ILÖK
Institut für Landschaftsökologie

AG Angewandte Landschaftsökologie und Ökologische Planung

vogelwarte.ch

Conspecific attraction in habitat selection of the Eurasian wryneck (*Jynx torquilla*) – a conservation strategy?

Masterthesis by Paula Schatte
paula.schatte@uni-muenster.de
Matriculation No.: 463 963

Supervisor: Prof. Dr. Tillmann K. Buttschardt (WWU Münster)
Co-Supervisor: Dr. Matthias Vögeli (Schweizerische Vogelwarte)

Abstract

Conspecific attraction has already been used as a suitable and cost-effective measure for species conservation. However, this mechanism has not yet been specifically investigated for woodpeckers (*Piciformes*), despite existing evidence of conspecific attraction in this order. Using an experimental approach, we tested conspecific attraction using vocal playback treatment for the wryneck (*Jynx torquilla*). Playback treatment was found to have a positive effect on the prospecting period of the wryneck but showed no effect on the establishment and breeding periods. The effect of the playback was independent of habitat characteristics. We therefore assume that habitat selection of the wryneck depends on conspecific attraction in the initial phase and is determined by habitat quality in the further course. Consequently, it should be possible to attract wrynecks by playback-treatment to habitats suitable for this species and thus achieve successful establishment regarding species conservation.

Keywords. conspecific attraction, wryneck, *Jynx torquilla*, playback, habitat selection, avian conservation techniques

Kurzfassung

„Artspezifische Anziehung“ kann als eine gute und kostengünstige Maßnahme für den Artenschutz genutzt werden. Für Spechte (*Piciformes*) wurde dieser Mechanismus bislang jedoch noch nicht spezifisch untersucht, obwohl Hinweise auf „artspezifische Anziehung“ in dieser Ordnung bestehen. Mit einem experimentellen Ansatz haben wir „artspezifische Anziehung“ unter Nutzung von Klangattrappen für den Wendehals (*Jynx torquilla*) getestet. Es zeigte sich, dass Klangattrappen einen positiven Effekt während der Prospektionsphase des Wendehalses haben, jedoch keinen Effekt in der Etablierungs- und Brutphase. Die der Klangattrappen ist dabei unabhängig von Habitatcharakteristiken. Wir gehen daher davon aus, dass die Habitatselektion des Wendehalses in der Anfangsphase von der „artspezifischen Anziehung“ abhängt und erst im weiteren Verlauf durch die Habitatqualität bestimmt wird. Folglich besteht die Möglichkeit, Wendehälse durch Playback in für diese Art geeignete Lebensräume zu locken und so eine erfolgreiche Etablierung in Hinblick auf den Artenschutz zu erreichen.

Table of Contents

Introduction

Migratory birds are driven by different ecological factors that influence their immigration and are crucial for their redistribution at the breeding grounds in Central Europe. Returning from wintering grounds requires reoccupation of breeding habitats each year with limited to no prior knowledge of habitat quality. As actively dispersing organisms migratory birds are able to choose among breeding habitats with different key characteristics such as size, quality and conspecific density (Rushing *et al.* 2021).

Drivers of habitat selection

There are various theoretical approaches to explain habitat selection (Rushing *et al.* 2021). The diverse set of potential cues for habitat selection makes it a multi-step process that is difficult to unravel, as it is likely that each bird species has evolved in a species-specific manner, adapting to the presented obstacles by prospecting a particular breeding habitat. *Prospecting* can be described as the process by which individuals evaluate the relative quality of potential sites before accepting and to establish oneself. The longer the prospecting period, the more factors could positively or negatively influence an individual's fitness. After the prospecting period, the *establishment* period starts, characterized by attempts to find a mate. Establishment is followed by the *breeding* period, which describes the time from mating to (in the best case) successful breeding and rearing of the offspring. In general, the costs of habitat selection are dominant during the prospecting and establishment period, while the benefits of habitat selection predominate during the breeding period (Stamps 2001).

Because individuals cannot explore a habitat and establish a territory at the same time, there is likely to be a trade-off between the costs associated with finding high-quality habitat and the fitness benefits they can expect after settling into new habitat. As a result, time and energy that are invested in exploring and meeting conspecifics during the habitat selection must be diverted from activities that would lead to an increase in fitness during breeding. Here, indirect cues of habitat quality (conspecific attraction and habitat imprinting) can serve to reduce settlement costs in areas occupied by conspecifics (Stamps 2001).

Conspecific attraction describes how newcomers are attracted to areas occupied by previous settlers (Stamps 1988, Ward & Schlossberger 2004). Birds benefit from reduced search and establishment costs due to the presence of conspecifics as an indirect cue of habitat quality. Habitat imprinting defines the preference of a species to settle in post-migration habitat with similar characteristics of the pre-migration habitat (Stamps 2001).

Understanding the mechanisms behind habitat selection, including conspecific attraction as an important indirect driver of habitat selection, is crucial for species conservation. This is particularly true in the case of anthropogenic land-use changes, which affect the mechanisms of habitat selection and may require the respective species to adapt its strategies (Stamps 2001).

Conspecific attraction in habitat selection

Although conspecific attraction has been investigated for over 25 years, knowledge gaps are still considerable. Most published studies have shown responses to conspecific attraction in birds (Buxton *et al.* 2020). This does not necessarily mean that positive responses are guaranteed, since studies without responses may not have been published. In particular, the long-term consequences of manipulating songbirds through conspecific attraction methods are not well understood (Ahlering *et al.* 2010, Buxton *et al.* 2020). Colony breeders were first investigated, since attraction by conspecifics appeared more obvious in colony breeders (Ahlering *et al.* 2010). However, conspecific attraction is also likely to occur in territorial songbirds and has been observed since a focus on territorial songbirds emerged 10 years ago (Ahlering *et al.* 2010, Buxton *et al.* 2020).

The following clues indicate potential attraction of conspecifics in habitat selection (Ahlering *et al.* 2010): Spacing (coloniality, aggregated territories/patchy distributions), behaviour and life history (extra-pair mating behaviors, large juvenile to adult ratio in population, few breeding opportunities – e.g. low survival, migratory behaviour), and breeding phenology (short breeding season, asynchronous breeding).

Potential benefits of conspecific attraction include increased mating success, protection from predators, and selection of high-quality habitats. Conspecific attraction of birds in habitat selection depends on two factors: presence and frequency of conspecifics (can be manipulated by decoys) and song of conspecifics (can be manipulated by playback). Vocalization plays a strikingly unique role in bird populations in contrast to other animal species. The use of playback as a manipulation method is therefore of special interest when it comes to birds. Thus, playback has been tested to a greater extent than decoys (Ahlering *et al.* 2010, Buxton *et al.* 2020).

Playback as tool for wryneck conservation

Through the combination of knowledge gained from restoration ecology and modern technology, it is possible to restore extensive areas (Zerbe & Wiegleb 2009). A major problem, however, is the difficulty of attracting target species to these sites and establishing them in the long term. Conspecific attraction has the potential to be an effective conservation tool as it can increase the success of management (Lewis *et al.* 2021), making conspecific attraction research particularly important for endangered bird species. It combines the possibility of directly manipulating species with a rapid response (Ahlering *et al.* 2010). This tool could be particularly useful for recolonizing restored habitats (Buxton *et al.* 2020).

The focus of this thesis is to test whether wrynecks respond to experimentally manipulated vocalizations of conspecifics as drivers for wryneck establishment and whether this mechanism can be used for wryneck conservation. We therefore chose a study area where conspecifics used to occur but disappeared mainly due to habitat degradation caused by agricultural intensification. Conservation measures such as habitat restoration and the installation of nest boxes have not led to a recolonization by the wryneck. The study area thus offers optimal conditions for testing whether wrynecks can be attracted to restored and formerly colonized habitats.

