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Responses of an alpine bird species
to human activities
at high altitude

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FOREWORD

The present PhD thesis is a collection of scientific papers and manuscripts having the objective to deepen the knowledge about human and alpine species interactions. To reach this goal, I used an alpine bird species as a model, and I studied its reactions to human activities at high altitude. The target species is the Alpine Chough, *Pyrrhocorax graculus*, a high elevation bird which can develop tolerance to human presence and has an opportunistic behaviour since it can feed on human food scraps. Therefore, it can obtain some benefits other than negative effects from human presence and activities. Among the several effects that human activities can have on wildlife and especially on birds, I initially focused on the direct disturbance due to human presence nearby foraging flocks, and I compared Alpine Chough reactions in two areas that differed in disturbance level. Subsequently, during my period abroad, I experimented with an alternative method to study the species' activity patterns in tourist areas characterized by the presence of anthropogenic food availability, evaluating whether bird behaviour was influenced by climate and/or the presence of people. Therefore, the first and the second data chapters mainly focused on behaviour and confirmed the highly opportunistic nature of the target species, shedding some light on how birds interact with humans, thus obtaining benefits that potentially mitigate the negative effects of coexistence. Afterwards, I decided to deepen the knowledge of Alpine Chough relationships with food sources, and the second part of the thesis took shape. Indeed, the first two studies indicated that one of the benefits that Alpine Chough can obtain from man is the presence of anthropogenic food, and trophic sources in general are one of the main driver in wild populations. In particular, I started investigating Alpine Chough's “natural” diet studying target species and key-prey abundance and their trend in space and time in both an undisturbed and a disturbed area, trying to understand whether trends were similar and whether there were some differences between areas. Results showed a strong link between predator and main prey. However, the two areas showed some differences indicating that some negative effects may act on prey in the more urbanized area.

The conclusions aim to highlight the most relevant findings of the three studies, with a critical look at the results, and an additional part dedicated to future perspectives. In the annex an additional paper that I co-authored is presented. This piece of work represents the starting point of my passion for mountain bird ecology, and although it deals with mountain ecotone birds and pastoral practices, it had a fundamental role in the progression of my research.

1. INTRODUCTION AND GENERAL FRAMEWORK

1.1. Human presence in high altitude areas: a very long-lasting relationship

Landscapes in Europe often reflect history, since human settlements and activities have always influenced natural landscapes, transforming them in semi-natural areas (Laiolo et al. 2004). In the Alps, pastoral activities have been practised for at least 6000 years and they have transformed the alpine environment, leading to the current landscapes: such areas are characterized by open zones below the elevational limit of the natural treeline since pre-existing shrublands and forests were cleared to increase the availability of grasslands for livestock (Laiolo et al. 2004). However, the intensity of land use has changed across the centuries: the development of industry led to depopulation of mountain areas after the Second World War, and the traditional agropastoral activities became less and less widespread, leading to agricultural intensification or to the abandonment of mountain areas (Laiolo et al. 2004), resulting in vegetation encroachment with a decrease in open habitats and reduced landscape heterogeneity (Laiolo et al. 2004).

As regards the Alps, more recently other changes in how humans interact with mountains have occurred, and therefore further modifications in high altitude habitats have happened. Indeed, in several Alpine valleys, the development of recreational activities has led to urbanization: the major winter skiing destinations in Europe are in the countries of France, Switzerland, Austria and Italy, that combined provide over 85% of Europe's skiing area according to Rixen and Rolando (2013). The relationship between man and mountain regions is a developing process that may go towards a more and more severe exploitation of alpine areas, since climate change may lead to a greater use of artificial snow and to the upward shift of human activities (Brambilla et al. 2016).

1.1.1. Climate change and human activities can act negatively on species

High altitude regions show great sensitivity to climate change, therefore while studying them it is fundamental to take into account any key driving factors. Alpine ecosystems are known to be sensitive to several factors. Such forces are linked with both rising temperatures and variations in mountain area management (Laiolo et al. 2004, Maggini et al. 2014, Probo et al. 2014). Mountain areas are more sensitive than lowlands to increasing temperatures (Böhm et al. 2001, Maggini et al. 2014, Flousek et al. 2015). The negative effects are shown in different *taxa*: Thuiller et al. (2005) studied the effects of climate change on plant diversity and showed how different regions may respond differently to increasing temperature, with the highest vulnerability in mountain areas. Similarly, Dirnbock et al. (2003) showed that alpine plant species with restricted habitat availability above the treeline will experience habitat loss. Dirnbock et al. (2011) studied the effects of climate change on five taxonomic groups, vascular plants, snails, spiders, butterflies, and beetles, showing that they may experience up to 77% habitat loss even under the weakest climate change scenario.

As concerns birds, Maggini et al. (2014) showed that mountain birds have different patterns of vulnerability, with those inhabiting alpine habitats showing significantly higher sensitivity to climate and land use change than species in other habitats. Flousek et al. (2015) demonstrated that species inhabiting high altitude habitats have more negative trends than low altitude species, and that some species shift towards higher altitude as reaction to warmer temperature. However, such species often have a negative trend despite the upward shift. In particular, Flousek et al. (2015) showed the decrease of fifty bird species ranges caused by climate change; moreover the study highlights a greater increase in temperature at higher altitudes, suggesting that the driving forces of global warming are potentially causing faster variations at higher elevations. Sekercioglu et al. (2008) showed that according to different scenarios of increasing temperature, by 2100, 500 (with a raise in temperature equal to 2.8°C) or 2500 (with a raise in temperature equal to 6.4°C) bird species could be extinct. One effect of global warming is phenological mismatch that causes reduction of food supply for breeding birds, since the timing of maximum food supply differs from the time of higher need of food, thus leading to reduced survival of nestlings (Flousek et al. 2015).

A diverse reaction to climatic variables may lead to a desynchronization between the phenology of different species and therefore cause modifications in the ecological interactions producing changes in the ecosystems: Thackeray et al. (2016) showed that the sensitivity to climate changes varies according to *taxon* and trophic level, and the variations in the timing of phenological events seem to be greater for primary consumers than the other trophic levels: in particular the study demonstrated how different trophic levels differ in the magnitude of seasonal climate sensitivity, with lower trophic levels having more pronounced variation and showing the greatest changes in seasonal timing for primary consumers. These variations are expected to accelerate in the near future leading to a greater extinction risk for populations or even for species (Dirnbock et al. 2003, 2011, Braunisch et al. 2013). Braunish et al. (2013) showed that species' range-shifts have been observed across all taxonomic groups and are expected to accelerate in the future, exacerbating the risks of species or population extinction.

Alpine habitats are exposed to different factors leading to negative effects, and some of these are independent of climate change such as the abandonment of traditional pastoral practices (Laiolo et al. 2004, Bazzi et al. 2015, Jähnig et al. 2018). Grazing has a positive effect, since it maintains a habitat mosaic and structural diversity, hence the abandonment of pastoral practices may be detrimental for biodiversity (Laiolo et al. 2004, Bazzi et al. 2015). Indeed, land abandonment is a potential factor affecting abundance and distribution of animal communities such as birds (Jähnig et al. 2018) and beetles (Tocco et al. 2013). As far as the Alps are concerned, Viterbi et al. (2013) showed that these mountains have a long history of human presence and exploitation - indeed human activities have shaped landscapes and therefore communities.

An additional potential threat for mountain areas is the construction of buildings and structures linked to recreational activities such as winter sports (Rixen and Rolando 2013). On one hand, developed valley bottoms act as barriers for species with seasonal vertical movements; on the other hand, ski area development causes habitat loss from resort areas and ski-pistes, but also soil erosion and changes in soil properties. Smoothing slopes by the removal of topsoil, boulders, and vegetation may lead to negative effects in vegetal and animal communities (Rixen and Rolando 2013). According to David et al. (2009), a major effect is linked to the increased flow and amount of sediment that lead to soil erosion and therefore to deterioration and fragmentation of ecosystems, interfering with flora and fauna (Geneletti et al. 2008, Negro et al. 2009). The negative impacts linked with recreational activities such as skiing are numerous and they harm soil and vegetation, thus leading to some negative effects on fauna. Viterbi et al. (2013) demonstrated that habitat structure is all important, indeed some species are less affected by climate and more by habitat structure and complexity, thus in some cases land use changes have stronger effects on species than climate change. Therefore, vegetation plays a fundamental role in determining the local community. The scarcity of vegetation on ski-pistes of alpine grasslands is likely the most relevant determinant of animal diversity and density. Several studies have shown negative effects of alpine ski-pistes on animals, such as birds (Rolando et al. 2007, Patthey et al. 2008, Caprio et al. 2011), and invertebrates with the decrease of invertebrate prey for birds (Negro et al. 2010, Tocco et al. 2013). Ski-piste revegetation promotes partial recovery of animal communities (Negro et al. 2013, Caprio et al. 2016). However, the recovery of vegetation is extremely difficult above the treeline because of the scarcity of soil and the peculiar traits of high altitude plant species (Rixen and Rolando 2013).

Besides habitat loss, humans can have direct impacts on wild species causing disturbance given by the presence of people in alpine ecosystems. Several studies show the correlation between human presence and changes in species physiology (Ellenberg et al. 2007, Arlettaz et al. 2015) and behaviour (Gill et al. 2007, Jiménez et al. 2013). As concerns the behavioral responses to human disturbance, the abundance of birds in areas close to paths seems to decrease with the increasing number of people frequenting the trail; moreover in some species, birds tend not to forage in zones that are too close to roads independent from food source availability (Gill et al. 2007). Wild species respond to human presence with vigilance behaviour: this attitude is not without costs in terms of energy since it consists of visually monitoring the potential danger, leading to a decrease in foraging rate (Gill et al. 2007). Energy consume rises when take-off (i.e. escape) happens, and species showing a greater escape distance are more sensitive to human presence, demonstrating their incapacity to habituate to it (Gill et al. 2007). A study carried out in by Remacha et al. (2013) demonstrated that reducing the number of visitors in terms of group size, in a lowland area used for wildlife watching tours, helped to minimize the impact on the bird community. Similar conclusions were reached by Juricic and Tellería (2000) while studying spatial and temporal feeding patterns, habitat selection and abundance of Blackbirds in a urban environment.

Negative effects of both climate change and land management seem to affect high altitude ecosystems more than the lowland ecosystems (Böhm et al. 2001, Chamberlain et al. 2012), and the destiny of high altitude species is of particular concern since climate change will probably induce operators and stakeholders to use artificial snow and to shift activities (e.g. skiing) and related structures (e.g. ski-pistes) to higher altitudes (Elsasser and Messerli 2001, Brambilla et al. 2016).

1.1.2. Positive interactions between man and wildlife: the ambiguous role of provided food

The negative interactions between human activities and wild species sometimes can be balanced by positive factors related to human presence. Indeed, on one hand people have caused the reduction or extinction of numerous species, but on the other hand humans try to be more and more respectful to nature, and despite that humans compete with wildlife for resources (e.g. humans use high altitude areas for recreational activities), they also supply (both intentionally and unintentionally) food and suitable sites for nesting. Indeed, human presence potentially means the presence of food sources in the form of human food scraps (e.g. picnic areas, tourists feeding wild animals, dumps, high altitude restaurants with terrace) and several bird species forage in human related habitats such that the presence of anthropogenic food has become a driving factor influencing bird distribution, behaviour and trend (Delestrade 1995, Gilbert et al. 2016). However, human provided food has an ambiguous effect since several studies have demonstrated that it can act both positively and negatively on wild bird species. It is necessary to distinguish between food provided intentionally in the form of supplementary food (hereafter supplementary food) with characteristics similar to the "natural" food source (i.e. seeds for granivorous birds etc.), and food provided intentionally or not, but in the form of human food scraps (hereafter anthropogenic food) with nutritional features that are completely different from the “natural" food (i.e. leftovers and organic waste). Oro et al. (2013) confirmed that the predictable anthropogenic food subsidies improve individual fitness leading to the increase of populations in opportunistic species, and West and Peery (2017) similarly showed that the consumption of anthropogenic food may lead to better body condition and a higher reproductive output. Indeed, human food scraps represent a highly predictable source of food, an all important feature since several studies have demonstrated that body mass decreases in birds can be induced by a reduction of either food abundance or food predictability, as shown by Acquarone et al. (2002). Wilcoxen et al. (2015) studied the effects of anthropogenic food, highlighting some positive effects indicating that the health of birds can improve with an increase in antioxidant levels. Other studies underline the potential importance of anthropogenic food, and in particular Schoech and Bowman (2003) showed that in suburban birds the access to predictable sources of high-quality human food allowed females to breed earlier thanks to the higher protein intake, but no evidence of either a positive or a negative effect of such variation was highlighted. However, when positive effects of human provided food are present, there is the possibility to drive down the carrying capacity in the case when food is removed (Kurosawa et al. 2003). Studies carried out on anthropogenic food showed that in the urban environment, the presence of food scraps can lead to the alteration of foraging behaviour, which affects population dynamics and therefore body condition and life span, with the result that only the "winners" have sufficient access to food resources and the opportunity to reproduce (Shochat et al. 2004). Furthermore, the positive effects of human provided food can hide negative outcomes: Grémillet et al. (2008) showed that in some cases where birds eat human food scraps, the junk food hypothesis can be verified. Indeed, when the optimal food source is scarce, species feed on other food items, but this alternative diet can act negatively on individual condition: in a study carried out on gannets *Morus bassanus*, non-breeding birds survived when complementing their diet with fishery waste, but the scarcity of the main food items led to low reproductive success (Grémillet et al. 2008). Moreover, a study based on anthropogenic food demonstrated that birds can undergo an increase in stress hormones due to moderate dietary changes, thus underlining that also mild variations in the diet may have important effects on body condition (Will et al. 2015). However, also supplementary food can act negatively, and a supplementation of a fat-rich diet during winter can worsen the oxidative state of breeding birds (Plummer et al. 2013), and in some cases the brood size proved to be reduced when birds had access to supplementary food (Harrison et al. 2010). Jones and Reynolds (2008) showed further negative effects that were potentially due to supplementary food exploitation by birds, including the fact that they may become dependent on human-provided foods, the impact of inappropriate or nutritionally inferior foods, the loss of foraging skills, and changes in movements and migration patterns. In conclusion, regardless of the kind of food, both types may have positive and negative outputs on wild species, and despite the capacity to exploit human food, may indicate plasticity and may be useful when “natural” food sources are scarce. It is necessary to distinguish the cases when such anthropogenic food source have positive effects and when they worsen an already negative situation of lack of food.

1.2. Aim

The present thesis is based on the study of the Alpine Chough in sites characterized by different levels of anthropic pressure. Alpine ecosystems are more and more threatened by several forces driving negative effects in mountain areas: climate change and human activities can act synergistically, influencing directly or indirectly numerous species. Although positive effects are likely fewer than negative effects, humans can also provide some positive outputs on wild species, and the provisioning of food and nest sites for birds is among such benefits. However, it's unclear how a given high altitude bird species can react to human presence since the general knowledge of alpine ecosystems and species needs to be further developed. Therefore, it's fundamental to deepen our comprehension of human and alpine species interactions. The main aim of the project is to provide a wider knowledge about human-alpine birds interactions and to shed some light on the different aspects of such interactions.

The first paper seeks to understand whether and how the simple presence of humans can affects the foraging behaviour of the target species, with the secondary objective to study the spatio-temporal trend of a key prey type since the distribution of food sources is a further element potentially influencing bird behaviour.

The second piece of work aims to verify whether and how Alpine Choughs modify their foraging behaviour according to climate and/or human activities, evaluating whether they can be influenced by the availability of anthropogenic food sources. We also tested the deployment of webcams to understand whether it could be a useful method to study social species in the alpine environment.

The third manuscript objectives are to test whether Alpine Chough and the abundance of its key-prey type are related in space and time, and to verify whether any such relationship varies according to the anthropogenic disturbance of the two sites.

1.3. The Alpine Chough

The Alpine Chough is a widespread palearctic bird that occurs almost exclusively above the treeline, depending on alpine pastures for foraging and cliffs for nesting (Rolando and Patterson 1993). This species has a diet that varies seasonally and it depends on the temporal availability of invertebrate and vegetable food (Rolando and Laiolo 1997), consisting mainly of berries in the cold season and arthropods in the warmer period (Laiolo and Rolando 1999).

During the reproductive period, corresponding to the summer, the Alpine Chough feeds mainly on grasshoppers that are particularly abundant in alpine meadows above the treeline (Koch et al. 2015) and its reproductive success depends on the availability of this food (Rolando et al. 1997).

Reproduction starts in April, with nest building and egg laying from late May to early June. The fledgling period starts at the end of July, when the young arrive on the foraging sites (Laiolo and Rolando 2001).

This species also behaves as a scavenger, eating food left by tourists, bars and restaurants: Alpine Choughs are known for being an opportunistic species, being able to tolerate human presence (Jiménez et al. 2013; Vallino et al. 2019), and during winter, when "natural" sources are scarce, they can attend high elevation sites to forage on human food (Rolando and Patterson 1993b; Delestrade 1995; Laiolo et al. 2001; Rolando et al. 2003).

The Alpine Chough is a gregarious bird that moves in flocks throughout the year, and it can form groups of tens of individuals (Delestrade 1994; Rolando et al. 1997), an aspect that influences individual behaviour and movements. Indeed, it is generally assumed that flocking may be advantageous to forage more efficiently (Rolando et al. 2001, Jiménez et al. 2013), and a recent study by Beauchamp (2017) proved that the intensity of the relation between flock size and vigilance can depend on the species being more developed in those that form larger groups. Furthermore, a study undertaken on the congener species, the Red-billed Chough *Pyrrhocorax pyrrhocorax*, proved the presence of a positive relation between greater flock size and decreased individual vigilance (Rolando et al. 2001).

The choice of using this species is based on several reasons: it belongs to the crow family and corvids play an important role in ecosystems since any modification in their behaviour, distribution and abundance may potentially lead to notable variations in competition and predation relationships (Jimenéz et al. 2013). Moreover, they have a marked plasticity, showing the capacity to react to environment perturbations, thus representing a good model to study flexible responses to external variable changes (Jimenéz et al. 2013).

1.4. Final remarks and knowledge gaps

The study of alpine ecosystems shows many gaps, and the lacking knowledge covers lots of aspects relative to alpine avifauna since few studies focus on alpine species (Chamberlain et al. 2012). As concerns the direct effects of human presence on bird behaviour, few data are available for both the alpine environment and the avian component. Indeed, lots of studies have been carried out on human-wildlife conflict or interactions, but the most studied *taxa* in this respect are mammals (Carter and Linner 2016 large carnivores, Spagnoletti et al. 2017 primates), while as concerns avifauna, numerous projects have been realized in urban or suburban environments, therefore highlighting issues related to lowland activities and urban development (Concepción et al. 2016, Tomasevic and Marzluff 2017), but few studies have taken into account mountain species. Several gaps are also present as concerns alpine birds' trophic ecology and diet. Indeed, since the knowledge of alpine species is poor, few data about trophic links are available, and trends of different group are often unknown. However, conservation of high altitude species is of major concern since they are sensitive to several forces acting negatively on them. Land use variations and the intensification of human activities are among the major challenges for conservation managers (Maggini et al. 2014), and therefore it's all important to deepen the knowledge of ongoing mechanisms among human activities and wildlife responses at high altitude. Since human presence can notionally provide both negative and positive effects on alpine birds, it's necessary to investigate with accuracy every situation to shed some light on the relationship between man and high altitude species.

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2. CHAPTER I

Behavioural responses to human disturbance in an alpine bird

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Abstract

Mountain habitats are threatened by several factors, including human activities at high elevation, although negative impacts can sometimes be balanced by positive effects related to human presence. Nonetheless, knowledge of such interactions is limited in alpine ecosystems. The Alpine Chough *Pyrrhocorax graculus*, a high elevation bird species, was used to assess the extent of behavioural responses in two alpine areas with differing levels of human disturbance, one a ski resort popular with tourists throughout the year, and the other a protected area with low tourist activity. Since the accessibility and distribution of food is a potential factor affecting bird behaviour, we focused on the availability of food types to better discriminate between the effect of food and direct disturbance. Human presence was negatively associated with intake rates and amount of time spent in a foraging patch (‘stay time’). Moreover, in the disturbed site, vigilance and flushing distances were shorter compared to the undisturbed area. However, intake rates were highest and stay times were shortest in the site where anthropogenic food (mostly discarded food items) was available. The abundance of a key prey type, grasshopper, changed significantly over space and time, and was lower in the more ski-developed area, probably due to the presence of ski-pistes. In conclusion, the study highlighted that human disturbance potentially affects foraging behaviour in Alpine Choughs, and that the effects could be both positive and negative. Further investigations are needed to better disentangle the effects induced by direct and indirect disturbance and, more generally, to evaluate the potential benefits and negative effects of anthropization on mountain biodiversity.

2.1. Introduction

Mountain areas are subject to a range of pressures, including climate change and alterations in land use, driving forces which are often linked to human activities, such as the abandonment of traditional pastoral practices (Probo et al. 2014; Bazzi et al. 2015; Jähnig et al. 2018). Climate warming is likely to push ski developments to higher elevations where snow conditions are more reliable, thus increasing pressure on high-elevation species (Brambilla et al. 2016). Indeed, the building of infrastructures related to winter sports has led to negative effects that act on a variety of *taxa* (Rixen and Rolando 2013) and restoration actions to re-establish previous communities have been at best only partially successful (Rixen and Rolando 2013; Caprio et al. 2016). Humans can also have a direct impact on wild species in alpine ecosystems, and several studies have shown the influence of human disturbance on changes in species physiology (Ellenberg et al. 2007; Arlettaz et al. 2015) and behaviour (Gill et al.

2007; Jiménez et al. 2013). Therefore, since one of the factors leading to potential negative effects on animal communities in mountain ecosystems is represented by human-wildlife interactions, studying the reactions of wild species to people is a key element in understanding the impacts of environmental change on mountain biodiversity.

In terms of the behavioural responses to human disturbance, wild bird species respond with vigilance behaviour that is not cost-free in terms of energy; indeed, increased vigilance due to disturbance may lead to a decrease in feeding rate, and energy consumption also rises when disturbance causes birds to flush (i.e. an escape response; Gill et al. 2007). A study carried out by Remacha et al. (2011) demonstrated that reducing the number of visitors in terms of group size in a lowland area used for wildlife watching tours helped to minimize the impact on the bird community. Similar findings were made by Fernández-Juricic and Tellería (2000) while studying spatial and temporal feeding patterns, habitat selection and abundance of Blackbirds *Turdus merula* in an urban environment. These negative interactions can sometimes be balanced by positive factors related to human presence. On one hand, people have caused the reduction or extinction of numerous species, since human activities are often associated with the development of infrastructure which causes direct and indirect costs to wildlife. On the other hand, human activities may also provide benefits to some species (e.g. through provisioning of food resources and nest sites; Kurosawa et al. 2003; Oro et al. 2013, West and Peery 2017; Jokimäki et al. 2017). Therefore, the presence of people potentially means the presence of food sources in the form of human food scraps (e.g. picnic areas, tourists feeding wild animals, rubbish dumps), and several bird species forage on anthropogenic food sources in human-related habitats, to the extent that it has become a driving factor influencing bird distribution, behaviour and trends (Delestrade 1995).

