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"Use of conspecific attraction to influence the breeding habitat selection of the Whinchat (Saxicola rubetra)"

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Table of content

Sworn declaration	IV
Acknowledgements	V
Abstract	VI
Kurzfassung	VII
1. Introduction	8
1.1. Habitat selection as a hierarchical process	8
1.2. Conspecific attraction	9
1.4. Conservation of Whinchat populations	13
1.5. Addressed research questions of this study	14
2. Material and Methods	16
2.1. Study area	16
2.2. Study species	17
2.3. Experimental design	21
2.3.1. Playback	22
2.3.2. Artificial perches	25
2.3.3. Habitat quality	25
2.4. Spatial factors	26
2.5. Statistical analysis	26
3. Results	28
3.1. Playback	29
3.2. Artificial perches	29
3.3. Habitat quality	30
3.4. Temporal aspect	34
4. Discussion	35
4.1. Playback	35
4.2. Artificial perches	
4.3. Habitat quality	
4.4. Spatial factors	
5 Conservation implementations	
6. References	
Annendix	57

"Through interpretation, understanding; through understanding, appreciation; through appreciation, protection."

- Tilden Freeman -

Sworn declaration

Hereby, I declare under oath that I wrote the submitted Master's Thesis autonomously, without any third-party assistance or information other than the provided sources. Sources for literal, paraphrased and cited quotes have been accurately credited.

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Vienna, March 2019

Signature

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Abstract

Background: Agricultural intensification of grasslands and shifts in the mowing phenology are the main reasons for the massive decline of the Whinchat (*Saxicola rubetra*) in Western and Central Europe. Hence, effective conservation measures are needed for this migratory songbird, which is in Switzerland confined to subalpine grasslands. Conspecific attraction, the tendency for individuals to settle near members of the same species, provides a conservation tool that has been successfully applied for several migratory passerines. Since birds use the presence of conspecifics as a cue to assess habitat quality, this behaviour can be exploited to influence the breeding habitat selection of individuals of a given species.

Aims: This study aimed to test whether experimentally provided conspecific vocalizations influence the breeding habitat selection of the Whinchat. If successful, the playback of conspecific vocalizations could be used as a conservation measure to redirect settling Whinchats towards suitable areas that are unaffected by early mowing. Additionally, this experiment aimed at testing whether an increased availability of perches improves Whinchat habitat quality and therefore influences breeding habitat selection.

Methods: In 2018, a controlled playback study using local conspecific vocalizations was conducted in the Lower Engadine on 79 experimental plots, which were simultaneously employed for testing the influence of an increased availability of perches. Established plots represented meadows of three different habitat quality levels (low, intermediate and high) along a distance gradient to existing large Whinchat populations (core areas).

Results: The playback and the increased availability of perches did not affect the breeding habitat selection of the Whinchat. Nevertheless, the habitat quality influenced the species' settlement, whereby low habitat quality plots were avoided. Furthermore, Whinchat settlement events were strongly related to the distance to the nearest core area. Consequently, Whinchats preferably settled in plots of high or intermediate habitat quality within approximately 2 km to the nearest core area.

Conclusion: The playback of conspecific vocalizations and the use of artificial perches did not prove being useful tools for conservation measures. Conservation management for the Whinchat in the Lower Engadine must focus on the conservation and improvement of the existing large core areas and their surroundings up to 2 km distance. Further studies are necessary to address the importance of conspecific attraction for breeding habitat selection of the Whinchat and to unmask the relationship between social factors, breeding site fidelity and habitat characteristics.

Kurzfassung

Die Intensivierung der Grünlandbewirtschaftung und die zeitliche Verlagerung der Mahd sind zwei Hauptgründe für den drastischen Rückgang des Braunkehlchens (*Saxicola rubetra*) in West- und Mitteleuropa. Daher braucht es effektive Maßnahmen zur Förderung dieses Langstreckenziehers, der in der Schweiz subalpine Wiesen besiedelt. Die Tendenz von Individuen, sich in der Nähe von Artengenossen niederzulassen, wird als soziale Attraktion bezeichnet. Da Vögel die Anwesenheit von Artgenossen nutzen, um die Qualität des Habitats zu beurteilen, kann dieses Verhalten genutzt werden, um die Wahl des Bruthabitats eines Individuums zu beeinflussen. Bei verschiedenen Zugvögeln ist soziale Attraktion bereits erfolgreich als Instrument zur Artenförderung eingesetzt worden.

Ziel dieser Studie war es experimentell zu testen, ob das Abspielen von arteigenen Gesängen die Wahl des Bruthabitats beim Braunkehlchen beeinflusst. Sollte diese Methode erfolgreich sein, kann das Abspielen von arteigenen Gesängen als Maßnahme zur Artenförderung genutzt werden, um die Ansiedlung des Braunkehlchens in geeignete, spät gemähte Gebiete zu lenken. Im selbigen Experiment wurde ebenfalls getestet, ob das Ausbringen von künstlichen Sing- und Sitzwarten zur Verbesserung der Habitatqualtät beiträgt und somit die Wahl des Bruthabitats für das Braunkehlchen beeinflusst.

Dafür wurde 2018 im Unterengadin auf 79 Flächen ein kontrolliertes Playback-Experiment mit lokalen Braunkehlchengesängen durchgeführt. Darüber hinaus wurde der Einfluss von künstlichen Sing- und Sitzwarten getestet. Die Flächen wurden in drei verschiedene Qualitätsstufen (niedrig, mittel und hoch) eingeteilt und befanden sich entlang eines Distanzgradienten zu den bestehenden Kerngebieten.

Sowohl das Playback-Experiment als auch die künstliche Erhöhung des Wartenangebots hatte keinen Einfluss auf die Wahl des Bruthabitats beim Braunkehlchen. Jedoch beeinflusste die Habitatqualität die Ansiedlung des Braunkehlchens, wobei Flächen tiefer Qualität gemieden wurden. Darüber hinaus zeigte das Ansiedlungsverhalten des Braunkehlchens ein starkes räumliches Muster, das von der Nähe zum nächsten Kerngebiet bestimmt wurde. Folglich besiedelten Braunkehlchen bevorzugt Flächen mittlerer und hoher Habitatqualität innerhalb von 2 km Distanz zum nächsten Kerngebiet.

Das Abspielen von arteigenen Gesängen und Ausbringen von künstlichen Sing- und Sitzwarten sind als Maßnahme zur Artenförderung für das Braunkehlchen ungeeignet. Folglich sollten sich Förderungsmaßnamen auf den Schutz und die Aufwertung von bestehenden Kerngebieten und deren unmittelbare Umgebung im Umkreis von etwa 2 km fokussieren. Weitere Studien zur Bedeutung von sozialer Attraktion und dessen Einfluss auf die Wahl des Bruthabitats beim Braunkehlchen sind nötig, um den Zusammenhang von sozialen Faktoren, Standortstreue und Habitateigenschaften zu verdeutlichen.

1. Introduction

1.1. Habitat selection as a hierarchical process

The choice of the optimal breeding habitat is essential for the reproductive success of birds (Cody 1985). Habitat selection in birds is a hierarchical series of choices leading to their particular distribution in their breeding grounds (Jones 2001, Ahlering et al. 2010). This annually repeated decision-making process begins at a macro-habitat scale (geographic region, landscape) and then the focus narrows down towards micro-habitat selection for nest sites and feeding locations (Block & Brennan 1993, Ahlering et al. 2010). Compared to habitat use, where species use an accumulation of environmental components in order to meet numerous life history needs (e.g. foraging, breeding, etc.), without insinuating a conscious choice (Hutto 1985, Block & Brennan 1993), habitat selection is the inborn and learned behavioural response that allows birds and other animals to recognize and differentiate various environmental components (Block & Brennan 1993). Habitat selection further incorporates the understanding of complex behavioural and environmental processes (Jones 2001). These habitat selection processes result in characteristic habitat use patterns (distributional use of environmental conditions), influencing the change of survival and, ultimately, the fitness of individuals (Block & Brennan 1993, Jones 2001). Therefore, habitat selection has to be addressed as a hierarchical process and not a distributional pattern with several extrinsic factors (such as habitat accessibility or weather patterns) influencing this process (Hutto 1985. Jones 2001).

Breeding habitat selection relies on information and can be affected by numerous factors such as the availability of food, the vegetation type and the presence of conspecifics (Stamps 1988, Brown & Brown 1996, Clark & Shutler 1999, Ahlering et al. 2010, Grendelmeier et al. 2017, Szymkowiak et al. 2017). Although the ecological and evolutionary consequences of breeding habitat selection can be crucial for individuals, the mechanisms behind it are, however, poorly understood (Hildén 1965, Cody 1985, Orians & Wittenberger 1991). Therefore, understanding the mechanisms behind breeding habitat selection of a species, and the processes affecting it, may contain fundamental information (Bruinsma & Koper 2012, Devries et al. 2018). The choice of the right breeding habitat is essential and expected to reflect the underlying habitat specific fitness consequences of a species (Cody 1985, Devries et al. 2018). Nesting site selection can have important consequences for the reproductive success of birds, which further strongly impacts population growth in many species (Devries et al. 2018). Since species management and species conservation often focus on population growth and promoting settlement in new areas, additional knowledge concerning the processes influencing habitat selection is fundamental for future conservation initiatives, which may help to prevent

population declines (Swaisgood 2007, Ahlering et al. 2010, Bruinsma & Koper 2012, Devries et al. 2018).

1.2. Conspecific attraction

Essential information about the breeding habitat can be acquired as a result of direct interactions with the physical environment, using trial and error tactics or from previous reproductive performances, so called personal information (Danchin et al. 2004, Ahlering et al. 2010). Furthermore, information can be obtained by monitoring the interactions of con- or heterospecifics among one another, a term called social information (Danchin et al. 2004, Grendelmeier et al. 2017). Social information can be based on specifically designed signals to provide information or on inadvertently provided cues by individuals engrossed in efficient performance of activities (Danchin et al. 2004). The presence of conspecifics in a given habitat can be a social cue that provides information about the quality of the habitat, which can further guide the settlement decision of individuals (Stamps 1988, Ahlering et al. 2010, Szymkowiak et al. 2017). Conspecific location cues can bias settlement decisions of individuals for habitats that are already inhabited by other individuals of their own species, a phenomenon also knows as conspecific attraction (Stamps 1987, 1988, Ward & Schlossberg 2004, Szymkowiak et al. 2017). This indirect technique to estimate the quality of habitats is seemingly a less costly habitat selection strategy. Conspecific attraction studies are particularly common in migratory birds, as their annually repeated movement forces migratory birds to restructure communities on a yearly basis, giving researchers the opportunity to observe how conspecific aggregation takes place (Nocera & Betts 2010). In territorial songbirds, conspecific attraction provides important cues about habitat use and individuals that prefer to settle close to conspecifics are less likely to settle in empty or newly created habitat patches (Schlossberg & Ward 2004, Vogel 2011). Since conspecific location cues are not available for individuals arriving first in the breeding grounds, they decide to settle based on other information (e.g. previous breeding experience), whereupon their presence may further serve as social cue for other individuals (Stamps 1988, Szymkowiak et al. 2017).

1.3. Agricultural intensification and declining grassland birds

Many ground-nesting grassland bird populations which depend on farmland habitats have been declining over the last decades (Donald et al. 2001, Grüebler et al. 2012, Korner et al. 2018). This trend has been observed since the 1960s, particularly in the lowlands of Central and North-western Europe. Human induced land use changes and an increase in land use intensity affect survival patterns of ground-nesting grassland birds and are considered to have a strong impact on bird populations (Grüebler et al. 2008). The therewith associated landscape changes cause deterioration of grassland habitat quality. This may reduce the carrying

capacity of a habitat and, eventually, a species' population size (Müller et al. 2005). If most of a species' habitat is affected by habitat deterioration, large-scale reductions in population size or even extinction are potential consequences (Müller et al. 2005).

Agricultural intensification of grassland management has been described as the main reason for the decrease of suitable habitat for ground-nesting grassland birds, resulting in nest losses and lower nest survival rates, and ultimately leading to declines in their populations (Müller et al. 2005, Britschgi et al. 2006, Grüebler et al. 2012). Agricultural land use has undergone major changes in the past, which potentially cause changes of plant, insect and bird populations (Fig. 1) (Robinson & Sutherland 2002). Donald et al. (2001) clearly showed that population declines and range compression of farmland birds were higher in countries with more intensive agricultural use. Most of the ground-nesting grassland bird species, including the Whinchat (Saxicola rubetra), are seemingly unable to adapt to the rapid and drastic changes that have occurred in the agricultural practices in the last decades all over Europe (Müller et al. 2005).

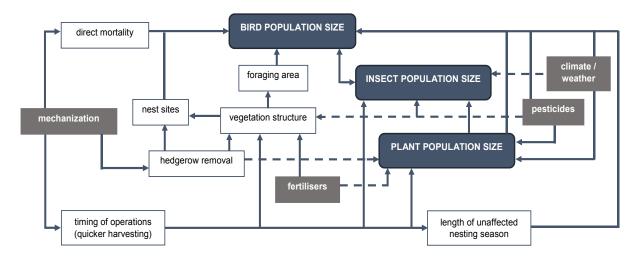


Fig 1: Potential causes of population change in plant, insect and bird populations resulting from changes of agricultural land use. Major drivers for population changes are shaded in grey (Robinson & Sutherland 2002, modified). Note: This figure is not intended to be comprehensive and only illustrate major drivers and their interactions.