While conspecific attraction using playback has been caried out for several years in a wide variety of colonial waterbirds and songbirds (Ahlering *et al.* 2010, Buxton *et al.* 2020), little is known about conspecific attraction in woodpeckers (*Piciformes*). Some studies have shown evidence of conspecific attraction (Robles *et al.* 2008, Mermod *et al.* 2009) but to the best of our knowledge none actually investigated it in an experimental approach. Thus makes our study the first to focus on the wryneck to experimentally test conspecific attraction.

Three research questions were developed:

1) Do wrynecks preferentially establish in experimental plots with playback of conspecific vocalizations?

Since wrynecks fulfil five of seven clues of potential conspecific attraction in habitat selection stated by Ahlering *et al.* (2010), we expect that wrynecks preferentially establish in experimental plots with playback of conspecific vocalizations. In Switzerland, well-established wryneck populations are patchily distributed (Knaus *et al.* 2018). Wrynecks have a short life expectancy and therefore a large juvenile to adult ratio (Glutz von Blotzheim & Bauer 1994). The Central European populations are considered short-distance migrants (van Wijk *et al.* 2013). Due to their migratory behaviour, they have a short breeding season and must recolonize their habitat each year (Schaub *et al.* 2010). Males as well as females sing courtship songs (Glutz von Blotzheim & Bauer 1994), which may increase the possibility of a response to attraction by conspecifics. We assume that our first research question applies to the first two colonization periods, prospecting, and establishment period, because songs play a particularly important role in these phases.

2) Do habitat characteristics influence the feedback that wrynecks show in response to the playback of conspecific vocalizations on experimental plots?

Migrating birds are under pressure to find a suitable habitat as soon as possible. Breeding success and early settlement have been found to be positively linked: the earlier the habitat is colonized, the higher is the breeding success (Stamps 2001, Buxton *et al.* 2020, Rushing *et al.* 2021). As described previously in detail, migratory birds must select a breeding habitat without prior knowledge of habitat suitability. Therefore, migratory birds are likely to initially use cues other than habitat quality for habitat selection. We expect that wryneck habitat selection is influenced by conspecific attraction first and by habitat characteristics second. Thus, we assume that wrynecks are positively influenced by playback during the prospecting period. The establishment and breeding periods are probably more heavily characterized by habitat feature quality as these periods are highly dependent on resources provided by the breeding side.

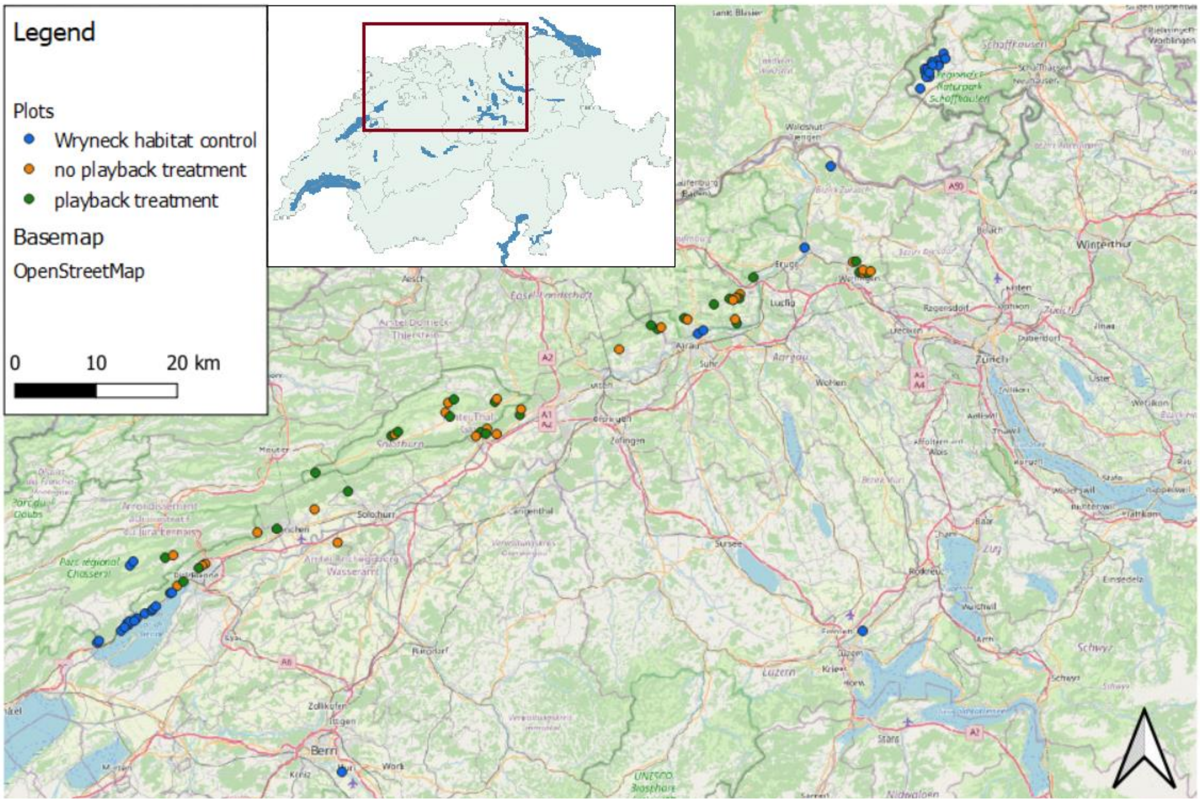

Figure 1. Study area. Green dots indicate the experimental plots with playback treatment in 2020, orange dots indicate the experimental plots without playback treatment in 2020. Blue dots indicate sites with proven wryneck presence aside from the playback experiment in 2020.

3) Is it possible to use playback of conspecific vocalizations as a wryneck conservation strategy?

This study allows us to assess not only the role of conspecific attraction in wryneck habitat selection, but also the potential use of playback as a cost-effective and easy-to-use tool for wryneck conservation management. For conservation, breeding success plays a key role, because species conservation is especially dependent on the reproduction rate. Therefore, to answer the third question, the success of the playback in relation to the third colonization period, the breeding period, is crucial. Based on our preliminary considerations, we assume that wrynecks do not solely rely on conspecific attraction for habitat selection, but also evaluate habitat quality. Accordingly, establishment is expected to be limited to high quality habitats where breeding success can be assumed. We therefore set successful establishment as a prerequisite for answering our third research question.

Methods

Study area

The study area for the playback experiment covered the region along the southern foothills of the Jura Mountains in Switzerland between Biel in the west and Wettingen in the east, involving the cantons of Bern, Solothurn, and Aargau (Fig. 1). An expert-based GIS modelling approach developed within a wryneck conservation project of the Swiss Ornithological Institute has identified numerous sites in this area as suitable habitat for the species (Lanz 2016, Schuck & Lanz 2017). The surroundings of the southern foothills of the Jura are characterized by intensive agriculture, while part of the southern foothills themselves offer highly structured habitats such as vineyards, extensive meadows and pastures, as well as forests. In proximity to this study area additional data – land use parameters – was sampled a) in two regions holding wryneck populations with more than 15 breeding pairs (north bank of Lake Biel and Hallau, canton of Schaffhausen) and b) locations with probable or confirmed wryneck broods in 2020 (Fig. 1), as well as in the study area itself.