Much research on the effects of human disturbance on birds has been carried out in urban or suburban environments, highlighting issues related to urban development (Concepción et al. 2016; Tomasevic and Marzluff 2017; Bàtary et al. 2018), or focusing on the effect of supplementary food sources provided by humans (Schoech et al. 2007; Robb et al. 2008; Hanmer et al. 2017; West and Peery 2017; Støstad et al. 2017). However, gaps are still present as regards the alpine avifauna, and the present study aims to address this using the Alpine Chough *Pyrrhocorax graculus* as a model species.

The Alpine Chough is a widespread palearctic species that occurs almost exclusively above the treeline, depending on alpine pastures for foraging and cliffs for nesting (Rolando and Patterson 1993b). This species has a diet that varies seasonally and it depends on the temporal availability of invertebrates and vegetable food (Rolando and Laiolo 1997), and consists mainly of berries in the cold season and arthropods in the warmer period (Laiolo and Rolando 1999). During the reproductive period in summer, the Alpine Chough feeds mainly on grasshoppers. It is known to be an opportunistic species, having developed habituation to humans (Jiménez et al. 2013), and it is also a scavenger that commonly eats food discarded by tourists, especially around bars and restaurants (Rolando and Patterson 1993a; Delestrade 1995; Laiolo et al. 2001). However, it is unknown how this association with humans, and in particular the availability of anthropogenic food, affects the behaviour of the species. The aim of this research was to assess whether and how the behaviour of Alpine Chough is affected by human presence. Since food availability is a further factor that is likely to affect bird behaviour, the spatio-temporal trend of a key prey type was studied to better distinguish between food availability and disturbance effects. The study was carried out in two areas with different levels of anthropogenic pressure.

2.2. Materials and methods

2.2.1. Study areas

The study sites were located in the North-Western Italian Alps in the Aosta Valley and included the tourist area around Cervinia in Valtournenche (45.9336° N, 7.6292° E) and the Dondena basin in Mont Avic Natural Park (45.6518° N, 7.5621° E, hereafter MA). MA is a relatively undisturbed area with few buildings (mainly mountain huts and facilities used by shepherds) that was visited by around 11000 people from June to August 2015 during the summer (unpubl. report, Mont Avic Natural Park 2016). The area of Cervinia is a popular tourist destination, characterized by a higher anthropization due to leisure activities such as skiing and other outdoor pursuits, and to the presence of high elevation ski resorts, bars and restaurants. The Cervinia skiing complex includes 72 ski pistes in Italy (and 78 on the Swiss side), 200 km of tracks covered with artificial snow and a snowpark as high as 2800 m a.s.l.. Tourists can participate in activities such as cross-country skiing, heliskiing on the glacier, trekking and down-hill skiing, and therefore Cervinia is frequented by tourists year-round. Just during the summer 2017, 63000 people visited the area (Cervino spa pers. comm.). There is already evidence that human presence may have an effect on Alpine Choughs in Cervinia in that the local population remains at high elevations in winter, roosting in buildings, whereas in other populations, there is usually movement towards valley bottoms (Rolando et al. 2003). At Cervinia, Alpine Choughs used two zones, a lower one including grasslands, pastures and ski runs between 2000 and 2700 m a.s.l. where individuals fed on natural items (Plan Maison, hereafter PM), and a higher one where birds fed on human food provided by restaurants (Plateau Rosà, hereafter

PR) that was characterized by rocky patches and ski lift buildings with restaurants as high as 3500 m a.s.l. on the border between Italy and Switzerland. To highlight differences in human disturbance, the total number of people frequenting the areas were counted on every day of fieldwork.

Neither PM not MA showed any evidence of availability of human-derived food resources (pers. obs), so a comparison of behavioural responses in these two sites relates to human disturbance and natural food availability. However, human-derived food was frequently available and exploited at PR. Comparisons between PM and PR were therefore mainly associated with differences between natural (PM) and human-derived (PR) food, as both of these sites, which were within the Cervinia area, were relatively disturbed.

2.2.2. Fieldwork

Foraging behaviour

Observations were carried out from June to August 2016-2018 on an almost daily basis (except in conditions of heavy precipitation) from 8 a.m. to 5 p.m. During the first year's fieldwork, zones frequented by Alpine Choughs were first located during pilot visits, and from then we focussed on these areas as potential locations of foraging flocks.

In 2016 in PM only, the number of items ingested by Alpine Choughs in a fixed period of one minute was counted (henceforth 'intake rate') by following one focal individual that was chosen randomly when a group landed in a feeding area. Flock size was also recorded. The feeding events were recorded on different days, both in undisturbed and disturbed conditions, the latter being defined as the proximity (i.e. less than 50 m) of people walking along nearby trails.

In 2017 and 2018, both MA and Cervinia (PM and PR) were studied, when the foraging behaviour of Alpine Choughs was evaluated by recording individual stay time and intake rate. The latter was calculated *a posteriori* as the ratio between the number of items ingested and the stay time of the individual in minutes, and since it was obtained in a different way compared to the 2016 intake rate (i.e. a different time scale), the analyses were carried out separately. Stay times were recorded using a chronometer and were defined as the time spent on a foraging patch by a focal individual chosen randomly within a landing flock. The stay time was stopped if the focal individual flew for more than 50 m (i.e. to separate small foraging movements from genuine changes in foraging location). The duration of observations corresponded to the stay time of the individual. The flock size (i.e. number of individuals in the foraging group) was also recorded.

Responses to direct human disturbance

To study the changes in behaviour linked to human presence, additional variables were recorded when humans were seen approaching a flock, namely vigilance distance (i.e. the distance in m, between humans and the first individual which stopped foraging due to human presence) and flushing distance (i.e. the distance in m, at which the first individual in the foraging flock flew away due to human presence). Distances were recorded using laser range-finders (Bushnell V4 6.6 x 5 x 3.4 mm).

Spatio-temporal prey distribution

To study natural food availability, sampling was carried out along elevational transects to study key-prey distribution and phenology in the summer 2016 and 2017. The location of transects was determined following preliminary visits at the beginning of the field season, selecting places where

Alpine Choughs were observed foraging. There were two elevational transects in each area, formed of six to seven sampling plots sited on grasslands. Plots were separated by 100 m elevation along a given transect. The abundance of grasshoppers on ski-pistes is usually very low (Negro et al. 2010). To test for an indirect effect of ski-pistes on nearby pastures, in 2017 we chose a transect at the border of a ski- spiste. In MA, the transects started at 2100 m a.s.l., while in PM the lowest plots were located at 2000 m a.s.l., and in both areas the maximum elevation of transects was around 2700 m a.s.l.. In each plot, a 6 m^2 area was randomly chosen and a one meter pole was passed horizontally through the vegetation, covering the whole area: during this procedure, grasshoppers that flushed were counted to determine their abundance (Rolando and Patterson 1993a). During fieldwork some individuals were also collected to identify grasshopper species.

2.2.3. Data analysis

Data collected in 2016 were used to assess the effect of disturbance and flock size (and interaction between flock size and disturbance) on intake rate using Generalized Linear Models (GLMs), specifying a Poisson error distribution and a log link function.

Individual stay time (seconds) and intake rate (number of items ingested / time of observation) from 2017 and 2018 were analysed using Generalized Linear Mixed Models with the glmmADMB package in R (Skaug et al 2016). In order to determine variations in individual stay time and intake rate, we tested elevation (and its quadratic term), study site, disturbance and period, and interactions between study site and flock size, study site and disturbance, and elevation and period, in a statistical hypothesis testing framework, with the null hypothesis that stay time and intake rate were not dependent on site, disturbance, elevation or period considered, specifying a Gaussian error distribution.

Flock size was tested as a dependent variable in a model to test the effect of site, period and elevation, specifying a Poisson error distribution. Periods were created by dividing the field season into several intervals lasting 14 days. Since overdispersion was found in preliminary Poisson GLMMs, Negative Binomial GLMMs were performed. Flock identity was fitted as a random factor in all models to account for possible non-independence of observations carried out in the same flock. As far as possible, no multiple observations were made on the same individual as long as the flock was visible. Study site was included as a three level factor (PM, PR and MA). Final models were identified after a model reduction procedure whereby non-significant terms were dropped from a model until only significant terms ($p \leq 0.05$) remained. Finally, vigilance and flushing distances (in m) obtained by approaching foraging birds were modelled to test the effect of site (PM and MA), flock size, period and elevation and interactions with site and period using a GLM and setting a Gaussian distribution of errors and an identity link function. Prior to modelling, elevation was scaled and centred.

Grasshopper data were used for a preliminary analyses taking into account the two areas separately to evaluate the distribution of prey in relation to space and time, and subsequently the overall differences between the two sites and between transects within the same area in terms of prey abundance were studied. Successively, data were modelled to test the effect of elevation and its quadratic term, site and period on the abundance of grasshoppers, specifying a negative binomial error distribution due to overdispersion, and specifying plot as a random effect. Periods were defined in 14 day intervals as in the previous analysis. Prior to modelling, altitude was scaled and centred.

In the results, means are presented ± standard deviation and model-derived parameter estimates are presented as estimate ± standard error. Analyses were carried out following Zuur et al. (2009) using R 3.2.2 (R Development Core Team 2015).

2.3. Results

The daily counts of people in 2017 and 2018 showed a clearly higher number of people at Cervinia, where the daily average was 358.54 ± 89.37 people (N = 42), while in MA it was 69.78 ± 272.26 people (N = 61) (Poisson GLM: number of people at site MA relative to Cervinia, estimate -1.48 ± 0.03, z value -54.03, p <0.0001).

2.3.1. Foraging behaviour

Interaction terms were never significant in tested models. During the first year in Cervinia, 60 feeding events were observed, while in the following two field seasons 445, 624 and 154 observations were made in MA, PM and PR, respectively. Data collected in 2016 at Cervinia showed that the intake rate was lower when Alpine Choughs were disturbed by people (N = 26). Interestingly, intake rates increased with flock size irrespective of disturbance (figure 1), (GLMM: Flock size 0.014 ± 0.002, z value 6.937, P<0.001; Disturbance -1.125 ± 0.209, z value -5.378, P<0.001, DF 53)

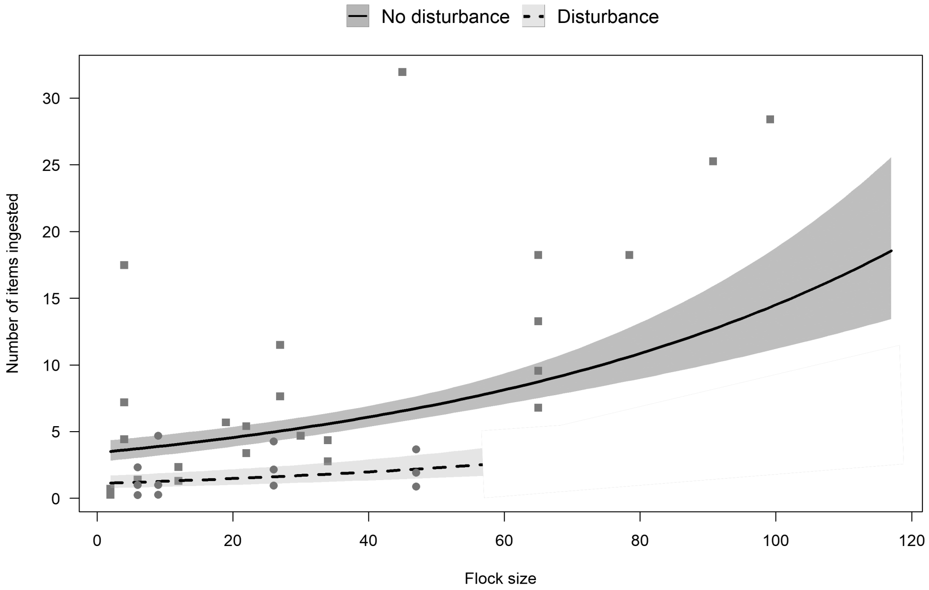

Figure 1. Curves depicting the influence of people disturbance and flock size and the number of items ingested in one minute. Squares indicate undisturbed points and circles disturbed ones.

Data collected in 2017 and 2018 showed that individual stay time was significantly shorter in MA and PR than in PM, and when the birds were disturbed by tourists or vehicles (figure 2). Furthermore individual stay time was longer in late July (i.e. P4) than in early June (i.e. P1) (table 1).

Table 1. GLMM of individual stay time in relation to the effect of site, disturbance and period; Estimated parameters, standard errors (SE), z values and significance (p) are given. PM is set as the site reference level and Period1 is set as the Period reference level.

Variables	**Estimate**	**SE**	**z value**	**p**
(Intercept)	3.842	.031	3.73	0.00019 ***
Site MA	-0.987	0.503	-1.96	0.04994 *
Site PR	-2.724	0.988	-2.76	0.00582**
Disturbance	-1.846	0.583	-3.17	0.00155**
Period2	-0.473	1.037	-0.46	NS
Period3	0.259	1.056	0.25	NS
Period4	3.684	1.111	3.32	0.00091 ***
Period5	-1.089	1.190	-0.92	NS

Alpine Choughs grouped in smaller flocks at PR (mean number of individuals = 3.69 ± 3.33 individuals, N = 154) and MA (mean number of individuals = 5.95 ± 7.98 individuals, N = 445) than at PM (mean number of individuals = 10.18 ± 15.42 individuals, N = 624), GLMM: Site MA 0.323 ± 0.151, z value 2.14, $P<0.05$; Site PR 1.602 ± 0.479, z value 3.34, $P<0.001$, DF 602 (figure 3).

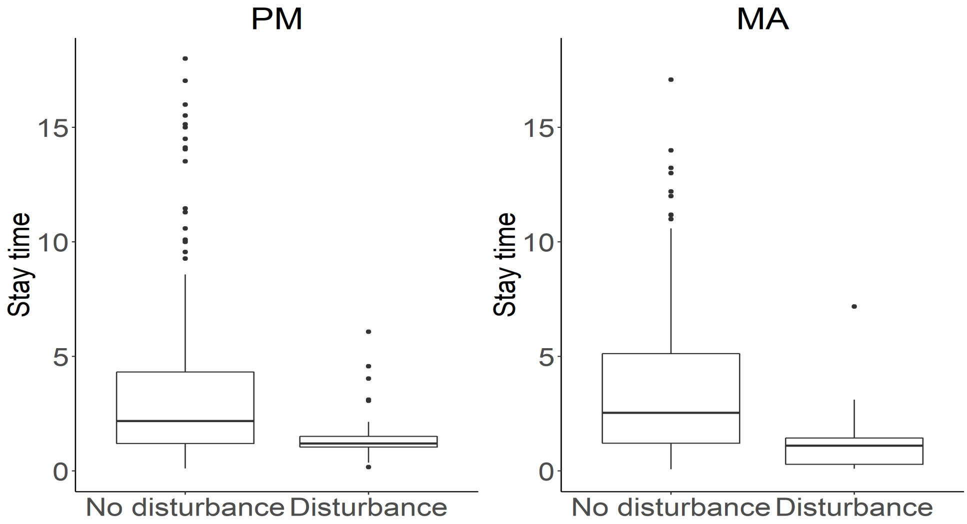

Figure 2. Boxplot showing the difference between Alpine Chough stay time with and without human presence in MA and PM. In the figure the x axis indicates disturbance and no disturbance.

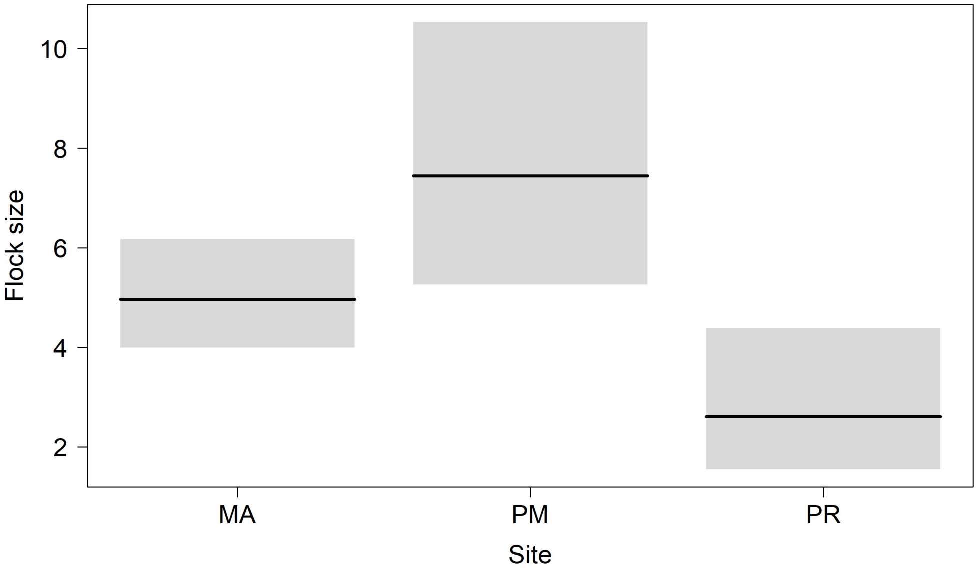

Figure 3. Backtransformed data of the GLMM of flock size in relation to the site; PM: Plan Maison, MA: Mont Avic, PR: Plateu Rosa. Flock size was higher in PM and lower in PR.

Intake rates were significantly higher at PR (mean number of items/minute equal to 14.18 ± 9.83 items ingested, N = 154) than MA (mean number of items/minute equal 6.09 ± 6.44 items ingested, N = 445) and PM (mean number of items/minute equal to 5.62 ± 5.46 items ingested, N = 624) and on average they were higher in late June (i.e. P2) than in early June (i.e. P1) (table 2).

Table 2. GLMM of intake rate in relation to the effect of site and period. Estimated parameters, standard errors (SE), z values and significance (p) are given. PM is set as the site reference level and Period1 is set as the Period

reference level.

Flock size	Estimate	SE	z value	p
(Intercept)	2.496	1.478	1.69	0.0913 .
Site MA	1.781	0.670	2.66	0.0079 **
Site PR	11.051	1.385	7.98	<0.0001 ***
Period2	3.790	1.490	2.54	0.0110 *
Period3	0.904	1.514	0.60	NS
Period4	0.135	1.583	0.09	NS
Period5	2.396	1.696	1.41	NS

Responses to direct human disturbance

Vigilance and flushing distances were significantly greater at MA than at PM. In MA, mean vigilance distance was 66.23 ± 14.31 m (N = 31), while in PM, it was 38.96 ± 14.57 m (N = 79) (Gaussian GLM: vigilance distance at site MA relative to PM estimate 27.27 ± 3.12, t value 8.75, p <0.0001, figure 4). Mean flushing distance was 27.91 ± 15.75 m at PM (N = 79), and 65.96 ± 14.51 m at MA (N = 31) (Gaussian GLM: take off distance at site MA relative to PM estimate 38.05 ± 3.36, t value 11.32, p <0.0001, figure 5). Interestingly, vigilance and flushing distances almost coincided at MA.

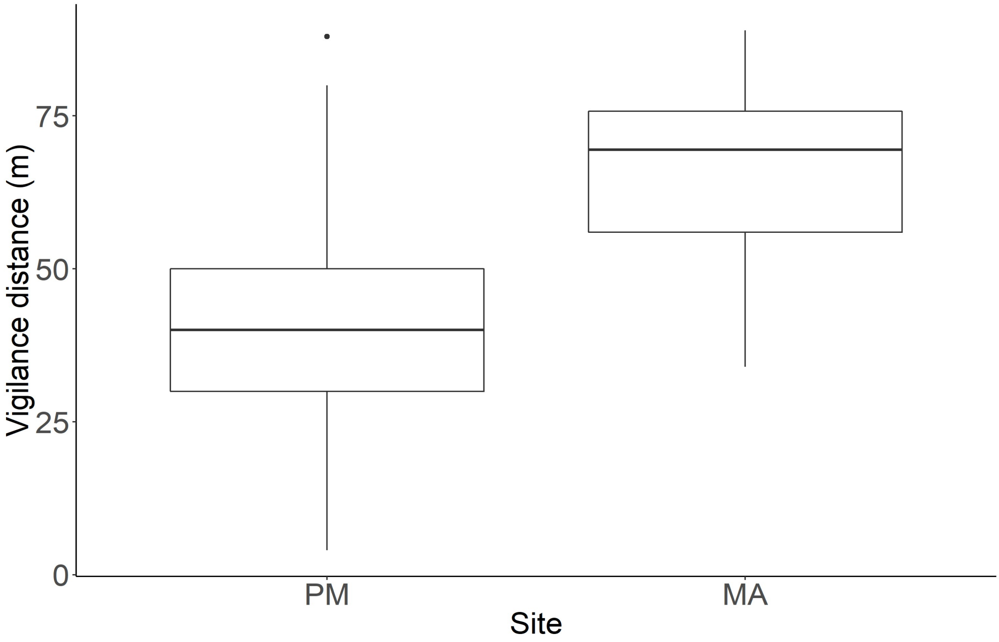

Figure 4. Boxplot showing the difference between Alpine Chough vigilance distance at PM and MA.

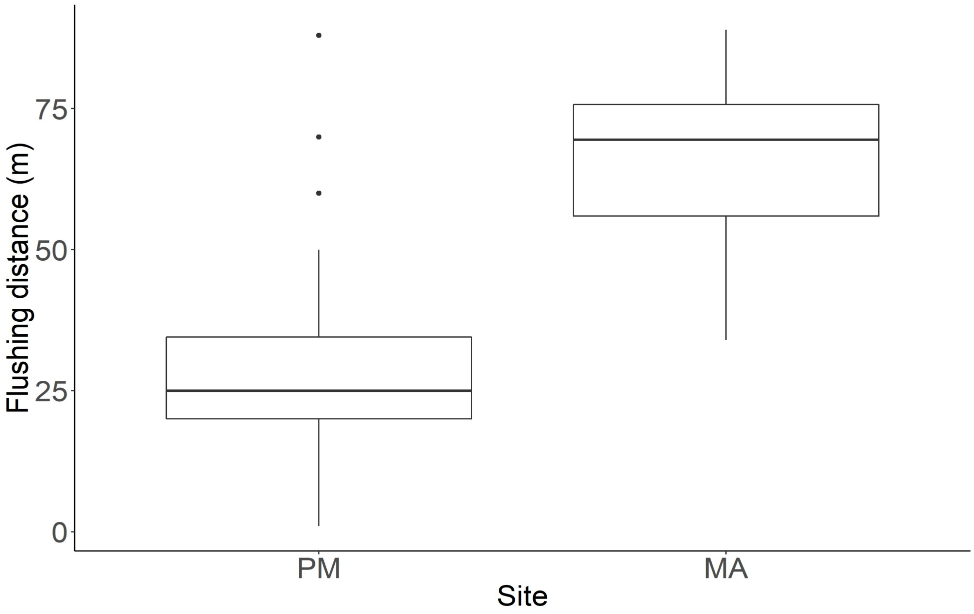

Figure 5. Boxplot showing the difference between Alpine Chough flushing distance at PM and MA.