In case of the Whinchat several studies provide evidence that changes in land use and grassland management have a massive impact on reported population declines (Bastian & Feulner 2015, Grüebler et al. 2015a). Especially the shift of the mowing phenology with earlier mowing dates (primarily the first mowing date) and increased harvest activities are the main reasons for reduced nest survival, a key factor lowering the reproductive success of Whinchats, which may also explain their current negative population trends (Donald et al. 2001, Müller et al. 2005, Grüebler et al. 2008, Perlut et al. 2008a, b, Grüebler et al. 2012, Strebel et al. 2015). Grüebler et al. (2008) detected a temporal shift in nest destruction from the nestling stage to the pre-hatching stage between 1988 and 2008. This shift to earlier mowing dates and the intensification of farming practice enable more frequent grass cuts, which can be realized due

to technical mowing advances that increase the speed and efficiency of mowing machines as well as new storage techniques that favour earlier mowing dates (Grüebler et al. 2008). Due to the improvement of the infrastructure in mountainous areas, farmers can operate with larger and heavier agricultural machinery, which results in more mechanically and intensively exploited agricultural surface (Bosshard 2015). Destroyed or damaged eggs, killed or injured nestlings and fledglings are the result of these sudden and radical changes of the habitat, turning potential source populations into sink populations (Müller et al. 2005, Grüebler et al. 2008).

Agricultural change is most likely to have consequences on the food availability of birds (Wilson et al. 1999). The intensification of farming practices in recent years, especially, has led to a decreased abundance and diversity of grassland invertebrates throughout most of the season (Britschqi et al. 2006). This is an indirect threat affecting the foraging efficiency and reproductive success of birds. The agricultural intensification of modern grassland management (e.g. more frequent mowing, fertilization and the utilization of pesticides) affects the diversity and vegetation structure of meadows, which entails serious consequences for the Whinchat (Fig. 2) (Bastian & Bastian 1996). Fertilization and more frequent mowing, for example, changes the vegetation composition and structure, leading to lusher plant growth and higher plant density, which impedes the visibility and access of prey for the Whinchat (Oppermann 1990, Bastian et al. 1994, Grüebler et al. 2015b). The incessant pollution of agricultural land due to the use of synthetic pesticides in particular is one of the major driver of insect loss in recent years (Dudley & Alexander 2017, Sánchez-Bayo & Wyckhuys 2019). Consequently, the intensification of modern grassland management has a strong and not negligible impact on grassland birds by altering the abundance, diversity, availability and accessibility of arthropod prey (Di Giulio et al. 2001, Marini et al. 2008).

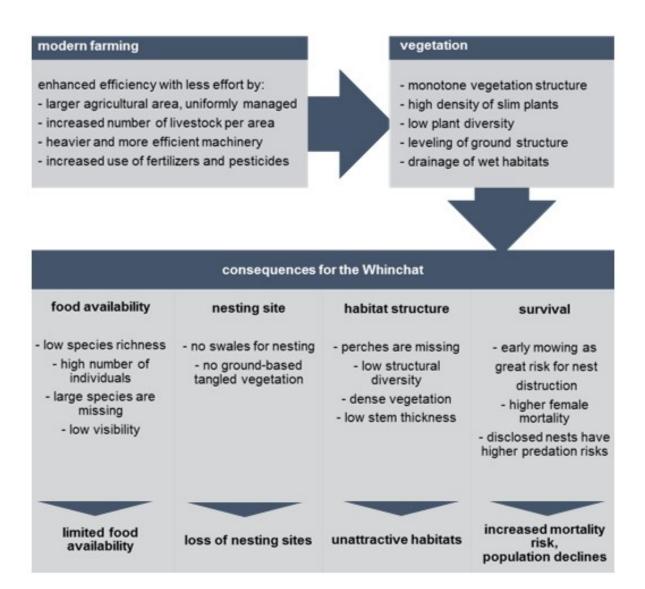


Fig 2: Influence of intensive grassland management on the vegetation structure and deduced consequences for the Whinchat (by Bastian & Bastian 1996, modified).

The results of Bastian et al. (1994) and Oppermann (1999) showed a clear relationship between habitat use of Whinchats and food availability. Whinchats tend to occupy habitat with a high diversity of arthropods, but not with higher abundances of arthropods. Like most meadows in the lowlands of north-western and central Europe, Whinchat habitats have already lost their former plant and animal diversity due to agricultural intensification (Müller et al. 2005). Thus, the Whinchat mainly inhabits extensively managed sub-alpine grasslands (Horch & Spaar 2015). The consolidation of parcels and the subsequent removal of shrubs and bushes often accompany the agricultural intensification of grassland, which particularly lower the botanical diversity and plant structures of grassland habitats (Horch et al. 2008). Whinchats rely on these vertical structures in their breeding habitat and show the tendency to use habitats with a high availability of perches such as herb stems, tall weeds, shrubs or trees but also artificial perches like posts, fences or power lines (Cramp 1988, Glutz von Blotzheim 1988, Oppermann 1990, Fischer et al. 2013). Moreover, it is assumed that an increased number of

perches has a positive impact on the habitat quality and subsequently on the establishment and colonisation of potential Whinchat breeding habitats (Siering & Feulner 2017). This is why artificial perches have been used to improve potential breeding habitats as a conservation measure for the Whinchat for several years.

All these drastic changes of grassland habitats have also reached the alpine area, threatening one of the last refuges for the Whinchat as well as the last strongholds of remaining whinchat populations in central Europe (Müller et al. 2005).

1.4. Conservation of Whinchat populations

To stop further Whinchat population declines and to secure viable populations, effective conservation measures are needed (Müller et al. 2005, Grüebler et al. 2012). In several regions in Switzerland the Swiss Ornithological Institute has implemented conservation measures in the framework of the Swiss Species Recovery Programme for Birds (Horch et al. 2008, Horch & Spaar 2015). These measures ranged from nest protection, small-area grassland management, increased supply of natural perches and a large-scale adapted grassland management. Such measures are cost-intensive and time-consuming approaches to protect breeding habitats and only a large-scale adapted grassland management seems to be a promising long-term conservation measure (Horch & Spaar 2015).

Previously, conservation of bird populations has focused on identifying and managing threats such as habitat loss, habitat destruction or predators, but conservationists have recently learned that it may be insufficient to conserve a certain species by simply focusing on its external environment (Ward & Schlossberg 2004, Kappes et al. 2011). For species that exhibit conspecific attraction, playback could be used to attract birds to settle in high quality habitats, where factors limiting survival and reproduction are controlled (Ward & Schlossberg 2004). Focussed management of these areas is essential to mitigate limiting factors and to prevent them from turning into population sinks. This could be a substantial advantage for species whose numbers are declining due to selection of ecological traps.

Conspecific attraction is therefore a factor that can potentially be used to influence the breeding habitat selection of Whinchats and redirect them towards suitable habitats unaffected by mowing events throughout the whole breeding season (Ward & Schlossberg 2004, Anich & Ward 2017, Grendelmeier et al. 2017). Thus, conspecific attraction has the potential to be an effective and inexpensive conservation measure, as it is easy to implement if appropriate habitats are available (Schlossberg & Ward 2004, Ahlering et al. 2010).

1.5. Addressed research questions of this study

This study aims at testing whether playback of Whinchat vocalizations, as an experimentally provided social cue, can exploit the mechanism of conspecific attraction to influence the species' breeding habitat selection. If successful, broadcasting conspecific vocalizations could be applied as an effective conservation measure for the Whinchat. Further, it was tested whether an increased availability of perches improves the habitat quality for Whinchats and therefore influences its breeding habitat selection in the study area. The outcomes of this study are likely to contribute to the conservation management of the Whinchat. The final objective is to design and apply conservation measures based on the obtained results to ensure the continued existence of the Whinchat in the study area as well as in other regions of Switzerland. Furthermore, the outcomes of this study may provide important information for the use of conspecific attraction in a conservation framework with other bird species.

This study aims to answer the following questions:

Does the experimentally provided playback of conspecific vocalizations influence the breeding habitat selection of the Whinchat?

Whinchats show several characteristics that may favour conspecific attraction, such as asynchronous migration, aggregated distribution patterns, higher ratio of juveniles in the population and a short breeding season (Glutz von Blotzheim 1988, Müller et al. 2005, Ahlering et al. 2010, Border et al. 2017a). Therefore, I expect that Whinchats will preferably select plots where the playback of conspecific vocalizations is experimentally provided.

Does the experimentally increased availability of artificial perches influence the breeding habitat selection of the Whinchat?

For several years, artificial perches have been used as a conservation measure to enhance the quality of potential breeding habitat of the Whinchat (Siering & Feulner 2017). Although it seems that artificial perches have a positive influence on the establishment and colonisation of potential breeding habitat, this conservation measure has never been experimentally tested. Whinchats rely on vertical structures in their breeding habitat and tend to use perches such as herb stems, tall weeds, shrubs or trees but also artificial perches like posts, fences or power lines (Cramp 1988, Glutz von Blotzheim 1988, Siering & Feulner 2017). Since an increased availability of perches is expected to have a positive impact on the habitat quality and subsequently on the settlement behaviour of the Whinchat, I expect that Whinchats will preferably select plots with an increased availability of artificial perches.

How does habitat quality affect the breeding habitat selection of the Whinchat?

Although Whinchats colonize open grasslands with different habitat quality, their breeding success decreases in breeding habitats with low habitat quality (Britschgi et al. 2006). Since Whinchats experience greater breeding success in high quality habitats and successful breeding Whinchat males tend to occupy the same breeding territory in the next year (Müller et al. 2005, Britschgi et al. 2006, Shitikov et al. 2015), I expect that Whinchats will preferably select experimental plots with high habitat quality, characterized by the botanical diversity of the experimental plots.

Is the settlement pattern on the experimental plots spatially related to the existing large Whinchat populations in the study area?

The Whinchat population is not homogeneously distributed in the Lower Engadine, where four large Whinchat populations with more than 35 occupied territories (core areas) remain. Whinchats seemingly prefer to settle close to territories already occupied by conspecifics, which can lead to high settlement densities under optimal conditions (Glutz von Blotzheim 1988). Therefore, I expect that Whinchats will preferably select experimental plots close to the existing large Whinchat populations.

2. Material and Methods

2.1. Study area

The study was carried out in the Lower Engadine (46°50` N, 10°23` E) (Fig. 3), an inner-Alpine valley situated in the south-east of Switzerland (Grüebler et al. 2008, Strebel et al. 2015). The Lower Engadine is part of the canton Graubünden and has a dry and mild summer climate with an average annual precipitation of 695 mm (37% from June to August), which is only 40% of the precipitation recorded in areas located in the outer chains of the northern Alps at similar altitudes (Müller et al. 2005; Britschgi et al. 2006). The elevation of the Lower Engadine reaches from 1035 m (Martina) to 3410 m (Piz Linard) above sea level (a.s.l.).

The landscape of the Lower Engadine is defined by mostly wooded north-facing slopes, a valley floor pervaded by various human infrastructure and agriculturally used areas — dominated by meadows which have experienced an increase in management intensity over the last decades — and moderately steep south-facing slopes used for agriculture (mainly meadows and pastures) with steeper, wooded areas (Korner et al. 2017).

Although agricultural intensification, in particular, has led to large changes in the avifauna of the Lower Engadine in the last decades, important populations of threatened bird species like the Whinchat (*Saxicola rubetra*), the Skylark (*Alauda arvensis*) or the Red-backed shrike (*Lanius collurio*) still persist in the valley (Korner et al. 2017). Numerous studies have been conducted in the Lower Engadine by the Swiss Ornithological Institute, and a detailed Whinchat monitoring programme has been in progress since 2006. Therefore, the Lower Engadine was the ideal study area.

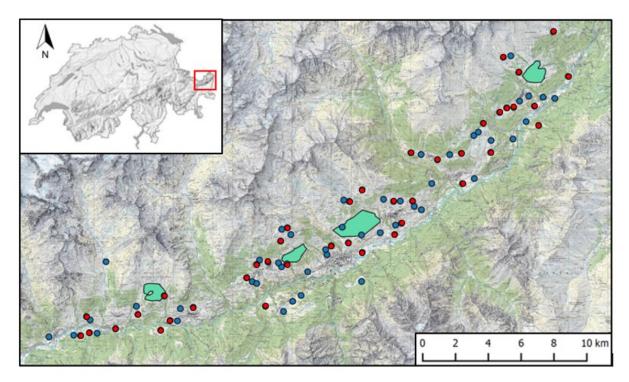


Fig. 3: Map of the study area in the Lower Engadine between Lavin and Martina. The experimental plots (n = 39) are shown as red dots and control plots (n = 40) as blue dots. The four existing large core areas (> 35 occupied territories) of the Whinchat present in the study area are shown in turquoise. The map inset indicates the geographical location of the Lower Engadine in the Southeast of Switzerland.

2.2. Study species

The Whinchat is a ground-breeding, insectivorous passerine and an indicator species of open grassland, cultivated at a low intensity level (Müller et al. 2005, Britschgi et al. 2006, Grüebler et al. 2015b). In general, this species uses open grasslands with a high availability of small-scale structures as breeding habitat such as extensive wildflower meadows but occasionally it is also found in pastures (Cramp 1988, Glutz von Blotzheim 1988, Müller et al. 2005). It prefers gently sloped terrains with moist or wet meadows as breeding grounds (Cramp 1988). This makes the Whinchat highly susceptible to agricultural intensification of grasslands (Müller et al. 2005). Although the Whinchat is present on a wide range of different plant associations, it needs a diverse vegetation structure that changes among the breeding season (Glutz von Blotzheim 1988, Oppermann 1990). Besides vegetation that provides adequate cover for Whinchats to establish their nests, they require low-growing and patchy vegetation as foraging areas that are overtopped by natural or artificial perches (Glutz von Blotzheim 1988, Oppermann 1999). Whinchats build their well-camouflaged ground nests often in close range to shrubs, bushes or other perches. These structures are ideal bases for hunting and are often used before entering the nest (Glutz von Blotzheim 1988, personal observation).

