of documented Penduline Tit encounters for each month cumulated over the study period 1968-2018.



Data about excursions

Data about excursions into the study area was obtained with help of Thomas Zuna-Kratky accessing his old notebooks and logs. All historical records of other bird species or of amphibians in a sextant during the study period were considered as "observer present in sextant" and labelled as excursion into respective sextants. The information about excursions into the study area made it possible to not only make statements about presence, but also about absence of Penduline Tits (at a temporal resolution of the following periods: before 1981, 1981-1989, 1990-1999, 2000-2006, 2007-2012, 2013-2018). Reasons for this arrangement of years: Before the 90ies, the area was only visited irregularly. During the 90ies, regular and systematic surveys took place. From 2000 onwards, noticeable changes in the population demand for shorter time periods. The year 2013 marks the start of the online reporting-tool “ornitho.at” and the start of data collection for the new Austrian breeding bird atlas, which resulted in a substantial increase of documented data.

Dividing the number of encounters in a sextant by the number of excursions in that same sextant during a certain time period, led to the new category “Encounters per Excursion”. To visualize and analyse this data, two separate subsets were prepared:

Dataset a) All sextants where there was either no information about Penduline Tit encounters (=NA) **or** the number of excursions (=NA) were not included in analysis; i.e. all NA’s in the data were removed. As a result, the minimum amount of encounters or excursions in included sextants was 1, the dataset consisted of 276 rows (Figure 8A and B).

Dataset b) For comparison, sextants without information about Penduline Tit encounters (=NA), but with information about the number of excursions, were included in this dataset as zero-encounter sextants (=513 additional rows of data, figure 8C and D).

Habitat Structure & Sextant Quality

Sextant Quality

The total number of sextants with Penduline Tit records in the study area during 1969-2018 was 177. For certain analyses, sextants were categorized into different “quality classes” reflecting the change in Penduline Tit abundance over time (see Table 1 and Figure 3).

Table 1. Definition of the quality classes used to subcategorize all sextants. The quality classes weight the sextants in respect to the total amount and constancy of findings between 1969-2018. Summarized encounters over 5-year periods were taken for categorisation to reach a meaningful amount of encounters for most sextants.

Sextant quality class	**Definition**
Good (n=19)	Encounters at least in 4 five-year-periods + encounters in the most recent five-year-period (2014-2018)
Formerly Good (n=13)	Encounters at least in 3 five-year-periods + but no encounters in most recent five-year-period + maximum of one encounter between 2004 – 2013
Medium (n=19)	Minimum of 5 encounters in total during 2 five-year-periods, OR less encounters during at least 3 five-year-periods. When in conflict with “new”, “medium” wins
Bad (n=31)	Maximum of 1 encounter in total + no encounter during the last 4 five-year-periods
New (n=14)	Encounters between 2009 - 2018 + Maximum of two encounters before, with the sum of encounters between 2009 – 2018 then needing to be higher than that number
Rest (n=81)	All other sextants

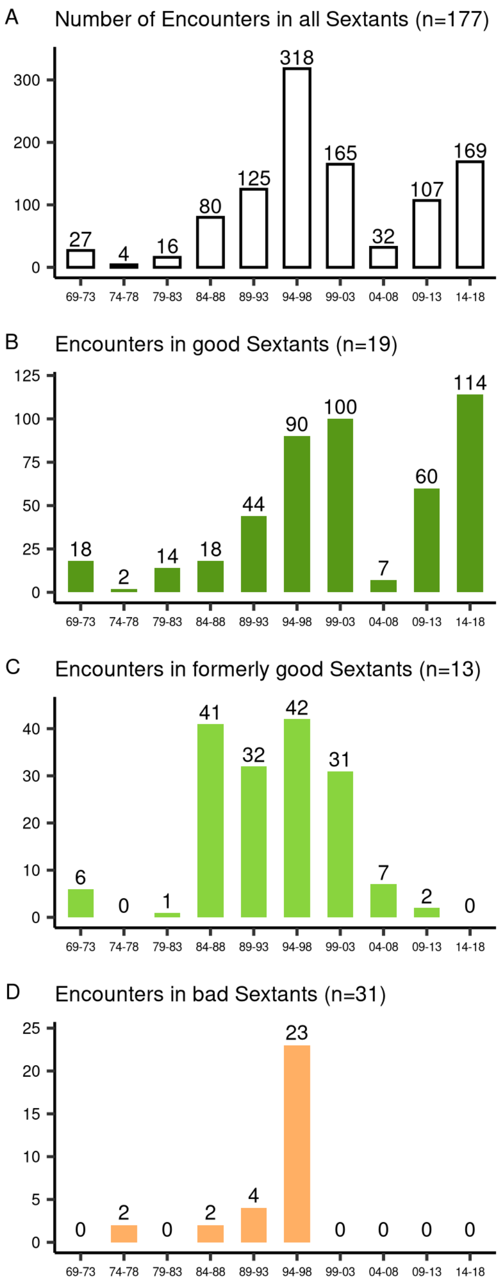


Figure 3. Number of encounters for different sextant quality classes for five-year periods over the whole study period.

Habitat Structure

Digitalized mappings of the riparian zone of the respective rivers, i.e. the study area, were used to calculate the percentage of different landscape elements in each sextant (Bierbaumer 2013, Stelzhammer 2013, Stelzhammer 2014, Zuna-Kratky unpubl.). Some of the classes overlap with other classes (usually periodically dried up shallow waters overlap with fields, fallows or meadows). For many sextants, not the whole area was mapped. For these two reasons, the amount of all classes of landscape elements of a sextant taken together usually does not add up to 100% (see Figure 4).

Waters (2)

For statistical analysis, only two classes of waters were distinguished: deep waters and shallow waters. The original mappings were much more detailed, but statistical analysis at this level of detail would have resulted in sample sizes too small to draw any meaningful conclusions. But for better traceability, the following list includes the sub-categories:

- deep waters (usually not falling dry)
    - main river
    - stream
    - deep waters close to river
    - anthropogeneous waters close to river
    - anthropogeneous waters on the landside of the dyke
    - deep waters on Slovakian side
- shallow waters (some falling dry at least in parts during the course of a year)
    - shallow waters close to river
    - shallow waters away from river
    - shallow waters on the landside of the dyke
    - temporarily filled shallow waters in landscape depressions (“Sutten”) close to river
    - temporarily filled shallow waters in landscape depressions (“Sutten”) away from river

Land-use Types (4)

Four classes of land-use types were distinguished:

- field: field with changing crops every year
- fallow: field with grass and greens, unchanging for some years in a row
- meadow: permanent grassland, including pastures

- special: agricultural landscape element of ecological value (mostly very small-scale)

Woods (5)

Five classes of woods were distinguished:

- riparian forest: "softwood" forest, regularly flooded. Characteristic species are willows, poplars and alders
- riparian forest (anth): anthropogeneous softwood forest, often hybrid-poplar cultures used for forestry and old pollard willows
- alluvial forest: "hardwood" forest, less commonly flooded. Characteristic species are oak, maple, ash and linden tree.
- alluvial forest (anth): anthropogeneous hard-wood forest, mainly ash tree cultures used for forestry
- other woods: all forest types and small woods which don't fit the above categories

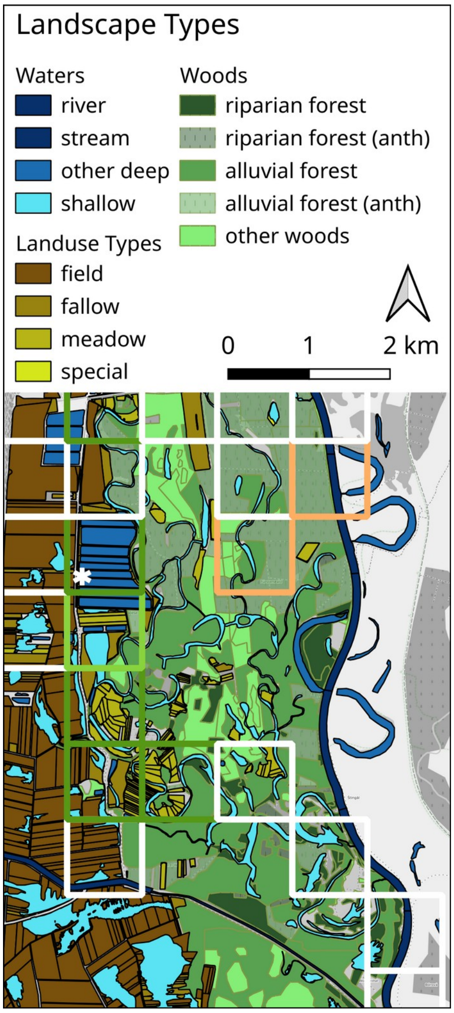


Figure 4. Landscape elements as used in analysis (except: “river”, “stream” and “other deep” together formed the “deep waters” category). “anth” = anthropogeneously influenced. Map shows area south of Hohenau with the sedimentation basins close to the field station of the local ringing association "Auring" (marked with a white star: 48.58324° N, 16.90829° E). As one can see, only scarce data was available for the area east of the main river. Sextant borders are coloured in respective quality class (green: good, light green: formerly good, orange: bad, white: all others – see also Figure 6).