2.3.2. Arthropod data

A total of 13 species of grasshoppers of the families *Acrididae* and *Tettigoniidae* were collected and identified in the two study areas. Results of a negative binomial mixed model showed that there was a non-linear relationship between abundance of grasshoppers and elevation, and a significant difference in abundance between periods, with all the tested periods showing higher abundance with respect to Period1 (table 3).

Table 3. GLMM of the effect of elevation and periods on grasshopper abundance.

Grasshopper abundance	Estimate	SE	z value	p

(Intercept)	1.439	0.276	5.21	<0.00001 ***
Site MA	0.457	0.253	1.80	0.07113
Elevation	-0.019	1.129	-0.15	0.00065 ***
Elevation^2	-0.488	0.142	-3.43	0.00060 ***
periodP2	1.372	0.207	6.62	3.7e-11 ***
periodP3	1.226	0.211	5.81	6.3e-09 ***
periodP4	0.824	0.219	3.77	0.00016 ***
periodP5	0.554	0.237	2.34	0.01914 *
periodP6	0.7764	0.265	2.93	0.00340 **

The average number of grasshoppers/m^2 was higher at MA (mean number of grasshoppers/m^2 2.25 ± 2.38, N = 66) than at PM (mean number of grasshoppers/m^2 1.44 ± 1.56, N = 67), and the model suggested a difference between disturbed and undisturbed areas, even though significance was not fully attained (GLMM Negative Binomial: site MA estimate 4.57e-01 ± 2.53e-01, z value 1.80, p = 0.071). No significant difference was found between transects in PM, the transect near the ski pistes having similar densities to the more distant one (GLMM Negative Binomial: transect far from ski-piste grasshopper abundance estimate 0.18 ± 0.26, z value 0.69, P = 0.48).

2.4. Discussion

The present study highlights some behavioural responses that likely indicate either habituation or direct and indirect negative effects of human activities on Alpine Choughs. In particular, the presence of people was shown to be a possible factor affecting variations in foraging behaviour, such as the reduction in intake rate, the shortening of stay times, and, for the 2016 data, the increase in flock size, thus potentially negatively influencing the feeding process. The study of reactions to people approaching foraging flocks showed vigilance and take off distances were shorter in PM compared to MA, potentially suggesting that Alpine Choughs in PM can develop habituation. In particular, at the tourist site, Alpine Choughs showed a capacity to tolerate disturbance as they tended not to leave the foraging patch immediately when humans approached. On the contrary, in MA, as soon as the potential danger was perceived, the flock stopped feeding and flushed, thus losing a foraging patch and increasing the negative effect of disturbance. These results agree with Jiménez et al. (2013), who suggested that choughs can become habituated to the presence of people; a reduction in the flushing distance might indicate that choughs had learnt to perceive the perturbation (i.e. human presence) as less negative, thus giving them the possibility to remain in a potentially good foraging patch. However, Beale and Monaghan (2004) demonstrated that birds foraging in richer habitats can afford to stop foraging during disturbance, while individuals in poorer areas must forage for as long as possible since there are fewer resources; thus, birds may change their response according to the quality of the environment.

As regards the tourist area, a further potential response was represented by the observed variation in behaviour at PR. Indeed, once fledglings left the nests, Alpine Choughs abandoned natural pastures, moving to high elevation ski-dedicated sites (i.e. PR). Previous studies had already proved that Alpine Choughs are opportunistic and they can feed on food scraps (Rolando and Patterson 1993a; Delestrade 1995; Laiolo et al. 2001). However, due to its location at 3500 m a.s.l., the only food source the Alpine Choughs can feed on at PR is represented by leftovers, provided from the local restaurant, or given by tourists. Hundreds of tourists per day arrive at PR during the summer, and nearby the high elevation restaurant, small quantities of human food are available several times a day. At PR, flocks were significantly smaller than at

PM and this might be explained assuming that the food source can be exploited just by few individuals at a time since small quantities of leftovers are available. An alternative explanation is that the source of food is of poor quality, and it does not represent a good opportunity for a large number of individuals. However, at the present time we cannot know whether the birds that foraged at PR on different days are different individuals. At PR, Alpine Choughs had higher intake of items despite the shorter stay time compared to PM, which can easily be explained by the features of the source of food they exploit at PR. As already pointed out, exiguous leftovers are available piecemeal, and hence the time over which they can be consumed is limited. Since some indications suggest a slightly lower abundance of natural food in the tourist area, potentially linked with the presence of ski-pistes (Negro et al. 2010), PR could be a potentially good feeding site where human food supplements the overall scarce natural sources of PM.

At MA, smaller flock size, higher intake rates and shorter stay times than at PM were also found. Mont Avic Natural Park is characterized by low disturbance and some indications suggested that grasshopper availability was higher, hence the choughs can spend less time in foraging patches thanks to the high abundance of prey that allows several items to be ingested quickly. Furthermore, birds may not often need to activate anti-predatory behaviour through grouping in big flocks (Rolando et al. 2001), since disturbance caused by people is seldom present. However, the role of natural predation pressure, which could itself be affected by human disturbance, could also be important, although we have no data to assess this.

Behavioural differences among sites could also be due to factors other than human disturbance that were superficially examined in the present study, namely prey distribution and/or different invertebrate *taxa* exploitation (i.e.

other than grasshoppers). Indeed, a further factor potentially influencing movements and foraging behaviour is the spatio-temporal prey distribution. Grasshoppers are key Alpine Chough prey during the summer (Rolando and Laiolo 1997), and their abundance was highly variable in space and time, having a non-linear relationship with elevation and an increasing trend from early June onwards both in PM and MA. Therefore, the longer stay times recorded in late July could be linked with increasing prey abundance leading to increased stay times. Another potential explanation is given by the fledgling period occurring in late July (Delestrade and Stoyanov 1995; pers.obs.), and potentially leading to the necessity to stay longer on foraging patches to allow inexperienced young to feed.

Different studies have suggested that some potential benefits linked to human presence can be obtained by birds, such as food provisioning and availability of nest or roosting sites (Kurosawa et al. 2003; Oro et al. 2013; West and Peery 2017; Jokimäki et al. 2017). Previous research carried out in Cervinia on Alpine Choughs (Rolando et al. 2003) demonstrated that during winter, birds simply became urbanized, staying in the town throughout the cold period, while in other localities the populations moved to valley bottoms. Furthermore, that study demonstrated that habitat use was rather constant at Cervinia because birds stayed amongst buildings. The present study was carried out in the summer, during the breeding and post-breeding season of the Alpine Chough, and therefore no data relative to the winter period were collected; however, the present research shows that also during the warm season, it's likely that the local Alpine Chough population of PM can obtain benefits from human activities, while in MA the birds leave high elevations as soon as the first snow falls (M. Bocca pers. obs.). Indeed, the presence of buildings could be useful to Choughs since they can build nests in ski-lift stations, as was observed at PM (pers. obs.). Moreover, birds can seek out areas of high human presence in order to exploit food scraps left by restaurants which are predictable and easier to obtain than invertebrates on grassland patches. Indeed, natural food sources are characterized by temporally and spatially highly variable prey abundances, while anthropogenic food is typically more predictable and obtainable (Bridge et al. 2008; Oro et al. 2013). Moreover, in Cervinia, Alpine Choughs nest between 2800-3500 m a.s.l. (Rolando and Patterson 1993a), and therefore feeding at 3500m is energy saving since the distance in elevation between foraging site and nesting/roosting cliffs is shorter. However, there is increasing evidence of some negative effects given by supplementary food exploitation. Indeed, the negative outcomes of this source of food (here intended as any kind of consumable source such as from bird feeders and rubbish dumps) can potentially act both on behaviour and body condition (Shochat 2004; Gilbert et al. 2016). According to a study carried out on seabirds, even modest dietary changes can activate physiological responses in birds (Will et al. 2015). Moreover, previous research designed the "junk food" hypothesis according to which the shift from high quality to low quality food exploitation is due to the decrease in optimal prey abundance leading to detrimental effects on predators (Grémillet et al. 2008). Therefore, further investigation is needed to shed some light on the potential negative effects concealed in a diet based on human food scraps. In this sense, it is desirable to deepen the knowledge about the features of food eaten by Alpine Choughs, thus examining food sources from a chemical point of view to understand whether the diverse types have also different chemical composition and calorie contents. A further aspect that need to be examined in the future is the behaviour of Alpine Choughs in tourist sites during winter, when the exploitation of human food sources is potentially more developed since they can stay in town

(Rolando et al. 2003). Therefore, studies about the time spent on human food sources during winter are advisable to understand how much they rely on this type of food during another crucial season for birds.

2.5. Conclusion

The present study showed probable development of behavioural responses in Alpine Choughs subject to human presence, both in a tourist area and a more natural area. Responses may have both negative (e.g. higher energy expenditure for the birds due to escape costs, Gill et al. 2007) or positive (e.g. habituation and consequent enhancement of birds' foraging success, Jiménez et al. 2013) effects. When habituation is present, further benefits can be obtained by human presence at high elevations, namely food sources that are easy to predict and obtain, and nest sites (Bridge et al. 2008; Oro et al. 2013; West and Peery 2017; Jokimäki et al. 2017). However, there is increasing evidence that human-provided food can have detrimental effects on avifauna (Shochat 2004; Gilbert et al. 2016). Therefore, further investigation is needed to shed some light on the potential negative effects concealed in a diet based on human food scraps. Moreover, the spatio-temporal distribution of natural food availability is a further factor potentially affecting birds and the shift in their diet to human food, and therefore the composition of the natural diet and the potential negative effect of ski-pistes on the arthropod community in the tourist area need to be further studied. The extent to which the responses recorded here affect only the behaviour of the Alpine Choughs, or whether there are wider population-level consequences cannot be known from our study, although there is observational evidence of a possible population decline at Cervinia: the maximum dimension reached by a single flock in this study was 180 individuals (EC 2017-07-13), whereas Rolando et al. (2003) recorded flocks of up to 300 individuals in the same area in the past. Systematic long-term monitoring is needed to assess the extent of population-level impacts of human disturbance on this species.

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3. CHAPTER II

Webcams as a remote tool for eco-ethological research: A pilot study on the Alpine Chough

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Abstract

Ski resorts increasingly use webcams to share panoramic views. We tested preinstalled webcam effectiveness as a remote tool for eco-ethological studies. Our target species was the Alpine Chough *Pyrrhocorax graculus*, a social and opportunistic species of high mountain environments, and our aim was to understand whether and how some factors influenced Alpine Chough attendance of tourist sites provided with bar terraces. We used flock size and time spent at the ski resort as response variables, and assessed how strongly they were related to the number of tourists and weather condition information obtainable with webcams. We analysed about 14,000 pictures taken at 10 minute intervals at three ski resorts sites in the European Alps in France, Italy and Switzerland. Results showed that the maximum flock size changed across ski resorts, while it decreased with low temperatures and increased with the number of tourists, but the strength of the relationships varied between resorts. Flock size also decreased on days with snow. Frequency of presence around restaurants (measured as the number of pictures showing birds/day) increased with the intensity of cold and the number of tourists. Finally, in one site birds stayed more continuously when the temperature was lower. In conclusion, Alpine Choughs proved to be able to modulate their presence at the ski resorts according to each factor that we included in the study, thus human presence, cold intensity and snow condition. Furthermore, the results obtained suggest that preinstalled webcams, despite a few specific caveats can be successfully employed in eco-ethological research, but such method can be improved with prior fieldwork and, when necessary, with the combined use of additional data on demographic traits (reproductive output and survival).

3.1. Introduction

Human and wild birds interactions have been studied in several ways and different effects of such relation have been highlighted. An increasing number of alpine species are threatened directly or indirectly by human activities that potentially induce disturbance for animals such as birds (Chamberlain et al. 2016). The construction of buildings and ski pistes for winter sports, for instance, causes severe habitat loss (Rixen and Rolando 2013). Furthermore, climate change is going to push ski developments to higher altitude influencing more and more high elevation species (Rixen and Rolando 2013, Brambilla et al. 2016). Even the daily presence of people can potentially disturb wild birds, leading to modification in species physiology and behaviour (Ellenberg et al. 2007, Gill et al. 2007, Arlettaz et al. 2015). The abundance of birds in areas close to paths decreases with an increasing number of people, and birds tend to avoid foraging in sites that are too close to roads (Gill et al. 2007, Remacha et al. 2013). Many species trade-off foraging and vigilance, and increasing human presence may lead to longer times spent monitoring human presence (Gill et al. 2007).

The impact of human presence can be mitigated by positive effects, because human presence can be associated with increased food supply and nesting or roosting sites (Kurosawa et al. 2003, Oro et al. 2013, Jokimäki et al. 2017, West and Peery 2017). In opportunistic species, for instance, human derived food can improve individual fitness and reproductive outputs, especially when "natural" food is scarce (Acquarone et al. 2002, Oro et al. 2013, West and Peery 2017). The presence of human derived food may then become an all important factor potentially affecting demographic trends and movements (Delestrade 1995, Rolando et al. 2003, Gilbert et al. 2016).

Species' sociality may modulate responses to human presence. The decision of where to forage is usually driven by food availability, but in gregarious species foraging in flocks, sociality may influence such decisions as well. These species can develop different tactics of social foraging, so that a group of interacting individuals searching for a food patch can improve foraging success (Fernández-Juricic et al. 2004). Even if birds search for food on their own, they can exploit the food discoveries of their neighbours ("scrounging") (Lendvai et al. 2006). Flocking in social birds may also influence predation events: it contributes to an early detection of predators (Rolando et al. 2001, Jiménez et al. 2013) and to a reduced individual predation risk (Hamilton 1971).

The Alpine Chough, *Pyrrhocorax graculus*, a palearctic bird of high altitude ecosystems, is an excellent target species in this framework. It is a highly social, gregarious corvid forming social groups of tens of individuals (Delestrade 1994, Rolando et al. 1997, Delestrade 1999). Vallino et al. (2019)

demonstrated that direct human disturbance causes a reduction of feeding rates and stay times of birds foraging on alpine pastures. Interestingly, disturbance may be reduced by particular behavioural responses developed in those areas more frequently visited by tourists (Jiménez et al. 2013, Vallino et al. 2019). Despite the potential disturbance induced by humans, Alpine Choughs frequent ski resorts where, especially in winter, they behave like scavengers by feeding on scraps discarded from high altitude bars and restaurants (Rolando and Patterson 1993a, Delestrade 1995). Higher densities of birds occur around high altitude touristic areas where they move around restaurants when tourists are present (Storch and Leidenberger 2003). The potential foraging advantage of flocking, however, is unclear, because in larger flocks birds feed faster, but stay for a shorter time in patches (Delestrade 1995, Rolando et al. 1997, Vallino et al. 2019). Moreover, it cannot be excluded that the increased intraspecific competition associated with flocking, particularly when food is limited, can be detrimental for individuals that are less efficient foragers (Delestrade 1999). Recent long term research carried out in the French Alps showed that survival of females decreased with increasing flock size, likely because their food provisioning is prevented by males, which are dominant (Chiffard et al. 2019).

Ski resorts in the Alps increasingly use high resolution webcams to share panoramic views and promote themselves in the industry of winter recreational activities. Cameras can record the presence of middle-size birds like an Alpine Chough, and are equipped with remote access. Therefore, webcams may be a potential useful tool for eco-ethological studies without the physical presence of the observer in the field. Technological advances are opening a new world of monitoring biodiversity and in the last few years the use of camera traps for ecological purposes increased: the opportunity to do observations remotely is increasing the range of possibilities that researchers have to collect meaningful information about ecology and ethology thanks to the realization of observations during period of the year, period of the day, and environments that are hard to be investigated (Kucera et al. 2011). Alpine Choughs study is usually demanding in terms of fieldwork effort since they live in the alpine environment: in practical terms it means that monitoring them may lead fieldworkers to hike a lot including relevant ascent, accordingly to workers' accomodation, and fieldwork can include days with bad weather condition both during the summer and during winter. Furthermore, it can be financially expensive whether the fieldworkers have to stay in the field for a long period, so they can either find an accomodation close to the site or drive every day from home to the study area; such situation is more complicated when there is more than one study area.

The present research aims to test the effectiveness of webcams as a remote tool for studying winter bird synanthropy. Preinstalled fixed webcams were used to study the effect of anthropogenic and environmental variables on the winter flocks of Alpine Choughs in search of human food at ski resorts. We focused on flock size and time spent at the site as response variables, and assessed if they were related to the number of tourists and weather conditions (minimum temperatures and snowfall events). We assumed that both low temperature and heavy snow cover could negatively affect the winter availability of natural food sources and increase energy requirements, possibly encouraging birds to search for anthropogenic food.

3.2. Materials and methods

3.2.1 Selection of webcams

We remotely collected data on winter foraging flocks of Alpine Choughs at high altitude ski resorts by using Panomax webcams (Landesstraße, Henndorf, Austria, www.panomax.com). Panomax has 368 public webcams in 16 countries all around in the world, 70 of which are located in the European Alps. We focused on very popular alpine ski resorts whose camera view included both restaurant terraces used by tourists and choughs to feed, and the roofs of buildings used by birds to rest. Among webcams meeting the above requirements, we chose three sites located in the French, Swiss and Italian Alps (figure 6). Other webcams were excluded since one or more requirements were not met: several were located in the lowlands, while many of the high altitude webcams were placed in sites without restaurants and other buildings, or Alpine Choughs were not detected. At every site, cameras provided pictures of the area every 10 minutes, from 8 to 17. We focused on the winter period collecting a total of 13,704 pictures (i.e. 4,568 for each site), from December 14, 2018 (when the French camera provided the first picture) until March 8, 2019. We used all pictures to count birds attending the ski resort at any time of the day; pictures taken between 12 and 15 (when most of the skiers attended bars and restaurants) were used to count the maximum number of tourists. People were counted in a priori defined areas including the restaurant terrace (figure 7). For each picture, webcams also provided temperature from which we extracted daily minimum temperature. Snowfall data were provided by webcams as snow fallen during the night. However, webcams indicated snowfall events even for light snowfalls, when pictures showed no fresh snow presence. Therefore, we opted for indicating snowfall events only when they were noticeable and pictures showed a visually detectable uniform layer of fresh snow, so we indicated the presence/absence of snow on a daily basis according to the presence/absence of fresh snow.

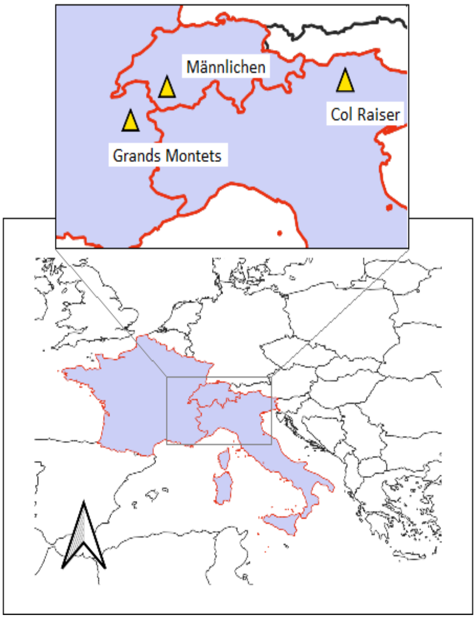

Figure 6. Location of the three study areas in the French, Swiss and Italian Alps.

Figure 7. Webcam views in the three study sites included both the restaurant terraces used by tourists and birds to feed, and the roofs of buildings used by birds to rest. People were counted in *a priori* defined areas including the restaurant terrace (red line). From top to bottom: the French site (Grandes Montets, GM), the Italian site (Col Raiser, CR) and the Swiss site (Männlichen, M).

3.2.2 Study sites

The chosen sites were located on flat terrain delimited by cliffs. Surroundings were characterized by snow covered grasslands and ski pistes; the Swiss site showed no tree cover, while conifers were present in the French and in the Italian site.

The French site was in the area surrounding the Lognan ski lift station named Grands Montets, below the Aiguille des Grands Montets in the Chamonix Mont-Blanc valley (45.9685°N, 6.943083°E, hereafter GM). GM was located at 1,972 meters above sea level (m.a.s.l.) and consisted of a ski lift station and a restaurant with a terrace. Observations of Alpine Choughs with colour rings used for long term studies on this population revealed that a flock up to 100 individuals frequented GM around midday and in the afternoon, while during the morning they generally descended to the closest villages, Argentiere and Le Tour (A. Delestrade personal observation).

The Italian site was in the area around Almhotel Col Raiser at Santa Cristina Valgardena in the Dolomites, north eastern Italian Alps (46.584972°N, 11.745167°E, hereafter CR). CR was located at 2,106 m.a.s.l. and consisted of a ski lift station, a restaurant with a terrace and some chalets. Large flocks of up to 100 individuals were known to visit localities about five kilometers from the site to feed on berries (such as *Sorbus* sp.) during winter. Irrespective of the season, birds might feed at high elevation around restaurants, at about 2,500 m.a.s.l., but they also had the possibility to descend to the valley bottom at about 1,000 m.a.s.l. (I. Prugger personal observation).

The Swiss site was in the resort of Männlichen (46.613139°N, 7.941083°E, hereafter M) and was located in Wengen, in the Swiss Bernese Pre-Alps. M is placed at 2,225 m.a.s.l. and consisted of a hostel, a restaurant with terrace and few cabins used as shops.

During this study, we included data from both non holiday and holiday periods. In particular we defined holiday period as the interval of time between the start and end dates of scholastic holidays in France, thus from the end of January to the beginning of March. This period also coincided with school holidays in Switzerland, while in Italy the break was shorter and fell between Christmas and January 6. However, the Italian site that we used in this study is especially used by tourists from Germany (whose holidays almost coincided with the Italian ones), Switzerland and Austria (astat.provincia.bz.it), where the latter's holiday period included February.

3.2.3. Data analysis

For the data analysis we used observations taken in a given day (every ten minutes) to calculate three daily parameters of flocking behaviour. They were: 1) the maximum flock size, 2) the frequency of presence, measured as the number of pictures showing birds (daily presence), thus an index of time spent on the site, and 3) the duration of the periods of continuous presence, measured as the longest series of pictures showing birds (long continuous presence, LCP). We used a generalized linear mixed model (GLMM) to analyze maximum flock size and daily presence, using Poisson and associated over-dispersed distributions for the response variable. Site was used as a random effect to account for the repeated observations design, but the low number of sites (3) in addition to having sites also as a fixed effect often led to a random effect variance of 0. We used zero-inflated Generalized Poisson distributions to account for different components of overdispersion. As fixed factors, we used day of year (with 1= January 1), either as a linear effect or a second order polynomial, minimum temperature (Tmin), maximum number of people, and holiday periods. To assess if holiday periods, snow, Tmin and maximum number of people had different effects at different sites, we used interactions between site and snow, holiday period, Tmin and maximum number of people. We used zero inflated models, thus models mixing a component with structural 0s (i.e., expected number of choughs is null) and a (generalized) Poisson component with the (positive) mean a function of the covariates. GLMMs were fit using the R package *glmmTMB* (Brooks et al. 2017). The relative fit of models was compared using AICc (calculated using the *AICc* function in *MuMIn*; Barton 2019), and we used the simplest models among models with the lowest AICc value for inference, focusing on parameter estimates and their uncertainty. Residual plots were used for all models to assess model fit. In particular, we assessed the autocorrelation of residuals, and as the first-order autocorrelation was <0.25 for all three sites, we used models with no autocorrelation. For LCP, as the distribution of the longest run of 1s in a binary sequence is not known analytically (e.g., Gordon et al. 1986), we used simulations to calculate the probability of different daily LCP. We then calculated a standardized difference between observed LCP and expected LCP by using: st_LCP=(LCP_obs-E[LCP])/sd(LCP).

