Behavioural responses to human disturbance in an alpine bird

This is a pre print version of the following article:

Original Citation:

Availability:
This version is available http://hdl.handle.net/2318/1696854 since 2020-02-19T10:40:04Z

Published version:
DOI:10.1007/s10336-019-01660-z

Terms of use:
Open Access
Anyone can freely access the full text of works made available as "Open Access". Works made available under a Creative Commons license can be used according to the terms and conditions of said license. Use of all other works requires consent of the right holder (author or publisher) if not exempted from copyright protection by the applicable law.
This is an author version of the contribution published on:

Questa è la versione dell’autore dell’opera:

[Journal of Ornithology, 2019, DOI: https://10.1007/s10336-019-01660-z]

The definitive version is available at:

La versione definitiva è disponibile alla URL:

http://link.springer.com/article/10.1007/s10336-019-01660-z
Behavioural responses to human disturbance in an alpine bird

Cristina Vallino*1, Enrico Caprio*1, Fabrizio Genco, Dan Chamberlain1, Claudia Palestrini1, Angela Roggero1, Massimo Bocca2, Antonio Rolando1

1Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina 13, 10123, Turin, Italy.
2Mont Avic Natural Park, La Fabrique, 164, 11020, Champdepraz, Italy

* corresponding author: cristina.vallino@unito.it +0116704521 https://orcid.org/0000-0003-3671-3128
enrico.caprio@unito.it +0116704521 https://orcid.org/0000-0002-5997-5959

Dan Chamberlain https://orcid.org/0000-0002-5381-2024
Claudia Palestrini https://orcid.org/0000-0001-6241-2009
Angela Roggero https://orcid.org/0000-0003-0108-6304
Antonio Rolando https://orcid.org/0000-0002-3432-1780

Keywords
Alpine Chough, grasshoppers, habituation, foraging

Acknowledgments
We thank Cervino spa for allowing us the use of ski lifts, and for the data provided. We also thank Professor Bruno Massa for help with grasshopper identification, and all fieldworkers: Gioele Brotto, Sara Beggiato, Francesca Bosio, Luca Calcagno, Julia Milan, Giorgio Gentile and Alessandro Lago.

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.

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; Bátyar 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. Materials and methods

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 nor 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. 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 \textit{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-spite. 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 m² 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.

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 ≤ 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).

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).

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    | 1.031 | 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: Plateau 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        |

3.1.1. 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

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 *** |
| Elevation²            | -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/m² was higher at MA (mean number of grasshoppers/m² 2.25 ± 2.38, N = 66) than at PM (mean number of grasshoppers/m² 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).

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 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.

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.

Ethical approval: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Data policy: The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

References

Arlettaz R, Sébastien N, Marjana N, Peter V, Rupert P, Jenni-Eiermann S, Patthey P, Genoud M (2015) Disturbance of wildlife by outdoor winter recreation: allostatic stress response and altered activity–energy budgets. Ecological Applications 25: 1197–1212. https://doi.org/10.1890/14-1141.1

Bátary P., Kurucz K., Suarez-Rubio M., Chamberlain D. (2017). Non-linearities in bird responses across urbanization gradients: A meta-analysis. Global Change Biology, 24, 1046-1054.

Bazzi G, Foglini C, Brambilla M, Saino N, Rubolini D (2015) Habitat management effects on Prealpine grassland bird communities. Italian Journal of Zoology 82: 251–261. https://doi.org/10.1080/11250003.2014.983566

Beale CM, Monaghan P (2004) Behavioural responses to human disturbance: a matter of choice? Animal Behaviour 68: 1065–1069. https://doi.org/10.1016/j.anbehav.2004.07.002

Brambilla M, Pedrini P, Rolando A, Chamberlain DE (2016) Climate change will increase the potential conflict between skiing and high-elevation bird species in the Alps. Journal of Biogeography 43: 2299–2309. https://doi.org/10.1111/jbi.12796

Bridge ES, Schoech SJ, Bowman R, Wingfield JC (2009) Temporal predictability in food availability: effects upon the reproductive axis in Scrub-Jays. (2009)J. Exp. Zool 311A: 35-44.https://doi.org/10.1002/jez.493

Caprio E, Chamberlain D, Rolando A (2016) Ski-piste revegetation promotes partial bird community recovery in the European Alps. Bird Study 63: 470–478. https://doi.org/10.1080/00063657.2016.1216520

Catalan J, Ninot JM, Mercè Aniz M (2017) The High Mountain Conservation in a Changing World. Advances in Global Change Research 62: 3-36. https://doi.org/10.1007/978-3-319-55982-7

Concepción ED, Obrist MK, Moretti M, Altermatt F, Baur B, Nobis M.P (2016) Impacts of urban sprawl on species richness of plants, butterflies, gastropods and birds: not only built-up area matters. Urban Ecosystems 19: 225-242. https://doi.org/10.1007/s11252-015-0474-4
Delestrade A (1995) Impact of human activity on foraging flocks and populations of Alpine Chough *Pyrrhocorax graculus*. Avocetta 19: 189-193.

Delestrade A, Stoyanov G (1995) Breeding biology and survival of the Alpine Chough *Pyrrhocorax graculus*. Bird Study, 42:3, 222-231, DOI: 10.1080/00063659509477171

Ellenberg U, Setiawan AN, Cree A, Houston DM, Seddon PJ (2007) Elevated hormonal stress response and reduced reproductive output in Yellow-eyed penguins exposed to unregulated tourism. General and Comparative Endocrinology 152: 54–63. https://doi.org/10.1016/j.ygcen.2007.02.022

Fernández-Juricic E, Tellería JL (2000) Effects of human disturbance on spatial and temporal feeding patterns of Blackbird *Turdus merula* in urban parks in Madrid, Spain. Bird Study 47: 13–21. https://doi.org/10.1080/0006365009461156

Freppaz M, Filippa G, Corti G, Cocco S, Williams M W, Zanini E (2013) Soil Properties on Ski runs. In Rixen C and Rolando A (eds) The Impacts of Skiing and Related Winter Recreational Activities on Mountain Environments. Bentham Books, pp.46-64.