Whinchats are long-distance migrants with wintering grounds in sub-Saharan tropical Africa and leave them in the second half of March to migrate to their breeding areas (Cramp 1988, Glutz von Blotzheim 1988). The main migration through Switzerland begins in the middle of

April and cumulates in the beginning of May when they also start to establish their breeding territories (Glutz von Blotzheim 1988). Migration can prolong until beginning of June in higher elevations. Spring migration phenology starts with the arrival of mostly adult males in the breeding area. Subsequently, young males arrive in the breeding area. In general, male arrival is concluded after 10-20 days and local resettlements still occur during the whole breeding season. Female arrival follows a similar pattern, however, with an average delay of 3-10 days compared to male arrival. Depending on the weather conditions, the arrival of Whinchats can occur in intensive phases (Glutz von Blotzheim 1988). In 2018, the arrival of Whinchats in the study area peaked in the second week of May (Fig. 4).

Immediately after arriving from their wintering grounds, males start to establish and defend large territories that shrink in size when conspecifics arrive and establish their territories (Glutz von Blotzheim 1988). Whinchats seem to prefer settling down close to already established territories, which can lead to an aggregated distribution pattern with high settlement densities under optimal conditions (Glutz von Blotzheim 1988, Border et al. 2017a). In the Lower Engadine, populations with high densities can be found in Scuol (Pedras, 70 occupied territories in 2018) and Tschlin (Pra Grond, 71 occupied territories in 2018), where about half of the territories covered an area of one ha or less in 2018 (Swiss Ornithological Institute, unpublished data). In 2018, the male settlement in the study area peaked in the end of May (Fig. 4).

Compared to first-year breeders, adult Whinchats show a higher tendency to return to their previous breeding territories (Schmidt & Hantge 1954, Bastian 1992, Bezzel & Stiel 1997, Müller et al. 2005, Border et al. 2017a). Whinchat males which bred successfully the previous year often occupy the same territory in the next year, whereas unsuccessful breeders apparently tend to emigrate towards other sites in the breeding area (Müller et al. 2005, Shitikov et al. 2015). The familiarity with a territory from a previous year, and particularly with food resources in this territory, is likely to give site-faithful males an advantage over intruding males (Greenwood 1980, 1982, Sedgwick 2004). In this sense, dominant males tend to establish territories with a higher diversity of arthropods during breeding season (Bastian et al. 1994). Site fidelity can directly influence the survival of individuals as well as population dynamics and demography (Hoover 2007).

Male Whinchats immediately start their courtship behaviour as soon as a female Whinchat arrives in a territory (Glutz von Blotzheim 1988). Thus, pair-bonding is concluded rather quickly and, with pairs of the previous year, often within the same day. Nesting site selection, as a subset of habitat selection, is only done by the female (Jones 2001). When selecting the nesting site and collecting nesting material, the female is constantly followed by the singing male (Frankevoort & Hubatsch 1966). The Whinchat nest has a diameter of 12-16 cm and is

built only by the female within 2-3 days (Glutz von Blotzheim 1988). The average clutch size is 5-7 eggs with an average incubation time of 11-14 days (Glutz von Blotzheim 1988, Müller et al. 2005, Grüebler et al. 2008). Fledglings leave their nests within 11-15 days. However, they stay within close range of the nest until they are completely fledged at the age of 17-19 days (Glutz von Blotzheim 1988).

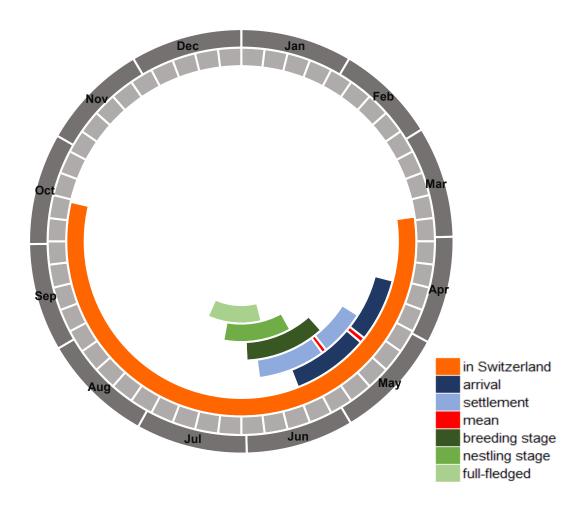


Fig. 4: Breeding phenology of the Whinchat in the Lower Engadine in 2018. The dark grey bars represent the months and the light grey bars the weeks for 2018. The presence of the Whinchat in Switzerland (orange bar) is based on Maumary et al. (2007). The data for arrival, settlement and full-fledged chicks were collected in the study area between the beginning of April until the end of July 2018. Data for the nest building period, egg laying and incubation period (combined as breeding stage) as well as the period between of hatching until chicks are full-fledged (nestling stage) were calculated based on information of Glutz von Blotzheim (1988).

In Switzerland, the Whinchat has disappeared almost entirely from the low- and midland, except for a few isolated populations (Fig. 5, Knaus et al. 2018). Thus, it primarily inhabits subalpine grasslands, managed at a low-intensity level (Horch & Spaar 2015).

Fig. 5: Distribution of the Whinchat in Switzerland 2013-2016. The values between 0 and 1 (white to dark red) indicate the species' probability of occurrence in relation to a wide set of environmental characteristics as well as accounting for spatial autocorrelation and detection probability (Knaus et al., 2018).

In Switzerland, the Whinchat population has been declining rapidly since the 1930s, a trend that continues in the past years (Fig. 6-7) (Horch & Spaar 2015, Knaus et al. 2018). According to most recent data, the population of the Whinchat in Switzerland is down to 7000-9000 breeding pairs (Knaus et al. 2018). The Whinchat has also disappeared from the lowlands of Switzerland's neighbouring countries and experienced massive declines in in the last decades (e.g. Austria: Uhl et al. 2017, France: Broyer et al. 2015, Germany: Siems-Wedhorn 2017). Its conservation status is cause for concern in many European countries and which is why it is listed as *vulnerable* (VU) on the Swiss Red List of threatened breeding birds, a list that follow the guidelines of the International Union for Conservation of Nature (IUCN) (Tucker and Heath 1994, Keller et al. 2010, Horch & Spaar 2015).



Fig. 6: Distribution of the Whinchat in Switzerland according to the four breeding atlases for Switzerland (1950–1959, 1972–1976, 1993–1996, 2013–2016) (Knaus et al. 2018).

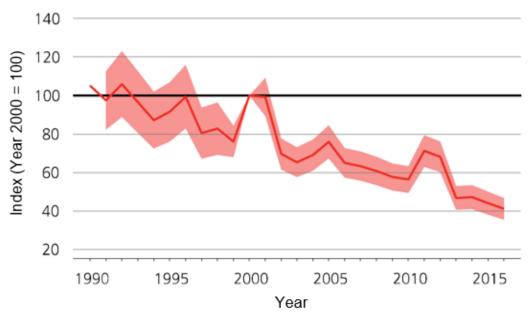


Fig. 7: Population trend of the Whinchat in Switzerland between 1990-2017. 2000 is the reference year with a set index of 100 (Knaus et al. 2018).

At the end of the 20th century, the Whinchat was still widely distributed in the Lower Engadine and there is evidence for a source-sink dynamic within the valley (Müller et al. 2005). Whinchat numbers and densities, however, have generally been decreasing since 2000 (Müller et al. 2005, Horch & Spaar 2015). Currently, a few large populations still exist, including one of the few Whinchat populations in Switzerland (Pra Grond in Tschlin) that has increased in number over the last years (Horch & Spaar 2015). Since 2008, more than 50% of these 130-ha sized low-intensity meadows of Pra Grond have been cut late (mostly after the 15th of July) due to agricultural subsidies to support biodiversity with first contracts signed in 2004. As a result, the local Whinchat population has increased from 43 occupied territories in 2003 to 71 occupied territories in 2018 (Horch & Spaar 2015, Swiss Ornithological Institute, unpublished data).

2.3. Experimental design

In order to provide evidence for conspecific attraction within territorial birds, it is essential to control experimentally for the effects of important resources on spacing behaviour (Stamps 1988). Therefore, an experimental design that controls for these factors is needed. To investigate whether conspecific attraction can influence the Whinchat's settlement behaviour, a controlled playback experiment was conducted in grassland meadows of three different habitat qualities and along a distance gradient to selected Whinchat populations of the Lower Engadine.

The experimental study was carried out in an area of about 70 km² and an elevation of 1039-2278 m a.s.l. (mean: 1540 m a.s.l.) on 79 circular plots with a radius of 150 m and a corresponding area of seven ha aiming to provide enough area for several Whinchat territories. The home range of Whinchats in the Lower Engadine has a mean size of 2.5 ha (±1.3 ha)

whereas breeding territories can cover one ha or less in areas with high population densities (Grüebler et al. 2015a, Swiss Ornithological Institute, unpublished data). The experimental plots were established based on local Whinchat monitoring data and with the objective to have a well-balanced experimental design among the different groups. Therefore, all available information (extensive monitoring data and local expertise of Mathis Müller, Swiss Ornithological Institute) was used with the aim of selecting plots unoccupied by Whinchats. However, it was not always certain whether Whinchats had been present on these plots in the preceding years.

The experiment was conducted between the 15th of April and the 27th of July 2018. Repeated observations on the experimental plots with more than 20 visits on average (range: 12-33 visits per plot, n total = 1717 visits) were made throughout the entire period. Each plot was observed for 20 minutes per visit to determine the occurrence of Whinchats, from the presence of an individual up to successful breeding pairs with fledglings. In average, the observation interval of each experimental plot was 3 days. All plots lacking Whinchat presence or settlement were excluded from further observations by mid-June. Plots in higher elevations were at least observed until the beginning of July. Starting in mid-June with the first observations of fledglings, the main task consisted of locating the nests in low and medium habitat quality plots. Confirmed nests were marked with two bamboo sticks and landowners or farmers were informed to ensure that these nests were not mown.

All fieldwork was documented on a tablet with the fieldwork-friendly program QField (QGIS Development Team, 2018; http://www.qfield.org/) and all Whinchat observations and nest locations were recorded with separate GPS coordinates. The details of each observation were specified as well as sex, age and behaviour of all observed individuals. Weather data, presence of other bird species and changes within the plot due to agricultural use (e.g., mowing event) were documented. The data were synchronized in QGIS after collecting in the field (QGIS Development Team, 2018) and transferred to datasheets in Microsoft Excel 2013.

2.3.1. Playback

Half of the experimental plots (n = 39) were equipped with playback stations, broadcasting local Whinchat songs (experimentally provided vocalizations), whereas the other half (n = 40) was used as control group. To test if broadcasting a sound with playback stations is affecting the breeding habitat selection of the Whinchat, half of the control group (n = 19) were operated with vocalizations of the Mistle Thrush (*Turdus viscivorus*) as noise control (Grendelmeier et al. 2017). These vocalizations were used because this species commonly occurred in the whole study area and therefore naturally integrated into the existing system. The MP3 sound files were downloaded from http://www.xeno-canto.org (last accessed on the 10th of April

2018). To test if the playback station itself is affecting the Whinchat, 21 playback station dummies were used as silent control (Grendelmeier et al. 2017).

Based on the guidelines of Ward & Schlossberg (2004) playback stations were built by the technical lab of the Swiss Ornithology Institute. Playback stations were attached to wooden posts at a height of 1.5 m and consisted of a waterproof box with two sound speakers, powered by solar panel (Fig. 8). The inside of the box was equipped with a lithium battery which stored enough energy to run the playback station for several days when weather conditions were miserable. Furthermore, a MP3-player with SD-card slot and a programmable micro controller were integrated to broadcast the playback of conspecific vocalizations at particular times.



Fig. 8: Playback station and silent control. The left picture shows a playback station that broadcasted the experimentally provided vocalizations of the Whinchat. The same stations were also used for the noise control groups. The right picture shows a polystyrene dummy that was used as silent control.

This study mainly focusses on the influence of conspecific attraction on the habitat selection of the Whinchat in the pre-breeding period between the first arrival of the species in the study area in mid-April to the beginning of nest-building in the middle of May (Fig. 4) (Ahlering et al. 2010). This period reflects the main arrival and settlement period of the Whinchat (Glutz von Blotzheim 1988). The pre-breeding period was chosen for two reasons. First, because Whinchats show an asynchronous migration pattern that Whinchats, a key point that favours the use conspecific attraction to attract later-arriving individuals (Glutz von Blotzheim 1988, Ahlering et al. 2010). Second, the presence of conspecifics (older, experienced settlers) in that period of time is assumed to correlate with previous breeding success in this location (Ahlering et al. 2010). Therefore, in species like the Whinchat where breeding-site fidelity of successful breeders seems to be strong, a bird settling close to these individuals should experience the same habitat specific components (Müller et al. 2005, Ahlering et al. 2010, Shitikov et al. 2015). So, the main aim was to attract unexperienced individuals which arrived later with the experimentally provided stimulus of conspecific attraction in the pre-breeding season.

Since the singing activity of male Whinchats drastically drops during the breeding season (Vaytina & Shitikov 2017, personal observation), the playback stations were stopped in the middle of the breeding season when first signs of breeding attempts were observed (e.g. nest building). Doing so, breeding pairs were protected from a potential external stress factor. Indeed, a single playback study indicated a negative effect of conspecific attraction on the preference of nesting sites of the Thorn-tailed Rayadito (*Aphrastura spinicauda*), which tended to avoid nest building at sites with a simulated presence of conspecifics after the settlement phase (Quilodrán et al. 2014).