We used the simulations to calculate P-values, i.e. probabilities to observe differences larger than the observed differences.

We used R 3.6.2 (R Development Core Team 2019) for analyses and plots.

3.3. Results

Results showed that the daily maximum flock size varied among sites with M, GM and CR showing the smallest (median =2, min-max=0-15) intermediate (median=35, min-max=0-109) and largest (median=70, min-max=0-150) maximum flock size, respectively (figure 8). The model with the best relative fit (table 4) showed that daily maximum flock size was negatively affected by daily Tmin at all sites, but with different effect sizes (-0.041 95% CI [-0.061; -0.022] for CR, -0.089 [-0.11; -0.063] for GM, -0.11 [-0.19, -0.03] for M; differences between sites are given in table 5). Daily maximum flock size was also positively affected by the maximum number of people present at restaurant terraces, with a stronger effect at M 0.018 [0.010; 0.024], weaker at GM 0.0074 [0.0038; 0.011] and close to zero at CR -0.0018 [-0.0069; 0.0034]. Days with snow had smaller maximum flock size (-0.36 [-0.60, -0.13]). Maximum flock size was related to the daily presence: the daily presence increased with the maximum flock size at M and GM (figure 9).

The daily presence was related to daily Tmin, the number of tourists and holiday periods, but with variable effect sizes (table 6). Low temperature led to a lower number of pictures with Alpine Choughs at M (-0.13 [-0.21; -0.06]), but the effect was smaller at GM (-0.053 [-0.087; -0.019]) and CR (-0.018 [-0.046; 0.010]). High tourist numbers led to higher number of presence at M (0.023 [0.016; 0.029]), with a smaller effect at GM (0.006 [0.002; 0.010]) and no evidence for such an effect at CR (-0.0001 [-0.009; 0.007]; table 7). Holiday periods led to lower number of pictures with bird presence at CR (-0.80 [-1.20; -0.40]), with no evidence for an effect at M (-0.068 [-0.64; 0.50]) and GM

(0.046 [-0.28; 0.38]). The analysis of the duration of the periods of continuous, uninterrupted presence of birds (LCP) showed that at CR and GM Alpine Choughs were present in a continuous way (mean standardized difference between observed length of longest sequence and expected length under a binomial distribution: CR: 5.84; GM: 5.92), while at M their presence was less continuous (mean standardized difference 2.77; all P-values < 0.01). Furthermore, at GM presence was more continuous when Tmin was lower (figure 10).

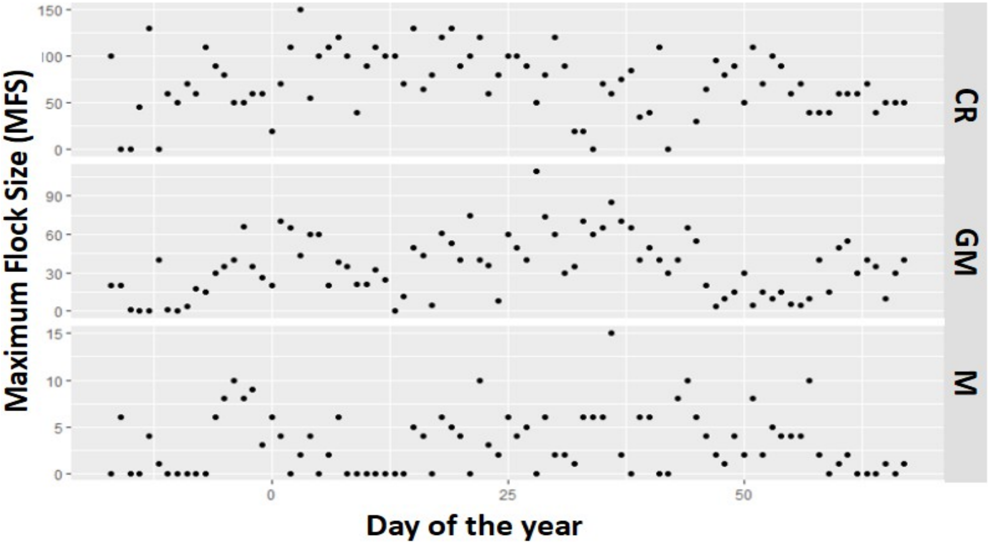

Figure 8. Flock size variations according to date and site.

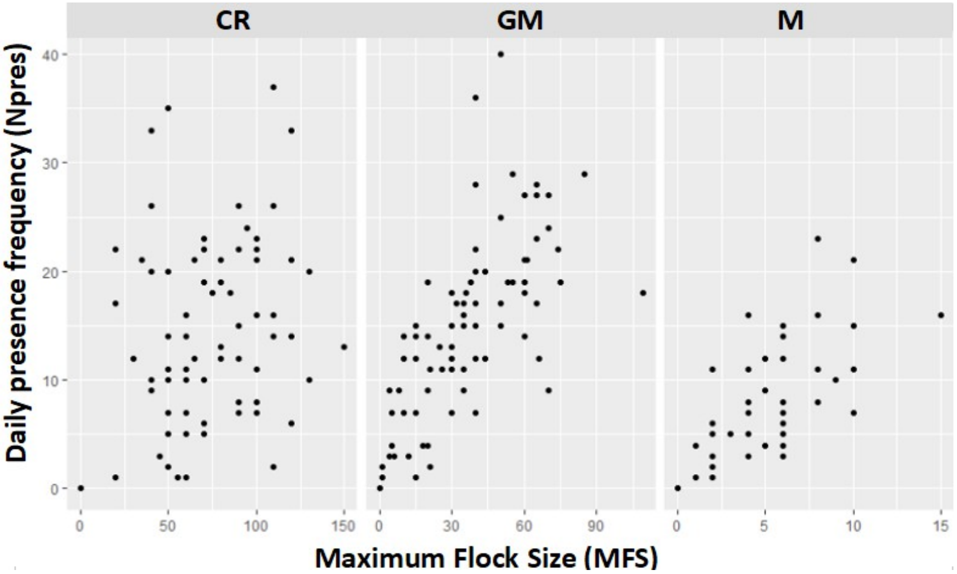

Figure 9. Variation of daily number of presence of Alpine Choughs each 10 minutes according to maximum flock size.

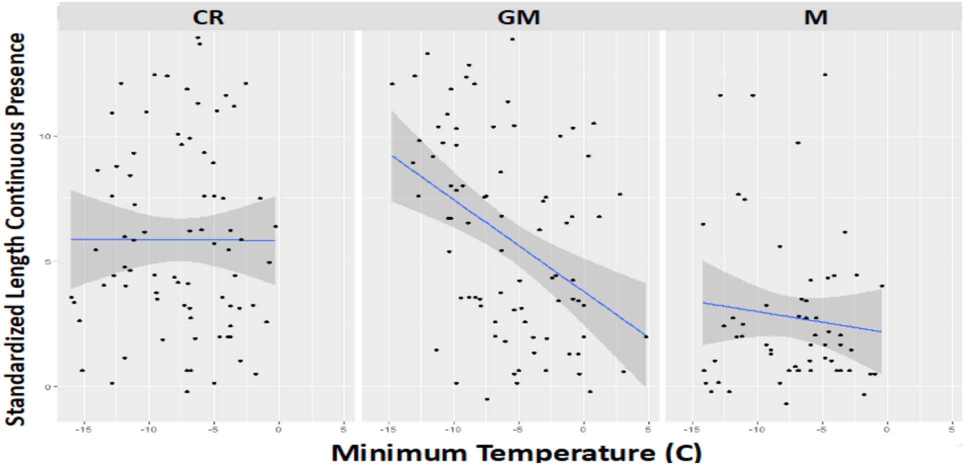

Figure 10. The figure shows the standardized continuous presence (0 = expected length under a binomial distribution) of Alpine Choughs according to

the minimum temperature and the site. Presence of birds was more continuous at CR and GM, where values are often greater than 5.

Table 4. Model selection for Maximum Flock Size. Models were ranked according to AICc, and the five best models with the same structure for the structural zeroes are shown. The best model is indicated in italic and first. We also provide AICc values with different distributions and structure for structural zeroes to show that they gave poor fit to the data. All models included site as a random effect.

Structural 0s	Poisson/Generalized Poisson model	Distribution	AICc	AIC weight
doy	*(maxpeople+Tmin)*site+snow*	*Gen Poisson*	*1885.9*	*0.55*
doy	(maxpeople+Tmin)*site+snow+holidays	Gen Poisson	1887.8	0.21
doy	(maxpeople+Tmin+snow)*site	Gen Poisson	1889.4	0.09
doy	maxpeople*site+Tmin+snow	Gen Poisson	1891.3	0.04
doy	(maxpeople+snow+Tmin)*site +holidays	Gen Poisson	1891.5	0.03
none	(maxpeople+Tmin)*site+snow	Gen Poisson	2022.4	
1	(maxpeople+Tmin)*site+snow	Gen Poisson	1898.4	
doy^2	(maxpeople+Tmin)*site+snow	Gen Poisson	1886.2	

doy	(maxpeople+Tmin)*site+snow	Poisson	2992.3	

Table 5. Zero inflated model of daily maximum flock size in relation to minimum temperature (Tmin), daily maximum number of people (maxpeople), and site (M and GM) using CR as reference category. Interactions are indicated with ":" between variables, and they are given as differences between each level (sites) and the reference site. Conditional and zero-inflation models are shown in table 5.a and 5.b, respectively. GM: the French site (Grandes Montets), CR: the Italian site (Col Raiser), M: the Swiss site (Männlichen). The random effect site was estimated as 0 for this model.

5.a. Conditional model

Daily maximum flock size	**Estimate ± Std. Error**	**z value**	**P-value**
Intercept (site=CR)	4.097 ± 0.140		
Tmin (site=CR)	-0.041 ± 0.010	-4.10	<0.001
Maxpeople (site=CR)	-0.0018 ± 0.0026	-0.67	0.50
Intercept Site=GM	-1.416 ± 0.208	-6.80	
Intercept Site=M	-4.308 ± 0.520	-8.30	
Tmin:site=GM	-0.048 ± 0.016	-2.90	0.0038
Tmin:site=M	-0.072 ± 0.043	-1.70	0.09
maxpeople:site=GM	0.0092 ± 0.0032	2.86	0.004
maxpeople:site=M	0.020 ± 0.0044	4.48	<0.001
Snow	-0.364 ±0.119	-3.06	0.002

5.b. Zero-inflation model (structural 0s)

Daily maximum flock size	**Estimate ± Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	-2.50 ± 0.403		
Doy	-0.084 ± 0.031	-2.73	0.006

Table 6. Model selection for number of Presence. Models were ranked according to AICc, and the five best models with the same structure for the structural zeroes are shown. The best model is indicated in italic and first. We also provide AICc values with different distributions and structure for structural zeroes to show that they were less parsimonious. All models included site as a random effect but the estimate for random effect was 0 for the best model. The overdispersion parameter for the selected model was 4.63.

Structural 0s	Poisson/Generalised Poisson model	Distribution	AICc	AIC weights
doy	*(holidays+maxpeople+Tmin)*site*	*Gen Poisson*	*1570.2*	*0.56*
doy	(holidays+maxpeople+Tmin)*site+snow	Gen Poisson	1571.9	0.24
doy	(holidays+maxpeople)*site+Tmin+snow	Gen Poisson	1574.1	0.08
doy	(holidays+maxpeople)*site+Tmin	Gen Poisson	1574.9	0.05
doy	(holidays+maxpeople+snow+Tmin)*site	Gen Poisson	1575.7	0.03
doy^2	(holidays+maxpeople+Tmin)*site	Gen Poisson	1569.5	
1	(holidays+maxpeople+Tmin)*site	Gen Poisson	1580.4	
none	(holidays+maxpeople+Tmin)*site	Gen Poisson	1606.2	
doy	(holidays+maxpeople+Tmin)*site	Poisson	1915.5	

Table 7. Zero inflated model of daily number of presence in relation to minimum temperature (Tmin), daily maximum number of people (maxpeople), holidays and site (M and GM) using CR as reference category. Interactions are indicated with ":" between covariates. Conditional and zero-inflation models

are shown in table 7.a and 7.b, respectively. GM: the French site (Grandes Montets), CR: the Italian site (Col Raiser), M: the Swiss site (Männlichen).

7.a. Conditional model

Daily number of presence	**Estimate ± Std. Error**	**z value**	**P-value**
Intercept (site=CR)	2.712 ± 0.200		
Holidays	-0.804 ± 0.204	-3.92	<0.001
Tmin (site=CR)	-0.018 ± 0.014	-1.27	0.20
Maxpeople (site=CR)	-0.001 ± 0.004	-0.27	0.78
Intercept:Site=GM	-0.650 ± 0.282		
Intercept:site=M	-3.36 ± 0.527		
holidays:site=GM	0.857 ± 0.266	3.19	0.001
holidays:site=M	0.799 ± 0.358	2.06	0.039
Tmin:site=GM	-0.036 ± 0.022	-1.54	0.123
Tmin:site=M	-0.118 ± 0.039	-2.98	0.003
maxpeople:site=GM	0.007 ± 0.004	1.57	0.11
maxpeople:site=M	0.023 ± 0.005	4.47	<0.001

7.b. Zero-inflation model

Daily number of presence	**Estimate ± Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	-2.45 ± 0.43		
Doy	-0.083	0.034	0.014

3.4. Discussion

Environmental drivers of flocking behaviour at ski resorts

Results obtained from the study of about 14000 webcam pictures demonstrated that Alpine Choughs feeding on scraps can modulate their flocking behaviour at ski resorts according to three main environmental drivers, thus the number of tourists, cold intensity and snowfall. The three study sites showed evident differences in the number of birds, with the smallest flocks at

M and the largest at CR. In all sites, the daily maximum flock size increased when minimum temperature decreased and when the number of tourists at restaurants increased. Similarly, the time spent (frequency of presence) around the restaurant increased when the minimum temperature decreased and increased when the number of tourists increased. Continuous presence during the day was also affected by daily minimum temperature, at least in one site, GM, where Alpine Choughs stayed more continuously when temperature was lower. We also found that the presence of fresh snow caused a decrease in the maximum flock size in all ski resorts. This may be explained by assuming snowfall has a significant effect on Alpine Chough movements, by inducing birds to move to lower areas for feeding, thus reducing flock size at higher ski resorts. Villages at lower elevations occur at all three sites. The small villages of the valley bottom around Chamonix (French site) were regularly visited by birds looking for food scraps (C. Vallino personal observation).

A generic association between tourist presence and birds looking for food is well known in scavenger species. Storch and Leidenberger (2003) showed that in summer, during the post fledging period, Alpine Choughs moved around restaurants when tourists were present. Our results formally demonstrated that birds were also attracted by tourist activity in winter, and that Alpine Choughs were not influenced by the presence of people *per se*, but rather by the *number* of people gathering at the site. These corvids have not only learnt to associate the presence of people with the presence of food, but they also clearly know that more people discard more scraps.

In high elevation ecosystems, weather conditions may significantly affect several aspect of bird biology. Results of a 27 year demographic research project on marked Alpine Choughs at GM suggested that high winter and spring temperatures may affect spring survival, especially of females (Chiffard et al.

2019). The present study demonstrates that harsh weather conditions may also drive birds' flocking behaviour. Alpine Choughs tended to concentrate and stay longer around restaurants of ski resorts (i.e. both the number of birds in flocks and the time spent at the site increased) when cold intensity increased. Since human supplied leftovers represent predictable food (Bridge et al. 2008, Oro et al. 2013), we hypothesize that birds are prone to exploitation in case of increased need of energy intake, thus when the temperature drops and "natural" food sources are scarce.

The opportunistic use of food provided by man may be facilitated by the pronounced sociality of the Alpine Chough, that it is known to forage and move in flocks throughout the year (Cramp and Perrins 1994, Delestrade 1994, Rolando et al. 1997, Delestrade 1999). In the present study, the daily presence frequency increased with maximum flock size.

Benefits derived from foraging in flocks include a reduced predation risk, possibly due either to the presence of more vigilant individuals, allowing a reduction of single birds' investment in vigilance, or to a diminished risk of individual predation, when the predator can choose among many potential prey (Hamilton, 1971, Lima 1995, Roberts 1996, Rolando et al. 2001). Accordingly, vigilance is expected to decrease in larger groups since they potentially provide more safety against predators. Alpine Chough displays a decline in vigilance with group size, and the same was shown in the Red-billed chough *P. pyrrhocorax* (Rolando et al. 2001). This relationship might help to understand the apparent paradox of birds exploiting human food scraps despite human disturbance. In large flocks, the disturbance due to the presence of people would be counterbalanced by benefits provided by the availability of anthropogenic food and, maybe, by a diminished vigilance activity.

An additional benefit of gathering in winter at ski resorts is that these sites could provide protection against predation. Alpine Chough predators are certainly disturbed by human presence and keep away from those areas.

The ecological topic of this research (i.e. the flocking behaviour of Alpine Choughs foraging on scraps at ski resorts) falls within the never-ending discussion about costs and benefits of anthropogenic food, with several studies providing evidence of both (Acquarone et al. 2002, Kurosawa et al. 2003, Schoech and Bowman 2003, Shochat et al. 2004, Oro et al. 2013 , Will et al. 2015, West and Peery 2017). The availability of anthropogenic food for Alpine Choughs at many alpine ski resorts is so large and constant that it represents a case of supplementary food unintentionally provided to wild birds. Supplementary feeding represents a major intervention in avian ecology, as feeding influences almost every aspect of bird ecology, including reproduction, behavior, demography, and distribution (Robb et al. 2008). However, this human intervention may produce positive impacts, such as aiding species conservation programs, and negative ones, such as increased risk of disease transmission (Robb et al. 2008) or reduced breeding when food is provided during winter (Plummer 2018).

Adaptation and supplementary feeding

A flexible feeding behaviour allows choughs to exploit all opportunities of high elevation ecosystems: when the snow melts, for instance, birds can forage on wet ground around snow patches to extract *Typula* larvae (Rolando and Patterson 1993a). The flocking behaviour *per se* may also be an adaptive trait, favouring both optimal foraging and antipredator protection. The continuous use of anthropogenic food may interact with the adaptation process. In the Alpine Chough, the standard organization of flocks foraging on natural grasslands, with birds regularly spaced and in close visual contact with one another, may be disrupted in birds foraging on scraps left around by tourists. The flock disruption hypothesis is supported by previous observations that showed a dramatic reduction of flock size and stay times in birds foraging at high elevation restaurants compared to those foraging on pastures in late summer (Vallino et al. 2019). The availability of anthropogenic food is also responsible for the disruption of winter movement patterns. In valleys with little ski development, flocks of Alpine Choughs showed circadian migration movements, flying towards snow free valley bottoms to look for food in the morning, and coming back to the roosts in high elevation cliffs in the afternoon. Vice versa, in ski developed resorts, birds stayed in town all day, roosting on buildings and opportunistically feeding on scraps (Rolando et al. 2003).

Webcams as remote providers of eco-ethological data

The results of the present study proved that webcams may be a useful remote tool for eco-ethological research. This conclusion is also supported by some general remarks: i) preinstalled webcams allow data collection for free, and can therefore be useful for projects with small budgets; ii) the use of this kind of technology allows a huge amount of data to be collected in shorter time frame than in the field (fieldwork is always time consuming); iii) working at high elevation can be prohibitive in cases of extreme weather conditions, whilst using webcams means observations can be collected in virtually all environmental conditions; iv) webcam monitoring of flock behavior may last all day long and over the winter season, which is never possible for the field observer.

Despite the above quoted advantages, this study also highlighted some caveats. First, we don't know what a minimum species size would be to be sufficiently detectable through the webcams. As far as choughs is concerned, pictures captured only a part of the flock because not every bird was always correctly located in front of the camera. Therefore, an error term should be taken into account when estimating flock size. Second, despite the use of high definition images, colour rings of marked individuals at GM could not be discerned. Therefore, the remote observer has no way of knowing whether the same individuals were attending the site over time, or if there was a high turnover of individuals. Third, is not possible to have information about the portion of the environment that is not included in the webcam view. Parts of the above mentioned caveats can be mitigated by the by the installation of webcams specially set for research purposes, and the combination of remotely collected data with fieldwork or additional available data about study areas and populations (e.g., demographic data). Fieldwork can be useful to obtain more precise information about the effective flock size and the attendance of the site by marked birds: therefore, it would be possible to include such fieldwork data in the study to limit potential mistakes. Moreover, visiting the study site is useful to have a global vision of the area and to notice important features such as the presence of alternative food sources or further factors influencing bird movements.

3.5. Conclusions

In this study, we used preinstalled webcams to identify environmental factors that drive the winter flocking behaviour of Alpine Choughs feeding on scraps at ski resorts. We focused on flock size and time spent at the site as dependent variables, and tested if they were correlated with the number of tourists and/or weather conditions (minimum temperatures and snowfall events). Results suggested that Alpine Choughs tended to concentrate opportunistically around restaurants when the number of tourists or the intensity of cold increased. Therefore, birds could modulate their presence at the feeding sites according to precise environmental variables. This tuning capability may suggest that the Alpine Choughs frequenting high elevation resorts in winter have developed addiction to anthropogenic food, raising concerns about the long term effects on adaptation processes and on preservation of populations. To better understand the effect of this kind of food, future research should compare reproductive outputs (offspring weight and survival, for instance) of supplemented and non supplemented populations. Moreover, given that the effect of anthropogenic food may depend on the type of food provisioned (Plummer at al. 2018), specific analyses of nutritional profiles should also be planned.

In methodological terms, the results obtained suggest that preinstalled webcams, have a few caveats, but they can be successfully employed in eco-ethological research, on condition that the use of remotely collected data is combined with prior and simultaneous fieldwork, thus allowing the evaluation of data in the light of more precise and contextual information recorded in the field.

As pointed out before, Panomax at the time of the data collection for the present study had about 360 webcams around the world: whether other companies operate similar systems they represent a huge potential resource. If these companies could be engaged to make some slight adjustments, without compromising their goals, then this could offer a new branch of research.