Study species

The Eurasian wryneck (*Jynx torquilla*) is near threatened in Switzerland (Keller *et al.* 2010) and a priority species of the Swiss Species Recovery Program (Spaar & Ayé 2016). The wryneck population in Switzerland has declined over the last 50 years due to the loss of structural diversity caused by the intensification of agriculture (Söderström *et al.* 2001, Hübner *et al.* 2004, Knaus *et al.* 2018) and the concomitant decline of xerothermophilous ants living in open areas (Seifert 2008). More recently, the wryneck has been found to colonize new habitats, such as vineyards and orchards surrounded by more intensive agriculture (Weisshaupt *et al.* 2011, Knaus *et al.* 2018). Generally, the wryneck is limited by the availability of ants and cavities (Coudrain *et al.* 2010). While ant diversity has no high impact, their accessibility is decisive for wryneck occupancy (Mermod *et al.* 2009). Since the wryneck is a secondary cavity breeder, the availability and the amount of cavities are crucial habitat features for the wryneck (Mermod *et al.* 2009, Tolkmitt *et al.* 2009, Coudrain *et al.* 2010). However, habitat selection by the wryneck is most likely dependent not only on habitat quality, but also on social cues. Zingg *et al.* (2010) showed a positive relation between the presence of wrynecks and the probability of newly colonized sites by wryneck breeding pairs. Consequently, the wryneck seems to be a species in which conspecific attraction plays a certain role for breeding habitat selection.

The first wryneck individuals arrive in Switzerland from mid-March until the beginning of April. Wrynecks are already singing during this prospecting period. The prospecting period transitions smoothly into the establishment period, during which settlement takes place. Mating lasts about 20 days and ends with the beginning of the breeding season in the second half of May, which lasts until July, when the young birds are fledged and fully independent (Glutz von Blotzheim & Bauer 1994). Only around 20 % of pairs make a second brood (Tolkmitt *et al.* 2009). With the independence of the young from the first brood, the post-breeding period begins. It lasts from August to mid-September, when the wrynecks leave Switzerland (Glutz von Blotzheim & Bauer 1994).

Experimental design

We used playback as a social cue for the attraction experiment (Ahlering *et al.* 2010). In 2019 a pilot study with 33 experimental plots was done. All plots of 2019 were included in the experiment in 2020 and 18 experimental plots were added to a total number of 51. The plots that received playback treatment in 2019 were used as plots without playback treatment in 2020. Plots without playback treatment in 2019 consequently received playback treatment in 2020. The attraction experiment was carried out on 84 experimental plots in total, 2019 and 2020 (Tab. 1). One to 36 (mean = 7.24) nest boxes available for the wryneck were placed on each experimental plot.

Our experimental plots were categorized into three main habitat categories according to the predominant land use on the experimental plot: meadows, pastures, and vineyards. The playback devices were distributed evenly among habitat categories (Tab. 1).

Land use data was collected between June and July 2020 to characterize the habitat quality of the experimental plots. In addition to the 51 experimental plots from 2020, 38 plots with proven wryneck occurrence were used as habitat control plots, resulting in a total of 89 plots for the habitat quality analysis (Fig. 1). The nearest and most stable populations (Lake Biel and Hallau) were included into the habitat control plots. We selected eight land use characteristics that have an important influence on the wryneck breeding habitat selection (Coudrain *et al.* 2010, Weisshaupt *et al.* 2011). We collected the proportion of vineyards, meadows, pastures, orchards, fallow land, crops, forest patches, hedges, and anthropogenic habitat. In addition to land use characteristics, we defined two structural parameters to characterize wryneck habitat: the amount of bare ground at vineyards, pastures and meadows, and the number of trees at meadows and pastures.

Playback treatment

We defined circular experimental plots with a radius of 200 m (i.e. 12.6 ha) according to the 4.8 ± 2.4 ha average home-range area of wrynecks (Weisshaupt *et al.* 2011). Thus, at least two pairs of wrynecks could occupy one experimental plot. The playback devices were placed in the center of the experimental plots. The distance between two neighboring experimental plot centers was at least 400 m to avoid pseudo replication.

We built a playback device with following components to provide the acoustic cue: a ATMEGA 328P microcontroller, a DFPlayer Mini with Adafruit 3.7 W Class D audio amplifier, two Visator FR 8 WP speakers and a DS3231 Real Time Clock powered by a 3600 mAh rechargeable Li-Ion battery with

Table 1. Number of playback devices on the experimental plots

		2019	2020	2019 + 2020
No Playback	vineyards	4	6	10
	pastures	5	10	15
	meadows	7	10	17
Playback	vineyards	4	6	10
	pastures	6	9	15
	meadows	7	10	17
N		*33*	*51*	*84*

solar charger and solar panel. The playback software was coded in Arduino IDE.

The broadcasted playback sound was a male courtship song recorded in the study area from Herbetswil (Lüthi 2018). The playback was broadcasted daily during the pre-breeding period of wrynecks from mid of March to June (Glutz von Blotzheim & Bauer 1994). Since selection pressure on potential breeding habitat is highest during the pre-breeding period, the social attraction effect is potentially strongest at that time. The playback was broadcasted one, three and five hours after sunrise, one hour before sunset and once in the night, at one o'clock a.m. for one minute, respectively. In total, we played five minutes of wryneck courtship song per day. At the first evidence of a wryneck settlement, we individually assessed whether playback should be continued or stopped to avoid potential disturbance by the playback during the breeding season. The playback devices ran from March 21 to June 10 in 2019, and from March 18 until June 21 in 2020. The playback volume was adjusted to mimic natural conditions. Broadcasted wryneck songs were audible up to ca. 100 m.

Monitoring

We monitored wrynecks as described by Südbeck *et al.* (2005). Wrynecks react very strongly to conspecific songs in the pre-breeding period, which makes playback of their songs a reliable method to assess territory occupancy. Hence, we used playback for monitoring provided by a portable Bluetooth speaker using the same courtship song as for the attraction experiment. Each visit of an experimental plot was documented in QField version 1.4 and took approximately 30 min to ensure that we did not miss the presence of wrynecks. We visited each experimental plot once a week from April 6 to May 29 in 2020 (8 visits per experimental plot). From that time until June 21, we focused on 23 experimental plots (3 visits per experimental plot) with the highest potential for wryneck presence.

Data analysis

In a first step, we analyzed the effects of playback treatment and habitat characteristics on the presence of wrynecks (attraction experiment). Therefore, we used binomial generalized linear mixed effect models (binomial GLMMs) implemented with the 'glmer' function of the 'lme4'-package version 1.1-26. GLMMs are the most satisfactory method of dealing with e.g., presence/absence data, including the ability to adjust the data for variability that cannot be managed using common generalized linear models (GLMs) (MacKenzie *et al.* 2002). GLMM incorporate fixed-effects parameters and random effects in a linear predictor, using maximum likelihood. For binomial models, the logit link function is used. The maximum likelihood is given by an integral over the random effects space, which must be approximated for a GLMM. The 'glmer' function uses the adaptive Gauss-Hermite quadrature, which is the most reliable approximation for GLMMs (Bates *et al.* 2020). Furthermore, we applied Bayesian modeling using the 'arm' package of R, which, unlike the frequentist method, allows for a more comprehensive range of statistical distributions as well as more complex dependence structures (Zuur *et al.* 2009). The models were evaluated using the 'DHARMa'-package of R, a residual diagnostic for mixed regression models, especially tailored to generalized linear mixed effect models by the 'lme4'-package (Hartig 2020). All models were performed in R Studio version 3.6.2.

The presence of wrynecks was defined by the detection of at least one wryneck on a given experimental plot during monitoring and was binary coded, 1 for presence and 0 for absence. To analyze the effect of playback on wryneck presence we performed one GLMM with the wryneck presence as dependent variable and playback treatment (1 for playback treatment, 0 for non-playback treatment) as explanatory variable with the presence/absence data from all 84 experimental plots. We used the plot identity as a random effect to control for the potential influence of replicates, since we analyzed data from 2019 and 2020. To analyze the influence of habitat features on the wryneck's responses to playback, we included a categorial explanatory variable in a second model with three habitat levels: vineyards, pastures and meadows.