To mimic natural conditions as closely as possible, locally recorded songs of the Whinchat were used as experimentally provided stimulus (hereafter referred to as playback) (Ahlering et al. 2010). The Whinchat songs used were recorded in the study area (Tschlin – Pra Grond) in May 2017. The recordings of two individuals showing the largest song repertoire and highest quality were selected to adequately equip the playback stations. These two individuals are presumably older males (at least in their second breeding season), since older males tend to have a larger song repertoire compared to first-time breeding Whinchats in their second year (Vaytina & Shitikov 2017). All data files of the two individuals were edited with the program Raven Pro 1.5 (Bioacoustics Research Program 2014). Background and other disturbing noises were filtered out and heterospecific bird vocalizations were muted, since they could have had unintended effects on the target species (Ahlering et al. 2010). Afterwards, the sound files were cut and amplified. In the next step, different files of one individual were merged to create one audio file (.wav format, sampling frequency 44.1 kHz, resolution: 16 bit) of 10 minutes with the program Audacity® (Audacity Team 2018). The same procedure was applied for the noise control (Mistle trush). Finally, the playback stations were equipped with the sound files.

The playback stations were installed from the beginning of April till mid-May, depending on the accessibility due to the snow cover in the study plots. The playback stations were established as the centre of the experimental plots. They were installed close to already existing natural or artificial structures to avoid interference with current agricultural use. The volume of the songs broadcasted by the playback stations was set at natural level. In general, they were audible for max. 120 m, depending on the topology and the landscape or vegetation structure of the experimental plots. The playback stations broadcasted in the morning during five sessions, starting 90 minutes before sunrise. Each session consisted of 50 minutes broadcasting and a 10-minute break. In the evening, the playback stations were active during two sessions. The evening sessions, beginning two hours before sundown, consisted of 30 minutes of broadcasting and a 30-minute break. The playback stations were also active at night during four sessions since Whinchats are nocturnal migrants (Glutz von Blotzheim 1988). Each night session comprised 10 minutes of broadcasting and a pause of 50 minutes.

The playback stations were removed in the beginning of June at plots without Whinchat settlement. At plots with settlement of Whinchats, playback stations were removed with the first signs of a breeding attempt between the beginning and middle of June at lower elevations. The playback stations in higher elevations remained active until mid-July at the latest.

2.3.2. Artificial perches

The experimental setup was additionally used to test whether an increased availability of artificial perches and/or the combination of conspecific attraction and an increased availability of artificial perches can influence the breeding habitat selection of the Whinchat. Therefore, selected experimental plots (n = 15) were equipped with 20 bamboo sticks with a length of 120 cm and a diameter of 1 cm. The sticks were placed around the playback station with a distance of at least 20 m, and along structures or borders of different agricultural parcels, to avoid a potential interference with the current agricultural use. These artificial perches were placed with a minimum distance of 20 m among each other, where no natural or other artificial perches were present. Consequently, the density of perches at the plots ranged from 10 to 20 perches per ha. Since the importance of this conservation measure decreases during the breeding season, artificial perches were installed before the Whinchat's arrival in early April (Siering & Feulner 2017).

2.3.3. Habitat quality

The experiments were conducted in meadows divided into three levels of habitat quality (Tab. 1). The level of botanical diversity of the plots was used to group the experimental plots (low, intermediate and high botanical diversity). To this, an identification key developed for a biodiversity-friendly agri-environmental scheme was used (Jenny et al. 2011). Low botanical diversity was defined as a lush vegetation, dominated by grass-like plants (mostly due to sown seed mixes). Among flowers present in plots of low botanical diversity, only indicator species for high nutritious soils were found (e.g. Anthriscus sylvestris, Taraxacum officinale). Plots of this category were predominantly intensively cultivated, sown meadows with a multi-cut regime markedly influenced by intensive fertilization and/or irrigation. Plots with intermediate botanical diversity were intensively managed, seminatural meadows with low flower density. Species indicating high nutritious soils, but also species indicating more extensive grassland management were to be found there (e.g. Centaurea scabiosa, Salvia pratensis [~1 specimen/m²]). Plots with high botanical diversity were traditionally managed, seminatural meadows with high flower density dominated by species indicating more extensive grassland management (e.g. Centaurea scabiosa, Salvia pratensis [>1 specimen/m²]) (Britschgi et al. 2006; Jenny et al. 2011). The experimental plots were characterized twice in terms of their botanical quality and intensification level between the beginning of May and mid-June. on the basis of signs of fertilization and irrigation. Furthermore, already existing natural and artificial

perches were documented and, depending on the number of perches found there, each experimental plot was consequently assigned to one of three different categories (none, few and abundant).

Tab. 1: Distribution of the experimental groups. Number of plots of each habitat quality, type of experimental treatment (playback/no playback) and category of artificial perch availability are listed below.

habitat quality	playback	no playback	perches	no perches
high quality	12	11	2	21
intermediate quality	17	17	12	22
low quality	10	12	2	20

2.4. Spatial factors

The distance to existing large populations (hereafter referred to as *core areas*) was defined as the distance between the plot centre and the border of the nearest core area in the Lower Engadine (hereafter referred to as *distance*). The populations of Ardez Murtera, Ftan Furmièrs, Scuol Pedras / Sent Tuffarolas and Tschlin Pra Grond were defined as core areas (Tab. 2, Fig. 3). The distance from each plot to the border of the nearest core area ranged from 0 to 5.3 km (mean: 2.5 km, n = 79). Moreover, connectivity indices for each plot were calculated following Hanski et al. (1994). These indices took in account the distance to each of the four core areas and their number of occupied territories. Since distance and connectivity indices showed very similar results, distance was used for the sake of simplicity. This factor is also easier to quantify and more useful in a practical conservation framework.

Tab. 2: Selected core areas of the Lower Engadine. Location, core areas, the size of each core area and the occupied territories (number of territories occupied by male Whinchats) are shown below.

Location	core areas	size [ha]	occupied territories (2018)
Ardez	Murtera	55	37
Ftan	Furmièrs	45	36
Scuol/Sent	Pedras/Tuffarolas	180	116
Tschlin	Pra Grond	83	71

2.5. Statistical analysis

To document the settlement process and the subsequent breeding events, several binary response variables were defined at the level of the experimental plots. *Presence* was defined as at least one Whinchat observation on a given experimental plot. *Settlement* was defined as at least three Whinchat sightings within 10 days on an experimental plot as well as signs ofterritorial behaviour (singing male or conspecific aggressions). *Pair-bonding*, which includes the settlement decision and the mating choice for female Whinchats, was defined as the sighting of at least one Whinchat pair within the boundaries of a plot at least twice within 10 days as well as signs of courting behaviour. *Breeding attempts* were defined as signs of a brood (eggs, fledglings, feeding adults, active or used nest) of at least one Whinchat pair within

plot boundaries. *Successful breeding* was defined as at least one sighting of a Whinchat fledgling in a given experimental plot. An additional response variable for presence (hereafter referred to as *presence [prop]*) was defined as the ratio between the number of visits on an experimental plot with presence of Whinchats and the total number of visits for this experimental plot. With this response variable it was possible to cope with single visits of individuals that probably used the study area only as stopover during migration. The response variables for presence, settlement, pair-bonding and successful breeding had a binary character (0 = negative event, 1 = positive event), whereas presence [prop] was expressed as a proportion, thus with a range from 0 to 1.

The characterization of all explanatory variables was made in the next step. The playback and the increased availability of artificial perches were separately coded as explanatory variables with a binary character (playback/no playback, perches/no perches). Habitat quality was expressed as a categorical variable with three levels of botanical quality (low, intermediate and high quality). The distance to the nearest Whinchat core areas was expressed in km and as a continuous variable. Before commencing the statistical analysis, all explanatory variables were checked for collinearity. Therefore, a heterogenous correlation matrix consisting of Pearson product-moment correlations between numeric variables, polyserial correlations between numeric and ordinal variables, and polychoric correlations between ordinal variables was used (R Documentation: R Core Team 2018).

The data were analyzed within a generalized linear model framework using Generalized Linear Models (GLM) constructed via maximum likelihood techniques using the package Ime4 (Bates et al. 2015) in the R environment (R Core Team 2018).

All models (except those with presence [prop] as a response variable) were built using a binomial distribution of errors and a logit link function. The models with presence [prop] as a response variable were computed with a quasi-binomial error distribution and a logit link function to account for overdispersion. A model selection procedure was applied starting with a general model including all explanatory variables and their interactions. Non-significant interactions and factors were removed performing a stepwise backward selection to obtain the best fit model for each response variable (hereafter referred to as *final model*). The explanatory variables explicitly tested for in this study, i.e., playback and perches, remained in the final models irrespective of their statistical significance.

To account for temporal aspects of Whinchat's settlement, a model with the Whinchat settlement date for each experimental plot as response variable was built which included all the above-mentioned explanatory variables. The altitude of each plot was added as an explanatory variable. This model was computed using a gaussian error distribution and an identity link function because the response variable analysed followed a normal distribution.

3. Results

During the whole observation period (April-July 2018), 1599 Whinchat observations were made on the experimental plots. Whinchats were present on 55 plots and settled on 36 plots. Pairbonding took place on 27 plots and breeding attempts were made on 24 plots. Successful broods were recorded on 13 plots (Tab. 3). Whinchats mainly settled on the south facing slopes of the study area, whereas northern facing slopes were mostly avoided. In terms of altitude, settlement ranged from approximately 1170 to 2150 m (total range: 1040–2280 m) with a mean of 1526 m. The highest plot with the recording of a successful breeding pair was located at an altitude of approximately 2150 m. In cooperation with the nest protection project of the Swiss Ornithological Institute (Wirth & Horch 2019), 18 nests, which would most likely have been destroyed by mowing events, were protected on 8 individual plots.

Tab. 3: Overview of all response variables. Each response variable corresponds to a different phase of the Whinchat breeding cycle. Number and percentage of positive events are listed below for each phase of the Whinchat breeding cycle and the percentage of positive events of settled Whinchats for subsequent breeding events. Furthermore, the number of positive events for each playback treatment and habitat quality is given.

	number of plots with positive events		plots with positive events (only with positive settlement)	Playback (n = 39)	no Playback (n = 40)	high habitat quality (n = 23)	intermediate habitat quality (n = 34)	low habitat quality (n = 22)
	n	%	%	n	n	n	n	n
presence	55	69.6	-	27	28	16	26	13
settlement	36	45.6	-	20	16	13	18	5
pair-bonding	27	34.2	75.0	13	14	10	14	3
breeding attempt	24	30.4	66.7	11	13	9	13	2
successful breeding	13	16.5	36.1	5	8	7	5	1

In total, 46 pairs were found on the experimental plots and 40 nests were detected with a minimum breeding outcome of 78 fledglings. Marked nests (n = 28), which were protected from mowing had a breeding outcome of 68 fledglings (Tab. 4).

Tab. 4: Number of pairs, total number of nests, number of saved nests, minimum number of fledglings and minimum number of fledglings of saved nests are listed for each playback treatment and habitat quality.

	Playback (n = 39)	no Playback (n = 40)	high habitat quality (n = 23)	intermediate habitat quality (n = 34)	low habitat quality (n = 22)
	n	n	n	n	n
number of pairs	21	25	18	25	3
total number of nests	17	23	17	22	1
number saved nests	9	9	5	13	0
min. number of fledglings	33	51	35	46	3
min. number of fledglings (saved nests)	11	14	4	21	0

When testing for collinearity among all explementary variables, the correlation coefficients were below 0.2, except for the correlation between the level of botanical diversity and the altitude of the experimental plots (polyserial correlation: -0.65). The variable with the most relevant biological meaning, in this case diversity, was retained for the subsequent analysis (Green 1979).

3.1. Playback

The playback did not affect the response of the Whinchat in selected stages during the breeding cycle (Tab. 6). The predicted probabilities for all response variables during the Whinchat breeding cycle did not differ significantly between the two treatments (Fig. 9). Consequently, the experimentally broadcasted songs did not influence the presence, settlement and pair-bonding of the Whinchat.

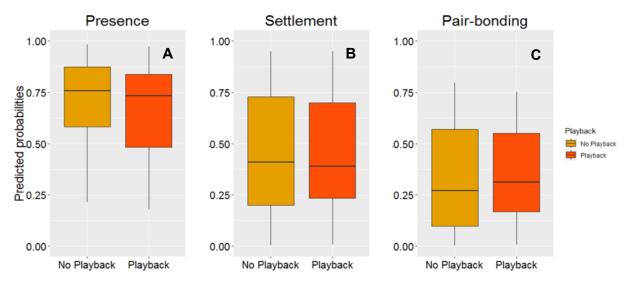


Fig. 9: Response of the Whinchat to the playback for different stages during the breeding cycle (presence (A), settlement (B) and pair-bonding (C)). The different treatments are plotted on the x-axis and the y-axis provides the predicted probabilities for each stage and treatment. The thick line within the box represents the median (Q2) and the box represents the inter-quartile range (50% of the data) from the lower quartile (Q1) to the upper quartile (Q3) for each breeding stage. The lower and upper whiskers represent the values outside the 50% inter-quartile range.

3.2. Artificial perches

No statistically significant effects were detected for the increased availability of artificial perches on the response of Whinchats in either of the stages of its breeding phenology (Tab. 6). This result remained the same even when taking into account the already existing natural and artificial structures for each plot.