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4. CHAPTER III

Flocking of foraging Alpine Choughs reflects the availability of grasshoppers and the level of human development in high elevation ecosystems

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Abstract

Mountain ecosystems are subject to many pressures, including changes in land use, rising temperatures and increasing recreational activities. These factors may disrupt food webs, threatening the survival of organisms and, ultimately, ecosystem functioning. However, few studies focus on the trends of different groups joined by trophic links in alpine ecosystems. The Alpine Chough, *Pyrrhocorax graculus*, a gregarious bird that moves in flocks, is an ideal target species within this framework since it has a grasshopper-based diet during the summer and may inhabit sites heavily developed for recreational activities. We tested therefore whether flock size co-varied with grasshopper abundance along an elevational gradient in two alpine areas with different levels of human disturbance. Alpine Chough flock size and grasshopper abundance were measured along elevational transects. The median flock size was analysed in relation to grasshopper abundance and biomass, also accounting for effects of

period (i.e. from June to mid-August), site, and elevation, by performing negative binomial GLMMs. In both study areas, flock size increased where the abundance of prey increased, i.e. flocks of Alpine Choughs were larger at the elevational belt where grasshoppers were more abundant. This result may indicate the capacity of the species to follow large scale fluctuations in their key insect prey. On the other hand, the relationship between flock size and grasshopper biomass (weight measured in mg) was positive at the natural site and negative at the tourist site. This suggests that in the area with a high level of human pressure, other factors, such as the availability of human food, may disturb the natural relationship between Alpine Choughs and their key prey. Overall, our results indicate that flocking of foraging Alpine Choughs reflects both the abundance of grasshoppers and the level of human development.

4.1. Introduction

High elevation ecosystems are sensitive to environmental change (Böhm et al. 2001; Maggini et al. 2014; Flousek et al. 2015) and they are currently subject to a number of increasing pressures (Dirnböck et al. 2003; Thuiller et al. 2005; Dirnböck et al. 2011; Braunisch et al. 2013; Viterbi et al. 2013), including temperature increases (Sekercioglu et al. 2008; Dirnböck et al. 2011; Chamberlain et al. 2013), changes in land use (Laiolo et al. 2004; Probo et al. 2014; Bazzi et al. 2015; Jähnig et al. 2018), and increases in recreational activities (Arlettaz et al. 2013; Rixen and Rolando 2013).

In the Alps in particular, much research has shown that both land abandonment (Laiolo et al. 2004; Bazzi et al. 2015; Koch et a.l 2015), and ski-piste construction (Rolando et al. 2007; Patthey et al. 2008; Negro et al. 2010; Caprio et al. 2011; Negro et al. 2013; Caprio et al. 2016), by acting on habitat mosaics and structural diversity, may negatively affect animal communities, such as birds and invertebrates. The destiny of high elevation animal species is of particular concern, because climate change will cause the shift of both vegetation and human activities. For instance, it's likely that operators and stakeholders will shift skiing activities and ski-pistes to higher elevations (Elsasser & Messerli 2001; Brambilla et al. 2016).

The study of high elevation food webs in this transforming environment is particularly urgent because any change in trophic interactions between organisms may affect organism survival and, ultimately, ecosystem functioning. Climate change, for instance, can affect trophic relations through the phenological mismatch that may cause reduction of food supply for breeding birds (Flousek et al. 2015; Thackeray et al. 2016). However, studies on food web components and/or on trends in different groups joined by trophic links are scarce. Indeed, studies focussing on the distribution and trends of alpine species (Chamberlain et al. 2012), and relationships between predators and prey in human impacted high elevation areas, have been severely neglected so far (Vallino et al. 2019). The Alpine Chough, *Pyrrhocorax graculus*, a gregarious bird that moves in flocks throughout the year, is an excellent target species in this framework. It is generally assumed that flocking may be advantageous to detect predators (Rolando et al. 2001; Jiménez et al. 2013), and has a survival value in relation to food finding (Ward and Zahavi 1973), for instance through sharing information about food localization (Fernández-Juricic et al. 2004).

The diet of the Alpine Chough is highly varied and depends on the temporal availability of invertebrates and vegetable food (Rolando and Laiolo 1997). This species is also known to be a scavenger that may eat food discarded by high elevation bars and restaurants (Rolando and Patterson 1993a; Delestrade 1995). Higher densities of birds occurred around high altitude touristic areas where they moved around restaurants when tourists were present

(Storch and Leidenberger 2003). In summer, however, the main food resources are grasshoppers (Orthoptera), that are particularly abundant in alpine meadows above the treeline (Koch et al. 2015). Grasshopper remnants may be found in over 80% of droppings (Rolando and Patterson 1993a; Rolando & Laiolo 1997; Laiolo & Rolando 1999). Therefore, Alpine Choughs and grasshoppers represent a predator-prey interaction of alpine ecosystems. Several studies have demonstrated that the distribution of avian predators may reflect those of their prey (Davoren et al. 2003; Katayama 2012), and that experimental reductions of the abundance of grasshoppers can drive concomitant suppressions of predator bird densities (Norelius & Lockwood 1999; Pescador et al. 2019). However, such studies have never tested the response of an alpine species.

Here, we tested whether Alpine Chough flock size co-varied with grasshopper abundance and biomass along an elevational gradient in two alpine areas. As grasshoppers are important food items for the Alpine Chough, we expected flock size to match spatially and temporally with prey abundance and biomass. We surveyed two areas differing in human pressure, with the most urbanized site characterized by high altitude restaurants and bars where anthropogenic food is available for Alpine Choughs. Therefore, we expected to find a weaker relationship between choughs and natural key prey in the most urbanized area, and a stronger relationship in the natural site, where alternative food sources are absent.

4.2. Materials and methods

4.2.1. Study areas

The study was conducted in the north-western Italian Alps (in the Aosta Valley region) and included the tourist area around Cervinia (45.9336° N, 7.6292° E, hereafter C), and the Dondena basin in Mont Avic Natural Park

(45.6518° N, 7.5621° E, hereafter MA). MA is a relatively undisturbed area with few buildings (mainly mountain huts and facilities used by shepherds) that was visited by around 11,000 people from June to August 2015 during the summer (unpublished report, Mont Avic Natural Park 2016). The area of Cervinia is a popular tourist destination, characterized by a marked anthropization due to leisure activities, such as skiing and other outdoor pursuits, and to the presence of high-altitude ski resorts, bars and restaurants. The Cervinia skiing complex includes 72 ski pistes in Italy (plus an additional 78 ski pistes on the Swiss side), 200 km of tracks covered with artificial snow and a snowpark that reaches as high as 2800 m a.s.l. Tourists can participate in activities such as cross-country skiing, heliskiing on the glacier, trekking and downhill skiing; consequently, Cervinia is frequented by tourists year-round. During the summer of 2017 alone, 63,000 people visited the area (Cervino spa, personal communication). Ski developments are particularly concentrated at Plateau Rosà (3500 m asl), where a lot of restaurants and bars around the cable-car station produce garbage all year round.

4.2.2. Fieldwork

Alpine Chough survey

Direct observations on birds feeding in pastures were carried out almost daily from June to August 2016-2017 from 8 a.m. to 5 p.m. We surveyed all the sites potentially frequented by Alpine Choughs, walking along transects or reaching favourable observation points. Observations were made on daily basis, changing the time of day each site was observed to account for possible daily variations in behaviour. For each observation, we recorded flock size (i.e. counting the number of individuals in the foraging group) and elevation (for more details see Vallino et al. 2019). Since most birds were not marked, we could not distinguish single individuals.

Grasshoppers and habitat description

In 2016 and 2017, two elevational transects were placed in each area to monitor the distribution and phenology of grasshoppers. Each transect was formed by seven to eight sampling plots located on grasslands and spaced at intervals of 100 m in elevation along each transect. Plots were monitored from June to mid-August and were placed from 2000 m asl (C) or 2100 m asl (MA) to 2700 m asl. These elevations have been demonstrated to be most frequented by Alpine Choughs at Cervinia during the summer (Rolando and Patterson 1993a). The locations of transects were selected based on observations of foraging Alpine Chough during a pilot study in 2015. In each plot, we surveyed grasshoppers three times during each visit, each time passing a one meter pole, kept close to the ground, through the vegetation for two meters, therefore sweeping a total area of 6 m^2. Grasshoppers that flushed were counted to determine their abundance/m^2 (Rolando and Patterson 1993a). To obtain the biomass (i.e. the weight of the grasshoppers expressed in milligrams), we collected 100 individuals at different developmental stages. In the lab, grasshoppers were measured (body length, from the head to the end of abdomen, in mm), dried and weighed. Through this procedure, we identified three reference body length classes (i.e. ≤ 10 mm, 10 – 15 mm, > 15 mm) and derived the relative average weight of each class. For each plot, we measured the body length of six randomly selected individuals to obtain a unique value indicating the average body length of local grasshoppers. Finally, the global biomass of grasshoppers in the plot was obtained by multiplying the average weight of the corresponding body length class (i.e. that encompassing the average body length of grasshoppers in the plot) by the number of grasshoppers counted.

In every grasshopper sampling plot, we described the habitat composition by visually assessing the percentage cover of rocks, mosses, grass, shrubs, bare ground and snow in a circle of 10 m radius. The presence of a stream, a path or active grazing was also recorded, however none of them proved to be relevant during the analysis. To describe habitat structure, we also measured the height of 20 randomly selected stems per plot in order to derive an average grass height value.

To describe taxonomic diversity, in 2017 during the realization of transects and in 2019, we randomly collected grasshoppers. In 2017, we collected 3 random individuals for each plot every time that we repeated the transect, although only adults could be used for identification. Therefore, in 2019 in late July and August (when most individuals were at the adult stage), along the same transects and at the same plots identified in the previous field seasons, we collected additional individuals. Collected grasshoppers were stored in plastic tubes until their preparation in the laboratory, where they were identified *a posteriori* (species nomenclature and taxonomic order follow Massa et al. 2012).

4.2.3. Data analysis

Alpine Chough flock size

We modelled Alpine Chough flock size (i.e. the number of birds observed foraging together) in relation to period, site, elevation and its quadratic term and interactions between study site and elevation, and between period and elevation, by means of a Generalized Linear Mixed Model, in a statistical hypothesis testing framework. Periods were defined as 14 day intervals which corresponded to grasshopper sampling sessions (i.e. period 1, 2, 3, 4 and 5 corresponding to early June, late June, early July, late July, and early August, respectively). Continuous variables were centred and scaled in order that effect sizes of variables measured at different scales could be directly compared in model outputs (Zuur et al. 2009). Since overdispersion was found in preliminary Poisson GLMMs, Negative Binomial GLMMs were performed using the R package lme4 (Bates et al. 2015). Multiple observations were carried out on the same day, hence date was fitted as a random factor to account for possible non-independence. The final model was identified after a model reduction procedure whereby non-significant terms were dropped from the full model until only significant terms ($p \leq 0.05$) remained (Zuur et al. 2009).

Grasshopper abundance and biomass

For habitat variables, since structure and composition are intrinsically correlated, we reduced the number of variables, minimizing the effects of multicollinearity and revealing patterns in the data by performing a Principal Component Analysis (PCA: Gaunch 1984). We modelled grasshopper abundance and biomass in relation to period, site, habitat structure (i.e. the scores of the first four Principal Components), elevation and its quadratic term and interactions between study site and elevation, and period and elevation, using a Generalized Linear Mixed Model. Plot identity was fitted as a random factor to account for possible non-independence of observations in the same plot. Since overdispersion was found in a preliminary Poisson GLMM of abundance of grasshoppers, we performed Negative Binomial GLMMs, while for biomass we specified a Gaussian distribution of errors and an identity link function. Prior to modelling, elevation was scaled and centred.

All models were built with all explanatory terms fitted. Final models were selected following a backward stepwise procedure, by progressively dropping non-significant variables.

All models were built with all explanatory terms fitted. Final models were selected following a backward stepwise procedure, by progressively dropping non-significant variables.

Alpine Chough and grasshopper relationship

To assess whether Alpine Chough flock size was linked to grasshopper abundance, we considered all the flocks observed and grasshoppers counted within 100 m elevational belts (one grasshopper sampling plot per belt). For each altitudinal belt and period, we extracted the median value of flock size (i.e. the most frequent number of individuals observed) and we modelled the median flock size in relation to the abundance and biomass of grasshoppers per period, site, elevation and its quadratic term and interactions between study site and grasshopper abundance or biomass. We used the median flock size as the response variable because the mean would have been particularly susceptible to the influence of outliers and extreme values. Since overdispersion was found in preliminary Poisson GLMs of median flock size, we performed Negative Binomial GLMMs. Prior to modelling, elevation and grasshopper abundance were scaled and centred. Preliminary analysis showed that median flock size had a positive relationship with grasshopper abundance and a negative relationship with biomass at C site. Therefore, we decided to introduce the residuals of the relationship between grasshopper biomass into the model as a function of grasshopper abundance.

Median flock size was modelled with the residuals of the linear model of grasshopper biomass as a function of abundance (appendix VI, fig. 4), site, elevation and the interaction between residuals and site. Residuals measured whether grasshopper biomass found in an elevational belt was above or below the expected value given by the modelled relationship between biomass and abundance. Positive values of the residuals indicated elevational belts with a measured biomass that was above the expected given the number of grasshoppers found, while negative values represented sites where biomass was below the expected values given the relationship with abundance.

4.3. Results

Alpine Chough flock size

Overall, we observed 949 flocking events: the elevational belt where the highest numbers of flocks were observed was 2400-2500 m asl at Cervinia (236 observations) and 2200-2300 m asl (198 observations) at Mont Avic (appendix I). Flock size was smaller at MA than at C (mean number of individuals ± SD equal to 5.89 ± 8.01, N = 405 at MA, 9.56 ± 14.81, N = 544; median flock size equal to 3 at MA, and 4 at C; Negative Binomial GLMM: chough flock size at MA relative to C estimate -0.51± 0.13, z value -3.81, Pr <0.001). Flock size showed no relationship with period or elevation. Birds foraged on high elevation pastures, but at C in late July they moved to Plateau Rosà at 3500 m asl to feed on scraps.

Grasshopper abundance, biomass and habitat

As a whole, 15 grasshopper species were identified *a posteriori*. The most abundant, ubiquitous species was *Chorthippus biguttulus biguttulus* (Linnaeus, 1758), followed by *Aeropus sibiricus* (Linnaeus, 1767) (appendix II).

In the habitat ordination analysis, the first four principal components (PC1, PC2, PC3, PC4) accounted for 73.15% of the total variation in the habitat structure matrix, with eigenvalues > 1 (table 8). Rock cover and moss cover were positively correlated with PC1, while average herbaceous vegetation height, standard deviation of herbaceous vegetation height and grass cover were negatively correlated with PC1, suggesting an elevational gradient with greater vertical grass extent and grass cover in lower elevation plots, and higher moss and rock cover at higher elevations. Shrub cover and trail presence were negatively correlated with PC2, while bare ground cover and grass cover were negatively correlated with PC3 and ski-piste presence nearby the sampling plot was positively correlated with PC4.

The grasshopper abundance model showed a significant interaction between period and elevation as a result of the phenology of grasshoppers, whose peak abundance reached the maximum value at different elevations in different periods, showing the maximum at about 2300 m. asl in period 2 (figure 11). As shown in table 9, grasshopper abundance had minimum values in period 1 and maximum values in period 2, with intermediate values in other periods. The relationship with elevation was quadratic, with lower values at 2000 and 2600 m. asl and reaching the maximum value at 2300 m asl.

Results of grasshopper biomass models indicated that prey biomass was related to period and included PC1 (table 10). Grasshopper biomass increased in period 2 and had a peak in period 3 compared to the reference category (i.e. period 1). Also, the biomass was higher in sampling plots with greater coverage and height of grass, and decreased in plots with higher percentage of rocks and mosses.

Relationship between Alpine Chough and grasshoppers

The median flock size per 100 m elevational belt was positively related to the abundance of grasshoppers, thus the number of Alpine Choughs in the flocks and the number of prey increased in tandem (figure 12). The median flock size was lower in site MA (figure 12) and had a quadratic relationship with elevation (figure 12, appendix IV), with maximum median flock size at 2500 m. asl. The median number of Alpine Choughs showed a significant interaction between grasshopper biomass and site, thus median flock size increased with increasing grasshopper biomass in MA, while it decreased with increasing grasshopper biomass in C (figure 13). The model included a quadratic relationship with elevation with maximum median flock size at 2500 m. asl (figure 13, appendix V). This contrasting result was further confirmed by modelling the residuals of the relationship between grasshopper abundance and biomass and median Alpine Chough count. Our results showed an interaction between the residuals and site, meaning that the size of flocks was larger in C in elevational belts with grasshopper abundance that was below the expected values. Conversely, in MA the relationship between median flock size and residuals was positive, meaning that flock size increased in elevational belts with higher grasshopper biomass. The results showed an interaction between residuals and site - median flock size increased with higher values of residuals in MA, but decreased in C (figure 14, appendix VI).

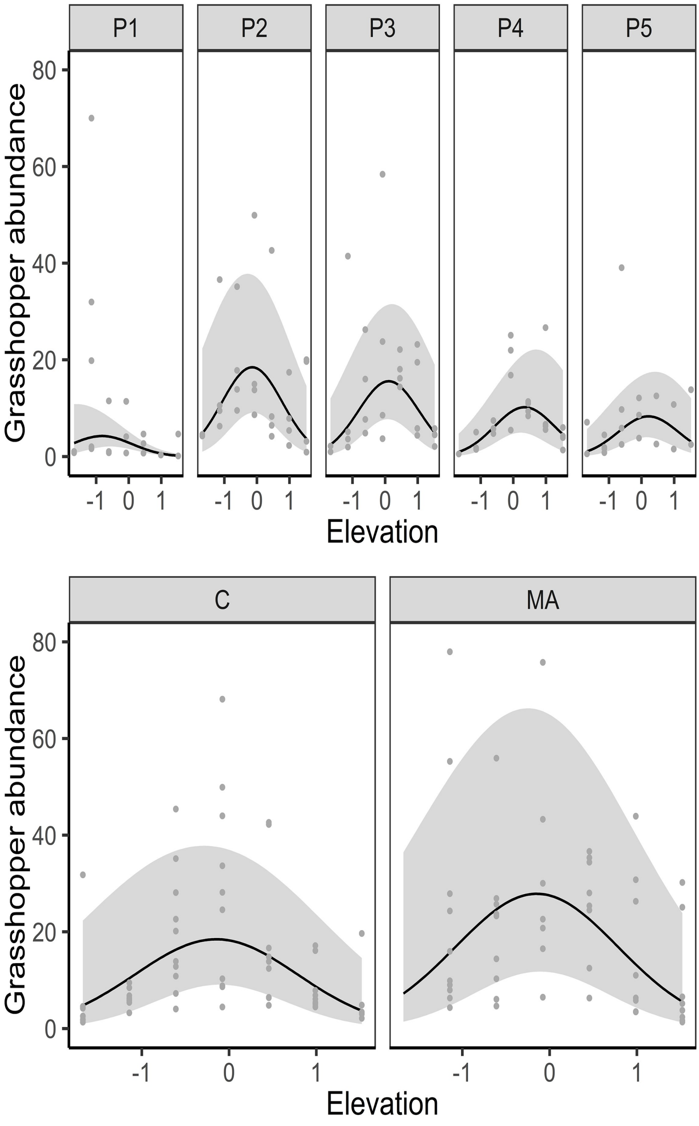

Figure 11. Graphs showing grasshopper abundance trends during the different sampling periods (top) and in the two study areas according to elevation (bottom). In the top figure, grasshopper abundance and standardized elevation are shown on the y and x axes respectively; P1, P2, P3, P4 and P5 correspond to early June, late June, early July, late July, and early August, respectively. In bottom figure grasshopper abundance and elevation are shown on the y and x

axes in C and MA site. Shaded areas represent 95% confidence limits.

Table 8. Results of principal component analysis carried out on average herbaceous vegetation height (VHM) and standard deviation (VHSD), cover data and trail presence. The highest loadings are given in bold italic type.

Variables	PC1	PC2	PC3	PC4
VHM	***-0.401***	0.358	0.338	-0.146
VHSD	-0.386	0.352	0.357	-0.069
Shrub cover	0.030	***-0.564***	0.332	-0.094
Trail presence	-0.097	***-0.504***	0.345	-0.176
Ski-piste cover	-0.006	0.035	-0.044	***0.842***
Snow cover	0.140	-0.033	-0.317	-0.121
Bare ground cover	0.077	-0.002	***-0.436***	-0.345
Rock cover	***0.462***	0.329	0.201	-0.172
Moss cover	***0.445***	0.253	0.190	-0.153
Grass cover	***-0.493***	0.024	-0.401	-0.195
Eigenvalues	1.567	1.407	1.295	1.104
Variance explained	24.57	19.8	16.78	12

Table 9. GLMM of grasshopper abundance in relation to period (with Period 1 set as reference category), elevation, elevation squared (indicated as 'Elevation^2') and site (MA = Mont Avic). Interactions are indicated with the ':' between variables.

Grasshopper abundance	Estimate ± Std. Error	z value	Pr(>|z|)
(Intercept)	1.044 ± 0.298	3.50	0.000456 ***
Period 2	1.837 ± 0.236	7.77	7.92e-15 ***

Period3	1.673 ± 0.237	7.06	1.64e-12 ***
Period 4	1.191 ± 0.242	4.93	8.44e-07 ***
Period 5	1.032 ± 0.258	4.00	6.30e-05 ***
Elevation	- 0.946 ± 0.248	-3.78	1.56e-04 ***
Elevation^2	- 0.577 ± 0.143	-4.04	5.42e-05 ***
Site MA	0.41 ± 0.250	1.64	0.10 .
Period 2:elevation	0.775 ± 0.251	3.08	0.002 **
Period 3:elevation	1.070 ± 0.254	4.21	2.54e-05 ***
Period 4:elevation	1.340 ± 0.267	5.02	5.07e-07 ***
Period 5:elevation	1.186 ± 0.281	4.22	2.42e-05 ***

Table 10. GLMM of grasshopper biomass according to period, PC1 and site (MA = Mont Avic).