In a second step, we analyzed the wryneck occurrence in our study area, including the plots in the surrounding regions (Fig. 1), as a function of habitat quality. Occurrence was defined as probable or confirmed wryneck breeding in 2020, as well as wryneck presence on the experimental plots, and was binary coded, 1 for occurrence and 0 for non-occurrence. Therefore, we conducted a GLM with wryneck occurrence as the dependent variable and the proportion of vineyard, pasture, and meadow cover, as well as the structural parameters of tree number and proportion of bare ground as explanatory

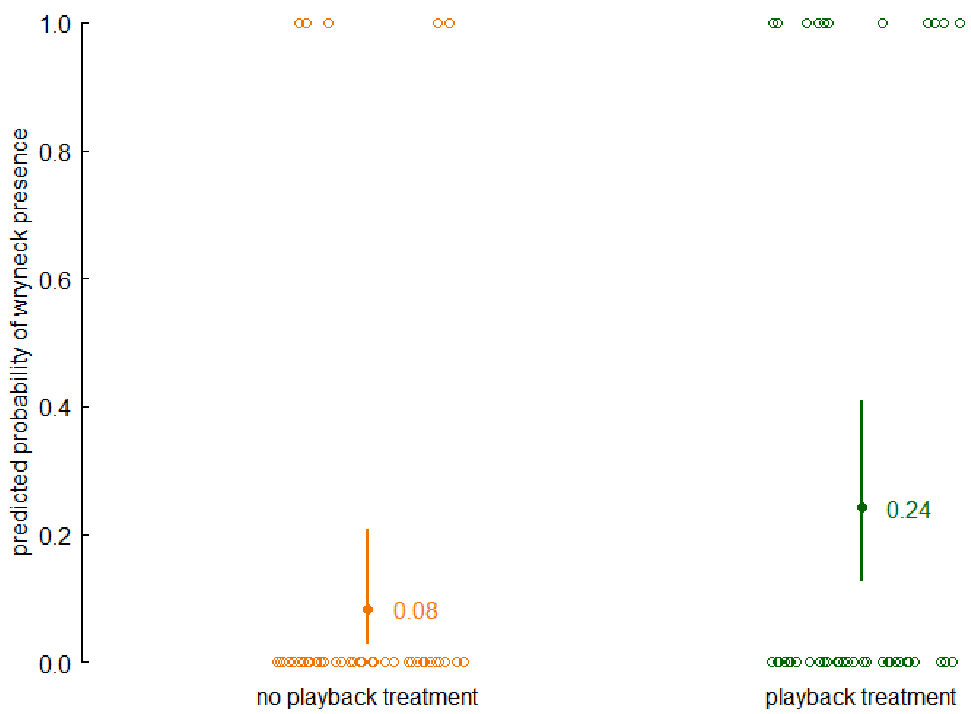

Figure 2. Effect of playback on wryneck presence on experimental plots visualized by estimated mean with 95% credible intervals. Plots without playback treatment: n = 42; plots with playback treatment: n = 42. The open circles represent the raw data from experimental plots.

variables with occurrence/non-occurrence data from 89 plots. To match our two analysis steps, we decided to focus on the habitat variables already used in the first step of our analysis (attraction experiment), although we had collected data on more detailed land use characteristics. Two additional structural habitat variables were also included in the models: number of trees and proportion of bare ground. All explanatory variables were tested for quadratic effects. Single terms were maintained in the model when quadratic effects resulted statistically significant. A statistically significant quadratic effect was found only for the structural habitat variable 'number of trees'.

Results

Playback experiment

In both study years, we detected wryneck presence on 17 experimental plots, 12 with playback treatment, 5 without playback treatment. The playback treatment had a positive effect on wryneck presence with a Bayesian estimated effect of 1.25 (95% credible interval (CrI) = -0.04-2.51; Z = 1.83; P = 0.0725). The posterior probability of the hypothesis that there is a difference between the two experimental treatments yielded a value of 0.97.

The predicted probability of wryneck presence on experimental plots with playback treatment was 0.08 (95% CrI 0.03-0.22), while the predicted probability of wryneck presence on those without playback treatment was 0.24 (95% CrI 0.13-0.42). Thus, the probability of wryneck presence on plots with playback treatment was three times higher than on plots without playback treatment (Fig. 2).

When considering the habitat characteristics, wryneck presence was detected on 6 experimental vineyard plots (*n* vineyard plots = 20; playback = 3; no playback = 3), 8 pasture plots (*n* pasture plots = 30; playback = 6; no playback = 2), and on 3 meadow plots (*n* meadow plots = 34; playback = 3; no playback = 0).

Habitat characteristics do not affect the response of wrynecks to the playback

Table 2. Results of playback experiment analysis including the Bayesian estimated effects (95% CrI), z-values, p-values (. represents a nearly significant effect), and predicted probability of wryneck presence with and without playback treatment.

	Estimate (95% CrI)	Z-value	p-value	Predicted probability of wryneck presence (95% CrI) without playback	Predicted probability of wryneck presence (95% CrI) with playback
Vineyards	1.29 (0.04-1.56)	1.84	0.0664 .	0.16 (0.05-0.42)	0.41 (0.17-0.70)
Pastures	-0.23 (-1.70-1.27)	-0.31	0.7540	0.13 (0.04-0.35)	0.35 (0.16-0.61)
Meadows	-1.74 (-3.53-0.07)	-1.78	0.0747 .	0.03 (0.01-0.15)	0.11 (0.03-0.33)

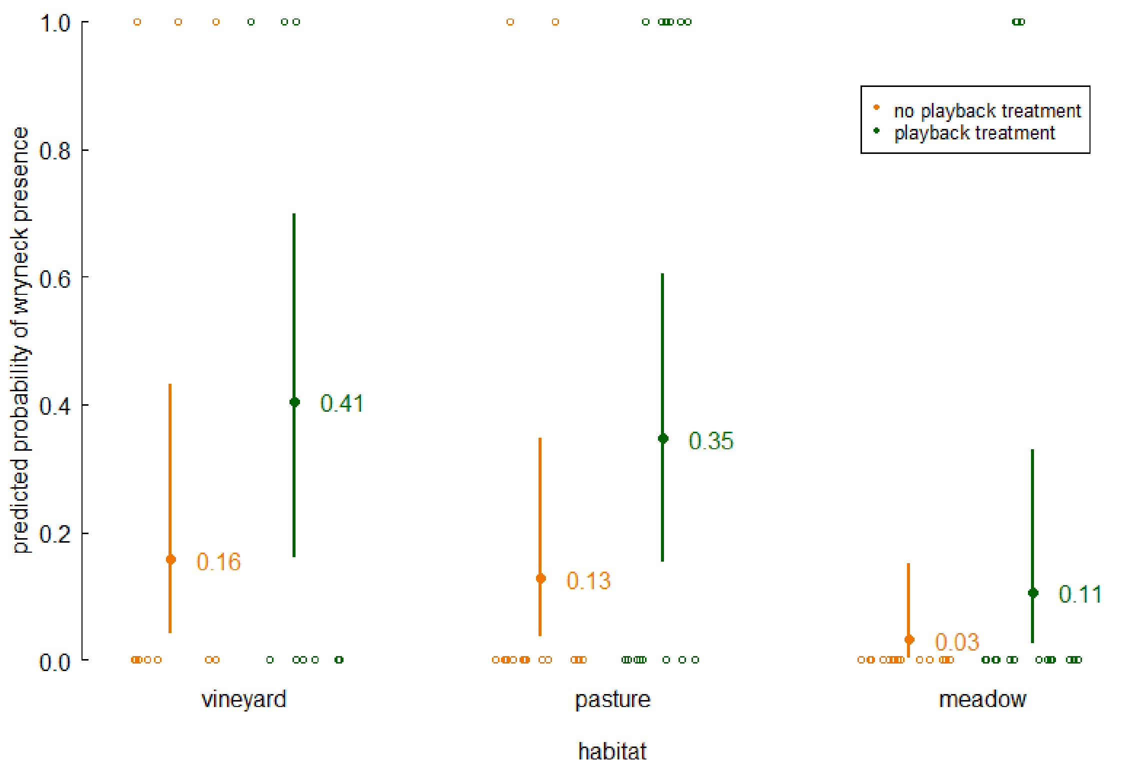

Figure 3. Effect of playback on wryneck presence visualized separately for each habitat level, visualized by estimated mean with 95% credible intervals. n vineyard plots = 20, playback = 10, no playback = 10; n pasture plots = 30, playback = 15, no playback = 15; n meadow plots = 34, playback = 17, no playback = 17; total n playback = 42, total n no playback = 42. The open circles represent the raw data from experimental plots.