The interaction of playback and the availability of artificial perches showed a statistically significant effect on the settlement of the Whinchat (Fig. 10, Tab. 6). The predicted probabilities for Whinchat's settlement did not differ between the treatment (playback) on plots without an increased availability of artificial perches. Therefore, the interaction of the playback and the increased availability of artificial perches apparently influenced the settlement of the Whinchat leading to a higher probability of settlement on plots with playback vocalizations and an increased availability of artificial perches. However, the sample size for each group in this experiment was unbalanced and did not cover the whole range of the experimental design for the factor distance, which results in a lower range and mean of distance for the two groups with an increased availability of perches compared to the groups without an increased

availability of perches (Tab. 5). Furthermore, the plot groups with an increased availability of artificial perches were unbalanced as well in terms of their habitat quality.

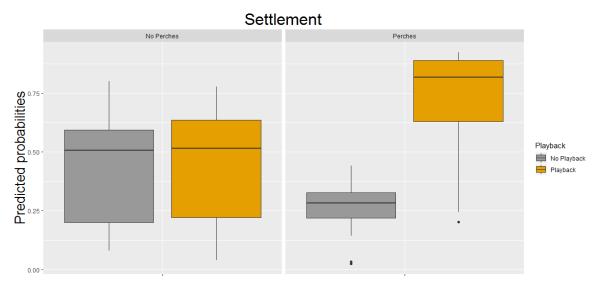


Fig 10: Response of the Whinchat to the playback in combination with the availability of artificial perches for the settlement of Whinchats. The left box represents the results for the playback treatment (playback and no playback) without an increased availability of artificial perches, whereas the right box represents the results for the playback treatments with an increased availability of artificial perches. The different treatments are plotted on the x-axis and the y-axis provides the predicted probabilities for each stage and treatment. The thick line within the box represents the median (Q2) and the box represents the inter-quartile range (50% of the data) from the lower quartile (Q1) to the upper quartile (Q3) for each breeding stage. The lower and upper whiskers represent the values outside the 50% inter-quartile range.

Tab 5: Results for the interaction of the playback and the increased availability of artificial perches. Total number of plots, number of settled and un-settled plots as well as mean distance and distance range are listed above. Further, the number of plots for each combination of the explanatory variables and the three habitat qualities (low, intermediate and high) are given.

explanatory variables	total (n)	settlement (n)	no settlement (n)	mean distance [km]	distance (range) [km]	low habitat quality	intermediate habitat quality	high habitat quality
perches x playback	8	7	1	1.12	0.00 - 2.44	1	6	1
perches x no playback	8	2	6	1.60	0.28 - 3.81	1	6	1
no perches x playback	31	13	18	2.03	0.67 - 4.94	9	11	11
no perches x no playback	32	14	18	1.99	0.00 - 5.23	11	11	10

3.3. Habitat quality

The models detected a significant effect of the habitat quality on the response variables (Tab. 6). Low habitat quality showed a negative effect on the probability of presence, settlement and pair-bonding of the Whinchat, whereas high habitat quality has a significant positive effect on the presence and settlement of Whinchats (Fig. 11-13). Intermediate habitat quality showed no significant effect for all selected stages. Hence, Whinchats preferred plots with intermediate or high habitat quality during all selected stages of Whinchat's breeding habitat selection.

3.4. Spatial factors

The distance to the nearest core area was strongly and statistically significantly related to the studied response variables (Tab. 6), showing a negative relationship with the presence, settlement and pair-bonding of the Whinchat. Consequently, the negative value of the estimate

indicated that the probability for a positive event (e.g. settlement) decreased with distance (Fig. 11-13).

Tab. 6: Output of the final logistic regression models testing for factors influencing the presence, settlement, pair-bonding and the date of settlement of Whinchats. Estimates of fixed factors, standard errors, t-values and p-values are given. Significant terms are shown in bold.

response variable	explanatory variable	estimate	std. error	t-value	p-value
presence	intercept	2.814	1.153	2.439	0.015
•	playback	0.079	0.555	0.142	0.887
	perches	1.832	1.108	1.654	0.098
	distance	-1.088	0.483	-2.253	0.024
	intermediate quality	-1.485	1.378	-1.078	0.281
	low quality	-3.368	1.399	-2.408	0.016
	distance x intermediate quality	0.797	0.564	1.395	0.163
	distance x low quality	1.503	0.605	2.485	0.013
presence	intercept	-3.389	0.227	-14.928	0.001
[prop]	playback	0.232	0.193	1.203	0.233
	perches	-0.029	0.227	0.127	0.899
	distance	-0.727	0.190	-3.817	0.001
	intermediate quality	-0.637	0.334	-1.907	0.061
	low quality	-1.732	0.536	-3.234	0.002
	distance x intermediate quality	0.462	0.227	2.038	0.045
	distance x low quality	0.609	0.289	2.110	0.038
settlement	intercept	1.910	0.759	2.517	0.012
	playback	-0.052	0.605	-0.086	0.931
	perches	-1.453	1.052	-1.381	0.167
	distance	-0.915	0.227	-3.299	0.001
	intermediate quality	-0.118	0.658	-0.181	0.857
	low quality	-1.728	0.750	-2.304	0.021
	Playback x perches	3.179	1.575	2.017	0.044
pair-bonding	intercept	1.332	0.703	1.895	0.058
	playback	-0.152	0.550	-0.277	0.782
	perches	-0.075	0.703	0.106	0.916
	distance	-0.940	0.297	-3.171	0.002
	intermediate quality	-0.132	0.643	-0.205	0.838
	low quality	-1.641	0.804	-2.042	0.041
date of	intercept	111.927	11.245	9.953	0.001
settlement	playback	5.922	3.548	1669	0.105
	perches	-7.143	2.995	-2.385	0.023
	height	0.016	0.007	2.437	0.020

Whinchats tended to avoid plots with low habitat quality and preferably occurred on plots with high habitat quality. The distance to the nearest core area was negatively related with presence, resulting in higher probabilities of presence close to core areas. In this model, a positive effect of the interaction between the distance to the nearest core area and the habitat quality was detected. However, this weak effect was overridden by the univariate effect of distance (Fig. 11).

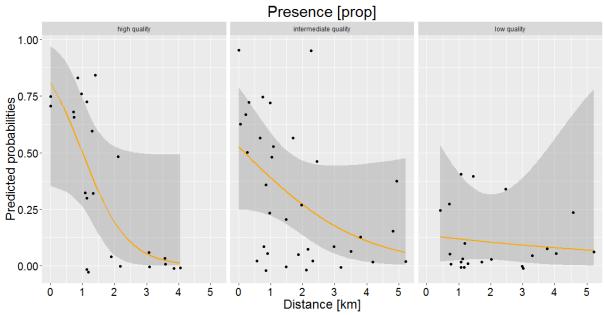


Fig. 11: Predicted probabilities (orange lines) of a logistic regression model for the presence [prop] of Whinchats at three levels of habitat quality in relation to the distance to the nearest core area. The distance is plotted on the x-axis and the y-axis provides the predicted probabilities for each habitat quality. The shaded areas represent the 95% confidence intervals. The points show the raw proportional data of presence in relation to the distance to the nearest core area for all experimental plots.

Both habitat quality and distance to the nearest core area explained Whinchat's settlement pattern. Whinchats tended to avoid settling in plots with low habitat quality and prefered colonising plots of intermediate and high habitat quality. The preference of Whinchat's settlement did not differ among plots with intermediate and high habitat quality. Probability of settlement and distance to the nearest core area were strongly and negatively related, resulting in higher probabilities of settlement close to core areas. Settlement at a distance closer than 2 km to the next core area resulted in a probability of settlement higher than 0.5 for high and intermediate habitat plots. Finally, the model detected a statistically significant and positive effect of the interaction between playback and increased availability of artificial perches.

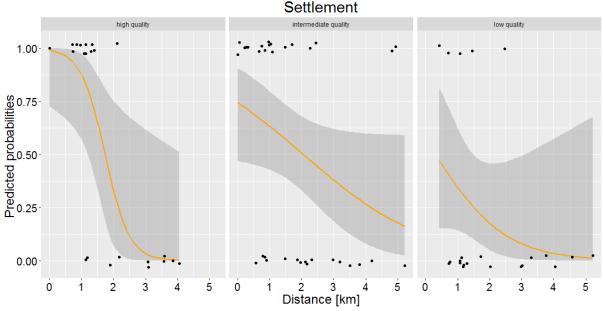


Fig. 12: Predicted probabilities (orange lines) of a logistic regression model for the settlement of Whinchats at three levels of habitat quality in relation to the distance to the nearest core area. The distance is plotted on the x-axis and the y-axis provides the predicted probabilities for each habitat quality. The shaded areas represent the 95% confidence intervals. The points show the raw proportional data of settlement in relation to the distance to the nearest core area for all experimental plots.

The model outputs show that pair-bonding of Whinchats was less likely to occur in plots with low habitat quality. The distance to the nearest core area, again, was negatively related to the probability of pair-bonding, resulting in higher probabilities of pair-bonding close to core areas (Fig. 13).

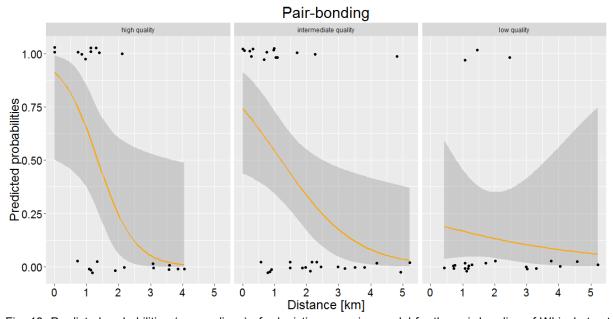


Fig. 13: Predicted probabilities (orange lines) of a logistic regression model for the pair-bonding of Whinchats at three levels of habitat quality in relation to the distance to the nearest core area. The distance is plotted on the x-axis; the y-axis provides the predicted probabilities for each habitat quality. The shaded areas represent the 95% confidence intervals. The points show the raw proportional data of pair-bonding in relation to the distance to the nearest core area for all experimental plots.

3.4. Temporal aspect

Fig. 14 (A) indicates the difference in the date of settlement between the two experimental groups. The date of settlement, however, did not differ significantly between the treatments (Tab. 6). Thus, the playback had no influence on the date of settlement of the Whinchat. (B) The altitude of each experimental plot affected the timing of Whinchat's settlement significantly. The predicted date of settlement increased with altitude (approx. three days per 200 m).

Furthermore, the corresponding model detected a statistically significant and negative effect of the increased availability of artificial perches on the date of settlement, implying that plots with an increased availability of artificial perches were settled earlier compared to the control group.

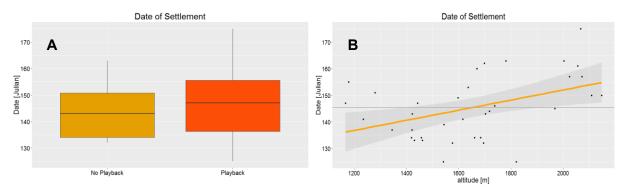


Fig. 14: Temporal influence on the date of settlement of Whinchats. A: Influence of the playback on the date of settlement of the Whinchat. Different treatments are plotted on the x-axis and the y-axis provides the Julian date (range: $125 = 5^{th}$ of May $2018 - 175 = 24^{th}$ of June 2018) for each treatment and plot. The thick line separating the box represents the median (Q2) and the box represents the inter-quartile range (50% of the data) from the lower quartile (Q1) to the upper quartile (Q3) for each breeding stage. The lower and upper whiskers represent the scores outside of the middle 50%. B: The orange line shows the relationship between altitude and the date of settlement of Whinchats. The altitudinal range is plotted on the x-axis; the y-axis provides the Julian date. The orange line represents the predicted probability for the date of settlement for each altitude and the shaded areas show the 95% confidence intervals. The grey line represents the mean date of settlement (145.3 = 25^{th} of May 2018) and the points show the raw settlement data points in relation to the altitude of each experimental plot.

4. Discussion

In this study, the breeding habitat selection of Whinchats was experimentally investigated. It was explicitly tested whether this decision-making process can be influenced by exploiting the mechanism of conspecific attraction. Furthermore, the impact of an increased availability of artificial perches on the habitat quality of potential Whinchat breeding habitat was tested. The experiment revealed that the playback and the increased availability of perches did not affect the breeding habitat selection of the Whinchat.

Nevertheless, this study shows that habitat and spatial factors can explain the settlement pattern of the Whinchats in the study area. In particular, it shows that (1) the habitat quality of meadows affects the settlement of Whinchats in the study area and (2) the settlement pattern of Whinchats in the study area is strongly related to the distance to the nearest core area.

Furthermore, the results indicate that the timing of Whinchats' settlement is not so much influenced by the playback but by the altitude of the experimental plots.

The results obtained from this study provide essential information for species conservation and future management not only for Whinchats in the study area but also for Whinchat populations showing similar a decline in numbers.

4.1. Playback

Although Whinchat's characteristics fulfil many requirements for potential conspecific attraction (e.g. asynchronous migration, aggregated distribution patterns, higher ratio of juveniles in the population and a short breeding season), the experimentally provided conspecific vocalizations did not influence the breeding habitat selection of the Whinchat (Glutz von Blotzheim 1988, Müller et al. 2005, Ahlering et al. 2010, Border et al. 2017b). In contrast to the expected outcomes of this study, Whinchats were neither attracted nor deterred by the experimentally provided conspecific vocalizations in any of the selected stages during their breeding cycle.