Grasshopper biomass	**Estimate ± Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	-0.018 ± 0.166	-0.11	0.914
Period 2	0.383 ± 0.157	2.44	0.0169 *
Period3	0.549 ± 0.160	3.42	0.0009 ***
Period 4	0.305 ± 0.164	1.85	0.0668
Period 5	0.216 ± 0.170	1.27	0.2068
PC1	-0.139 ± 0.050	-2.80	0.0063 **
Site MA	0.358 ± 0.196	1.82	0.0819

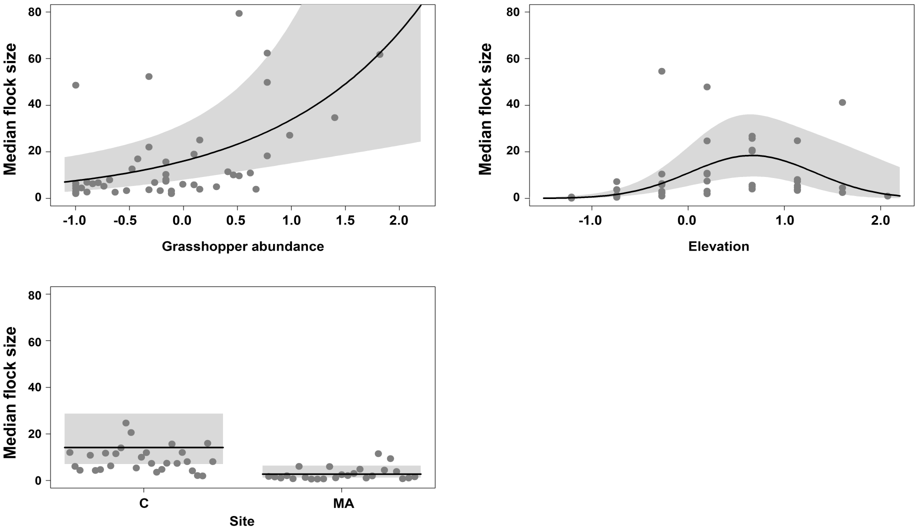

Figure 12. Relationship between median flock size and grasshopper abundance (centred and scaled), site and elevation (centred and scaled). Shaded areas represent 95% confidence limits.

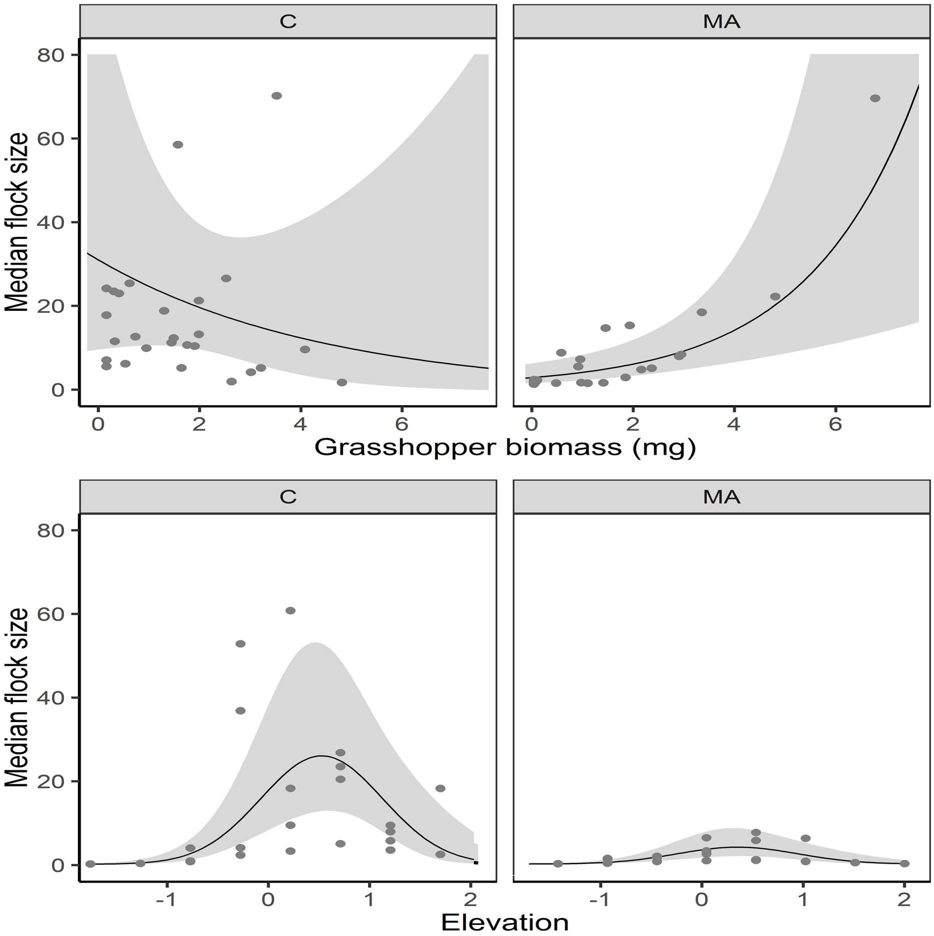

Figure 13. Relationship between median flock size and grasshopper biomass (mg), and median flock size and elevation for each site. Shaded areas represent 95% confidence limits.

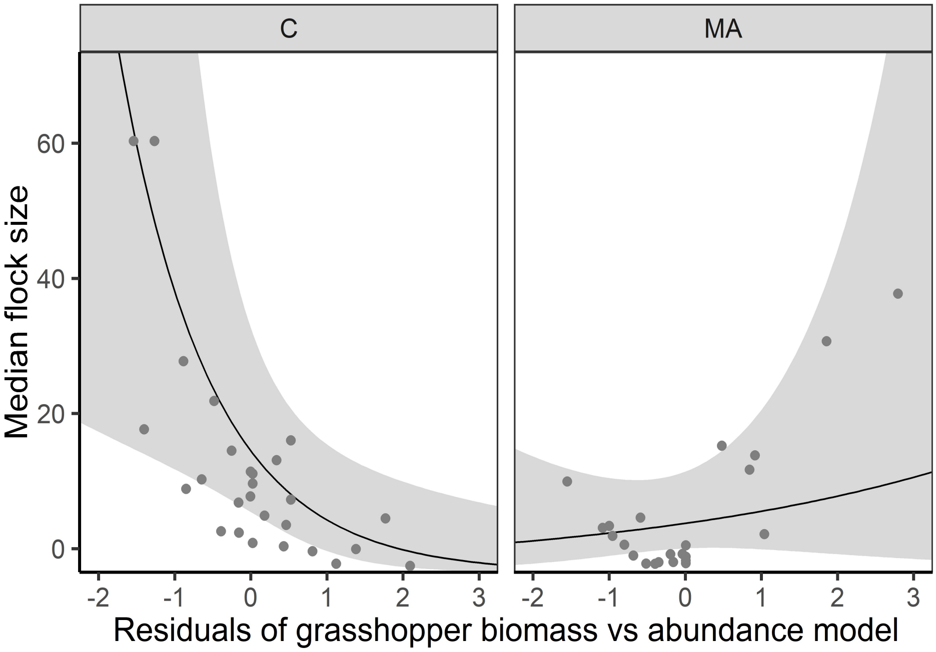

Figure 14. Relationship between median flock size and interaction between residuals of the model of grasshopper biomass and abundance (both centred and scaled) for each site. Shaded areas represent 95% confidence limits.

4.4. Discussion

The present study was carried out in two areas with different levels of human development.

MA and C had numerically different Alpine Chough populations. A maximum flock size of 180 individuals was observed at C in 2017 (Vallino et al. 2019). At the same site, Rolando et al. (2003) recorded up to 300 individuals in the 1990s. Conversely, at MA, the population was estimated as being formed of around 60 individuals according to Bocca (2000), but we recorded a maximum flock size of 30 individuals (CV 22-06-17). Period showed no significant relationship with flock size, thus indicating that flock size depended on other factors, like elevation. Conversely, period, along with elevation, influenced the abundance of grasshoppers, which had a peak in late June, at an intermediate elevation. Furthermore, the interaction between period and elevation proved that during the summer, grasshopper abundance increased with elevation, but with different rates in different sites, thus potentially following climatic and environmental parameters such as increasing temperature and grass growth (Wachter et al. 1984; Van der Plas et al. 2012). Grasshopper biomass was extrapolated *a posteriori* by weighing samples in the lab which may be a source of bias since it does not take into account each individual sampled in the field; nonetheless, we are confident of the robustness of our approach due to the results of grasshoppers abundance (estimated in the field) which corroborate with the results obtained from grasshopper biomass.

Flock size and grasshopper abundance

In both sites, the number of birds in flocks had a linear relationship with prey abundance and a non-linear relationship with elevation. Therefore, flocks were larger at the elevational belt where grasshoppers were more abundant. This result suggests that Alpine Choughs can follow large scale fluctuations of the most abundant and key insect prey. However, the ability to follow the fine scale variations of grasshopper abundance may be obstructed by some factors, such as the Alpine Chough's heterogeneous diet composition, and the species' pronounced sociality. Indeed, the diet includes several invertebrate groups and other food sources (Rolando and Patterson 1993a; Rolando and Laiolo 1997; Laiolo and Rolando 1999) and therefore it is likely that Alpine Chough are not entirely dependent on grasshoppers. Sociality is important in this species (Cramp and Perrins 1994), and it could also play a role in influencing foraging behaviour and flocking. Indeed, Alpine Choughs seem to prioritize group bonds over foraging success, with flocks formed by young individuals and adult females staying together with adult males (which have access to food first) even when food is scarce and not sufficient to feed every component of the flock (Delestrade 1999). Moreover, the potential benefit gained from feeding in big flocks is doubtful, since the number of items ingested increases in relation to the number of birds forming the group (Rolando et al. 1997, Vallino et al. 2019), but the time spent in the foraging patch decreases (Rolando et al. 1997). Therefore, other than prey abundance distribution, sociality may also affect the selection of the foraging patch and influence flock size.

Flock size and grasshopper biomass

The relationship between flock size and grasshopper biomass was site dependent, being positive at MA (as expected given that abundance and biomass are correlated), but negative at C., where large flocks concentrated where there were many grasshoppers, although prey had a smaller size. Moreover, in this area, the high availability of anthropogenic food may have disturbed the natural relationship between Alpine Choughs and the biomass of the key prey. Indeed, the presence of human-discarded food may influence the foraging behaviour of Alpine Choughs, as proved by Storch and Leidenberger (2003), who demonstrated that higher densities of birds can be found around high elevation areas frequented by humans. Storch & Leidenberger (2003) also showed that Alpine Choughs can shape their range according to the presence of such food sources, and that they frequent more areas around mountain restaurants when more people are present, i.e. around lunch time. This is in line with the ranging behaviour of Alpine Chough flocks observed at C in late summer, when they abandoned pastures and moved to Plateau Rosà to feed on scraps left by restaurants and bars. Previous research carried out in these very same areas has documented other aspects of human impacts on flocks. Tourist presence in summer has been shown to directly disturb foraging behaviour, by reducing both feeding rates and the time spent in patches (Vallino et al. 2019). The urbanization at C has significantly changed the ranging behaviour in winter, when birds stay in the town all day, roosting on buildings and occasionally feeding on scraps, whereas other populations in the Aosta valley display circadian migration movements, flying in flocks towards snow free valley bottoms to look for food in the morning, and coming back to the roosts in high elevation cliffs (often above 3000 m asl) in the afternoon (Rolando et al. 2003). A further potential factor influencing chough relationships with grasshopper biomass at C site is that the peak of prey abundance took place in late June, while the maximum biomass was reached in early July.

4.5. Conclusions

Environmental changes occurring at high elevation will likely affect food webs and relationships between trophic levels (Flousek et al. 2015, Thackeray et al. 2016). However, several gaps are present in relation to the understanding of trends and interactions of alpine species joined by trophic links. The present study considered a generalist alpine bird species and its main insect prey. Results demonstrated that even a generalist predator species, by modulating flock size, may be able to cope with large scale variation in the abundance of key prey - birds were concentrated in elevational belts that had the highest grasshopper densities.

Flock size, however, was positively associated with grasshopper biomass in the natural park (as expected given that abundance and biomass are correlated), but negatively associated with it in the tourist ski-developed area, suggesting that in this area other factors, like the availability of human food and the relative scarcity of grasshoppers, may disturb the natural relationship between Alpine Choughs and their key prey. In this regard, it is interesting to note that in the ski-developed site, birds were seen to move to a high cable-car station to feed on scraps in late July, suggesting, in keeping with previous research (Rolando et al. 2003, Vallino et al. 2019), that development for leisure activities and the massive presence of tourists in mountains may markedly affect the flocking behaviour of the Alpine Chough. All in all, our results indicate therefore that flocking of foraging Alpine Choughs may reflect both the availability of grasshoppers and the level of human development.

We acknowledge that our study area is limited to only one natural site and one touristic area and that important factors that influence grasshoppers (e.g. micro-habitat parameters; Joern 1982, and grazing Wettstein et al. 1999, Jauregui et al. 2008) and birds (e.g. social factors, Delestrade 1999) were not fully considered in this study. Finally, a more detailed knowledge of Alpine Chough diet would be useful to identify potential factors (e.g. the exploitation of other food sources and their availability) influencing the relationship between this species and its key prey.

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5. DISCUSSION AND CONCLUSION

5.1. Major results and final remarks

Alpine ecosystems are sensitive to many factors such as rising temperatures and variations in mountain area management (Laiolo et al. 2004, Maggini et al. 2014, Probo et al. 2014, Bazzi et al. 2015, Jähnig et al. 2018), the construction of buildings and structures linked with recreational activities such as winter sports (Rixen and Rolando 2013), and direct impacts on wild species causing disturbance that can cause lead to in species physiology (Ellenberg et al. 2007, Arlettaz et al. 2015) and behaviour (Gill et al. 2007, Jiménez et al. 2013). During my PhD project, I focused on the interactions between an alpine bird species, the Alpine Chough, and humans in high elevation areas.

Alpine Chough foraging behaviour and human presence

The first paper focused on Alpine Chough behaviour, and the major objective was to deepen the knowledge about the effect of direct human disturbance on Alpine Choughs during foraging events. Therefore, our aim was to understand whether the presence of people could negatively affect feeding behaviour. Thanks to our study, we confirmed that the target species can modify its behaviour according to human activities, as proposed in a previous study by Jiménez et al. (2013). Moreover, we also demonstrated that such variations in behaviour can lead to either increased or decreased foraging success. Indeed, according to the level of disturbance, different reactions to human presence were shown by chough populations. In particular, habituation was found in Alpine Choughs living in the more disturbed site only, while it was absent in the less disturbed area. In particular, in situations where humans approached a flock of foraging Alpine Choughs, birds could either develop habituation, going ahead with the foraging activity (Jiménez et al. 2013) or escape (Gill et al. 2007), thus leaving the foraging patch, and the adoption of such different behaviour is due to the context of where the population lives. Thus, populations living in more disturbed areas can potentially become more and more confident with humans, while populations inhabiting less urbanized areas with fewer people tend not to develop habituation. Therefore, as the very word indicates, the habituation process needs time to happen, and results suggest that the disturbance event must be repeated several times in order to be perceived as a non-disturbance event. Furthermore, these two possible reactions lead to different effects on the individuals, since in the first case choughs don't lose the foraging patch, while they lose it in the second case. Therefore, at first glance, habituation should provide benefits to birds, while conversely its absence should negatively affect them. Moreover, when habituation is present, food sources can be obtained easily, such as human food scraps (Oro et al. 2013). However, there are indications of negative effects due to the exploitation of anthropogenic food (Shochat 2004; Gilbert et al. 2016). Nonetheless, other factors need to be taken into account to have a broader framework, since other parameters can impact choughs. However, our first study gave some general indications, suggesting that choughs can live in areas with a high level of human disturbance, adopting behavioural changes that help them to better relate to the context.

Alpine Chough attendance of human tourist sites during winter

The second part of the project was also focused on Alpine Chough behaviour, but it had the aim to understand whether and how chough movements and attendance of places frequented by humans were influenced by climate and human food presence during winter in tourist sites. Indeed, especially during winter, choughs commonly use high elevation tourist sites to forage on human food (Rolando and Patterson 1993b; Delestrade 1995; Laiolo et al. 2001; Rolando et al. 2003, Storch and Leidenberger 2003). Therefore, human presence was used as indicator of human discarded food availability since we considered ski-resort sites characterized by bars and restaurants with terraces where people could leave leftovers. During this study, we used webcams to test whether they can be employed to investigate social species in the alpine environment. The latter may be characterized by harsh environmental conditions that make working at high altitude energy and time consuming, thus the knowledge of alpine bird populations is often poor. Therefore, testing different methods to collect data in such environments can be useful to highlight good alternatives to fieldwork. During this study, we found that Alpine Choughs were influenced by the number of tourists, the cold intensity, and the presence of fresh snow. Flock size increased when minimum temperature decreased and when the number of tourists at restaurants was higher. This first result indicated that cold intensity may influence chough flocking behaviour, leading them to concentrate around restaurants at ski resorts. Moreover, human food scraps represent predictable food (Bridge et al. 2008, Oro et al. 2013), and this was clearly indicated by the fact that Alpine Choughs are able to associate the presence of people with the presence of food, and they also know that more people means more scraps. Conversely, we found that snowfall events led to smaller flocks, probably due to the exploitation of other lower elevation areas to feed.

Results of the present study highlighted that webcams may be useful for eco-ethological research, since they allow free data collection, they permit the collection of huge amounts of data in shorter times than that possible in the field, they facilitate the collection of data when fieldwork is prohibitive due to bad weather, and they allow to monitor flock behavior all day long and all across the winter season. However, this study also highlighted some caveats: flock size was an estimation based on those birds that were visible in the pictures, it was impossible to read colour rings, just a limited area in front of the camera was visible, and the use of webcams without field observations lacks information about local vegetation, nesting/roosting and movements. Therefore, pre-installed webcams can be successfully employed in eco-ethological research. However, taking some precautions, such as combining the use of webcams with a little fieldwork, can further facilitate the work.

Alpine Chough and grasshopper relationship: the influence of human disturbance

Finally, in the third study, we took into account the spatio-temporal distribution of natural food availability as a further factor potentially affecting birds together with human presence, as highlighted in the first study. The main objective was to study Alpine Chough and its key prey to understand whether the abundance of prey and predator were related in space and time. We developed the study in two areas with differing levels of anthropogenic disturbance in order to highlight eventual influence of human presence on such relationships. Results suggested that Alpine Choughs can follow large scale fluctuations of their key prey, grasshoppers, but the ability to follow the fine scale variations of such prey abundance may be obstructed by the fact that other insects are present and used to feed, and by sociality. Other than key prey abundance, we took into account key prey biomass, and we found a negative relationship between chough and prey biomass in the more urbanized area. The tourist site showed slightly lower abundance of grasshopper than the other site, and showed the presence of ski-pistes. Therefore, ski-pistes may have reduced the presence of natural pastures with adequate coverage and height of grass, and consequently led to smaller grasshoppers. The negative relationship between Alpine Choughs and grasshopper biomass can be explained by the presence of anthropogenic food that may have disturbed the natural relationship between Alpine Choughs and their key prey.

Therefore, results showed a clear relationship between Alpine Choughs and their key prey. However, some indications suggested that man can alter such relationships, especially when high levels of human influence on the alpine ecosystem are present.

5.2. Conclusions and future perspectives

The three studies presented here had the main objective of contributing to the knowledge of an avian alpine species, trying to shed some light on human-avifauna interactions in high elevation ecosystems. We confirmed that the Alpine Chough has the capacity to vary its behaviour, and we demonstrated that it can modify its attitude according to the situation of a certain area, thus different populations living in a given site can adopt divergent strategies either to avoid or to accept disturbance. Such strategies show both benefits and negative effects at the same time. However, some potential effects (either positive and negative) still need to be studied in order to be fully understood. We also demonstrated that although this species is linked to human activities now, it is also influenced by environmental factors such as temperature and snow during winter. However, even and especially during the most challenging season, Alpine Choughs were proved to be able to exploit positively the presence of humans at high altitude through the frequentation of high elevation sites where anthropogenic food is left by tourists. Finally, we highlighted that although human food seems to play an all important role in chough diet during winter, Alpine Choughs and grasshopper abundance have a positive relationship during the summer, when choughs use grasshoppers as their main prey. However, even during this warm period, indications suggested that the presence of recreational activities may ruin the relationship between Alpine Choughs and their key prey in two ways, i.e. the presence of ski-pistes that alter grasshopper biomass, and the availability of human food that attracts choughs which abandon natural foraging patches to move to areas with anthropogenic food.

In conclusion, human supplied food sources seem to be all important in influencing Alpine Chough behaviour and movements. However, during the realization of the three studies, we could often observe choughs foraging on natural patches where grasshoppers were not the exclusive prey. Therefore, a more detailed knowledge about Alpine Chough natural diet would be useful to have a deeper knowledge of the species ecology.

As far as diet is concern, a further aspect that needs to be taken into account is the availability of anthropogenic food: such factor represents an interesting and unclear point in avian ecology (Robb et al. 2008) since this human intervention may produce both positive and negative impacts (Robb et al. 2008; Plummer 2013) depending on the quality of food provided and on the species. Therefore, research on the effects of anthropogenic food specifically on Alpine Choughs is required. Moreover, climate change is known to potentially influence interactions between predators and prey (Flousek et al. 2015, Thackeray et al. 2016), therefore it will likely affect Alpine Choughs and their prey. Hence there is the need to focus on a more detailed knowledge of Alpine Chough diet to identify potential factors influencing the relationship between this species and its key prey, and to evaluate which changes may affect the high altitude community according to different climate change scenarios.

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APPENDICES

Appendix I. GLM of the relationship between grasshopper biomass and abundance.

Grasshopper biomass	**Estimate ± Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	1.457 ± 0.122	11.96	-2e-16 ***
Grasshopper abundance	1.563 ± 0.123	12.73	-2e-16 ***

Appendix II. List of grasshopper species identified *a posteriori* and their abundance in the two study areas. Species nomenclature and taxonomic order follow Massa et al. 2012.

Species	N in C	N in MA	Total N
Anonconotus alpinus (Yersin, 1858)	2	16	18
Anonconotus baracunensis Nadig, 1987		1	1
Anonconotus ghilianii (Camerano, 1878)	2	4	6
Anonconotus alpinus/ghilianii		4	4
Platycleis grisea (Fabricius, 1781)	5		5
Bohemanella frigida frigida (Boheman, 1846)	4	5	9
Epipodisma pedemontana (Brunner von Wattenwyl, 1882)		8	8
Omocestus haemorrhoidalis (Charpentier, 1825)	21		21
Omocestus rufipes (Zetterstedt, 1821)	4	1	5
Omocestus viridulus (Linnaeus, 1758)	37	2	39
Stenobothrus lineatus lineatus (Panzer,1796)	32		32
Aeropus sibiricus (Linnaeus, 1767)	20	33	53
Aeropedellus variegatus (Fischer de Waldheim, 1846)	1	4	5
Chorthippus apricarius apricarius (Linnaeus, 1758)	14		14
Chorthippus biguttulus biguttulus (Linnaeus, 1758)	69	80	147

Juvenile forms	24	50	74
TOTAL ABUNDANCE	235	208	443

Appendix III. GLM of the median flock size in relation to grasshopper abundance, elevation and site.

Median Alpine Chough flock size	**Estimate ± Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	-2.739 ± 0.354	-7.74	9.64e-15 ***
Grasshopper abundance	0.746 ± 0.251	2.97	0.003 **
Elevation	1.590 ± 0.436	3.64	0.00027 ***
Elevation^2	-2.33 ± 0.635	-3.67	0.00024 ***
Site MA	-1.631 ± 0.451	-3.61	0.0003 ***

Appendix IV. GLM of the median flock size in relation to grasshopper biomass, elevation and site.