treatment. The predicted wryneck presence on plots with playback treatment is on average three times higher than on plots without playback treatment, regardless of habitat characteristics (Tab. 2 & Fig. 3). The highest Bayesian estimated mean (1.29) was calculated for vineyard plots with playback, with a posterior probability of 0.98 compared to vineyard plots without playback. Both pasture and meadow plots had a negative effect on wryneck presence compared to vineyard plots. The Bayesian estimated mean was -0.23 on pasture plots with a posterior probability of 0.63 when comparing with vineyard plots. For meadow plots a Bayesian estimated mean of -1.74 was calculated, with a posterior probability of 0.97 in comparison to vineyard plots (Tab. 2).

Habitat quality analysis

The probability of wryneck occurrence is positively correlated with the proportion of vineyards (Fig. 4). All other variables showed no statically significant relationships with wryneck occurrence (Fig. 5).

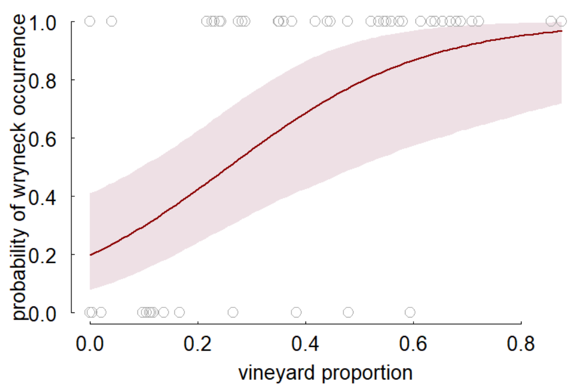

Figure 4. The probability of wryneck occurrence is positively related to the proportion of vineyard. Total plot number for the function of habitat quality n = 89; plots with wryneck occurrence n = 48; plots without wryneck occurrence n = 41.

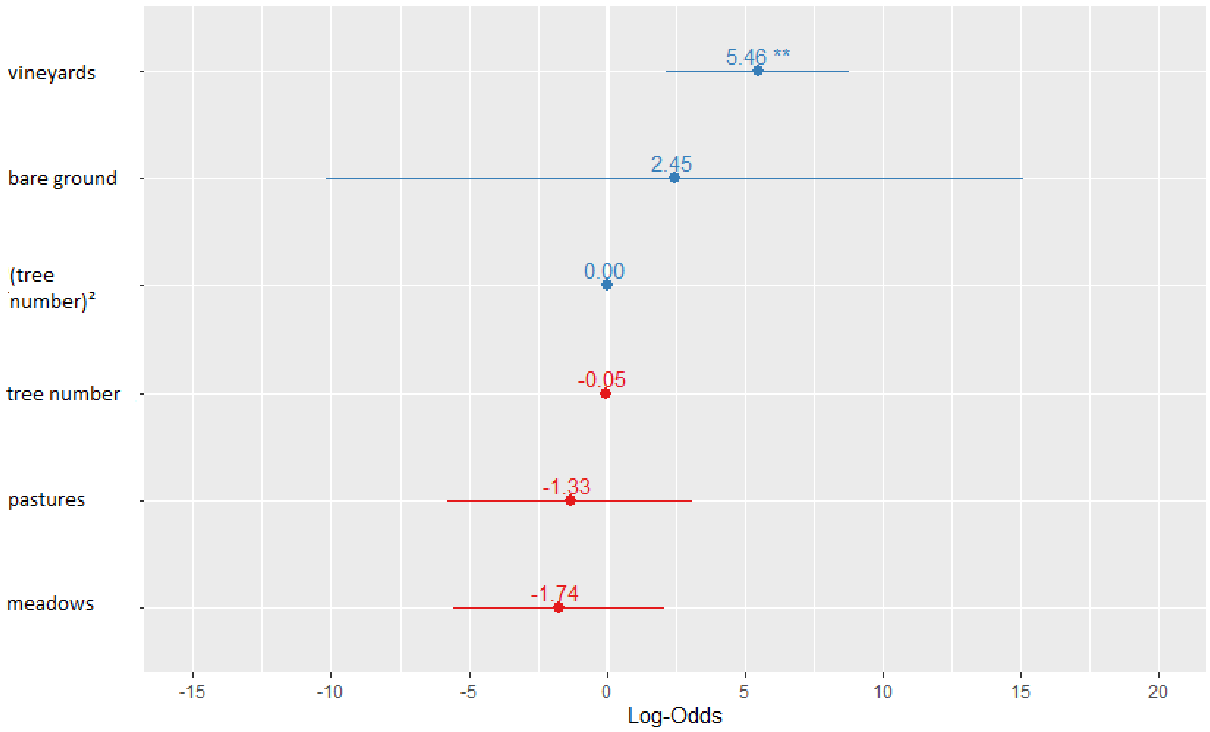

Figure 5. Effect plot of wryneck presence depending on land-use parameters. Plotted in R version 3.6.2 using the sjPlot-package (Daniel Lüdecke 2021).

Wryneck breeding behaviour

We recorded only a limited number of wryneck breeding events on the experimental plots in our study area. Hence, we did not include breeding success as a response variable in the statistic modelling approach. In 2019, four wryneck pairs (total experimental plots *n* = 33; breeding on plots with playback treatment = 3; breeding on plots without playback treatment = 1) made breeding attempts, with two successful broods on plots with playback treatment. In 2020 (total experimental plots *n* = 51) just one wryneck pair bred successfully on a plot without playback treatment. All successful breeding pairs reared a second brood in the same year.

Discussion

We investigated conspecific attraction of the wryneck in an area with low wryneck abundance to assess the effectiveness of playback for conservation management. We were able to show that playback has a promoting effect on habitat selection during the prospecting phase but does not lead to a statistically significant increase in establishment. It is thus unlikely that dispersal of the wryneck is a random process that explains the probability of immigration as a function of patch size and connectivity, uninfluenced by indirect cues and habitat quality.

Effects of playback to wryneck presence

We found evidence that playback positively affects wryneck prospection of our experimental plots. However, most wrynecks were seen only once and did not establish or mate on the experimental plots. Hence, our results are inconsistent with our first research hypothesis about preferential settlement of wrynecks on plots with playback of conspecific vocalizations. Although observations of wrynecks staying for several days on experimental plots with playback and vocalizing throughout this time span suggested breeding intention, successful establishment of wrynecks on our experimental plots was scarce. As wrynecks do not always establish the first available habitat, the establishment rate of habitat selection depends on the previous prospecting time. Birds search for the best possible habitat for as long as the trade-off between their own fitness and finding the highest quality breeding habitat allows (Stamps 2001). We therefore need to consider triggers of possibly low prospection independent of playback to explain the low establishment rate in our study area.

A likely explanation for a low prospection rate is that wrynecks were rare or absent in the study area. Indeed, breeding attempts by wrynecks were very scarce in the years before starting the experiment (Knaus *et al.* 2018). Thus, overflying, migrating individuals, or migration from nearby source populations are prerequisites for prospection in the study area.