There are three plausible, mutually non-exclusive explanations for the absence of the effect of the playback in this study:

First, the experimentally provided conspecific song by the playback stations may not have sufficiently reflected the natural conditions of Whinchat males in their breeding habitat although attempts were made to mimic natural conditions as closely as possible (Ahlering et al. 2010). When defending their territories, Whinchat males sing alternatingly from different perches within their territory borders and further interactions among singing Whinchat males, such as immediate song imitations and counter singing, or persecutions and display behaviour during flight are common (Glutz von Blotzheim 1988). In this study, many Whinchat males showed a behavioural response to the experimentally provided conspecific vocalizations. They started

intensive counter singing with the playback station while continuously reducing the distance until they sang perched on top of the playback station. This behaviour was mainly observed in the settlement phase and male Whinchats habituated rather quickly. Since only one permanently installed playback station in the middle of the plot was used in the experimental setup, natural conditions might not have been replicated properly.

Second, the experimentally provided conspecific vocalizations may not have provided the appropriate conspecific attraction cue for the Whinchat. For habitat selection, birds mainly use two conspecific attraction cues which could potentially be used to attract birds towards a selected site: (1) the presence and density of conspecifics and (2) conspecific vocalizations (Reed & Dobson 1993, Schlossberg & Ward 2004). Even though local Whinchat vocalizations from males with a large repertoire were used as conspecific vocalization, their properties (e.g. amplitude, frequency, timing, song type) could have been insufficient to affect Whinchat's decision to settle (Ahlering et al. 2010). Whinchat males preferably sing from high perches where they are highly visible. Since the experiment lacked decoys, the importance of optical cues for the breeding habitat selection of the Whinchat was possibly misjudged.

Third, the experimentally provided conspecific vocalizations in the pre-breeding season may not have represented the right timing for conspecific attraction cues for the Whinchat. Even if pre-breeding cues may be more effective if mating strategies underlie conspecific attraction, little is known about when pre- or post-breeding season cues are more likely to be used by birds (Ahlering et al. 2010, Chalfoun & Schmidt 2012). Considering Whinchat's biology, broadcasting conspecific vocalizations in the post-breeding season would not mimic natural conditions (Vaytina & Shitikov 2017). The placement of juvenile Whinchat decoys on the other hand could be an appropriate optical cue in the post-breeding season. This optical cue could potentially be used to provide biased information about the breeding success (increased number of fledged Whinchats) of a certain area, which could reveal essential information for Whinchats in the post-breeding season. Consequently, this cue may allow Whinchats to draw assumptions about the habitat quality of the area, which could influence their settlement decision the following year. Nevertheless, it is still unknown how and when Whinchats assess the quality of their breeding habitats.

Since Whinchat populations in Switzerland have been declining rapidly, especially in the past decades (Horch & Spaar 2015, Knaus et al. 2018), the Swiss Ornithological Institute has endeavoured to investigate the major threats to which Whinchats are exposed (e.g. Müller et al. 2005, Britschgi et al. 2006, Grüebler et al. 2008, 2012, 2015). Additionally, the implementation of conservation measures and the development of effective conservation tools were promoted to stop further population declines. Therefore, a limited pilot study of Rey & Spaar (2005) has already – though unsuccessfully – used playback as a social cue to influence

the settlement of the Whinchat in the Rhine valley. They assumed that the main reasons for failure were inadequate habitat quality in the pilot study area, a lack of visual dummies and inappropriate vocalizations recorded in other regions than the pilot study area. Furthermore, the next Whinchat population was located at more than 10 km distance.

Previous research has already provided evidence for the use of conspecific attraction as effective conservation tool, covering four major habitat types: forests, grasslands, shrublands and wetlands (for reviews see Ahlering et al. 2010 and Grendelmeier et al. 2017). A large majority of these studies, however, deals with non-passerine wetland species. When focusing on passerines, most studies were carried out with forest species, such as the European Pied Flycatcher (*Ficedula hypoleuca*), the Black-capped Vireo (*Vireo atricapilla*) or the Wood Warbler (*Phylloscopus sibilatrix*) (e.g. Alatalo et al. 1982, Ward & Schlossberg 2004, Grendelmeier et al. 2017, Szymkowiak et al. 2017). Only few studies were carried out with species inhabiting grassland habitats: Therefore, a small review was conducted to compare already published results with the outcomes of this study:

Ahlering et al. (2006) were able to attract Baird's Sparrows (*Ammodramus bairdii*) to previously unoccupied grassland habitats using conspecific vocalisations during the pre-breeding season. The Baird's Sparrow shows nomadic tendencies, and differs therefore significantly from the Whinchat, which has a tendency to return to its previous breeding sites (Glutz von Blotzheim 1988, Green 1992, Ahlering et al. 2006).

Vogel (2011) successfully attracted Henslow's Sparrows (*Centronyx henslowii*) to previously unoccupied habitats using conspecific song playback. Henslow's Sparrows inhabit dynamic grassland habitats, which may experience disturbances (e.g. late summer burn) that could transform suitable into unsuitable breeding habitats, and show low site fidelity (Dornak 2010). The temporal limitation of their breeding habitat could be one explanation for this low site fidelity. In contrast to Henslow's Sparrows, adult Whinchats – and successful breeders in particular – show a high tendency to return to previous breeding territories (Schmidt & Hantge 1954, Bastian 1992, Bezzel & Stiel 1997, Müller et al. 2005, Shitikov et al. 2015, Border et al. 2017a).

Virzi et al. (2012) tested the influence of conspecific attraction on the Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*), an endangered resident species of grasslands. They provided evidence that Cape Sable Sparrows use conspecific vocalizations as one cue for their settlement decisions. This is one of few studies showing that a resident bird species – unlike the Whinchat, which is a migratory species – uses conspecific attraction in making settlement decisions.

Andrews et al. (2015) showed that broadcasting conspecific vocalizations did not affect the settlement decision of Grasshopper Sparrows (*Ammodramus savannarum*) in the pre-breeding

phase, but the selection of breeding locations within the breeding season. Therefore, the presence of conspecific vocal cues seems to be an important factor, influencing the habitat selection of Grasshopper Sparrows during the breeding season. The singing activity of male Whinchats drops drastically towards the end of the breeding season, and during the breeding season mostly unpaired males sing (Vaytina & Shitikov 2017, personal observation). Therefore, it could be expected that conspecific vocalizations during breeding season are not likely to influence the settlement decision of Whinchats.

Harrison et al. (2009) were successful in attracting male Brewer's Sparrows (*Spizella breweri breweri*) towards suitable breeding habitats during peak settlement with broadcasting conspecific song in the pre-breeding phase. Although they were able to attract males that established territories in previously unoccupied experimental plots, the number of formed pairs did not differ compared to the control plots. One plausible explanation for this outcome is that the attracted males did not appeal to the females, so they chose to settle and mate elsewhere.

Nocera et al. (2006) influenced the settlement decision of first-time breeding Bobolinks (*Dolichonyx oryzivorus*), a social and synchronous breeding species, by using conspecific location cues (vocalizations and decoys). Bobolinks did not respond to the pre-breeding cues but heavily reacted to post-breeding cues, irrespective of habitat quality (20 of 22 plots were settled). They further studied a more solitary species, the Nelson's sharp-tailed Sparrow (*Ammodramus nelson*). Conspecific attraction cues did not influence the settlement decision of Nelson's sharp-tailed Sparrows, regardless of the timing.

The outcomes of these studies should be interpreted with caution, as most published literature on conspecific attraction present positive responses to conspecific attraction cues (Ahlering et al. 2010, Chalfoun & Schmidt 2012). Only very few papers indicate a lack of response to conspecific attraction cues, which raises the question whether only few studies actually found a lack of response or if studies with a lack of response are simply less likely to be published in a scientific journal.

Nevertheless, all these results are pointers towards the complexity, variability and individual response of conspecific attraction in birds. Even though the role of conspecific attraction in the settlement decisions of grassland songbird species has been explored, many aspects remain still unknown (Ahlering et al. 2006, Nocera et al. 2006, Ahlering et al. 2010, Vogel 2011).

This study suggests that future research on conspecific attraction of the Whinchat should focus on the type of cues used for conspecific attraction, on the timing of these cues and on reflecting natural conditions as accurately as possible. To comply with the suggestions mentioned, future conspecific attraction experiments in the pre-breeding season should be conducted on experimental plots, equipped with several playback stations at various points. These stations should rotationally broadcast different conspecific vocalizations of a local Whinchat male.

Furthermore, it is suggested that conspecific vocalization cues in the pre-breeding season should be combined with decoys such as Whinchat replications that could present Whinchats optical cues or mirrors that may even provide a simulated Whinchat interaction. For the post-breeding season, it is suggested that combined conspecific attraction cues should consist of juvenile Whinchats decoys as optical cue and the begging calls of juvenile Whinchats as conspecific vocalization. Lastly, if a study provides combined conspecific attraction cues that are present in the pre-breeding and post-breeding season, it could generate important knowledge about the right timing of the conspecific attraction cues for the Whinchat and about when they assess the quality of their breeding habitats.

4.2. Artificial perches

The experimentally increased availability of artificial perches did not influence the breeding habitat selection of Whinchats in the study area. These results are in contrast to the expected results and conservation measures that were applied before to improve potential breeding habitat for the Whinchat (e.g. Siering & Feulner 2017). However, the interaction of the playback and the increased availability of artificial perches showed a positive influence on the settlement decision of Whinchats. Furthermore, it seems as if the increased availability of artificial perches accelerates Whinchat settlement.

One possible explanation for the present lack of influence of an increased availability of artificial perches on the breeding habitat selection of the Whinchat may deal with the habitat characteristics in the study area in terms of the structural diversity. Siering & Feulner (2017) carried out their study in an agricultural fallow farmland of 30 ha, where natural perches are missing when Winchats arrive in their breeding grounds. In contrast, the vast majority of experimental plots in the study area were endowed with natural and artificial perches. In total, 34 experimental plots showed a high density and diversity of natural and artificial perches.

The result of the apparent positive influence of the interaction of the playback and the increased availability of artificial perches on the settlement decision of Whinchats needs to be interpreted with caution for three reasons. First, the sample size of the experiment and the different treatment groups is very small. Particularly, the two groups with an increased availability of perches had a low sample size (perches x playback: n = 8, perches x no playback: n = 8). Second, this small sample size did not cover the whole range of the experimental design for the factor distance. Especially, the group of perches x playback shows a lower mean and range of distance (range: 0–2.44 km, mean: 1.12 km) compared to the remaining groups. Third, the experimental groups were unbalanced in terms of the habitat quality. While the number of plots for each habitat quality is well-balanced for the two groups without an increased availability of artificial perches, both groups with an increased availability

of artificial perches only contained one plot with low habitat quality each. The findings could, therefore, be seen as a result of a statistical artefact. Furthermore, results showed that neither the playback, the increased availability of artificial perches nor the interaction of both factors affect any other selected stage of Whinchat breeding phenology.

The fact that an increased availability of artificial perches has an influence on the date of settlement of whinchats should also be interpreted with caution. The experimental plots with or without an increased availability of artificial perches show an unbalanced sample size (perches n = 8, no perches n = 32) as well as the different range and mean of height (perches: range = 1,280–1,821 m, mean = 1,522 m, no perches: range = 1,167–2,147 m, mean = 1,693 m, Wilcoxon rank-sum test: p-value = 0.086). Therefore, the results of this analysis have to be treated with caution because they could represent a statistical artefact.

Overall, the results of the test, as to whether an increased availability of perches improves Whinchat habitat quality, should be considered rather critically due to the intensity of the stimulus. Only a limited number of artificial perches (density: 10-20 artificial perches/ha) were set along structures or borders of different agricultural parcels to avoid interference with the current agricultural use. Since optimal hunting areas have a perch density of about 25 perches/100 m² (Oppermann 1992), the intensity of the stimulus (0.1–0.2 perches/100 m²) was rather weak. In comparison, the experimental plots of Siering & Feulner (2017) yielded a density of 40-50 perches per ha. The artificial perches were set in clusters and not homogenously distributed over the experimental plots. The resulting density ranged from 100 to 400 perches per 100 m² (25-50 perches/cluster, cluster diameter: 8-15 m). Oppermann (1999) showed that Whinchats in the north-western part of Germany preferred occupying habitats with a high density of available natural and artificial perches (50-100 perches/100m²). Even though this study only focused on existing natural and artificial perches and did not equip habitats with artificial perches, results are still comparable with this study and point out relationships between the availability of vertical structures and the habitat quality for Whinchats.

The implementation of artificial perches as a conservation measure is very labour-intensive due to the annual installation of artificial perches in spring and their removal in autumn. Therefore, it is not feasible on periodically mown meadows. In this study, where current grassland management was still pursued, most artificial perches were destroyed by the first mowing event on the plots.

Even though the increased availability of artificial perches did not influence the breeding habitat selection of the Whinchat, settled Whinchats used the experimentally provided artificial perches regularly at almost all plots with an increased availability of artificial perches. Further, it was also observed that Whinchats used the markings of protected nests heavily before

entering them, indicating the importance of a high density and diversity of perches for Whinchats in their breeding areas. Since the sample size was insufficient and not well balanced between the two groups, further research is needed to clarify the efficiency of artificial perches as conservation measure for the Whinchat in the Lower Engadine.

4.3. Habitat quality

This study revealed that the probability of occurrence and settlement for the Whinchat is associated with the habitat quality of meadows. Whinchats were only rarely observed in low quality habitat plots and avoided settling on these plots. As expected, Whinchats prefered settling in experimental plots with intermediate and high quality, indicating that both habitat types are equally attractive as breeding habitat for the Whinchat.