Median Alpine Chough flock size	**Estimate ± Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	3.266 ± 0.555	5.88	3.88e-09 ***
Grasshopper biomass	-0.233 ± 0.245	-0.95	0.34
Elevation	1.291 ± 0.428	3.02	0.00257 **
Elevation^2	-2.997 ± 0.671	-4.47	7.87e-06 ***
Site MA	-2.636 ± 0.617	-4.28	1.91e-05 ***
Grasshopper biomass x Site MA	0.711 ± 0.265	2.68	0.00731 **

Appendix V. GLM of the median flock size in relation to grasshopper abundance residuals, elevation and site.

Median Alpine Chough flock size	**Estimate ± Std. Error**	**z value**	**Pr(>|z|)**
(Intercept)	2.768 ± 0.357	0.34	9.14e-16 ***
Grasshopper residuals	-0.927 ± 0.361	-2.21	0.01034 *
Elevation	1.293 ± 0.380	-2.56	0.00068 ***
Elevation^2	-2.810 ± 0.610	3.40	4.06e_06 ***
Site MA	-0.944 ± 0.428	-4.61	0.02727 *
Grasshopper residuals x Site MA	1.171 ± 0.494	2.37	0.01779 *

Appendix VI. GLM of the relationship between grasshopper biomass and abundance.

Grasshopper biomass	**Estimate ± Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	1.457 ± 0.122	11.96	-2e-16 ***
Grasshopper abundance	1.563 ± 0.123	12.73	-2e-16 ***

ANNEXE

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ORIGINAL ARTICLE

The contribution of broadscale and finescale habitat structure to the distribution and diversity of birds in an Alpine forest-shrub ecotone

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Abstract

In a mountain context, the forest-shrub ecotone is an area of high biodiversity. Relatively little is known about the habitat requirements of birds in this habitat, yet it is facing potential threats from changes in grazing practices and climate change. Moreover, it is not clear at which scale habitat associations should be assessed in Alpine birds. Further information on key habitat components affecting bird communities of the ecotone is needed in order to inform management strategies to counteract potential habitat loss, and to better inform predictions of how bird communities may be affected by future environmental change. Data on bird occurrence and broadscale (land cover) and finescale (vegetation structure and shrub species composition) habitat variables were collected in an Alpine forest-shrub ecotone in Val Troncea (northwestern Italian Alps) in order to address two objectives: to identify the key habitat variables associated with the occurrence of individual species and with the diversity of the bird community; and, to assess which scale of habitat measurement (broadscale, finescale or both combined) is needed to model bird occurrence. Broadscale variables, or combinations of broadscale and finescale variables, tended to have the best performing models. When combined models performed best, shrub species identity was included in many cases. Shrubs also played an important role in explaining variations in species diversity and richness. Vegetation structure was of relatively little importance, either for individual bird species or for species richness and diversity. These findings suggest that management should strive to maintain a mosaic of habitats whilst minimizing forest encroachment, which could be achieved through targeted grazing. Broadscale habitat data and data on shrub species composition should provide a sufficient basis for identifying relevant species-specific habitat parameters in a mountain environment in order to model future scenarios of effects of habitat change on the bird community of the alpine forest-shrub ecotone.

Keywords Habitat management · Grazing · Mountains · Vegetation structure · Species distribution models · Habitat mosaic

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Zusammenfassung

Die Rolle von groß- und kleinräumigen Habitateigenschaften für Verbreitung und Diversität von Vögeln des Waldgrenz-Ökotons der Alpen

Das Waldgrenz-Ökoton der Alpen ist ein Gebiet, welches durch eine hohe Biodiversität gekennzeichnet ist. Obwohl aktuelle Bedrohungen durch Klimawandel und Veränderungen in der Beweidungspraxis omnipräsent in diesem Areal sind, sind die Habitatansprüche, welche für die Vögel in diesem Bereich gelten, bislang kaum erforscht. In welchem Maßstab diese Habitatanforderungen für Alpenvögel erfasst werden sollten, ist ebenfalls nicht bekannt. Es ist daher erforderlich, jene Habitatelemente zu identifizieren, die eine Schlüsselrolle für die Vogelgemeinschaften im Waldgrenz-Ökoton der Alpen spielen. Mit Hilfe dieser Informationen wird es in Zukunft möglich sein, potentiellem Habitatverlust entgegenzuwirken und Vorhersagen zu treffen, wie Vogelgemeinschaften des Ökotons auf zukünftige Umweltveränderungen reagieren könnten. Durch die Aufnahme von Daten über das Vogelvorkommen sowie groß- (Landbedeckungsdaten) und kleinräumigen (Daten zur Vegetationsstruktur und zur Straucharten-Zusammensetzung) Habitatdaten im Waldgrenz-Ökoton des Naturparks Val Troncea (NW Italien) wurden zwei Zielstellungen verfolgt: Die Identifikation von Habitatelementen, welche für das Vorkommen einzelner Arten sowie für die Vogeldiversität und den Vogelartenreichtum von wesentlicher Bedeutung sind und die Beurteilung des Maßstabs zur Habitatdatenaufnahme (großräumig, kleinräumig oder eine Kombination aus beidem), welcher erforderlich ist, um das Vorkommen einer Art modellieren zu können. Großräumige Habitatvariablen oder eine Kombination von groß-und kleinräumigen Habitatvariablen führte zu den besten Modellen. Wenn die besten Modelle durch eine Kombination von Habitatvariablen erzielt wurden, war die Identität der Strauchart eine oftmals beinhaltete Variable. Generell spielten Sträucher eine wichtige Rolle, um Variationen in der Vogeldiversität und dem Vogelartenreichtum zu erklären. Von geringer Relevanz für individuelle Vogelarten sowie Vogelartendiversität und -reichtum waren kleinräumige Habitatvariablen zur Vegetationsstruktur. Diese Ergebnisse zeigen, dass zukünftige Naturschutzmaßnahmen darauf abzielen sollten, das Habitatmosaik im Waldgrenz-Ökoton zu erhalten und einer Ausbreitung des Waldes entgegenzuwirken. Dies könnte durch gezielte Beweidung erreicht werden. Großräumige Habitatdaten sowie Daten zur Strauchartenzusammensetzung stellten zudem eine solide Basis dar, um relevante artspezifische Habitatansprüche für alpine Vogelarten zu identifizieren und potentielle Auswirkungen zukünftiger Habitatveränderungen auf die Vogelgemeinschaft des alpinen Waldgrenz-Ökotons modellieren zu können.

Introduction

Mountain biodiversity is under a range of environmental pressures, including land use change (Laiolo et al. 2004), increased human leisure activities (Rolando et al. 2007; Arlettaz et al. 2007), climate change (Sekercioglu et al. 2008; Dirnböck et al. 2011), and interactions between these factors (e.g. Brambilla et al. 2016). Climate change may be a particular problem given that the rate of warming in mountains is approximately double the global average, a trend that is expected to continue (Böhm et al. 2001). A consequence of climate change is that vegetation zones are likely to shift upwards—for example, the upper forest limit has shifted to higher elevations in many mountain regions in line with rising temperatures (Harsch et al. 2009). The loss of high-altitude open habitats as a consequence of such vegetation shifts has been identified as a potential future conservation problem (Sekercioglu et al. 2008; Chamberlain et al. 2013), especially as the proportion of species of conservation concern tends to increase with elevation (Viterbi et al. 2013). However, vegetation shifts in some areas have also been due to abandonment of grazing, which maintained the forest limit at a lower altitude than would be possible under only climatic constraints. This effect has had a greater effect than climate change on tree line shifts in the European Alps (Gehrig-Fasel et al. 2007).

The ecotone between the forest and the alpine grassland zone is characterized by a high structural diversity, typically being a mix of open grassland areas, pioneer forest and shrub species. It is therefore often an area of high biodiversity (Dirnböck et al. 2011). Whilst abandonment of grazing and vegetation shifts due to climate change may, at least initially, have the capacity to create new habitats, in particular through colonization by shrub species (Laiolo et al. 2004), there are also threats to this habitat. First, it seems plausible to consider that structural diversity is a key factor driving the relatively high biodiversity of the ecotone (e.g. MacArthur and MacArthur 1961), and grazing is likely to maintain a habitat mosaic that underpins the structural diversity, hence further abandonment of grazing may be detrimental. Second, many mountainous areas do not reach altitudes that are high enough to maintain the ecotone habitat given the likely magnitude of vegetation shifts (Dirnböck et al. 2011)—such areas are likely to be mostly forest in the future. Third, it cannot be assumed that all components of the vegetation community will respond simultaneously to climate change (Theurillat and Guisan 2001). For example, there is evidence that vegetation zones respond differentially to warming temperatures in the Alps (Cannone et al. 2007) , and that trees and shrubs may respond differentially to reduced snow cover resulting from climate change. Snow has insulating properties that benefit some shrub species from frost damage (Neuner 2014), and lower snow cover or earlier snow melt could potentially lead to a net loss of ecotone habitat.

Within the gradient of alpine habitats from mountain forest to the highest altitude nival zone (Kapos et al. 2000; Körner and Ohsawa 2006), the highest biodiversity is typically found in the forest-shrub ecotone, yet it has been little studied in an avian context. Whilst common species such as Dunnock *Prunella modularis*, Linnet *Carduelis cannabina*, Lesser Whitethroat *Sylvia curruca* and Wren *Troglodytes troglodytes* have been studied in lowland habitats (usually at higher latitudes), the few studies that have assessed habitat associations in these species in mountain habitats have considered only broadscale, usually remote-sensed, habitat data and have not considered more detailed measures of habitat complexity (Chamberlain et al. 2013, 2016). With a few exceptions, notably Black Grouse *Tetrao tetrix* (e.g. Patthey et al. 2012; Braunisch et al. 2016) and Ring Ouzel *Turdus torquatus* (von dem Bussche et al. 2008), there is as yet insufficient information to determine at which scale species-habitat associations should be assessed in order to plan conservation actions for the majority of common Alpine ecotone species in the context of environmental changes. Furthermore, such studies would also allow improvement of our ability to forecast potential effects of future environmental change for ecotone species. Species distribution models for typical ecotone species such as Dunnock, Wren and Tree Pipit *Anthus trivialis* show generally less good model performance, and greater inconsistency in model outcomes between different scenarios of change, compared with forest and grassland species (Chamberlain et al. 2013, 2016). This may be because these species are more dependent on finescale habitat characteristics, such as vegetation structure, and hence are not well-described by land cover and topographic variables that typically underpin many species distribution models.

Heterogeneity plays an important role in bird species diversity in a range of different habitats, including farmland (Benton et al. 2003), rainforests (Guerta and Cintra 2014), temperate forests (Freemark and Merriam 1986) and grasslands (Hovick et al. 2014). However, the role of heterogeneity in the forest-shrub ecotone is still not well understood. We would expect that, based on the influence of habitat diversity and structural vegetation diversity, species richness in the ecotone would be positively associated with measures of habitat heterogeneity. A recent study on Black Grouse in the Swiss Alps showed that horizontal and vertical structural heterogeneity was the best predictor of the occurrence of the species (Patthey et al. 2012). We similarly expect that ecotone species will in general be positively associated with habitat complexity. In this study, we consider complexity in terms of the diversity of vegetation structure, the heterogeneity in vegetation height, and also in terms of the habitat mosaic formed by shrubs, grassland and forest. We focus in particular on non-linear relationships between the bird community and shrub cover as a measure of the habitat mosaic, the expectation being that bird diversity and individual species occurrences will peak at intermediate values of shrub cover.

The specific objectives of this study are: (1) to assess key habitat attributes that influence bird diversity and individual species occurrence in an Alpine forest-shrub ecotone; and (2) to determine whether habitat cover and altitude are adequate to model species distributions in the ecotone, or if more detailed information on vertical vegetation structure and shrub species composition is needed.

Methods

Study area and point selection

The study was carried out in Val Troncea Natural Park (44°57′28″N, 6°56′28″E) in the western Italian Alps. At lower altitudes the area is dominated by larch *Larix decidua*. The natural tree line is typically found at around 2200 m a.s.l., but varies depending on local conditions. Typical shrub species are *Juniperus nana* (henceforth 'juniper') and *Rhododendron ferrugineum* (henceforth 'rhododendron'), which rapidly encroach upon wide areas of grasslands after the decline of agro-pastoral activities. Grasslands were mainly dominated by *Festuca curvula*, *Carex sempervirens*, and *Trifolium alpinum*. Scree and rocky areas occur predominantly at higher altitudes, above approximately 2700 m a.s.l.

Point counts were carried out in the forest-shrub ecotone, which we defined as the transition zone between forest and alpine grasslands. We included both natural ecotones where the tree line is limited by climatic conditions, and areas where open grassland has been maintained at lower altitudes, mostly due to grazing by domestic livestock, but also due to avalanches in some locations. Point count locations coincided with the centroids of a pre-existing grid at a scale of approximately 150 × 150 m [there was some variation, e.g. due to access constraints (Probo et al. 2014)] along the western-facing slope of the valley. Points were selected that had a minimum shrub cover of 5% and a maximum tree cover of 70% (i.e. representing the forest-shrub ecotone) within a 100-m radius according to vegetation surveys (see below). All points were spaced a minimum of 200 m apart.

Bird surveys

Point counts ($n=79$) were carried out from mid-May to mid-July over a period of 2 years (46 in 2015 and 33 in 2016) following the methods of Bibby et al. (2000), using a 10-min count period. At each point count location, all individual birds seen or heard were recorded within a 100-m radius (estimated with the aid of a laser range finder). Point counts commenced 1–1.5 h after sunrise and continued until 1200 hours. Surveys did not take place in excessively wet or windy conditions. Each point count location was visited once.

Broadscale and finescale habitat

Habitat data were classified into two categories representing 'broadscale' habitat data (land cover, altitude and other variables estimated at a resolution of the whole point count location), and 'finescale' habitat data (vegetation structure and shrub species composition estimated from plots at a finer scale of resolution within the point count location). Broadscale habitat comprised visual estimation of the percentage cover of canopy (i.e. vegetation above head height), shrubs (woody vegetation below head height), open grassland and bare rock (including scree and unvegetated areas) within a 100-m radius of the point's centre. The number of mature trees (greater than ca. 20 cm in diameter at breast height) within a 50-m radius of a point count location was also counted. These estimates have been shown to correlate well with estimates of land cover derived from remote sensing and have been used as the basis of predictive models for several species considered here (Chamberlain et al. 2013, 2016).

Finescale habitat data on vegetation structure and composition were collected at the centre of the point count location and along two 100-m-long transects, each divided into five plots spaced 20 m apart originating at the point's centre (thus there were 11 plots sampled per point count location including the central point). The compass bearing of each transect from the centre of the point to its perimeter was selected at random, the only constraint being that there had to be an angle greater than 90° between two transects at the same point. Following Bibby et al. (2000), on each plot, vegetation density was measured at three different heights (0 m, 0.5 m, 1 m) using a chequered board (50×30 cm), divided into 10×10-cm square subdivisions, placed vertically in the vegetation, the bottom of the board coinciding with the appropriate height class. To produce an index of vegetation density, an estimate was made of the number of squares of the board that were obscured by vegetation observed from a distance of 5 m. A square was considered obscured by vegetation when $<50\%$ of it was visible. The diversity of vegetation density over all 11 plots was then calculated with the Shannon diversity index $(H')=-\sum p_i \ln p_i$, where p_i is the proportion of squares obscured at the ith plot. Data were also collected on grass and shrub height (if present), and the SD of height calculated across the 11 plots was used as a measure of vegetation height heterogeneity for each point. The dominant shrub species at each plot within a 1-m radius was recorded and classified into four groups: rhododendron, juniper, bilberry (*Vaccinium myrtillus* and *Vaccinium gaultherioides)* and other (e.g. green alder *Alnus*

Table 1 Variables considered in the analysis, abbreviations used in the text, and the scale at which they were measured

Parameter	Category	Description
Canopy	Broadscale	Percentage cover of canopy (above head height) within a radius of 100 m of the point count centre
Shrubs	Broadscale	Percentage cover of shrubs within a radius of 100 m of the point count centre
Trees	Broadscale	Number of mature (greater than ca. 20 cm in diameter) trees within a radius of 50 m of the point count centre
Rocks	Broadscale	Percentage cover of rocks within a radius of 100 m of the point count centre
HCOV	Broadscale	Shannon index of broadscale habitat diversity ($H'=-\sum p_i \ln p_i$, where p_i is the percentage cover of the different habitat types)
Alt	Broadscale	Altitude of the point count location in metres a.s.l. estimated from a global positioning system
H1	Finescale	Shannon Index of vegetation density diversity at 1 m above the ground
H05	Finescale	Shannon Index of vegetation density diversity at 0.5 m
SDShrub	Finescale	Shrub height heterogeneity measured as the SD of the average shrub height at the point count location
Canfreq	Finescale	Frequency of vegetation sampling points for a point count location where canopy was present
Shrubfreq	Finescale	Frequency of vegetation sampling points for a point count location where shrubs were present
Rodfreq	Finescale	Proportion of vegetation sampling points for a point count location where rhododendron was the dominant shrub species
Junfreq	Finescale	Frequency of vegetation sampling points for a point count location where juniper was the dominant shrub species
Bilfreq	Finescale	Frequency of vegetation sampling points for a point count location where bilberry was the dominant shrub species

The broadscale category was measured at the whole point count location scale and the finescale category was measured at the plot level ($n=11$ for each point) *viridis*, willow *Salix* spp., and also young trees less than 2 m in height, mostly European larch *Larix decidua*). The frequency of plots in which a given group was present was calculated for each point (i.e. the maximum frequency was 11). All habitat variables used in the analysis are listed in Table 1 [a complete list of variables measured in the field, but not included in the models due to collinearity, are given in Electronic Supplementary Material (ESM) Table S1].

Data analysis

Birds detected within a 100-m radius of a point count location were used to analyse species richness (simply the number of species detected on each point count), species diversity (expressed using H') and species distribution (presence/absence of individual species) with regard to habitat composition and structure within the forest-shrub ecotone.

Data were analysed using an information theoretic approach with the MuMIn package in R [R version 3.3.2 (R Development Core Team 2016; Bartoń 2013)]. This entailed first deriving full models at each scale and for each dependent variable (richness, diversity or species presence) using a mixed modelling approach in the R package lme4 (Bates et al. 2015). Model-averaged parameter estimates were derived for all combinations of variables in each full model in order to identify variables that were most closely associated with bird distribution and diversity. p-values derived from the model-averaged parameter estimates and their SEs were considered to represent significant effects when $p < 0.05$. In addition, the Akaike information criterion corrected for small sample size (AICc) was determined for each individual model and was used to assess model performance at different scales (see below).

Prior to modelling, all variables within each set (i.e. broadscale or finescale) were scaled and centred. Variance inflation factors (VIFs) were calculated using the corvif function [package AED (Zuur et al. 2009)] to assess collinearity between continuous explanatory variables. All variables with a VIF > 3 were sequentially removed from the variable set until all VIFs were < 3. Inter correlations between remaining variables were then checked, and for those with Spearman correlation coefficients > 0.50, one of the pair was subsequently omitted (variables with a large proportion of zeroes were preferentially omitted, otherwise the choice was random). As a final check, variables that had been removed in the procedure to minimise collinearity were substituted for closely correlated variables (in particular between overall shrub cover or frequency, and the frequency of individual shrub species). Cases where the model with the substituted variable had a lower AICc were used in the final full model. As we were particularly interested in how the shrub-grassland habitat mosaic affected the bird community, we included a quadratic effect of variables representing shrub cover (including the frequency of individual shrub species) in all models. For other variables, non-linear effects were included in the models following visual assessment of scatter plots (following Zuur et al. 2009). Year was specified as random effect in every model to account for possible inter-annual effects.

Species richness and species diversity were analysed using generalised linear mixed models in relation to habitat variables, specifying a Poisson and a normal error distribution, respectively. The occurrence probability of the commonest species [present on 15% of points—Chamberlain et al. (2013) found that models performed persistently poorly below this threshold] in relation to habitat was analysed using binomial logistic regression, each species being recorded as either present or absent per point. At each scale, the residuals for all full models were extracted and tested for spatial autocorrelation using Moran's I (Moran 1950). There was no strong evidence of spatial autocorrelation across species or scales (see details in ESM Table S6 and S7), therefore this was not considered further.

At the end of the above process, for species richness and diversity and for each individual species, candidate models with model-averaged parameter estimates were derived for each combination of variables based on the full model for broadscale and finescale habitat variables separately. The next step was then to derive combined models based on the most important variables from both broadscale and finescale models, defined as those variables which were either significant ($p \leq 0.05$) or which approached significance ($p \leq 0.1$) from the broadscale and finescale model sets. In the few cases where no variables had $p < 0.10$, those with a high Akaike weight (> 0.50) in each scale-specific model were used in the combined model. The new data set was again subjected to variable set reduction according to VIFs and correlation coefficients, and subsequently combined models were derived, which were again subjected to model averaging.

The extent to which broadscale or finescale habitat structure, or a combination of the two, was necessary to model species diversity and distributions was assessed using AICc. At each scale (finescale, broadscale and combined) and for each dependent variable, models were ordered according to the AICc, where lower values indicate better performing models. Change in AICc relative to the top ranked model was calculated as ΔAICc. Models with ΔAICc < 2 were considered equivalent. Models from all three scales were compared in order to assess whether high model performance was associated with either broadscale or finescale habitat variables, or a combination of both. The importance of each variable at each scale was assessed by calculating Akaike weights based on all combinations of models (Burnham and Anderson 2002), which are expressed as the likelihood contribution of each model as a proportion of the summed likelihood contributions of all models. The weight for each variable is the sum of model weights for all models in which a given variable was present (Burnham and Anderson 2002).

Results

In total, 263 individuals of 29 species were recorded in 79 point counts over an altitudinal range of 1800–2600 m a.s.l. There were eight species that were recorded on at least 15% of the points: Tree Pipit, Water Pipit *Anthus spinoletta*, Dunnock, Northern Wheatear *Oenanthe oenanthe*, Lesser Whitethroat, Wren, Chaffinch *Fringilla coelebs*, Rock Bunting *Emberiza cia*. No significant model-averaged parameter estimates could be identified to predict Rock Bunting occurrence for broadscale or finescale models, therefore this species was not considered in further analyses.

Broadscale habitat structure

Details of model-averaged parameters of the model set for broadscale habitat structure are given in ESM Table S2. Bird species richness and diversity showed a positive relationship with the number of mature trees. Shrub cover showed a quadratic effect on bird diversity whereby diversity increased initially with the percentage of shrub cover, but declined after a shrub cover of approximately 55% was reached. Furthermore, diversity was negatively associated with altitude. Among individual species, Dunnocks showed a positive linear association with shrub cover, whereas both Lesser Whitethroat and Wren showed a quadratic association, where the probability of occurrence of Lesser Whitethroat and Wren peaked at ca. 45% and ca. 50% shrub cover, respectively. The number of mature trees showed a positive relationship with Chaffinch presence. There was also a negative effect of rock cover on Tree Pipit occurrence. Altitude was the only variable within the full model that was not linked to vegetation cover, and had different effects on the occurrence probability of Chaffinch, Wren (negative) and Northern Wheatear and Water Pipit (positive).