River Water Levels

Data of four water-level recording stations (LRS) along Thaya (Bernhardsthal), Morava (Hohenau + Marchegg) and Danube (Hainburg) was provided by via donau. Data constituted of daily mean water levels [cm] for each of the LRS from 1970 to 2018. For Hohenau, Marchegg and Hainburg, characteristic thresholds were obtained from official publications describing water levels at Morava and Danube river (KWM 1996[1] and KWD 2010[2]); thresholds can be found in Table 2.

Definitions for Morava (adapted from KWM 1996):

- LW (Low water): In the average year, 344 days are above that value (= 6% of all days during the reference-period 1957-1996 are below that value).
- HW (High Water): Smaller floodings are already present, the drain is 320m³/s. In the average year, 15 days are above that value (=95.9% of all days during the reference-period 1957-1996 are below that value).

Definitions for Danube (adapted from KWD 2010):

- LW: In the average year, 344 days are above that value (= 6% of all days during the reference-period 1981-2010 are below that value).
- HW: In the average year, only 3.6 days are above that value (= 99% of all days during the reference-period 1981-2010 are below that value).

Additionally to low and high water-levels, daily mean water levels of the first 6 months of each year were taken for analysis. Monthly mean water levels at Hohenau (Morava) for the whole study period are shown in Figure 5.

1 “Kennzeichnende Wasserstände March 1996” (characteristic water levels of Morava, Via Donau 1996)
2 “Kennzeichnende Wasserstände Donau 2010” (characteristic water levels of Danube, Via Donau 2010)

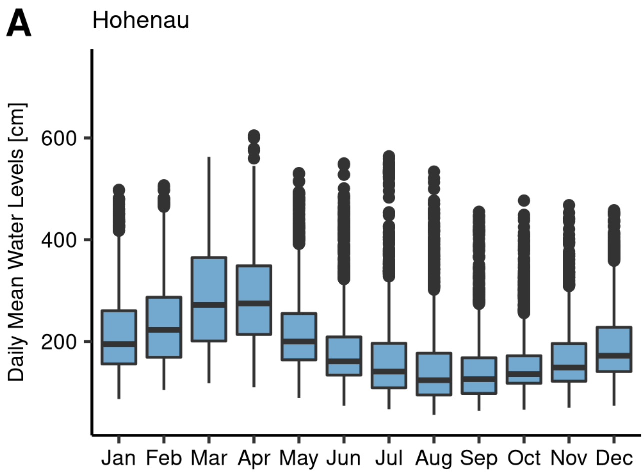


Figure 5. Daily mean water levels (median ± 25% (box) and up to 1.5 IQR[3] (whiskers)) of the Morava river during the course of the year between 1970-2018. Snowmelt in the catchment area leads to highest water levels usually between March and April. Peak maxima in June and August at Marchegg are due to some extreme water backlogs from Danube River.

Table 2. Characteristic water levels of recording stations along Thaya (Bernhardsthal), Morava (Hohenau and Marchegg) and Danube (Hainburg). Definitions differ between Thaya/Morava and Danube (see text). For analysis, I used official values where possible, and approximated the values for Bernhardsthal. "calc" = values calculated using my own data, i.e. the reference period of 1970-2018. "approx." = approximated value: I used the relative difference between my calculated values and official values (KWM 1996) of Hohenau and Marchegg to project the respective "KWM"-values for Bernhardsthal: 126 (calculated value of LW for Bernhardsthal) was multiplied by 1.26 (arithmetic mean of the relative difference between KWM-value and calculated value for Hohenau and Marchegg), and 341 (HW) by 1.07.

Location	**LW [cm]**	**HW [cm]**
Bernhardsthal $_{approx.}$	**159**	**354**
Bernhardsthal $_{calc\ (1970-2018)}$	126	341
Hohenau $_{KWM\ 96}$	**125**	**444**
Hohenau $_{calc\ (1970-2018)}$	94	415
Marchegg $_{KWM\ 96}$	**168**	**463**

3 1.5 times the interquartile range

Marchegg calc (1970-2018)	141	434
Hainburg KWD 10	**120**	**593**
Hainburg calc (1970-2018)	141	604

Climate - Temperature and Precipitation

Monthly mean precipitation and monthly mean temperature of the months March - June was obtained for the years 1969-2018 for Hohenau (ZAMG 2021a). Additionally, climate studies covering Austria and Europe were taken into account, some of which were using the HISTALP and HOM-START dataset of ZAMG (Auer et al 2007, Trömel & Schönwiese 2007, Dankers & Hiederer 2008, Auer et al 2010).

Data analysis

Population: Spearman's rank correlation was used to test for a connection between different time periods and the number of encounters per excursion (the latter being used as a proxy for local Penduline Tit population size).

Habitat Structure: For each of the 11 landscape elements (Figure 4), a boxplot-array distinguishing between the 6 sextant quality classes (Table 1) was drawn and used to visually pre-select landscape elements and quality classes of interest. As a result, 4 landscape elements and 3 quality classes were used for detailed statistical analyses: Wilcoxon rank-sum test (= Mann Whitney U) was then used to perform group-wise comparisons.

Water Levels: Spearman's rank correlation was used to test for a connection between year and median water levels, number of low waters and number of high waters for all four level recording stations.

Climate: Spearman's rank correlation was used to test for a connection between year and monthly mean temperature and monthly mean precipitation as measured by the weather station in Hohenau.

Regression lines or smoothed models were fitted in some graphs to aid the eye but were not used to deduce predictions.
Since this study is of investigative nature, trying to identify potential factors influencing population development of a species, I used a non-conservative alpha < 0.05 to identify significant effects. However, when multiple tests on one subject were performed, resulting p-values were adjusted using Holm-Bonferroni method.

Libre Office Calc (version 6.4.7.2) and R Studio (version 1.3.1073, R version 4.0.3) were used to handle and prepare data for analysis. R Studio was used to perform statistical tests and draw graphs. GIS-Data was handled and visualized using QGIS for Linux (version 3.16.0-Hannover). Some Graphs were fine-edited using GIMP (version 2.10.22). This document was written and layouted in Libre Office Writer (7.0.5.2) and Scribus (version 1.5.6.1).