Due to the high correlation between habitat quality and the altitude of the experimental plots, it was further impossible to address the relative importance of both variables for the breeding habitat selection of the Whinchat in the study area (Border et al. 2017b). The three different habitat quality levels were not homogenously distributed in the study area and plots with a high intensification level and subsequently low habitat quality were mainly situated on the valley floor, where meadows are easier to access and cultivate. Plots of intermediate and high habitat quality, on the other hand, were mostly found in higher elevations.

The presence of Whinchats on low quality habitat plots was mostly detected as single events only, indicating that these areas were unsuitable and, therefore, only used as stopover during migration. Low quality habitats were less attractive for Whinchats, an observation which was also made by other studies (e.g. Müller et al. 2005, Border et al. 2017b). Results show that the of grass-like plants dominated and lush vegetation of low habitat quality plots are not suitable as breeding habitats for the Whinchat. These habitats low in number of flowers further lacked vertical structures and showed marked signs of influence by intensive irrigation and fertilization.

Although the percentage of plots with a settlement or pair-bonding of Whinchats is equal for intermediate and high quality habitats, results show dramatic differences in the breeding success among the two types of habitat quality (Fig. 15). When looking at plots with positive settlement events only, Whinchats had breeding success on 54 % on high quality plots with a settlement of Whinchats. In turn, breeding was successful on only 28 % of the intermediate quality plots. The only factor explaining the differences between these two groups is the mowing date. High habitat quality plots were mostly governmentally subsidised as set-asides, where mowing occurs after the 15th of July (Grüebler et al. 2012), whereas intermediate habitat quality plots were mainly mown earlier.

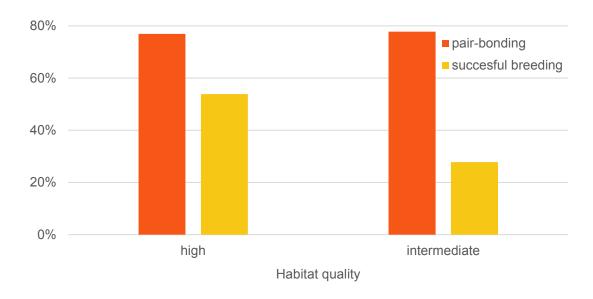


Fig. 15: Breeding success expressed in percentage of plots with a successful breeding Whinchat pair in the study area. The x-axis provides the stages of pair-bonding (orange) and successful breeding (yellow) for two levels of habitat quality and the percentage of plots with a pair-bonding event and a successful breeding Whinchat pair among each habitat quality are plotted on the y-axis. Only plots with a settlement of Whinchats were used for these results.

These results comply with the results of previous research (e.g. Müller et al. 2005, Broyer 2009, Grüebler et al. 2012, Strebel et al. 2015) which demonstrated (1) that Whinchats inhabit breeding habitats of different qualities with higher breeding success in high-quality habitats and (2) that the shift in the mowing phenology and the increased harvest activities are the main reasons for the population declines of the Whinchat.

When returning from their wintering grounds in spring, Whinchats try to set up new territories in breeding habitats that are quality ensuring and allow for a high breeding success (Müller et al. 2005). They make their settlement decision without knowing that sudden human-induced events such as early large-scale mowing events may radically change the habitat later on in the breeding season, transforming suitable habitats into ecological traps. In the phase of settlement, Whinchats seem to be unable to differentiate between traditionally managed, seminatural meadows providing high habitat quality and intensively manged, seminatural meadows, where mowing occurs earlier in the season due to intensification of grassland management. Consequently, these sudden human-induced events have a massive impact on their population trends (Müller et al. 2005, Grüebler et al. 2008). If earlier mowing events and the degradation of suitable habitat (e.g. vegetation structure, botanical diversity) proceed, local source populations are expected to become too small to support viable Whinchat populations in the study area (Müller et al. 2005).

Considering the experimentally controlled levels of habitat quality, the outcomes of this study provides important contributions to the knowledge about the implementation of conservation

measures for the Whinchat in the study area. They show that the probability of settlement is equal among meadows of intermediate and high habitat quality, however, the difference in their management has a dramatic effect on the whinchat. These results are particularly important for the nest protection in the area which should be carried out on meadows of intermediate habitat quality.

Even though the results of this study show a clear relationship between habitat quality and the settlement of Whinchats in the study area, closer examinations are necessary for future research. In this study, habitat quality was only determined based on botanical diversity along with the level of intensification and lacked important factors such as the availability of and change in food resources during the breeding season. Therefore, future research should focus on determining the key habitat characteristics of Whinchat's breeding habitat, including botanical diversity, vegetation structure and the availability of food resources.

4.4. Spatial factors

The outcomes of this study show a distinct spatial pattern of the Whinchats' settlement events, which can principally be explained by the distance to the nearest core areas. The distance to the nearest core areas showed a strong negative relationship with the settlement probability, resulting – as expected – in higher settlement probabilities in close proximity to the core areas. In a nutshell, Whinchats prefer settling in plots which provide a suitable habitat (high or intermediate habitat quality) within approximately 2 km of the nearest core area.

There are several non-mutually exclusive explanations for this spatial pattern:

One possible explanation for this pattern is natal philopatry and breeding-site fidelity. Natal philopatry refers to first-year breeders without breeding experience that return to the area where they were born, whereas breeding-site fidelity refers to individuals with breeding experience that return to the previous year's breeding ground (Greenwood 1980). Considering Whinchats, several studies showed that juvenile Whinchats might return to their natal area too, although their annual returning rates are very low (Schmidt & Hantge 1954, Bezzel & Stiel 1977, Müller et al. 2005, Shitikov et al. 2015). Adult Whinchats show a much higher tendency to return to their previous breeding territories. Successful breeders show particularly high breeding-site fidelity and tend to occupy the same territory the following year, whereas unsuccessful breeders are prone to emigrate from the breeding area (Schmidt & Hantge 1954, Bastian 1992, Bezzel & Stiel 1997, Müller et al. 2005, Border et al. 2017a). Breeding-site fidelity affects both sexes in Whinchats, often resulting in faithfulness to previous year's breeding partner as well. However, new pairings with proximate neighbours generally occur (Schmidt & Hantge 1954).

Even in hand, ageing Whinchats in spring is difficult and only possible with experience (Jenni & Winkler 1994). Hence, the data collected by observations in this study does not allow a clear separation between the two adult age groups (unexperienced first-year breeders and experienced breeders older than 2 years) to assess the age composition of Whinchats within close proximity to the core areas. As a consequence, it was impossible to disentangle the relative importance of both natal philopatry and breeding-site fidelity for the settlement of the Whinchat in the study area.

A second potential reason for the strong spatial pattern may be a result of small-scale habitat characteristics, since Whinchat breeding habitat is not distributed homogeneously within and in close proximity to the existing core areas. The breeding habitat choice of Whinchats is based on a complex combination of habitat characteristics (Müller et al. 2005, Border et al. 2017b). Therefore, there could be differences in small-scale habitat characteristics – not explicitly tested for in this study – between plots within 2 km of the next core area and plots further away. Most of all, they could vary in terms of microclimatic conditions, food availability, food accessibility and the suitability of the food resources as well as the abundance of predators (Border et al. 2017b).

The third possible explanation for this spatial pattern in the study area is the influence of conspecific attraction on the settlement of the Whinchat. Individuals might experience three potential benefits by using conspecific attraction, which can either emerge individually or combined (Stamps 1988, Ahlering et al. 2010). First, individuals can increase their mating success when using conspecific attraction. Whinchat males that settle in territories close to others may attract more females and could further increase the efficiency of the choice of mating partners (Ahlering et al. 2010). Second, individuals may experience a decreased predation risk when settling in aggregated clusters. Third, individuals using conspecific attraction may select habitat of higher quality. Whinchats experience greater breeding success in habitat of high quality and older experienced males tend to occupy the same breeding territory in the next year (Müller et al. 2005, Britschgi et al. 2006, Shitikov et al. 2015). Hence, settling close to these individuals should provide them with the same habitat quality if habitat quality is spatially autocorrelated (Ahlering et al. 2010).

Even though the playback experiment was not successful (probably due to an inappropriate choice of the conspecific attraction cue and/or timing), it is likely that the settlement pattern found is a result of individuals attracted to habitats already occupied by conspecifics. Indeed, Whinchats tend to settle close to already established territories, resulting in an aggregated distribution pattern (Glutz von Blotzheim 1988, Border et al. 2017a). In this sense, core areas with a large number of singing males and a high breeding success could act as an influential

conspecific cue providing crucial information about habitat quality in the study area (Stamps 1988, Ahlering et al. 2010, Szymkowiak et al. 2017).

For the first time, this study explicitly demonstrated that the probability of settlement for the Whinchat was strongly correlated with the distance to the nearest core area and decreased with distance. Therefore, the results provide important information for species conservation, which must be considered for future conservation measures in the study area and beyond. Species conservation management should focus on the protection and improvement of suitable habitats in the core areas and within approximately 2 km distance to the core areas. Therefore, a large-scale adapted grassland management is needed to secure Whinchat populations in the long term. Future research should investigate the age composition of Whinchats in the core areas as well as the ratio of breeding pairs and unpaired males. Therefore, it is necessary to consider previous year's breeding success and the difference in juvenile and adult survival.

5 Conservation implementations

In light of species conservation, the outcomes of this study provide an important contribution to the knowledge about the implementation of conservation measures for the Whinchat in the study area and beyond. Therefore, currently implemented Whinchat conservation measures need to be aligned and modified with regard to the results of this study (Fig. 16). In several regions in Switzerland, conservation measures have been being implemented as part of the Swiss Species Recovery Programme for Birds. These measures range from (1) nest protection, (2) small-area grassland management to a (3) large-scale adapted grassland management (Horch & Spaar 2015).

Indeed, the protection of nests can support the breeding success of local populations in the short run, although is not related to the prevention of further habitat degradation (Janett & Horch 2014). Furthermore, the protection of Whinchat nests can entail the risk of site fidelity towards poor-quality breeding habitats (Wirth & Horch 2016). Therefore, nest protection should only be a temporary solution to support local Whinchat populations and be replaced in the long term, otherwise, it only delays, but not prevents, the disappearance of local populations (Horch & Spaar 2015). However, the framework of nest protection can raise awareness for the major threats Whinchats are exposed to. This may further help to increase the acceptance of conservation measures among local farmers and the broad public to secure viable Whinchat populations. Since settlement and pair-bonding did not differ significantly between intermediate- and high-quality habitats, and high quality habitats are mostly mown after the 15th of July, nest protection should be conducted in areas without agricultural subsidies within close distance to the core areas (<2 km) to secure Whinchat populations in the short term.

Small-area grassland management such as increasing the supply of perches or leaving out small unmown meadow stripes hardly showed any effect in homogenous grasslands. Arriving Whinchats are unlikely to detect these small areas when making their settlement decision (Horch & Spaar 2015). The outcomes of this study for the use of artificial perches as conservation measure to enhance habitat quality of the Whinchat's breeding habitat also showed that the conducted implementation does not influence the settlement of Whinchats in the study area. Furthermore, these measures are time-consuming and labour-intensive approaches to protect breeding habitats and not feasible on periodically mown meadows. Therefore, these measures are not suitable for the study area, which consist mainly of meadows that provide a high structural diversity.

Considering the breeding phenology of the Whinchat, only a large-scale adapted grassland management with adjusted mowing dates, after the 15th of July seems to be a promising long-term measure (Horch & Spaar 2015). Therefore, large coherent areas of suitable meadow habitats with adjusted mowing dates in close distance to the core areas of the study area are

needed. Whinchats avoided settling in low habitat quality areas, which are unsuitable habitats and negligible for species conservation. When choosing suitable habitat, it should therefore be considered that Whinchats avoid settling in meadows close to large, closed forests and that meadows with a high proportion of hedgerows (>115 m/10ha) remain unsettled (Glutz von Blotzheim 1988).

proposed conservation measures

distance to core areas

close [< 2 km] low low priority areas for species conservation nest protection as short term measure contractually regulated areas with adjusted mowing date after the 15th of July

Fig. 16: Proposed recommendations for future implementation of conservation measures for the Whinchat in the study area. (Photo Whinchat: \bigcirc M. Burkhardt)

Species conservation of the Whinchat in the Lower Engadine should mainly focus on creating a coherent network of meadows with an adapted grassland management. Therefore, contractually regulated and adjusted mowing dates within the core areas and in close distance to them (<2 km) are indispensable in the long term. Besides a delayed mowing date, additional measures to promote biodiversity such as restricting fertilization, abandoning pesticides, avoiding irrigation and sowing flower-rich grassland seed mixes are necessary to secure suitable Whinchat breeding habitats and enhance the availability of food resources (Horch & Spaar 2015). Combined and well-implemented, these measures could improve the overall breeding success and, subsequently, the survival of a sufficient number of Whinchat populations in the long term (Müller et al. 2005). Many plant and invertebrate species suffering from the consequences of the intensification of agricultural use, too, would profit from the conservation measures addressed for the Whinchat (Di Giulio et al. 2001). These conservation measures could further be beneficial for other meadow-breeding birds, such as the Skylark (Alauda arvensis), the Tree Pipit (Anthus trivialis) or the Corn Crake (Crex crex) that rely on similar habitat conditions with delayed moving events to breed securely (Schmid et al. 1998, Müller et al. 2005).

Since Whinchats mainly inhabit extensively managed subalpine grasslands in Switzerland, particular importance can be attached to the ecological agriculture in these areas (Horch & Spaar 2015). Therefore, agricultural policy must adjust their environmental framework to increase the support for farmers of the subalpine regions, pursuing a biodiversity-friendly agricultural scheme. They need to be able to compete financially with farmers that adhere to intensive grassland management. For this purpose, rearrangements of agricultural subsidies need to move away from direct payments of farmers towards a system where measures and efforts that encourage biodiversity become financially favoured (Birrer et al. 2007). Only then, the modernisation of agriculture can be converted from intensive and unsustainable use of agricultural land towards an extensive and mainly biodiversity-friendly agri-environmental scheme where biodiversity is no longer a by-product of rural poverty or a lack of development (Korner et al. 2017).