Finescale habitat structure

Details of model-averaged parameters of the model set for finescale habitat structure are given in the ESM Table S3. A number of dependent variables showed significant quadratic effects (e.g. probability of occurrence or diversity peaking at intermediate frequencies), either for all shrubs (Northern Wheatear), or for individual shrub species (Wren and juniper frequency, Dunnock and rhododendron frequency, species diversity and bilberry frequency). Shrub height heterogeneity was positively correlated with Wren and Tree Pipit presence. A positive relationship of canopy presence was found for bird species richness and diversity, as well as for Chaffinch presence. In contrast, it showed a negative association with Northern Wheatear presence. Structural vegetation diversity was not selected in any model set (see ESM Table S3).

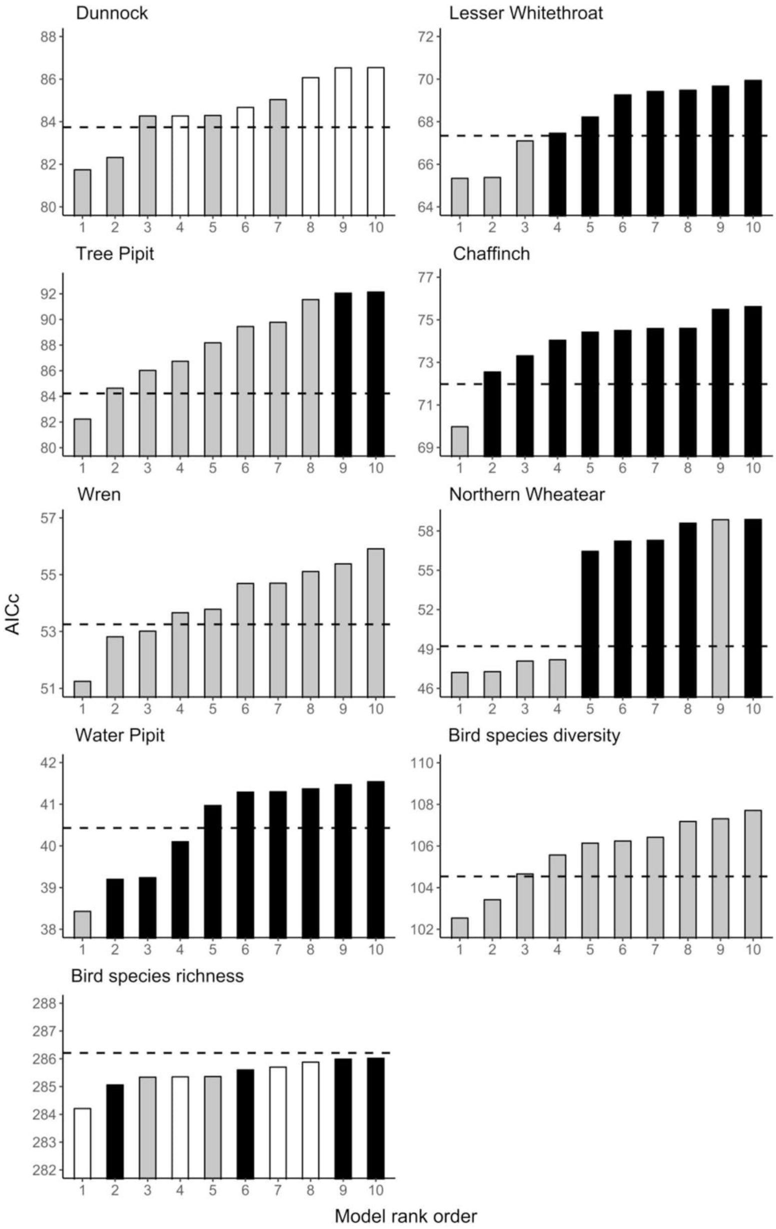
Combination of broadscale and finescale habitat structure

Details of significant model-averaged parameters of the final combined model sets are given in Table 2 (for a full list of parameters see ESM Table S4). In line with our expectation on effects of habitat mosaics on ecotone species, we here focus on shrub cover, but graphs of all significant variables in combined models are presented in ESM, Fig. S1. Shrub cover, as a broadscale variable, occurred in the combined model set for bird species diversity (Fig. 1) and Lesser Whitethroat (ESM Fig. S1). In a number of cases, individual bird species occurrences were closely associated either with shrub species identity or with shrub frequency (Table 2). Quadratic relationships between shrub species and bird species occurrence were found for Dunnock (rhododendron), Wren (juniper) and bird species diversity (bilberry; see Fig. 2). Tree Pipit occurrence declined with increasing rhododendron frequency (Fig. 2). Shrub height heterogeneity was closely related to Tree Pipit and Wren occurrences.

The frequency of canopy or the number of mature trees was retained in the combined models for bird species diversity, bird species richness and Chaffinch occurrence (positive associations) as well as for Dunnock occurrence (negative association). Altitude showed a negative relationship with the occurrence of Wren and Chaffinch, while it was positively associated with Northern Wheatear presence.

Model comparison

A summary of the ten highest ranked models for each species and each diversity measure across scales is shown in Fig. 3. The higher ranked models were mostly based on combined models (i.e. combinations of broadscale and finescale variables), or broadscale models alone. The best models (ΔAICc < 2) for Dunnock, Lesser Whitethroat, Northern Wheatear, Tree Pipit, Chaffinch, Wren and species diversity contained only combined models. Finescale models were in the best model set only for species richness, but combined and broadscale models performed equally well (i.e. ΔAICc < 2). Figure 3 also illustrates that, for many species, there was a high degree of model uncertainty in that there were often several models where ΔAICc < 2. In general, finescale habitat variables of high weight that were present in the combined (best) models were related to the presence of shrubs either overall (Northern Wheatear) or of specific shrub species (Dunnock, Lesser Whitethroat, Tree Pipit, Wren and bird species richness and diversity; Table 3).


Dunnock
88
86
84
82
80
Lesser Whitethroat
72
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68
66
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Tree Pipit
92
90
88
86
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82
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Chaffinch
77
75
73
71
69
Wren
57
55
53
51
Northern Wheatear
58
55
52
49
46
Water Pipit
42
41
40
39
38
Bird species diversity
110
108
106
104
102
Bird species richness
288
287
286
285
284
283
282
1 2 3 4 5 6 7 8 9 10
AICc
Model rank order

Table 2 Final significant model-averaged parameters of the model set derived by combining significant model-averaged parameters of broadscale and finescale habitat structure model sets for bird diversity, richness and the commonest species in the study area

Dependent variable	Parameter	Scale	Estimate ± SE	*z*	*p*
Lesser Whitethroat	Shrubs	*B*	2.171 ± 0.729	2.930	0.003
	Shrubs^2	*B*	− 2.041 ± 0.823	2.439	0.015
Tree Pipit	Rock	*B*	− 1.416 ± 0.648	2.151	0.032
	SDshrub	*F*	1.438 ± 0.514	2.754	0.006
	Rodfreq	*F*	− 1.120 ± 0.480	2.296	0.022
Dunnock	Trees	*B*	− 0.939 ± 0.471	1.963	0.050
	Rodfreq	*F*	1.601 ± 0.672	2.351	0.019
	Rodfreq^2	*F*	− 1.363 ± 0.589	2.286	0.022
Northern Wheatear	Alt	*B*	2.872 ± 0.482	5.873	≤0.000
	Shrubfreq	*F*	− 2.325 ± 0.469	4.884	≤0.000
	Shrubfreq^2	*F*	− 0.618 ± 0.031	19.595	≤0.000
Wren	Alt	*B*	− 2.435 ± 0.875	2.747	0.006
	Junfreq^2	*F*	0.583 ± 0.291	1.974	0.048
	SDshrub	*F*	1.096 ± 0.549	1.969	0.049
Chaffinch	Alt	*B*	− 1.533 ± 0.409	3.687	≤0.000
	Canfreq	*F*	1.238 ± 0.404	3.016	0.003
Species richness	Canfreq	*F*	0.169 ± 0.059	2.838	0.005
Species diversity	Shrubs	*B*	0.221 ± 0.062	3.508	≤0.000
	Canfreq	*F*	0.131 ± 0.053	2.451	0.014
	Bilfreq	*F*	− 0.171 ± 0.056	2.990	0.003
	Bilfreq^2	*F*	− 0.063 ± 0.025	2.491	0.013

The scale [broadscale (*B*), finescale (*F*)], estimate, SE, test value (*z*) and *p*-value are given for each parameter. Full details for all species and parameters are given in Table S4

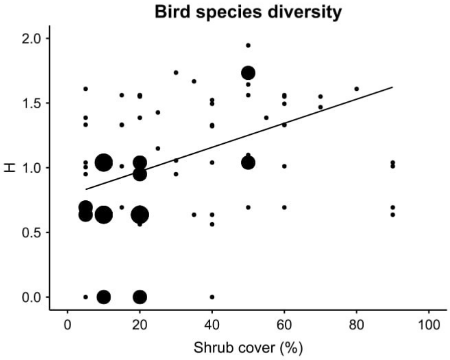

Fig. 1 Relationship between shrub cover (%) and bird species diversity based on the combined model. *Black circles* represent the Shannon diversity index (*H*′) value in relation to shrub cover for a given point count, where the *size* of the *circle* is proportional to the number of points for a given *H*′ value at a particular level of shrub cover

Discussion

The aim of this study was to describe species-specific habitat requirements within a mountainous forest-shrub ecotone in order to assess the relationships between the diversity and distributions of birds and environmental variables measured at different scales, and hence to identify potential conservation priorities and to inform future modelling methods. Through the combination of broadscale and finescale habitat data in final models, we determined key habitat characteristics which shaped bird species richness and diversity. Furthermore, this enabled us to pinpoint habitat elements which are specifically required by common ecotone species. Our expectations of positive associations between bird community measures (diversity and individual species occurrence) and habitat complexity were partially met in terms of shrub cover and to a lesser extent by shrub height heterogeneity, but there was no evidence that the diversity of vegetation structure was important.

Comparison of model scales

To make management recommendations, the identification of key habitat characteristics (e.g. vegetation structure or plant species composition) supporting bird species diversity or target species is essential. The decision at which scale this objective will be addressed varies among studies representing a trade-off between broadscale [remote-sensing techniques (Braunisch et al. 2016)] and finescale data collection [detailed vegetation measurements in the field (Patthey et al.

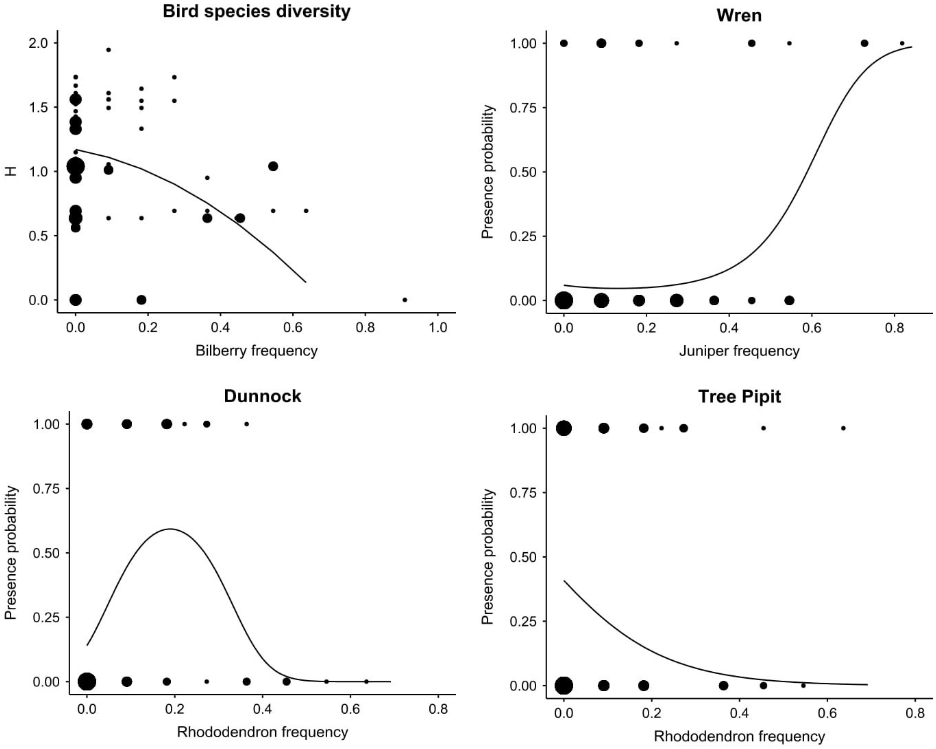

Fig. 2 Relationship between shrub species frequency (rhododendron, juniper, bilberry) and the probability of occurrence for individual bird species (Dunnock, Tree Pipit, Wren) and bird species diversity based on combined models. *Black circles* represent the point counts where a species was present/absent in relation to shrub species frequency, and the *size* of the *circle* is proportional to the number of points for a given category of presence/absence at a particular level of shrub frequency. For bird species diversity, *black circles* represent the H′ value in relation to bilberry frequency, where the *size* of the *circle* is again proportional to the number of points for a given *H′* value at a particular level of bilberry frequency

2012)]. Both techniques show advantages and disadvantages. Collecting broadscale data (for example, through remote-sensed data bases) allows large areas to be covered, but has the potential to miss relevant habitat features. Data collection in the field provides more detailed information, but is time-consuming and only applicable to smaller areas. Therefore choosing the appropriate scale is crucial as it directly determines the outcome of the study. The model scale comparison (broadscale, finescale or combined) applied to the same data allowed the assessment of the scale of data collection needed to identify habitat parameters determining bird species diversity or species-specific habitat requirements in the forest-shrub ecotone.

The comparison revealed that combined and/or broadscale models always performed better than finescale models for individual species. When combined models performed best, variables linked to shrub species identity (finescale variables) were included in several cases (Dunnock, Lesser Whitethroat, Tree Pipit, Wren and bird species richness and diversity). Other finescale variables were rarely included in the combined model set for individual bird species, or alternatively could be substituted by equivalent broadscale variables which had been excluded from the modelling process because of high collinearity between variables (e.g. Canfreq, a finescale variable which was highly correlated with canopy cover measured at the broadscale). Furthermore, finescale models were only included in the best model set (i.e. ΔAICc < 2) for species richness, but combined and broadscale models performed equally well. Variables that described vegetation structural heterogeneity or diversity were only rarely included in the best model sets: SDshrubs was in the best model set for Wren, Tree Pipit and species diversity, although for the latter, the variable was not significant and was of low variable weight (ESM Tables S4 and S5).

These results therefore suggest that structural vegetation may be less important for the identification of factors determining species diversity and species distribution in the majority of cases. However, to further our understanding of individual species and bird species diversity, data collection in the field should focus on habitat data which considers horizontal vegetation cover collected at a broad scale, but which includes species-specific estimates of cover of relevant shrub species in the area in order to model distributions of birds in the shrub-forest ecotone. The assessment of horizontal habitat cover can be done quickly and easily by eye from a single location for the whole area of a point count, including cover of easily recognizable shrub species such as juniper and rhododendron, whereas detailed structural vegetation measurements (as undertaken here) require considerable effort and access to a much greater area of a given point. The results further suggest that land cover datasets analogous to the data collected here should also be adequate for species distribution modelling in the studied habitat if they are able to estimate the cover of the dominant shrub species. Thus, broadscale habitat data and data on shrub species composition should provide a sufficient basis for identifying relevant species-specific habitat parameters in a mountain environment. Future species distribution models should seek to incorporate species-specific estimates of shrub cover, especially as the dominant species in the area are likely to respond differently to future climate change (Theurillat and Guisan 2001; Neuner 2014).

Factors affecting bird diversity and distribution at different habitat scales

There was some support that a habitat mosaic was beneficial for some individual species in that Dunnock, Lesser Whitethroat and Wren showed significant non-linear associations with either shrub cover or shrub species frequency in at least one model. Furthermore, shrub cover and frequency occurred in two final models and were positively correlated with bird species diversity (shrub cover) as well as Northern Wheatear presence (shrub frequency). The general overall importance of shrubs can easily be understood as they provide nesting habitat for shrub-nesting species, provide shelter in harsh weather conditions and can shield birds from predators.

In addition to overall shrub cover, individual shrub species were also important for some bird species. Bilberry cover was negatively related to bird species diversity, presumably because, in contrast to the other shrub species present, this species does not provide dense cover that could be suitable for nesting. Only Wren was positively associated with juniper frequency. It was also negatively associated with altitude, which may suggest a link to the different growth characteristics of juniper along the altitudinal gradient (Hallinger et al. 2010). At high altitudes (> 2000 m), this shrub species typically grows fairly low to the ground [10–30 cm (Aeschimann et al. 2004)], which may make it unsuitable for nesting (due to predation risk for example). Suitable Wren nesting habitat may only be found at lower altitudes (1800–2000 m), where juniper tends to be taller, and possibly less dense.

In contrast to juniper, rhododendron can still grow to heights suitable for nesting [30–120 cm (Aeschimann et al. 2004)] in the upper fringe of the ecotone and could therefore be seen as an attractive alternative for shrub-nesting species. In the combined models, rhododendron showed a non-linear association with Dunnock presence, and seems to be preferred as a nesting habitat over other shrub species (personal observation). In the Alps, rhododendron can form very large and dense patches on north-, west- and northwest-facing slopes within the subalpine belt (Pornon and Bernard 1996). Its distribution is highly dependent on winter snow cover, which serves as a protective layer against excessive irradiation and frost (Neuner et al. 1999). However, due to climate change, snow cover is predicted to decrease by the end of the century (Beniston et al. 2003). Taking potential snow accumulation into account, Komac et al. (2016) showed that rhododendron could experience an important reduction in its realized niche, and that its future habitat could be confined to areas which are today scree and rocky hillside habitats. This outcome suggests that, even if current habitat is maintained, climatic conditions might become less favourable for the persistence of rhododendron and that suitable habitat for shrub-nesting species in the forest-shrub ecotone will disappear.

Conservation implications

The loss of open habitats due to abandonment of grazing (Gehrig-Fasel et al. 2007; Roura-Pascual et al. 2005; MacDonald et al. 2000) and climate change (Lenoir et al. 2008; Pauli et al. 2007) is likely to continue in the future to the extent that significant areas of more open habitats, including the shrub-grassland ecotone, will be replaced by forest. To maintain ecotone habitat, it may therefore be necessary to counteract shrub and indeed forest encroachment in targeted areas in order to keep a heterogeneous character of the forest-shrub ecotone. Possible methods to counteract shrub-encroached areas could be mechanical shrub clearance or the

◂**Fig. 3** The ten best ranked models according to Akaike information criterion corrected for small sample size (*AICc*; where smaller AICc values indicate better performing models) for individual species, and for species richness and diversity. Each model is classified according to whether variables were finescale (*white bars*), broadscale (*black bars*) or a combination of the two (*grey bars*). The *dashed horizontal line* indicates ΔAICc = 2 (i.e. models *below the dotted line* are considered to be in the best model set)

re-establishment of grazing [e.g. rotational grazing systems with appropriate stocking level (Probo et al. 2014)]. However, mechanical shrub clearance can only be applied if the required equipment can be transported to the encroached areas, but accessibility by road is often limited in mountain areas. Moreover, encroached areas are frequently characterized by steep terrain, which influences the effectiveness of traditional grazing practices, as livestock tends to concentrate in flat areas and avoid steep slopes (Bailey et al. 1996; Mueggler 1965). Therefore, more specific pastoral practices involving targeted grazing are needed. The strategic placement of mineral mix supplements (MMS) would be one viable management option to be used in rugged shrub-encroached locations (Pittarello et al. 2015). The placement of MMS would lead to increased trampling in the surrounding 100 m of the MMS site, which would reduce shrub cover (Probo et al. 2013). A further more targeted option is the use of temporary night camps, where cows are fenced for up to 2 nights in shrub-encroached areas. Through intense trampling within the fenced area, shrubs get mechanically damaged and subsequently decrease in cover (Tocco et al. 2013; Pittarello et al. 2016; Probo et al. 2016). In the long-term, this pastoral technique has the additional advantage that it increases plant diversity (Pittarello et al. 2016), which in turn might positively influence invertebrate availability (Tocco et al. 2013) for birds. Any such initiatives would have to be managed carefully so as to open up encroached areas whilst maintaining a reasonable level of shrub cover. Similarly, grazing also has the potential to maintain open areas above the ecotone, which is important for Northern Wheatear and Water Pipit, both of which are open-habitat species at high altitudes. Although grazing could represent a viable management option in forest-ecotone areas, its potential direct or indirect effects on different bird species groups (e.g. grassland, ecotone, forest) are still unknown, and it is likely that some species might be more affected than others. Moreover, grazing management targeted in the wrong areas, or applied at intensive levels, could also be detrimental to biodiversity.

It should be noted that habitat requirements among the most common bird species within the forest-shrub ecotone can differ considerably. Chamberlain et al. (2013) argued that management for the maintenance of high-altitude grassland would be preferable to allowing forest expansion due to the high proportion of specialist species and species of conservation concern that could be negatively impacted. However, our data showed that forested areas with high shrub cover had the highest bird diversity. Nevertheless, there are important bird species in the ecotone that were not well covered by our methods (von dem Bussche et al. 2008; Braunisch et al. 2016), and the ecotone also has a high biodiversity of other taxa (Dirnböck et al. 2011). In order to meet a range of species-specific habitat requirements, it might therefore be important to sustain a high level of heterogeneity and to maintain a habitat mosaic within the ecotone (Pathey et al. 2012). Management recommendations need to be adopted at appropriate scales for areas differing in altitude, topography, shrub species composition and the degree of shrub encroachment (Braunisch et al. 2016). Depending on the targeted area, it might therefore be necessary to apply a combination of different management techniques and to adjust the time period of application to promote heterogeneity. There is the possibility of managing for diverse landscapes that can incorporate a range of needs for different habitat types which facilitates species resilience and resistance to environmental change (e.g. Brambilla et al., in press), but further work is needed on the most appropriate scale of management through which this can be achieved.

Table 3 Variables with the highest importance (Akaike weight > 0.70) for combined models, derived from all combinations of models for each dependent variable, grouped according to whether they were broadscale or finescale

Variable	Broadscale	Finescale
Tree Pipit	Rock, Shrubs^2	SDShrub, Rodfreq
Water Pipit	Alt	Canfreq
Dunnock	Trees	Rodfreq, Rodfreq^2
Northern Wheatear	Alt	Shrubfreq
Lesser Whitethroat	Shrubs, Shrubs^2	–
Wren	Alt, Shrubs	SDShrub, Junfreq^2
Chaffinch	Alt	Canfreq
Species richness	–	Canfreq
Species diversity	Shrubs	–

Full details are given in Electronic Supplementary Material Table S5. *Dash* indicates Akaike weight < 0.70 for a given scale. Variable codes are given in Tables 1 and S1

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