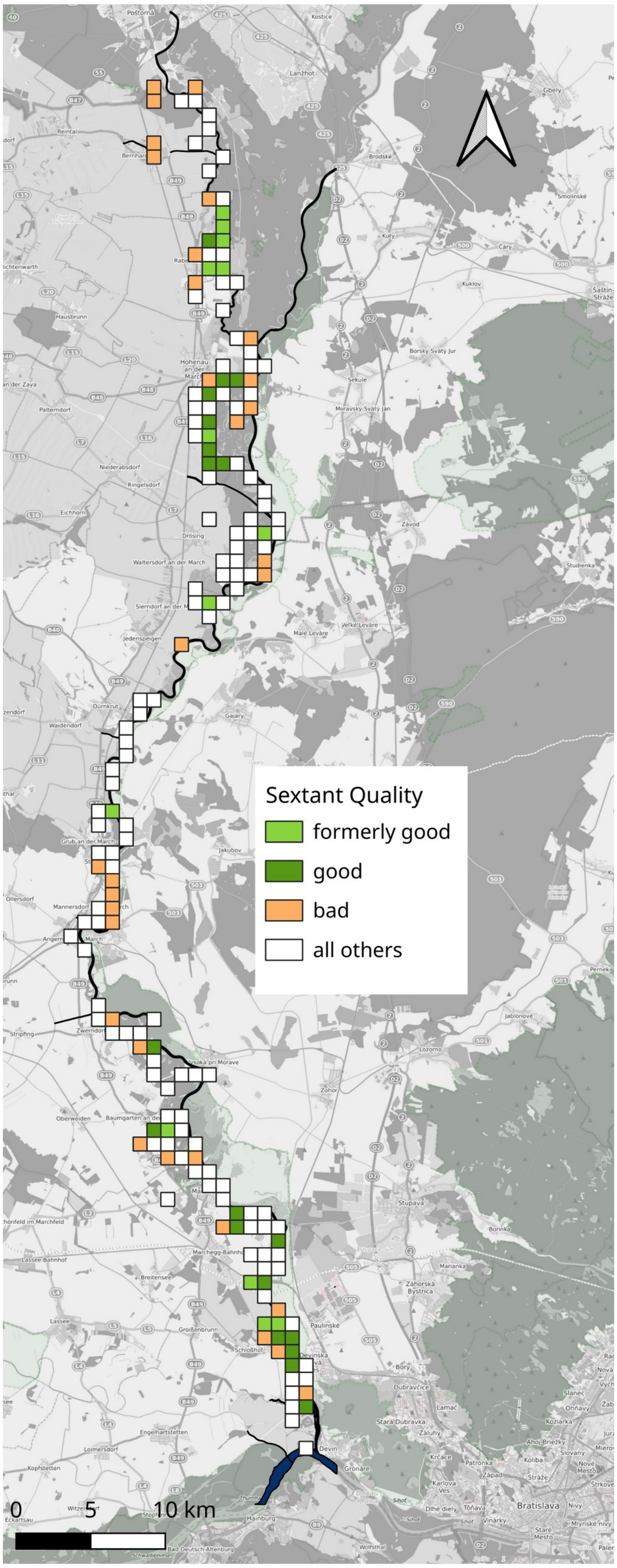
Results

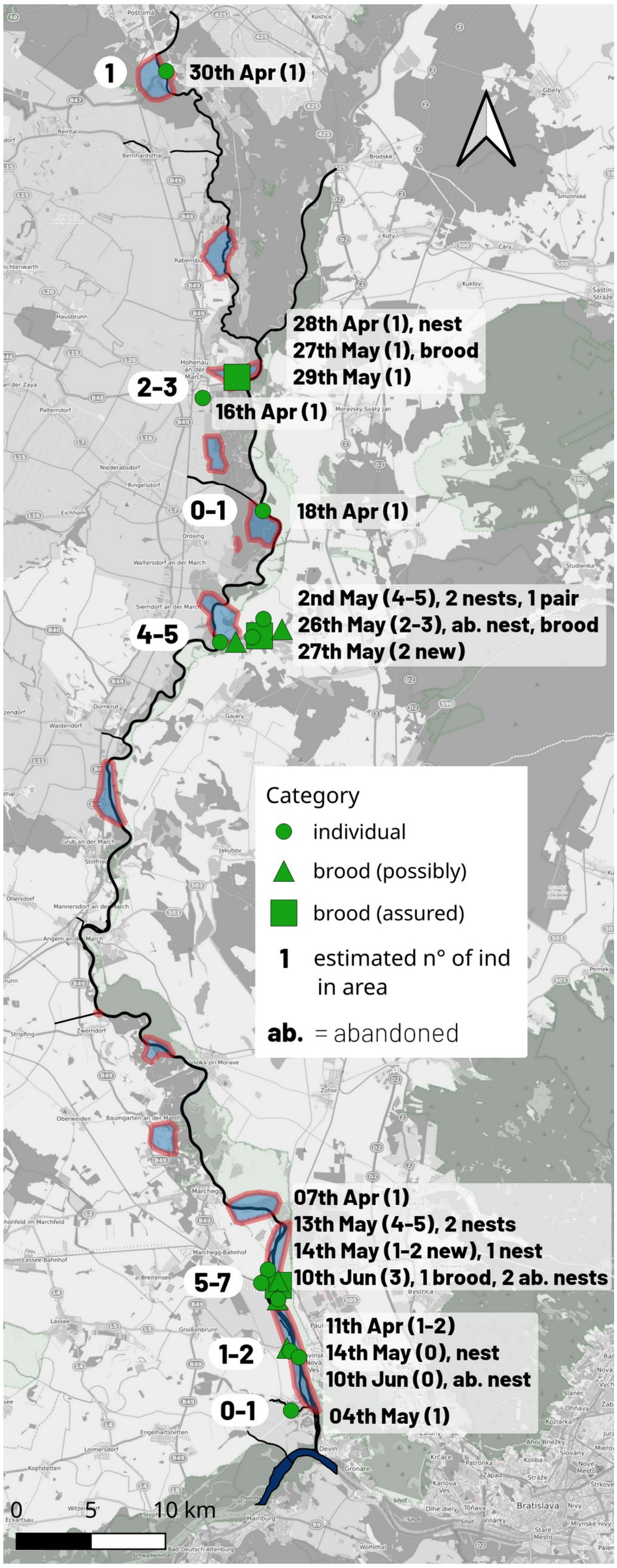
Survey Data (2018)

A total of three assured broods at the study areas (including Slovakian parts), and five occurrences where a brood seemed possible but not necessarily successful (1-2 individuals found building nest, but no brood found later on), were discovered. Only one assured brood occurred at the Austrian side of the study area east of Hohenau in the area "Hrudka". A finished nest, which was later found abandoned and partly destroyed, was located at the Austrian side of "Lußparz". The two main spots for Penduline Tits seemed to be on the Slovakian side of the river: 1) one brood and two further possible broods west of the Slovakian town Malé Leváre, close to the area "Hufeisen"; 2) within around 50m north and south of the train damn on the Slovakian side of "Alter Zipf", again with one assured brood and two possible ones. In total, between 4th April and 11th June 2018, 13-20 individuals were found to be present in the surveyed area (Figure 6B, for location and river names see Figure 1).

Figure 6A (next page, left). All sextants of the study with at least one occurrence during the study period 1969-2018 (n=177 sextants with records), with sextants coloured by quality class. Quality class weights the sextants in respect to the total amount and constancy of findings between 1969-2018 (see Table 1 and Figure 3 for definitions).

Figure 6B (next page, right). Survey areas 2018 and important encounters. Right of the green symbols, the date of encounters, overall number of individuals (in brackets) and additional information about the encounter are given. Numbers left of the green symbols represent the total number of individuals estimated being present in that area. Estimates were done in all conscience - lower and upper limits reflect the uncertainty due to the fact of a highly mobile species being mapped by a single observer.


Sextant Quality
formerly good
good
bad
all others
0 5 10 km


1
30th Apr (1)
28th Apr (1), nest
27th May (1), brood
29th May (1)
2-3
16th Apr (1)
0-1
18th Apr (1)
2nd May (4-5), 2 nests, 1 pair
26th May (2-3), ab. nest, brood
27th May (2 new)
4-5
Category
individual
brood (possibly)
brood (assured)
1 estimated n° of ind in area
ab. = abandoned
07th Apr (1)
13th May (4-5), 2 nests
14th May (1-2 new), 1 nest
10th Jun (3), 1 brood, 2 ab. nests
5-7
11th Apr (1-2)
14th May (0), nest
10th Jun (0), ab. nest
1-2
0-1
04th May (1)
0 5 10 km

Presence Data (1969-2018)

Between 1969 and the mid 90's, the number of Penduline Tit encounters increased in the study area. Subsequently, it decreased reaching a minimum between 2007-2009. Then, Penduline Tit numbers increased again to about half the number of the mid 90's (Figure 7).

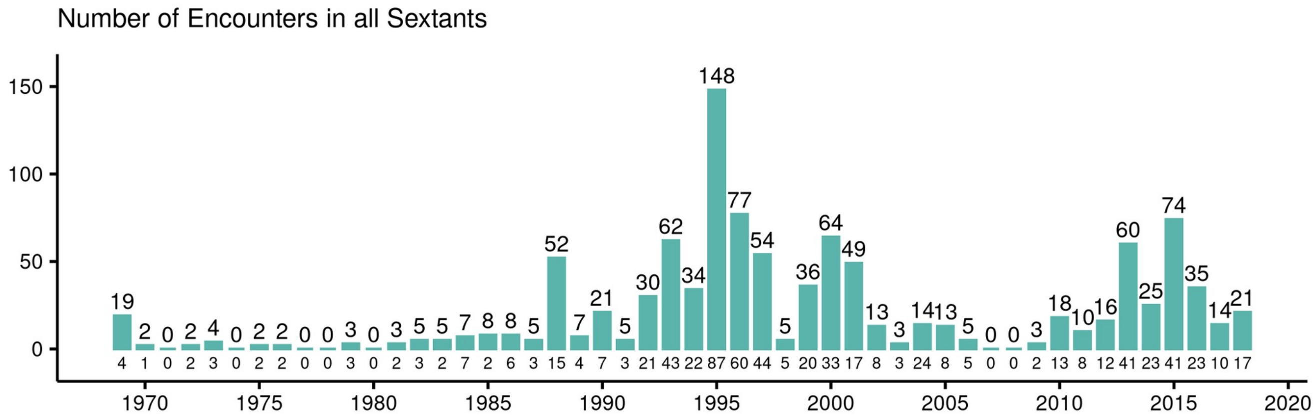


Figure 7. Number of all encounters in all sextants, for each year during the whole study period. Encounters of sextants where there was no information about number of excursions are included. Labels above the bars signify the amount of encounters during that year, small labels below state the number of sextants in which these encounters occurred.