6. References

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Appendix

Tab. 7: List of experimental plots of the Lower Engadine in 2018.

٩	Area	пате	Altitude Playback type	Perches	Habitat quality	Distance to core area [km]	Connectivity index	Start Playback	Presence [prop]	Presence	Settlement	Pair-bonding	Breedingattempt	Successful breeding	Saved nests	Mowing date (early < 24th of June > late)	Number of pairs	number of nests	min. number of fledglings observed per plot
2	Tschlin	Palavrain	1598 Whinchat 1	Perches	high quality	2.11	9.38	24.04.2018	0.48	1	1	1	0	0	0	early	1	0	0
3 6	Tschlin Tschlin	Planas Radosch	1544 Whinchat 2 2067 Whinchat 1	No Perches No Perches	intermediate quality high quality	1.70 1.34	14.10 20.26	14.04.2018 18.05.2018	0.56	1	1	1	1 0	1 0	1	early late	1	1	≥4 0
7	Ramosch	Motta	1518 Whinchat 1	No Perches	high quality	4.05	1.41	01.05.2018	0.00	0	0	0	0	0	0	late	0	0	0
8	Ramosch	Medras	1571 Mistle Trush	Perches	intermediate quality	3.51	2.35	01.05.2018	0.07	1	0	0	0	0	0	early	0	0	0
9	Ramosch	Sur Savogn	1718 Mistle Trush	No Perches	intermediate quality	4.83	0.76	03.05.2018	0.17	1	1	1	1	0	0	early	1	0	0
11 12	Sent Sent	Varclaina Battaglia	1421 Mistle Trush 1490 Whinchat 1	Perches No Perches	intermediate quality high quality	1.87 1.90	8.01 7.77	14.04.2018 14.04.2018	0.06	1	0	0	0	0	0	early early	0	0	0
13	Sent	Pazos	1420 Whinchat 1	Perches	intermediate quality	0.32	42.05	15.04.2018	0.70	1	1	1	1	1	1	early	4	4	?
14	Sent	Spinatscha	1457 Silent control	Perches	high quality	0.96	34.50	15.04.2018	0.79	1	1	1	1	1	1	late	1	1	≥2
16	Scuol	Clurin	1323 Mistle Trush	No Perches		0.72	24.48	15.04.2018	0.06	1	0	0	0	0	0	early	0	0	0
17	Sent	Chauennas	1422 silent control	No Perches	high quality	0.00	53.35	15.04.2018	0.72	1	1	1	1	1	1	early	4	4	≥2
18 19	Tarasp Tarasp	Sparsels Fontana	1465 Mistle Trush 1423 silent control	No Perches No Perches	intermediate quality low quality	1.97 2.47	6.62 3.95	15.04.2018 15.04.2018	0.27	1	0	0	0	0 1	0	early early	0	0	0 ≥3
20	Ftan Pitschen	Sadinas W	1661 silent control	Perches	intermediate quality	0.28	33.22	15.04.2018	0.52	1	1	1	1	1	1	early	1	1	6
21	Ftan Pitschen	Cumpcha	1703 Mistle Trush	No Perches	intermediate quality	0.23	34.79	15.04.2018	0.66	1	1	1	1	1	1	early	3	3	≥4
22	Ardez	Stra da	1542 Whinchat 1	No Perches	low quality	1.45		15.04.2018	0.38	1	1	1	0	0	0	early	1	0	0
23	Ardez	Muntatsch	1603 Mistle Trush	Perches	intermediate quality	0.90	10.32	15.04.2018	0.07	1	0	0	0	0	0	early	0	0	0
25 26	Tschlin Tarasp	Flütnas Chaposch	2056 Mistle Trush 1345 Whinchat 1	No Perches Perches	high quality intermediate quality	1.07 2.44	26.29 4.03	18.05.2018 15.04.2018	0.33	1	1	0	0	0	0	late early	0	0	0
27	Ardez	Munt	1821 Whinchat 1	Perches	intermediate quality	0.00	25.09	25.04.2018	0.93	1	1	1	1	1	0	late	3	2	≥5
28	Ramosch	Sur Savogn E	1670 Whinchat 1	No Perches	intermediate quality	4.94	0.80	03.05.2018	0.40	1	1	0	0	0	0	early	0	0	0
29	Lavin	Curtins zentral	1498 silent control	No Perches	intermediate quality	2.97	1.28	16.04.2018	0.09	1	0	0	0	0	0	early	0	0	0
30	Tschlin	Crusch	1461 silent control	No Perches	intermediate quality	1.08	26.22	14.04.2018	0.55	1	1	1	0	0	0	early	1	0	0
33 34	Ramosch Ramosch	Chantata 3 Chantata 2	1669 Whinchat 1 1720 silent control	No Perches No Perches	high quality high quality	3.08 3.57	3.59 2.23	30.04.2018 01.05.2018	0.05	1	0	0	0	0	0	late late	0	0	0
35	Ramosch	Chantata 1	1743 Mistle Trush	No Perches		3.85	1.72	01.05.2018	0.00	0	0	0	0	0	0	late	0	0	0
36	Vna	Prats	1586 Whinchat 1		high quality	3.60	1.51	14.04.2018	0.00	0	0	0	0	0	0	late	0	0	0
37	Sent	Marièrs W	1696 Mistle Trush	No Perches	high quality	0.85	22.10	24.04.2018	0.83	1	1	1	1	1	0	late	3	2	≥6
39	Sent	Muot San Peder E	2003 Whinchat 1	No Perches		0.76	25.62	18.05.2018	0.74	1	1	1	1	1	0	late	1	1	≥4
40 41	Vulpera Ftan	San Jon Pras üras	1459 Mistle Trush 1781 silent control	No Perches No Perches	intermediate quality high quality	2.31 1.13	6.68 14.29	15.04.2018 23.04.2018	0.00	0	0	0	0	0 1	0	late late	0	0	0 ≥2
42	Vna	Dadaint	1605 silent control	Perches	intermediate quality	3.81	1.27	14.04.2018		1	0	0	0	0	0	early	0	0	0
43	Ftan	Dorf NW	1699 Whinchat 2		low quality	0.71		15.04.2018	0.27	1	1	0	0	0	0	early	0	0	0
44	Guarda	Saglias	1590 Whinchat 1	No Perches	high quality	3.10	1.13	16.04.2018	0.00	0	0	0	0	0	0	late	0	0	0
45	Bos-cha	Ausagna	1627 silent control	No Perches		0.57	14.19	16.04.2018	0.00	0	0	0	0	0	0	late	0	0	0
46 47	Ftan Ftan	Dorf N Motta Naluns W	1738 Whinchat 1 2278 Mistle Trush	No Perches	high quality high quality	1.29 1.18	12.18 16.41	24.04.2018 17.05.2018	0.57	1	1 0	1	1	1 0	0	early late	1	1	≥3 0
49	San Niclà	Mot	1337 Whinchat 1	No Perches		2.17	8.77	25.04.2018	0.00	0	0	0	0	0	0	late	0	0	0
50	Sur En	Saglias	1449 Whinchat 1	Perches	intermediate quality	1.49	5.69	25.04.2018	0.00	0	0	0	0	0	0	early	0	0	0
51	Guarda	Pra Davant	1968 silent control		intermediate quality	2.26	2.61	19.05.2018	0.95	1	1	1	1	1	0	late	3	3	≥9
52	Scuol	Motta Naluns SW	2147 silent control		high quality	0.74	25.60	04.05.2018	0.65	1	1	1	1	1	0	early	1	1	≥4
53 55	Sent Martina	Battiv Plan Chanver	2024 Whinchat 1 1039 Whinchat 1	No Perches	intermediate quality low quality	1.04 1.17	18.82 23.98	18.05.2018 14.04.2018	0.50	1	1 0	1	1	1 0	0	late early	1	1	≥4 0
57	Strada	Chaflur	1101 Whinchat 1		low quality	1.19	23.35	14.04.2018	0.10	1	0	0	0	0	0	early	0	0	0
58	San Niclà	Baselgia	1064 Mistle Trush		low quality	2.01	10.28	14.04.2018	0.00	0	0	0	0	0	0	early	0	0	0
59	Seraplana	Plan Sura	1138 silent control		low quality	3.01	3.81	14.04.2018	0.00	0	0	0	0	0	0	early	0	0	0
60	Ramosch	Valgrisch	1129 Mistle Trush		intermediate quality	5.22	0.56	14.04.2018	0.00	0	0	0	0	0	0	early	0	0	0
62 63	Ramosch Vna	Bain Tschern Truoi	1452 Whinchat 1 1598 Whinchat 1		intermediate quality intermediate quality	3.20 4.19	2.17 0.97	14.04.2018 08.04.2018	0.00	0	0	0	0	0	0	early early	0	0	0
64	Ramosch	Plan da Muglin	1154 Whinchat 1		low quality	4.57	0.70	14.04.2018	0.21	1	0	0	0	0	0	early	0	0	0
65	Strada	Chasura	1127 Whinchat 1		low quality	0.76	36.06	14.04.2018	0.00	0	0	0	0	0	0	early	0	0	0
66	Sent	Plan du Crusch	1285 silent control		intermediate quality	2.17	5.96	15.04.2018	0.05	1	0	0	0	0	0	early	0	0	0
68	Sent	Zoppanaina	1180 Whinchat 1		intermediate quality	0.97	19.77	15.04.2018	0.22	1	1	1	1	0	0	early	1	0	0
69 73	Sent Sent	Duasasa Muot San Peder W	1167 Whinchat 1 2072 silent control		intermediate quality intermediate quality	0.85 0.98	24.17 21.14	15.04.2018 18.05.2018	0.38	1	1	0	1	1	0	early late	2	2	24
74	Tarasp	Sgne	1376 silent control			1.71	8.80	15.04.2018	0.00	0	0	0	0	0	0	early	0	0	0
77	Bos-cha	Las Palüds	1624 Whinchat 1	No Perches	intermediate quality	0.85	10.75	25.04.2018	0.00	0	0	0	0	0	0	late	0	0	0
78	Lavin	Planturen E	1392 Whinchat 2		low quality	3.76	0.58	16.04.2018	0.05	1	0	0	0	0	0	early	0	0	0
79	Lavin	Sur En Suot E	1388 Mistle Trush		low quality	2.98	1.27	16.04.2018	0.00	0	0	0	0	0	0	early	0	0	0
80 85	Ardez Strada	Saruns Sclamischot	1423 Mistle Trush 1074 silent control		low quality low quality	1.29 1.06	7.00 26.59	16.04.2018 14.04.2018	0.00	0	0	0	0	0	0	early early	0	0	0
86	Tschlin	Spinas	1431 Whinchat 1	Perches	intermediate quality	1.49	17.40	14.04.2018	0.18	1	1	0	0	0	0	early	0	0	0
88	Scuol	Via da Fläna	1370 Mistle Trush	No Perches	low quality	1.07	30.01	15.04.2018	0.00	0	0	0	0	0	0	early	0	0	0
89	Scuol	Russonch	1443 Whinchat 1		intermediate quality	0.67	37.80	15.04.2018	0.59		1	1	1	1	1	early	3	3	≥6
90	Sent	Pedras N	1637 Mistle Trush		high quality	0.00	55.99	23.04.2018	0.70	1	1	1	1	1	0	late	1	1	≥4
91 92	Sent Sent	Flüs Marièrs E	1576 silent control 1616 Whinchat 1		high quality high quality	1.39 1.13	12.89 16.69	23.04.2018 23.04.2018	0.84	1	1	1	1	1	0	late early	3 2	3	≥6 ≥7
94	Ftan	Motta Naluns E	2265 Whinchat 1		high quality	1.13	18.39	17.05.2018	0.70	0	0	0	0	0	0	late	0	0	0
95	Guarda	Giarsun	1392 Whinchat 1		intermediate quality	2.11	3.04	16.04.2018	0.00	0	0	0	0	0	0	early	0	0	0
96	Ardez	Saruns W	1409 Whinchat 1	No Perches	low quality	1.12	8.20	15.04.2018	0.05	1	0	0	0	0	0	early	0	0	0
97	Lavin	Sur En Suot W	1409 Whinchat 1		low quality	3.29	0.93	16.04.2018	0.05	1	0	0	0	0	0	early	0	0	0
98 99	Lavin Etan Ditection	Planturen W	1388 silent control 1684 Whinchat 1			4.05	0.44	16.04.2018		1	0	0	0	0	0	early	0	0	0
100	Ftan Pitschen Sent	Sadinas E Quadras W	1684 Whinchat 1 1280 Whinchat 1	Perches Perches	intermediate quality low quality	0.05 1.07	41.95 17.74	15.04.2018 14.04.2018	0.61	1	1	1	1	1 0	0	early early	1	0	≥1 0
101	Scuol	Fivench	2109 Whinchat 1		high quality	0.72	23.42	04.05.2018	0.45	1	1	0	0	0	0	late	0	0	0
102	Lavin	Crusch	1457 Mistle Trush	No Perches		5.23		16.04.2018		1	0	0	0	0	0	early	0	0	0
103	Sent	La Fuorcha	1296 silent control		intermediate quality	0.79	23.50	16.04.2018	0.11		0	0	0	0	0	early	0	0	0
104	Scuol	Talur	1236 silent control	No Perches	low quality	0.43	34.09	15.04.2018	0.25	1	1	0	0	0	0	early	0	0	0