The largest wryneck populations close to our study area, which may serve as source populations, are located at Lake Biel and Hallau (Fig. 1). Both populations are stable or growing and could thus attract additional wrynecks to breed. The absence of spatial patterns in our data indicate, however, that source-sink dynamics at this scale (several tens of kilometres) are unlikely. This is consistent with patterns found by Rushing *et al.* (2021) indicating that migrating individuals can assess habitat quality in relation to conspecific density when colonizing a new habitat. High habitat quality can supply a higher density of conspecifics than low quality habitats, allowing individuals to assess the regulating effects of the two mechanisms and to compensate for a mismatch between density and habitat quality. Density dependence in relation to breeding success is reduced and the reproductive output of the whole population is increased. If this is true, it would be likely that young birds from said areas would return to them or migrate to areas with similar conspecific density and habitat quality, instead of establishing new unoccupied habitats.

Another possible explanation related to the metapopulation concept and low establishment rates in our study area could be the model of 'habitat imprinting' (Stamps 2001). Species tend to settle in familiar habitats because they learn from experience gained in the pre-dispersal habitat, which improves adaptation to a similar post-dispersal habitat, or they use familiar cues from the pre-dispersal habitat to reduce costs of habitat selection at a suitable post-dispersal habitat (Stamps 2001). The nearest breeding populations of wrynecks are found in vineyards (Lake Biel and Hallau), which make up a small part of our experimental plots. It is therefore assumed that individuals from these source populations would prefer similar habitats to reduce the cost to colonize them. The highest predicted probability of wryneck presence on vineyard plots (Fig. 3) supports this hypothesis.

If we assume that birds colonizing our study area do not originate from nearby source populations, they must be migrating individuals. Thus, satellite-based geolocator experiments would be needed to evaluate the influence of spring migration on prospecting wryneck individuals as a function of playback treatment. Benefits and risks of such an approach would have to be carefully weighed against each other, because adult wryneck mean annual local return rate is around 20 % (van Wijk *et al.* 2013).

The 'social cues hypothesis' of habitat selection describes the attraction of individuals by conspecifics which is also determined by the habitat quality, the compatibility ability, and quality of the conspecifics (Rushing *et al.* 2021). This non-linear relationship shows highest settlement at medium conspecific density. At low species densities, habitats are not colonized; at high densities, already established individuals displace newcomers (Fletcher 2007). Accordingly, we hypothesize that wrynecks have not establish in our area because the stimulus provided by the playback is not sufficient to reflect a medium density of conspecifics. It is also possible that playback would have to be supplemented by decoys to achieve artificially induced establishment.

Conspecific attraction can occur in different forms: immediate (described up to this point) and delayed. Delays are caused by evaluating the reproductive success of conspecifics in one year and using the information gained for habitat selection in the following year (Danchin *et al.* 2001). However, playback does not simulate breeding success, making the occurrence of this effect unlikely in our experimental setup. The phenomenon of heterospecific cuing, i.e., gathering information about the song quality of heterospecifics to assess habitat quality (Morinay *et al.* 2020), cannot be considered in our study either, as social interactions within the wryneck bird community have been poorly studied so far.

In addition to conspecific attraction, weather conditions can influence the establishment of individuals. However, because weather variations have been found to have relatively little impact on reproduction (Tolkmitt *et al.* 2009, Ahlering *et al.* 2010) and populations in the surrounding area did not decrease during the duration of the study, we do not consider them relevant for the wryneck establishment. Similarly, the conditions in the wintering habitat do not seem to be critical. The wryneck seems to be able to compensate unfortunate conditions caused in migration and hibernation (Tolkmitt *et al.* 2009).

Establishment can be strongly influenced by the neighbourhood of conspecifics: areas that are too small to serve the establishment of conspecifics in addition to the already existing ones are therefore avoided (Stamps 2001). Even though we made sure that each experimental plot provided enough space for at least two breeding pairs, it is possible that wrynecks prefer areas that offer space for more conspecifics. This assumption is supported by the fact that wrynecks occupy extensive vineyards stretching over several kilometres at Lake Biel and Hallau, which are the closest larger and stable populations to our study area. Consequently, our evidence supports the suggestion by Rushing *et al.* (2021) that birds use a combination of species and habitat characteristics to select the highest quality habitat.

Relation between wryneck presence, occurrence, and habitat

The positive effect of playback treatment on wryneck presence during the prospection period is unrelated to our recorded habitat characteristics. These results are in line with our expectation that wryneck habitat selection is influenced first by conspecific attraction and second by habitat characteristics or quality.

Wryneck occurrence on all plots used for the habitat analysis was positively related to the proportion of vineyard, but unrelated to the proportion of meadows and pastures. In Switzerland, vineyards are among the preferred breeding habitats (Knaus *et al.* 2018). Vineyards cover large areas often on naturally biodiversity-rich, south-exposed dry slopes. In general, they are characterized by fairly high proportions of open ground and perches. Vineyards often yield, they are heterogeneous at the landscape level including surrounding habitats and/or habitat structures (hedgerows, forest edge, dry stone walls, dry rough grassland, etc.), and if they are managed at a small-scale they entail small-scale habitat heterogeneity (Guyot *et al.* 2017, Knaus *et al.* 2018). In addition, species-rich soil greening leads to a diverse insect diet and thus has a biodiversity-enhancing effect (Knaus *et al.* 2018, Barbaro *et al.* 2021). It follows that vineyards provide optimal conditions for a wryneck breeding habitat.

However, the wryneck also inhabits other habitats in Switzerland like intensive low-stem orchards, sparse larch forests and villages with adjacent habitats (Knaus *et al.* 2018). In a nutrient-poor landscape in Germany, wrynecks have been found colonizing dry and abandoned grasslands, old unused orchards, and areas with coppice forest character (Tolkmitt *et al.* 2009). All these biotopes share extensive meadows and pastures as a common feature and thus represent suitable habitat for wrynecks. Extensive pastures may be advantageous, because they offer more sward heterogeneity than extensive meadows (Vickery *et al.* 2001). Pastures are characterised by high temporal variability, depending on grazing intensity, which leads to higher temporal variability of bird communities as food resources are directly influenced (Söderström *et al.* 2001). However, the low establishment rate in our study area suggests that our experimental plots with meadow and pasture characteristics might not be suitable for wrynecks to become firmly established.

Bare ground has been repeatedly identified as an important habitat feature for the wryneck and other ground-foraging insectivorous farmland birds (Schaub *et al.* 2010, Weisshaupt *et al.* 2011). The absence of a correlation between wryneck occurrence and bare ground in our analysis (Fig. 5) is most likely due to the methodology we used. We roughly estimated bare ground cover for each land use patch, e.g., a fenced pasture. A more specific protocol across all experimental plots or using data obtained by remote sensing would likely have led to more accurate results.

Playback of conspecific vocalisations as a conservation strategy for wrynecks

In order to effectively protect a species, it is crucial to ensure the breeding success of that particular species in a target area, which is highly dependent on successful establishment. Because successful establishments in our study area were scarce, it is not possible to draw a scientifically robust conclusion from this data about the question whether playback is a useful tool as a conservation measure for the wryneck. To validate this method, the experiment would need to be implemented in a location where individuals are more likely to establish. That is, an area where some wrynecks breed regularly. Such a study design could provide more accurate information about the effects of playback on breeding success.

Nevertheless, the positive effect of playback on wryneck presence is indicating the possibility of a successful conservation strategy for this species through playback treatment. Despite the low density of wrynecks in the study area, the few recorded breeding events provide evidence for a successful attraction of wrynecks by the playback treatment to previously unoccupied, but suitable habitats to support population growth or to connect established populations. In total, we observed three breeding attempts on plots with playback treatment (two successful broods) and two on plots without playback treatment (one successful brood). These values are very similar to those reported under natural conditions of wryneck populations in Central Europe (Glutz von Blotzheim & Bauer 1994). Based on this evidence, we assume that the risk of using playback to attract wrynecks to unsuitable habitats (i.e., ecological trap) is low.