Dataset a)

The number of documented excursions into the region increased over the whole period, with a distinct drop in 2007-2012 (Figure 8A). The median number of encounters per excursion for the different time periods decreased continuously from 0.50 (1981-1989), to 0.31 (90-99), to 0.18 (00-06), to 0.06 (07-12) to 0.04 (2013-2018). The number of encounters per excursion decreased significantly over the course of the years ($r_s = -0.57$, $p < 2.2e-16$), see Figure 8B.

Dataset b)

The number of documented excursions into the region increased over the whole period, with a sharp rise after 2012. For most time periods, absolute number of excursions was twice as high as in dataset a (Figure 8C). The median number of encounters per excursion was 0.01 (1981-1989) and 0.18 (90-99), but zero in all other time periods due to the many zeros present in this dataset. The number of encounters per excursion decreased significantly over the course of the years ($r_s = -0.34$, $p < 2.2e-16$), see Figure 8D.

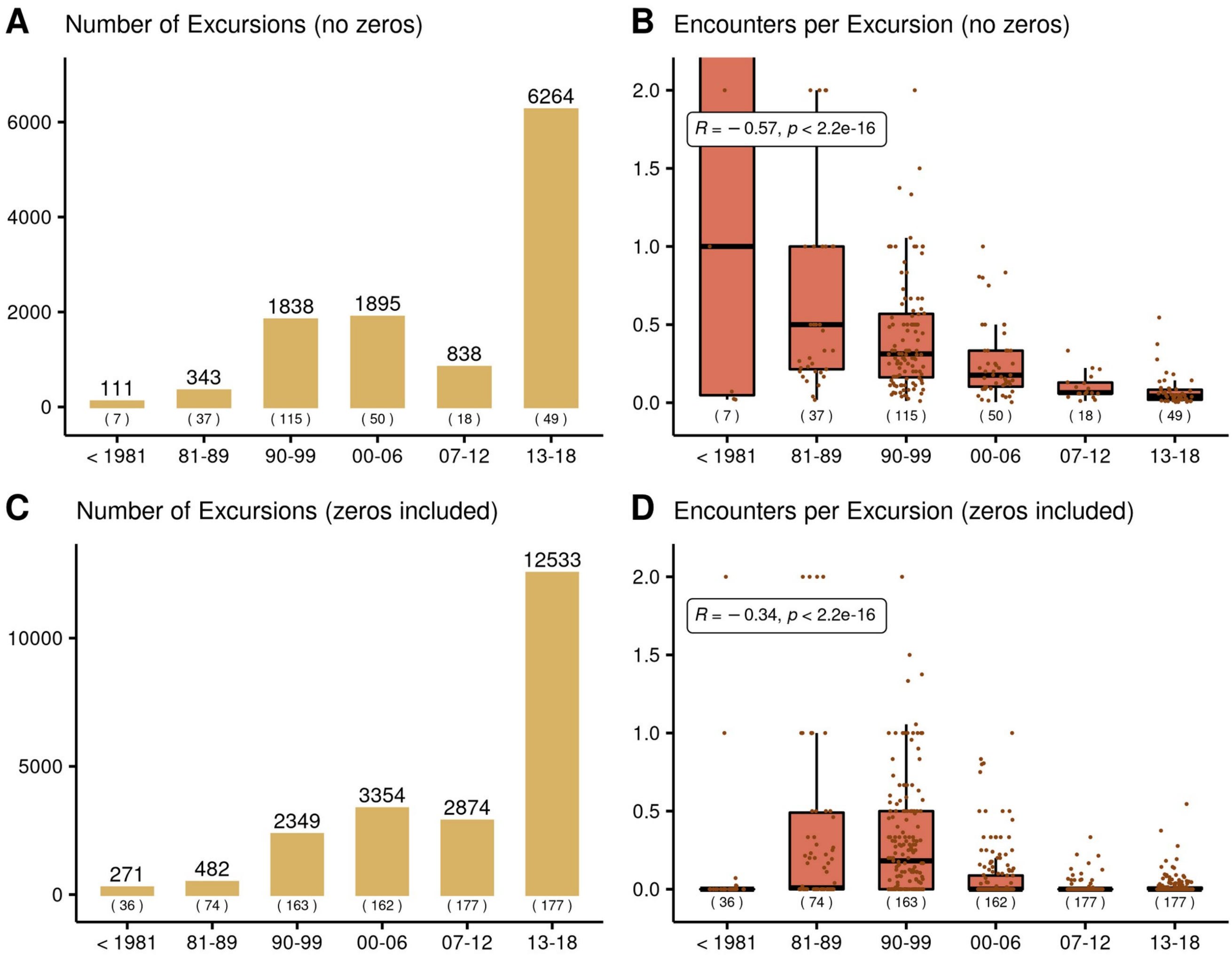


Figure 8. (A) Number of excursions into sextants of the study area during different time periods with at least 1 encounter (→ no zero-encounter sextants). Brackets below each plot give the number of sextants with sufficient data (=n, same sextants as in Figure 8C). (B) Number of Encounters per Excursion during different time periods in sextants with at least 1 encounter (→ no zero-encounter sextants). Brackets below each plot give the number of sextants with sufficient data (=n), also plotted as small brown dots. Result of a spearman rank correlation between the groups is plotted in the upper part of the graph. Y-values > 2.1 are not visible in this graph. (C) Same as 8B, but with zero-encounter sextants included, as defined in “dataset b”. (D) Same as 8C, but with zero-encounter sextants included.

Habitat Structure

Differences in the amount of certain landscape elements between sextants of different quality were tested using Mann-Whitney U-test. Only three of the six sextant quality groups are covered in detail: bad - formerly good, bad - good and formerly good – good. Only the landscape element “fallow”, “meadow”, “shallow waters” and “riparian forest” showed significant differences between sextant quality classes.

Fallow: The mean ranks of sq “bad” and sq “formerly good” were 19.2 and 30.3, with a significant difference between groups ($U = 99.5$, $Z = -2.67$, $p = 0.0067$, $r = 0.38$). There were no significant differences between sq “bad” and sq “good”, and between sq “formerly good” and sq “good”. The median of landscape cover with element “fallow” was 0.54% in bad sextants, 9.21% in formerly good sextants, and 2.88% in good sextants (Figure 9A).

Meadow: The mean ranks of sq “bad” and sq “formerly good” were 19.1 and 30.7, with a significant difference between groups ($U = 95.5$, $Z = -2.73$, $p = 0.0054$, $r = 0.39$). The mean ranks of sq “bad” and sq “good” were 19.8 and 34.8, with a highly significant difference between groups ($U = 118$, $Z = -3.53$, $p < 0.001$, $r = 0.48$). There was no significant difference between sq “formerly good” and sq “good”. The median of landscape cover with element “meadow” was 3.66% in bad sextants, 24.17% in formerly good sextants, and 17.16% in good sextants (Figure 9B).

Shallow waters: The mean ranks of sq “bad” and sq “formerly good” were 19.3 and 30.2, with a significant difference between groups ($U = 101$, $Z = -2.59$, $p = 0.0086$, $r = 0.37$). The mean ranks of sq “bad” and sq “good” were 22.0 and 31.2, with a significant difference between groups ($U = 186.5$, $Z = -2.16$, $p = 0.0302$, $r = 0.30$). There was no significant difference between sq “formerly good” and sq “good”. The median of landscape cover with element “shallow waters” was 4.16% in bad sextants, 10.54% in formerly good sextants, and 11.83% in good sextants (Figure 9C).

Riparian forest (/softwood forest): The mean ranks of sq “bad” and sq “formerly good” were 18.5 and 32.1, with a significant difference between groups ($U = 77$, $Z = -3.21$, $p = 0.0013$, $r = 0.45$). The mean ranks of sq “bad” and sq “good” were 20.2 and 34.2, with a significant difference between groups ($U = 129$, $Z = -3.31$, $p = 0.0013$, $r = 0.45$). There was no significant difference between sq “formerly good” and sq “good”. The median of landscape cover with element “riparian forest” was 2.74% in bad sextants, 10.64% in formerly good sextants, and 8.07% in good sextants (Figure 9D).

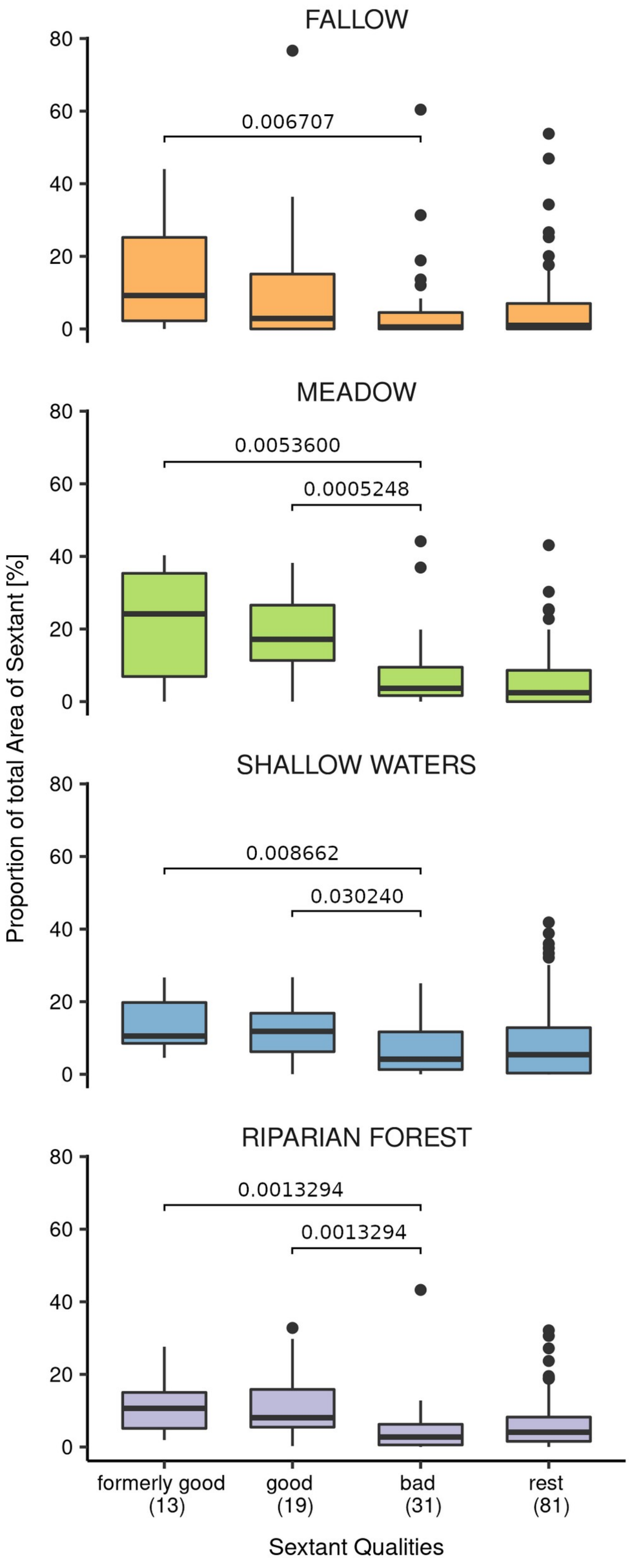


Figure 9. Amount of important landscape elements for different sextant qualities. Number of sextants in each quality-class (=n) is given in brackets on the lower x-axis. For definitions of the sextant quality classes see table 1 (note that "rest" is its own category, therefore doesn't include categories "medium" and "new"). For definitions of the landscape elements see Figure 4.

River Water Levels

If not stated differently, analyses in this section always refer to the time period between 1970-2018. Daily mean water levels over the first six months of each year were analysed using the median of each year to perform a Spearman rank correlation. Daily mean water levels decreased significantly between 1970 and 2018 (N = 47 years) at Bernhardsthal (r_s = -0.45, p = 0.0013), Marchegg (r_s = -0.34, p = 0.017) and Hainburg (r_s = -0.45, p = 0.0012). Only medians of water levels at Hohenau did not show a significant correlation with year (r_s = -0.16, p = 0.2748). Figure 10A shows the change in daily mean water levels over the study period of 47 years at Bernhardsthal.

The number of high and low waters signifies the number of days during a time period with daily mean water levels below certain threshold values (see methods and table 2). For all four LRS, no significant change in number of high waters during the first or second half of years could be detected over the course of the study period. However, for the period 2014-2018, not a single day with high water in the first half of years occurred at Bernhardsthal, Hohenau and Marchegg, and only one high water day occurred at Hainburg in 2014.

Number of low waters during the first half of years significantly increased at all four LRS: Bernhardsthal (r_s = 0.52, p = 0.00014), Hohenau (r_s = 0.38, p = 0.00679), Marchegg (r_s = 0.51, p = 0.00017) and Hainburg (r_s = 0.41, p = 0.00325) see Figure 10B.

The number of days with low waters also increased significantly during the second half of the years at Bernhardsthal (r_s = 0.43, p = 0.00224), Marchegg (r_s = 0.42, p = 0.00293) and Hainburg (r_s = 0.43, p = 0.00191), but not at Hohenau (r_s = 0.20, p = 0.168).

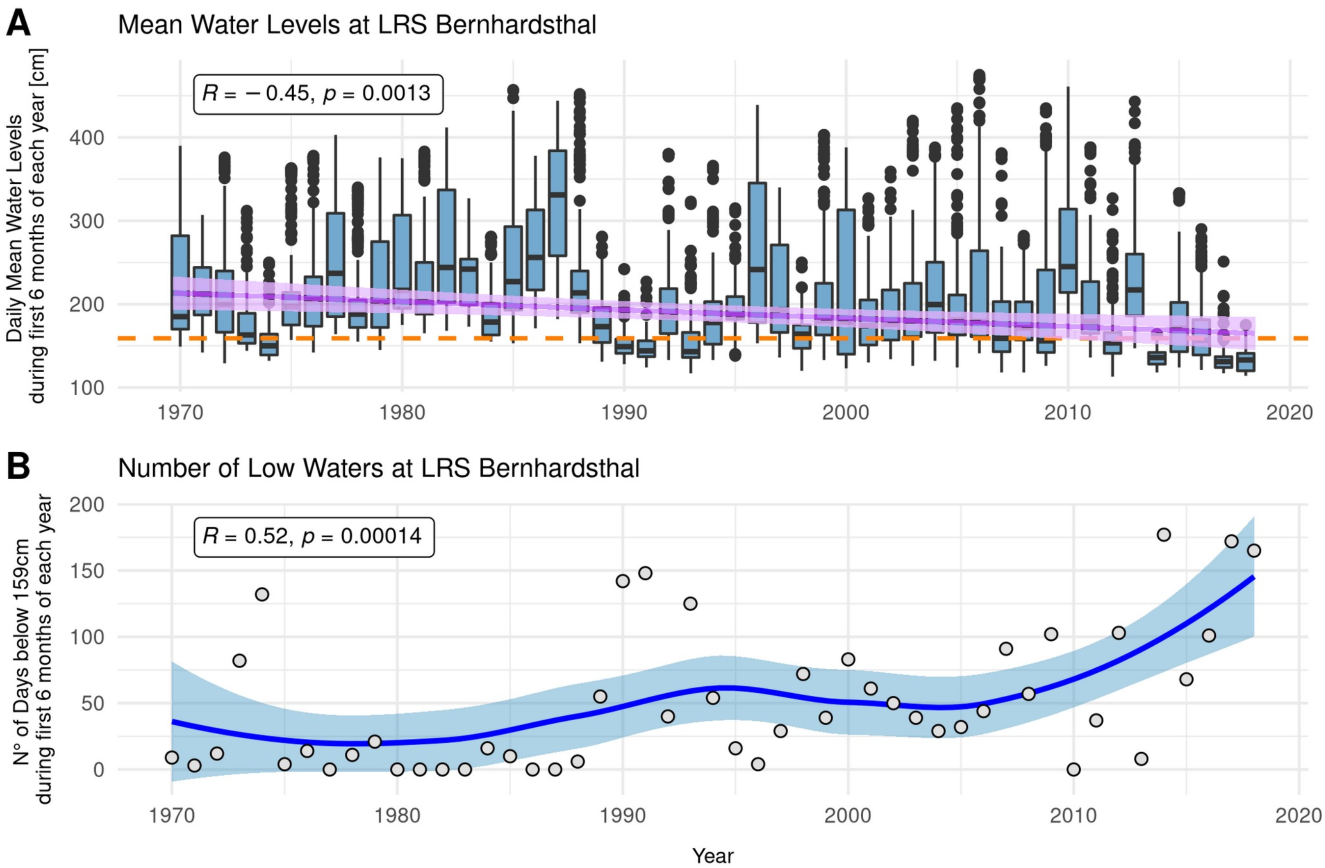


Figure 10. (A) Daily mean water levels (median ± 25% (box) and up to 1.5 IQR (whiskers)) of the first six months of each year over the period of 1970-2018 at LRS Bernhardsthal. Medians (thick horizontal line in each boxplot) were used to perform a Spearman Rank correlation with year, result printed in the top left. Regression line with 95% confidence interval added in pink. Dashed horizontal line represents the water level of 159cm, below which that day was considered as a day of low water, see Table 2 and Figure 10B. (B) Number of low waters during the first six months of each year over the period of 1970-2018 at LRS Bernhardsthal. Each data point represents the number of days during that period at which the daily mean water level was below 159cm. Local polynomial regression fitting (blue line) with 95% confidence interval was applied to aid the eye. Results of the performed Spearman Rank correlation are printed in the upper left part of the graph.