The wryneck pair from 2020 on an experimental plot without playback treatment most likely already settled and bred on this experimental plot in the previous year with a playback treatment, or it was a successfully hatched young from last year. This consecutive breeding event supports the assumption that playback is not only a possible but also sustainable conservation measure, since the probability of successful breeding increases significantly with the frequency of habitat occupancy (Mermod *et al.* 2009). In addition, every successful breeding pair on our experimental plots also successfully raised a second brood, which is the case for only 20% of the wrynecks and considered critical for population dynamics (Tolkmitt *et al.* 2009). In comparison to other conservation measures, playback is a very cost-effective method to attract birds to areas with suitable habitat, for example restored areas (Lewis *et al.* 2021). Hence, playback could boost the conservation efforts in such areas to be quickly colonized.

However, the use of playback must be applied with caution. Males arriving early in the breeding area tend to have a higher probability to breed than those arriving late (Amrhein *et al.* 2007). Thus, spending time on unsuitable plots with playback treatment reduces the chance of successful mating and reproduction. It is of utmost importance to only attract birds to habitats that appear suitable for the target to reduce search costs and declines in fitness (Stamps 2001). In addition, cultural bottlenecks would have to be taken into account in conservation strategies if populations decline (Lewis *et al.* 2021), even though wrynecks are still relatively common at present. For the wryneck, three limiting factors have to be considered: cavities, ant supply, and ant accessibility (Coudrain *et al.* 2010). Cavities can easily be provided by nest boxes suitable for the wryneck in the target areas (Zingg *et al.* 2010).

Because the wryneck is a ground foraging species (Knaus *et al.* 2018) it depends on short vegetation and bare ground to detect its prey (Weisshaupt *et al.* 2011). While the abundance of ant nests declines with increasing proportion of bare ground, the accessibility of ants for wrynecks increases (Coudrain *et al.* 2010, Schaub *et al.* 2010). Thus, an optimal vegetation structure of a wryneck foraging site is a small-scaled mosaic incorporating vegetated patches where food accumulates and bare patches where unrestricted access to food is ensured (Weisshaupt *et al.* 2011). Although short vegetation is linked with better food accessibility, wrynecks do not seem to show a preference for any particular sward height. Better accessibility of prey in short vegetation comes with avoidance of predation risk. Food accessibility and predation avoidance seem to be reasons why insectivorous birds appear to prefer foraging in sparse vegetation, despite higher food abundance in dense vegetation (Schaub *et al.* 2010).

The last two limiting factors can be improved by ant friendly management. The highest ant species richness has been found in nutrient-poor habitats (Seifert 2008), and fertilization of grasslands directly correlates with loss of ant species richness (Scherner 1989). The ants' preference for nutrient-poor habitats as well as the increased ant accessibility due to shorter vegetation cover (Coudrain *et al.* 2010), fits the wryneck's habitat selection of nutrient poor habitats such as heaths, abandoned grasslands, and extensive meadows (Wübbenhorst 2012). Thus, nutrient-reducing habitat management is recommended because atmospheric nitrogen deposition leads to higher biomass production, even in unfertilized habitats. Grazing-rotation or mowing regimes as a nutrient-poor management strategy would result in a mosaic of different field structures (Hübner *et al.* 2004, Fuhlendorf *et al.* 2006, Wübbenhorst 2012).

As previously stated, the small-scale vineyards in Switzerland, with their different management practices, provide in themselves very high-quality habitats for the wryneck. Alternating mechanical removal of ground vegetation is recommended to enhance a heterogeneous soil structure and to ensure feeding of ground-dwelling insects. Maintaining and promoting hedgerow structures and shrublands also has considerable positive effects on the avifauna biodiversity at landscape-level and thus ecosystem functioning and service provisioning (Barbaro *et al.* 2021). Such promotion of avifauna can serve as natural pest control (Guyot *et al.* 2017). In particular, the wryneck can contribute to the reduction of aphids as it feeds on ants, which in turn encourage aphids (Renault *et al.* 2005), ultimately leading to more sustainable viticulture.

Finally, nutrient-poor management methods in combination with high structured surrounding would also support endangered species such as the woodlark (*Lullula arborea*), cirl bunting (*Emberiza cirlus*), hoopoe (*Upupa epops*), common redstart (*Phoenicurus phoenicurus*), red-backed shrike (*Lanius collurio*), and common linnet (*Linaria cannabina*)

(Fuhlendorf *et al.* 2006, Guyot *et al.* 2017, Barbaro *et al.* 2021). Considering conspecific attraction, this results in the possibility of attracting entire bird communities to newly restored conservation sites or replenishing protected areas. However, a change in the bird community could also lead to unintended species declines, which is especially important to consider at sites with other threatened species (Lewis *et al.* 2021). At this point, further research on interaction within wryneck bird communities is needed.

Conclusion and management recommendations

Our results confirm the preference of wryneck settlements in locations with high densities of conspecifics and high habitat quality. In terms of habitat size, our results suggest that extensive areas, such as those created by viticulture in Switzerland, provide better conditions than isolated small-scale areas, as is the case in our study area.

For wryneck conservation management using playback, we recommend focusing on extensively used, semi-open habitats with available cavities, a high number of ants, and a bare ground cover of about 50%, where the probability of occurrence of the wryneck is highest (Coudrain *et al.* 2010, Weisshaupt *et al.* 2011).

Acknowledgments

My deepest thanks to my supervisors, Matthias Vögeli and Tillmann Buttschardt, who took very good care of me in addition to working on this project. I want to thank them, Michael Lanz, and the Swiss Ornithological Institute for their great support and work in the wryneck project. My thanks also go to our field assistant, Larissa Meyer, who went into the field with me and supported me in my work.

REFERENCES

Ahlering, M.A., Arlt, D., Betts, M.G., Fletcher, R.J., Nocera, J.J. & Ward, M.P. 2010. Research Needs and Recommendations for the Use of Conspecific-Attraction Methods in the Conservation of Migratory Songbirds. *Condor* **112**: 252–264.

Amrhein, V., Kunc, H.P., Schmidt, R. & Naguib, M. 2007. Temporal patterns of territory settlement and detectability in mated and unmated Nightingales Luscinia megarhynchos. *Ibis* **149**: 237–244.

Barbaro, L., Assandri, G., Brambilla, M., Castagneyrol, B., Froidevaux, J., Giffard, B., Pithon, J., Puig-Montserrat, X., Torre, I., Calatayud, F., Gaüzère, P., Guenser, J., Macià-Valverde, F.-X., Mary, S., Raison, L., Sirami, C. & Rusch, A. 2021. Organic management and landscape heterogeneity combine to sustain multifunctional bird communities in European vineyards. *Journal of Applied Ecology* **58**: 1261–1271.

Bates, D., Meachler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Scheipl, F., Grothendieck, G., Green, P., Fox, J. & Krivitsky, P.N. 2020. *Package 'lme4'*. https://cran.r-project.org/web/packages/lme4/lme4.pdf (accessed 23 February 2021).

Buxton, V.L., Enos, J.K., Sperry, J.H. & Ward, M.P. 2020. A review of conspecific attraction for habitat selection across taxa. *Ecology and evolution* **10**: 12690–12699.

Coudrain, V., Arlettaz, R. & Schaub, M. 2010. Food or nesting place? Identifying factors limiting Wryneck populations. *Journal of Ornithology* **151**: 867–880.