Climate - Temperature and Precipitation

While no significant correlation between year and monthly mean temperature was found for March (r_s = 0.14, p = 0.3321), in all other months temperatures measured at Hohenau increased significantly in the course of the study period 1969-2018 (April: r_s = 0.56, p = 2.277e-05; May: r_s = 0.41, p = 0.002988; June: r_s = 0.59, p = 5.609e-06; Figure 11). In contrast, no significant correlation of monthly mean precipitation and year was found at Hohenau.

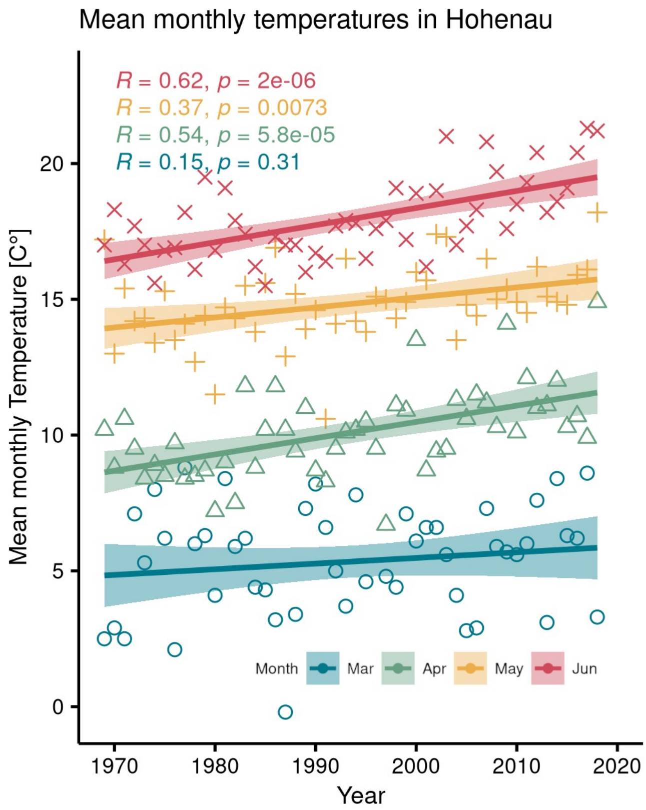


Figure 11. Monthly mean temperatures in Hohenau for the months March, April, May and June between 1969-2018. Pearson correlation statistics and regression lines with 95% confidence interval are added in the colors of respective month. Data taken from ZAMG Website (ZAMG 2021a)

Discussion

Population Trend

Survey data of Penduline Tit occurrences from 2018 around Marchegg are comparable in terms of area surveyed to the data of the study performed by Schleicher (1993). The author found 19 brood nests in a habitat of ~10km along Morava river (Austrian side only), whereas my findings for 2018 in the same area resulted in 4 brood nests (3 of which were on Slovakian side of the river, but very close to the site). Including all 4 brood nests still corresponds to a decrease of 79%. But being based on only one surveyed river stretch, and a pair of only two survey years, a comparison cannot be used to draw conclusions on the whole population of the study region. However, it fits well with the field experiences of Thomas Zuna-Kratky from the whole Morava-Thaya region (pers. comm.).

Analysing presence and excursion data of Penduline Tit occurrences between 1969 and 2018 draws a clearer but similar picture. When only including data points/sextants where information about both, encounters and excursions, is present (dataset a), the median “Encounter per Excursion” sank from 0.31 (1990-1999) to 0.04 (2013-2018) – a decrease of 87%. The decrease would be even greater if the median value of 0.50 between 1981-1989 would be considered – but the still low number of excursions during that time period and before might bias towards high values making the time period 90-99 more reliable. Coinciding with the start of the online reporting-tool “ornitho.at” in 2013, the number of recorded excursions skyrocketed (note the resulting steep rise of occurrences between the years 2012 and 2013 in Figure 7). And with only a limited number of birds present in the region, my calculated probability of observing a bird could be biased towards lower values. However, the low number of excursions between 2007 and 2012 were accompanied by a low amount of occurrences (see Figure 7 and 8A). This results in a comparable, low value for the periods 2007-2012 (0.06) and 2013-2018 (0.04) - emphasizing the consistency of the underlying trend of a decreasing Penduline Tit population. So in dataset a, the median number of encounters per excursion decreased from ~ 0.31 to 0.04 - 0.06 over the last 30 years, marking a decrease of 81 – 87 %. Dataset b shows that the underlying trend of a decreasing population persists even when all potential zero-encounter sextants are included in analysis.

To sum up, analysis of the available data suggests that Penduline Tit occurrences in the Austrian Morava-Thaya region decreased by 81 – 87 % between the 1980ies and 2018. This doesn’t necessarily reflect the real numerical decrease in local Penduline Tit population, but gives a good idea of its alarming dimension. It is in line with recent trends of the Italian Penduline Tit population, which were reported to have shrunk by 50 – 70 % between the 1980ies and 2007 (Brichetti & Grattini 2010). Accordingly, in the most recent version of the Austrian Red List, a decline of 41 – 50 % since 2005 is stated for the Penduline Tit population in Austria (Dvorak et al. 2017).

Habitat Structure

Only four landscape elements showed significant differences between groups. None of these elements differed significantly in its relative amount between *formerly good* and *good* sextants. Whereas sextants of both these groups contained a significantly higher amount of "meadow", "shallow waters" and "riparian forest" than *bad* sextants. "Fallow" differed only between *formerly good* and *bad* sextants, no difference was found between *good* and *bad* sextants.

Since the Penduline Tit has the highest conspicuousness during activities regarding breeding, while being relatively clandestine in other contexts, one can roughly equate "encounter during breeding period" with "breeding likely" (Zuna-Kratky, pers comm.), and safely assume that sextants with a high and/or regular history of encounters during breeding period contain good breeding habitats. This condition is met by *good* and *formerly good* sextants, but not by sextants of quality class *bad* and *rest* (Table 1). Compared to bad sextants, those containing good breeding habitats are characterised by a higher amount of riparian forest, shallow waters, and grassland. This is in line with previous assessments of the habitat structure preferred by Penduline Tits (Glutz von Blotzheim & Bauer 1993, Schönfeld 1994). Important habitat elements at breeding spots of Penduline Tits in Middle Elbe have been found to be the following (Schönfeld 1989a):

Night roosts: thickets with sufficient cover already before foliation (e.g.: *Prunus spinosa* and similar, but also *Rubus fruticosus* or former year vegetation of *Phragmites*).

Nesting trees: more or less distinct/solitary standing trees or big bushes (*Salix* sp., *Populus nigra*, *Betula* sp., *Alnus glutinosa*, *Ulmus laevis*).

Nesting material: lignified plants or other plants suitable to acquire fibres: stinging nettle (*Urtica* sp.), clematis (*Clematis* sp.), common hop (*Humulus lupulus*), reeds (*Phragmites* sp.), reedmace (*Thypha* sp.), bittersweet nightshade (*Solanum dulcamara*) and more.

Feeding areas: flowering groves and big trees where insects can be collected (alleys of *Populus nigra*, scattered fruit trees, *Populus tremula*, *Quercus robur*, and especially catkins of different willows).

This indicates that the species needs a high amount of structural heterogeneity and a decent mix of elements – which is reflected in the mix of landscape elements found to be important in this work. The spatial resolution of the elements analysed is not very high at first glance – but compared to the huge area analysed, it allows for credible conclusions. “Riparian forest” by itself is a category of habitat characterized by a high level of structural diversity, dynamics and change (Christian et al. 2011). Together with the categories of “meadow” and “shallow waters” as defined in this study, all the elements of high quality habitats of Penduline Tits mentioned above are represented. Many “shallow waters” in the region are accompanied by reeds; and “meadow” and “riparian forest” together contain thickets, bushes of different sizes, solitary trees and open areas, as much as patches with stinging nettle or other areas with a thick herbaceous layer and lignified plants like common hop (pers. obs.).

Regarding the landscape element “fallow”, an ambiguous effect could be found. Only *formerly good* breeding sextants (median cover of ~9%) showed a significantly higher amount of fallows as compared to *bad* sextants (1%); differences between *good* (3%) and *bad*, and between *formerly good* and *good* sextants were not significant. Here, the ephemerality of this landscape element might be important: the category included all fields planted with grasses and greens that lasted more than a year (usually used as animal food), including real fallows. The official agricultural status is still a field however, making it likely that crops change over time. A field that was mapped as “fallow” in the years of data acquisition (2012-2014), likely was not in this condition since/for more than a few years – while the time-period taken into account to form my categories of sextant quality ranged from 1969-2018. Therefore, changes in Penduline Tit abundance over this period cannot be easily ascribed to the amount of fallows as mapped between 2012-2014. For the other three landscape elements analysed, the temporal consistency is much higher. However, since farmers usually use their best fields to plant crops, and fields that have less good soil quality (or are otherwise less suitable to use as high-yield cropland, e.g.: very moist, threatened by floods, etc.) as a land to produce animal feed, at least some of the fields mapped as “fallow” should be found in this condition more regularly. So in my view, careful assertions regarding this category are justified as well. Looking at the data, a general trend towards a higher amount of fallow in better habitats can be ascribed. This might be explained by the open-land quality of this habitat, and the comparably higher diversity in comparison to regular fields. But the higher amount of fallow in better habitats doesn’t necessarily reflect the species general preference for this landscape element, it might rather be the best alternative in given habitat-reality. Furthermore, considering the above mentioned limitations of this category, it is improbable that recently observed, slight differences in the amount of fallow play a major role in explaining the differences in abundance of Penduline Tits between *good* and *formerly good* habitats.

The non-distinction between FG and G sextants regarding any of the analysed landscape elements rather hints towards some missed explanatory variable(s) regarding habitat structure: Since a lower population size likely results in only the best habitats being occupied (Schönfeld 1994, Hagemann 2001, Van Djik et al 2008), good sextants are expected to contain features explaining this preference. Reed cover might well be an important factor influencing habitat selection in Penduline Tits, since reeds are found in most habitats of the Penduline Tit, and they signify a common source for food, shelter and nesting material (Schönfeld 1989a, Glutz von Blotzheim & Bauer 1993, Schönfeld 1994). Unfortunately, in this study, there were no means to incorporate reed cover at a reasonable scale.

Quality classes *medium, new* and *rest* didn't show significant differences in any landscape element, which also hints towards data limitations: the set of landscape elements, as defined by this study, doesn't allow for fine-grained distinction between different population density progressions of Penduline Tits – only good and "non-good" breeding habitats could be distinguished. However, these landscape elements can be used as a basis to design GIS-based models to determine potential breeding sites of Penduline Tits in Central Europe – at a much finer scale (though less elaborately) as has been done in the European Breeding Bird Atlas 2 (Keller et al 2020). But to allow for more detailed assessments, it is advisable for future studies to have a distinct class of "reeds", and optionally one further variable measuring structural diversity of some sort – additionally to the still relatively coarse parameters of habitat structure analysed here.

River Water Levels

The median of daily mean water levels for the period January-June showed a significant decrease between 1970-2018 at three of the four water level recording stations in our study area. The decrease was stronger at Thaya and Danube, and less pronounced at Morava. Consistent with the decrease in mean water levels, the number of low waters during the first half of the year increased at all four level recording stations (LRS). Number of low waters also increased during the second half of year at three of the four LRS. While still no significant long-term change in the number of high waters could be detected for any of the LRS between 1970-2018, the last 5 years represented the longest period without high waters at Thaya and Morava (between Jan-Jun). It remains to be seen if this is part of normal fluctuations or the manifestation of a pattern.

The observed decrease in water levels – and increase in number of low waters – does not mean that less water is flowing in these rivers. It rather is a sign of riverbed degradation (deepening), which is a result of river regulations and/or dam building for hydroelectric power plants; bank reinforcements prevent the erosion of the river banks, while dykes keep the river in its bed and dams obstruct the input of fresh sediment from upstream. The long-term consequences of riverbed degradation on floodplains are severe. Through the decline of groundwater-levels and less-frequent inundations, the floodplains become increasingly disconnected from the river. Hydrological connectedness and associated disturbances by flooding events are a defining characteristic of floodplains, especially of the softwood riparian forest (Wirth et al. 2011). If these regimes change, succession towards other habitat types commences. Succession is a normal process in the constantly shifting habitat mosaic of healthy river ecosystems (Standford et al. 2005), but gets problematic when impeded water dynamics can't regularly recreate conditions for new pioneering communities.

Indication that succession is already changing floodplain habitats at Morava and Thaya are present: In the Czech Republic part of Thaya and Morava, a UNESCO biosphere reserve bordering Austria and Slovakia contains roughly 15.000ha of floodplain forest and meadows. A study comparing aerial photographs, found that in 1938, open woodlands represented 40.1% of the total 8500 ha of woodlands, and closed forest represented 50.8%; while in 2009, open woodlands decreased to 5.8%, and closed forest increased to 79.4% - with the total area of woodland staying the same. Additionally, uniformity of forests increased, and average age of forests decreased. Forestry intensification, logging and succession were identified as the most important drivers for the documented change in landscape composition (Miklín & Čížek 2014). Even though logging intensity is less pronounced in the Austrian part of the floodplains, a steady change of habitats can be observed as well. A study analysing vegetation composition in the area reported a tendency of backwater vegetation to become more uniform by succession (Scheiblhofer 2009). Changes in bird species composition provide additional (indirect) evidence for an ongoing reduction of the hydrological dynamic of the floodplain forest ecosystems of our study region. For the period 1998-2005, Teufelbauer & Zuna-Kratky (2006) documented a progressing transition from an avifaunal composition characterized by bird species typical for dynamic riparian forests (rich in structure, open and scattered appearance) to species assemblages dominated by "stagnation indicators" of post-dynamic habitats like reed beds and silt. Also Strohmaier et al. (2011) found a directional change in bird species composition over the complete Austrian part of Morava river between 1991 and 2008. The authors state that water and reed birds, so far, seem to have benefitted slightly from the current state of change in habitats, but that areas surpassing certain thresholds of uniformity showed a dramatic decrease in species diversity of water and reed birds, illustrating the inevitable long-term impact of the reduced hydrological dynamic (Strohmaier et al 2011). The Penduline Tit, being a characteristic species of open and structurally rich floodplain forests (Glutz von Blotzheim & Bauer 1993), is sure to be affected by these long-term trends since attractive breeding habitats become more rare.

A more timely negative response to changing water regimes might be a loss of diversity and abundance of at least some insects of the floodplains which have been found to respond positively to regular floods (Zulka 1994, Strelkova & Halgos 2012, Turic et al 2015). But it is unlikely that this would be a major factor shaping Penduline Tit abundance, since their main prey groups (Kristin 1995) don't rely on floods, and food availability in general doesn't seem to be a limiting factor for nestling survival (Hoi et al. 1994, Darolová & Hoi 1996). Given the high flexibility in nest site choice and the possibility to stay away for prolonged food trips due to the well-insulated nests, it is suggested that food availability is always above a critical level around nesting sites (Hoi et al 1994, Van Djik et al 2008). However, increased food availability at eutrophic sites (Raghi-Atri 1976) was proposed as a factor increasing survival during the post-fledging period (Flade et al 1986).

Habitat change due to succession as a result of river regulation isn't the only way human activity influences the transformation of habitats in the floodplains. Extensively farmed meadows and pastures have been decreasing drastically in the second half of the last century in the region (Kelemen & Oberleitner 1999), though a very slight recovery can be observed since the end of the 1990ies (Lapin 2010). Still, in 1946, around the town of Marchegg, meadows made up 43%, and pastures 18% of the area - while in 2009, only 11% meadows, and 1% pastures were left. At the same time, fields increased from 5% to 34% and forests increased from 18% to 37% (Lapin 2010). This constitutes a prominent change in landscape composition, likely impacting habitat quality for Penduline Tits (see also section "Habitat structure"). Especially meadows and pastures in proximity to floodplain forests should be of relevance to the species – given the previously discussed tendency of these forest to become more closed up, extensively managed meadows and pastures could be "simulating" some of their original features (i.e. open patches).

To sum up, reduced hydrological dynamics in the Morava-Thaya floodplains most likely still don't have immediate effects on the Penduline Tit; while resulting long-term changes in habitat composition due to succession, as well as habitat transformations due to changes in land-use practices, are very likely to be negatively affecting the local population.

Climate – Temperature and Precipitation

In Hohenau, for the months April, May and June, a significant increase in monthly mean temperature could be observed between 1969 and 2018. In the same period, no significant change could be found for monthly mean precipitation. This data represents the situation at one specific location, namely Hohenau. But long-term trends for eastern Austria in much more elaborate analyses fit with both findings: a general increase in mean temperatures, but no clear trend for this region in mean amount of precipitation (Auer et al. 2007).

As a thermophile species, the Penduline Tit should be profiting by increased temperatures. Since this doesn't seem to be the case (at this regional level), other and stronger factors must be at work as well. Precipitation doesn't seem to show a tendency at first glance. But total amount of precipitation isn't the only precipitation-related parameter of biological relevance: extreme weather events also affect species' distribution (Parmesan et al. 2000, Jentsch & Beierkuhnlein 2008), and breeding success of the Penduline Tit is negatively impacted by long lasting or extreme precipitation events (Schönfeld 1994). The percentage of broods lost due to bad weather events is summarized to range between 9-24%, depending on the location (Glutz von Blotzheim & Bauer 1993). With persistent rainfall, the pendulous nest, usually a good protection from weather, can become soaked and the inlet tube collapses, resulting in the loss of the brood (e.g. Franke 1954, Müller 1968, Hasse 1969).