Danchin, E., Heg, D. & Doligez, B. 2001. Public information and breeding habitat selection. In Clobert, J., Danchin, E., Dhondt, A. & Nichols, J. (eds.) *Dispersal*: 243–258: Oxford University Press.

Fletcher, R.J. 2007. Species interactions and population density mediate the use of social cues for habitat selection. *The Journal of animal ecology* **76**: 598–606.

Fuhlendorf, S.D., Harrell, W.C., Engle, D.M., Hamilton, R.G., Davis, C.A. & Leslie, D.M. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. *Ecological Applications* **16**: 1706–1716.

Glutz von Blotzheim, U.N. & Bauer, K. 1994. Wendehals - *Jynx torquilla*. In Glutz von Blotzheim, U.N. & Bauer, K. (eds.) *Handbuch der Vögel Mitteleuropas*: 881–916, 2nd edn. Wiesbaden: AULA-Verlag.

Guyot, C., Arlettaz, R., Korner, P. & Jacot, A. 2017. Temporal and Spatial Scales Matter: Circannual Habitat Selection by Bird Communities in Vineyards. *PLOS ONE* **12**: e0170176.

Hartig, F. 2020. *DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models*. https://cran.r-project.org/web/packages/DHARMa/vignettes/DHARMa.html (accessed 23 March 2021).

Hübner, G., Rauth, M. & Will, D. 2004. Wendehals und Landschaftspflegepraxis: Erkenntnisse einer Lebensraumanalyse im westlichen Oberfranken. *Natur und Landschaft* **79.**: 118–123.

Keller, V., Gerber, A., Schmid, H., Volet, B. & Zbinden, N. 2010. *Rote Liste Brutvögel: Gefährdete Arten der Schweiz,* 1019th edn.: Bundesamt für Umwelt, Bern, und Schweizerische Vogelwarte, Sempach.

Knaus, P., Antoniazza, S., Wechlser, S., Guélat, J., Kéry, M., Strebel, N. & Sattler, T. 2018. *Schweizer Brutvogelatlas 2013-2016: Verbreitung und Bestandsentwicklung der Vögel in der Schweiz und im Fürstentum Liechtenstein*. Sempach: Schweizerische Vogelwarte.

Lanz, M. 2016. Wendehalsförderung - auch ohne Hochstämmer? *Avinews*: 2–3.

Lewis, R.N., Williams, L.J. & Gilman, R.T. 2021. The uses and implications of avian vocalizations for conservation planning. *Conservation biology the journal of the Society for Conservation Biology* **35**: 50–63.

Lüthi, T. 2018. *XC417931 – Wendehals – Jynx torquilla*: https://www.xeno-canto.org/417931.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J. & Langtimm, C.A. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**: 2248–2255.

Mermod, M., Reichlin, T.S., Artlettaz, R. & Schaub, M. 2009. Vorläufige Ergebnisse einer Langzeitstudie zum Wendehals in der Schweiz. *Aktuelle Beiträge zur Spechtforschung - Tagungsband*: 78–81.

Morinay, J., Forsman, J.T. & Doligez, B. 2020. Heterospecific song quality as social information for settlement decisions: an experimental approach in a wild bird. *Animal Behaviour* **161**: 103–113.

Renault, C.K., Buffa, L.M. & Delfino, M.A. 2005. An aphid-ant interaction: effects on different trophic levels. *Ecological Research* **20**: 71–74.

Robles, H., Ciudad, C., Vera, R., Olea, P.P. & Matthysen, E. 2008. Demographic Responses of Middle Spotted Woodpeckers (Dendrocopos medius) to Habitat Fragmentation. *The Auk* **125**: 131–139.

Rushing, C.S., Brandt Ryder, T., Valente, J.J., Scott Sillett, T. & Marra, P.P. 2021. Empirical tests of habitat selection theory reveal that conspecific density and patch quality, but not habitat amount, drive long-distance immigration in a wild bird. *Ecology letters*: 1167–1177.

Schaub, M., Martinez, N., Tagmann-Ioset, A., Weisshaupt, N., Maurer, M.L., Reichlin, T.S., Abadi, F., Zbinden, N., Jenni, L. & Arlettaz, R. 2010. Patches of bare ground as a staple commodity for declining ground-foraging insectivorous farmland birds. *PLOS ONE* **5**: e13115.

Scherner, E.R. 1989. *Wendehals und Populationsbiologie: der "Vogel des Jahres 1988" und die Pflicht zur Forschung*. Laufen/Salzach: Bayerische Akademie für Naturschutz und Landschaftspflege (ALN).

Schuck, M. & Lanz, M. 2017. Comeback der Wendehälse: Projekte für den Spechtvogel. *ornis*: 18–21.

Seifert, B. 2008. Lebensraumansprüche, Biomasse und Erreichbarkeit für Spechte relevanter Ameisen. *Aktuelle Beiträge zur Spechtforschung - Tagungsband*: 20–27.

Söderström, B., Pärt, T. & Linnarsson, E. 2001. Grazing effects on between-year variation of farmland bird communities. *Ecological Applications* **11**: 1141–1150.

Spaar, R. & Ayé, R. 2016. Strategie Artenförderung Vögel Schweiz. *Rahmenprogramm der Schweizerischen Vogelwarte Sempach und des Schweizer Vogelschutzes SVS/BirdLife Schweiz, in enger Zusammenarbeit mit dem Bundesamt für Umwelt BAFU.*

Stamps, J. 1988. Conspecific Attraction and Aggregation in Territorial Species. *The American Naturalist*: 329–347.

Stamps, J. 2001. Habitat selection by dispersers: integrating proximate and ultimate approaches. In Clobert, J., Danchin, E., Dhondt, A. & Nichols, J. (eds.) *Dispersal*: 230–242: Oxford University Press.

Südbeck, P., Andretzke, H., Fischer, S., Gedeon, K., Schikore, T., Schröder, K. & Sudfeldt, C. (eds.). 2005. *Methodenstandards zur Erfassung der Brutvögel Deutschlands*. Radolfzell.

Tolkmitt, D., Becker, D., Reichlin, T.S.A. & Schaub, M. 2009. *Variation der Gelegegrößen des Wendehalses Jynx torquilla in Untersuchungsgebieten Deutschlands und der Schweiz*. Wernigerode: Nationalparkverwaltung Harz.

van Wijk, R.E., Schaub, M., Tolkmitt, D., Becker, D. & Hahn, S. 2013. Short-distance migration of Wrynecks Jynx torquilla from Central European populations. *The international Journal of Avian Science*: 886–890.

Ward, M.P. & Schlossberger, S. 2004. Conspecific Attraction and the Conservation of Territorial Songbirds. *Conservation Biology* **18**: 519–525.

Weisshaupt, N., Arlettaz, R., Reichlin, T.S., Tagmann-Ioset, A. & Schaub, M. 2011. Habitat selection by foraging Wrynecks Jynx torquilla during the breeding season: identifying the optimal habitat profile. *Bird Study* **58**: 111–119.

Wübbenhorst, J. 2012. Der Wendehals Jynx torquilla in Niedersachsen und Bremen: Verbreitung, Brutbestand und Habitatwahl 2005-2010 sowie Gefährdungsursachen, Schutz und Erhaltungszustand. *Vogelkundliche Berichte Niedersachsen*: 15–45.

Zerbe, S. & Wiegleb, G. (eds.). 2009. *Renaturierung von Ökosystemen in Mitteleuropa,* 1. Aufl. Heidelberg: Springer Spektrum.

Zingg, S., Arlettaz, R. & Schaub, M. 2010. Nestbox Design Influences Territory Occupancy and Reproduction in a Declining, Secondary Cavity-Breeding Bird. *Ardea* **98**: 67–75.

Zuur, A.F., Ieno, E.N. & Meesters, E. 2009. *A Beginner's Guide to R*. New York: Springer.