Even though mean monthly rainfall recorded by a weather station should give a rough idea of the precipitation-condition in an area during that time, such data represents only one single geographical point of measurements, averaged over a whole month. Given the small-scale variability of rainfalls, local and/or more extreme events are not necessarily reflected. Studies analysing data of many weather stations over a longer time can paint a better picture, even though geographical resolution is always a limiting factor. One such dataset is the HOM-START dataset by ZAMG. For the period between 1948 and 2009 an intensification of precipitation events with >20 mm rainfall/day is reported for the east and southeast of Austria (Auer et al. 2010, p.27), but no change in the number of consecutive wet days. A study conducted in Germany implies that between 1901 and 2003, the likelihood of extreme precipitation events (amount exceeding the 95th percentile of normal amounts) increased from 1.1% to 24.6% in Central Europe (Trömel & Schönwiese 2007, Jentsch & Beierkuhnlein 2008). Climatologists make sure to point out the high variability of precipitation events: even though global climate change will lead to an increase of extreme weathers such as high precipitation events, it does not mean that all regions are affected to the same degree (ZAMG 2021b). However, a study of the Joint Research Centre of the European Commission used a finegrained regional climate model for Europe (resolution ~12km) and compared 1961-1990 with predicted conditions in 2071-2100. The model predicts a 20-40% increase in the maximum 5-day precipitation amount, specifically during spring (Mar-May), in eastern Austria (Dankers & Hiederer 2008 Figure 41 and 42), while the amount of rare* 1-day and 5-day extreme precipitation events increases by 40-80mm (*happening on average every 20 years, Figure 43). The maximum number of consecutive dry days doesn't change in the region (~20 days), while the expected cumulative precipitation deficit during summer (Apr-Sept) amounts to roughly 200mm (Dankers & Hiederer 2008 Figure 44 and 45). The climate change scenario underlying this model assumes a medium-high amount of total global emissions until 2100 (scenario A2 in Nakicenovic et al. 2000, global total cumulative carbon dioxide emissions: 1450-1800 Gt C (= 5320-6600 Gt CO_2)). This assumption is not particularly optimistic, but also not totally far-fetched. The modelling can be seen as a way to illustrate trends we are currently already facing, and which are very likely to increase further: a variable but consistent increase in extreme weather events in Europe.

To sum up, both likelihood and intensity of extreme precipitation events are likely to increase in eastern Austria over the course of the coming decades. Especially during the breeding season of many birds, the number of high-precipitation events will likely increase. The total amount of yearly precipitation might not change significantly, but will likely undergo a shift towards winter and early spring - while during summer, a rainfall deficit might manifest more clearly (Dankers & Hiederer 2008). The changes in precipitation intensity might negatively impact Penduline Tit populations in eastern Austria, and presumably are a better predictor of Penduline Tit abundance than mean temperature at this regional level.

It would be interesting to combine datasets of extreme weather events with maps on spatial differences in population trends of European breeding bird species. This might shed more light on climate change impacts on European (bird) biodiversity. However, as has already been powerfully argued: *we know enough to **act** upon our knowledge* (Forister et al. 2019).

Big Picture

Of the parameters addressed in this work, increased precipitation intensity and habitat change (due to succession induced by human activity and land-use change) are the most likely "local" factors negatively influencing Penduline Tit abundance in the region. But even though being important without question, explaining the decrease in local Penduline Tit population by these factors alone would do no justice to the complexity of the issue. The species underwent long-term range expansions and contractions already in the past (Schönfeld 1994), and also today a decrease in range and/or abundance can be observed in many parts of Europe. Even though the overall population in Europe is considered to be stable, a negative trend can be observed in many parts of Western Europe, which were only populated some decades ago. In contrast, the species currently shows a northward expansion of its range in parts of Northern Europe (Keller et al. 2020). Mechanisms underlying these big-scale population dynamics are still poorly understood. Dispersion movements during and after breeding seem to play an important role in colonizing new areas (Flade et al. 1986). The species might have profited by the eutrophication of wetlands and apparently has found favourable transition habitats in open pit mines etc., enabling settlement (Flade et al. 1986, Schönfeld 1994, Hagemeijer & Blair 1997, Bauer et al. 2005). But being volatile by definition, i.e. subject to succession, these areas might nowadays not embody sufficient habitat quality anymore and result in lower reproduction rates. So source-sink dynamics come to play, where "sink" populations are dependent on regular immigration from other areas. If this immigration ceases for any reason (e.g.: source population now with lower reproduction rate, increased mortality in wintering areas or during migration), the sink population will vanish (Bauer et al. 2005). This dynamic might be active especially in border areas of Penduline Tit distribution: Populations in Central Europe, the north-western border area at that time, were reported to not have reached reproduction rates big enough to be self-sustaining, while already being present since more than 10 years at the time of publication (Flade et al. 1986). Accordingly, small populations (less than 10-15 breeding females) were found to be unable to become self-sustaining, since the special pair bonding mechanism usually leads to huge losses of broods under these circumstances (Schönfeld 1989b). So when looking at Penduline Tit population dynamics, not only regional factors influencing reproduction and survival have to be considered, but also factors being active in potential source or sink populations and in wintering areas (Bauer et al. 2005).

Several studies have found habitat transformation to be the main factor driving diversity loss in birds linked to wetlands (Peiró 2006, Jetz et al. 2007, Raquel 2017). The 50-70% decline of the Penduline Tit breeding population in Italy between 1980ies and 2007 was attributed at least partly to habitat loss (Brichetti & Grattini 2010). Accordingly, the destruction of habitats is emphasized as the main threat to the species (Bauer et al. 2005). Additionally, unfavourable (i.e. wet) weather conditions might drive the species away from Atlantic climates in europe, while increasing mean temperatures allow for the colonisation of northern continental and even boreal regions (see Keller et al. 2020).

Conclusion & Outlook

The Penduline Tit population of the floodplains along the rivers Morava and Thaya in eastern Austria showed a pronounced decrease over the last 30 years. The species has rightly been classified as "vulnerable" in the most recent version of the Austrian Red List, close attention should be paid to further developments. Softwood riparian forest, shallow waters and extensively managed meadows were identified as a mix of landscape elements marking good and persistent breeding habitats for this species. The observed increase in mean temperature during the breeding period did not have any noticeable positive impact on the local population. But long-term effects of climate change, such as the increase in likelihood and amount of extreme precipitation events, might already play a role in the region's negative population progression. Similarly, observed decreases in water level are unlikely to have a direct effect. But they surely mark a decrease in water dynamics and an ongoing change in the hydrological regime of the Morava-Thaya floodplains, manifesting in a succession towards more uniform habitats. This slow transformation might already lead to less attractive breeding sites for Penduline Tits, thus negatively impacting the local population.

To sum up, habitat structure, already affected by a loss of dynamic water regime in the local floodplains, was shown to have a direct influence on population density of Penduline Tits in the Morava-Thaya river system. Amount and intensity of precipitation events likely add another part to the explanation of a declining population in the area – while population dynamics at a bigger scale should also be taken into account.

To improve habitat quality for the Penduline Tit, dynamic processes at Morava and Thaya have to be restored and maintained. Together with a sustained encouragement of more extensive land-use practices, this will lead to a more open, diverse and patchy appearance of the riparian and alluvial area. Also most other species of dynamic riverine ecosystems can be expected to benefit of an increase in edge and transition areas (ecotones). Various measures to counteract riverbed degradation, such as the initiation of riverbed widening or artificial sediment input, have been successfully tested and partially implemented in some rivers in Austria (e.g. Habersack & Klösch 2012). But not all methods are suited for every river, and often opposing interests of nature conservation, river navigation, local citizens and farmers have to be brought into the equation. At Danube, this led to the "Integrated River Engineering Project for the Danube East of Vienna" (Klasz et al. 2009) with various testing sites, and the piloting phase being completed in 2016 (Via Donau 2019). At Morava, the LIFE+ project "Untere March-Auen" is reconnecting cut-off sidearms and old meanders since 2017, and similar actions are undertaken since 2016 in the project "Thaya2020"

(Via Donau 2016). These undertakings signify applaudable steps in the right direction, and have to be refined and expanded (see also discussion in Strohmaier et al. 2011). Allowing rivers to organically shape big parts of their floodplain again will certainly play a crucial role in our endeavour to ensure diverse ecosystems all over the world – not only resilient, but *antifragile* entanglements of life which are able to grow with the multitude of global challenges of our time (Equihua et al. 2020).

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