Gilbert NI, Carreia RA, Silva JP, Pacheco C, Catry I, Atkinson PW, Gill JA, Franco AMA (2016) Are white storks addicted to junk food? Impacts of landfill use on the movement and behaviour of resident white storks (*Ciconia ciconia*) from a partially migratory population. Movement Ecology 4:7 DOI 10.1186/s40462-016-0070-0

Gill JA (2007) Approaches to measuring the effects of human disturbance on birds. Ibis 149: 9–14. https://doi.org/10.1111/j.1474-919X.2007.00642.x

Grémillet D, Pichegru L, Kuntz G, Woakes AG, Wilkinson S, Crawford RJM, Ryan PG (2008) A Junk-Food Hypothesis for Gannets Feeding on Fishery Waste. Proceedings: Biological Sciences 275: 1149-1156.

Hamner HJ, Thomas RL, Fellowes MDE (2017) Provision of supplementary food for wild birds may increase the risk of local nest predation. Ibis 159: 158–167. https://doi.org/10.1111/ibi.12432

Jähnig S, Alba R, Vallino C, Rosselli D, Pittarello M, Rolando A, Chamberlain D (2018) The contribution of broadscale and finescale habitat structure to the distribution and diversity of birds in an Alpine forest-shrub ecotone. Journal of Ornithology 159: 1–13. https://doi.org/10.1007/s10336-018-1549-9

Jokimäki J, Suhonenb J, Vuorisaloc T, Kövér D, Kaisanlahti-Jokimäki M (2017) Urbanization and nest-site selection of the Black-billed Magpie (*Pica pica*) populations in two Finnish cities: From a persecuted species to an urban exploiter. Landscape and Urban Planning 157: 577–585. https://doi.org/10.1016/j.landurbplan.2016.08001

Jiménez G, Meléndez L, Blanco G, Laiolo P (2013) Dampered behavioral responses mediate birds’ association with humans. Biological Conservation 159: 477–483. https://doi.org/10.1016/j.biocon.2012.10.030

Kurosawa R, Kono R, Kondo T, Kanai Y (2003) Diet of Jungle Crows in an urban landscape. Global Environmental Research 7: 193–198.

Laiolo P, Rolando A (1999) The diet of the Chough (*Pyrrhocorax pyrrhocorax*) and the Alpine Chough (*Pyrrhocorax graculus*) in the Alps: seasonality, resource partitioning and population density. Rev. Ecol. (Terre Vie) 54: 133-147.

Laiolo P, Rolando A (2001) A comparative analysis of the breeding biology of the Red-billed Chough *Pyrrhocorax pyrrhocorax* and the Alpine Chough *P. graculus* coexisting in the Alps. Ibis 143: 33-40. https://onlinelibrary.wiley.com/doi/full/10.1111/j.1474-919X.2001.tb04167.x

Laiolo P, Rolando A, Carisio L (2001) Winter movements of the Alpine Chough: implications for management in the Alps. Journal of Mountain Ecology 6: 21–30.

Miehe G, Miehe S, Böhner J, Kaiser K, Hensen I, Madsen D, Liu J, Opgenoorth L (2014) How old is the human footprint in the world’s largest alpine ecosystem? A review of multiproxy records from the Tibetan Plateau from the ecologists’ viewpoint. Elsevier 86: 190-209. https://www.sciencedirect.com/science/article/pii/S0277379113004770
Mont Avic Natural Park Champdepraz (AO) Italy (2017) Environmental Statement EMAS 2015-2017 http://www.montavic.it/index.php/Per-saperne-di-piu/Certificazione-ambientale.

Negro M, Isaia M, Palestrini C, Schoenhofer A, Rolando A (2010) The impact of high-elevation ski pistes on ground-dwelling arthropods in the Alps. Biodiversity Conservation 19: 1853–1870 https://doi.org/10.1007/s10531-010-9808-y

Negro M, Rolando A, Barni E, Boccola D, Filippa G, Freppaz M, Isaia M, Siniscalco C, Palestrini C (2013) Differential responses of ground dwelling arthropods to ski-piste restoration by hydroseeding. Biodiversity Conservation 22: 2607–2634 https://doi.org/10.1007/s10531-013-0544-y

Oro D, Genovart M, Tavecchia G, Fowler MS, Martinez-Abrain A (2013) Ecological and evolutionary implications of food subsidies from humans. Ecology Letters 16: 1501–1511. doi:10.1111/ele.12187

Probo M, Lonati M, Pittarello M, Bailey DW, Garbarino M, Gorlier A, Lombardi G (2014) Implementation of a rotational grazing system with large paddocks changes the distribution of grazing cattle in the south-western Italian Alps. Rangeland Journal 36: 445–458. https://doi.org/10.1071/RJ14043

Remacha C, Pérez-Tris J, Delgado JA (2011) Reducing visitors’ group size increases the number of birds during educational activities: Implications for management of nature-based recreation. Journal of Environmental Management 92: 1564–1568. http://dx.doi.org/10.1016/j.jenvman.2011.01.006

Rixen C (2013) Skiing and Vegetation. In Rixen C and Rolando A (eds) The Impacts of Skiing and Related Winter Recreational Activities on Mountain Environments. Bentham Books, pp.65-78.

Rixen C, Rolando A (2013) The Impacts of Skiing and Related Winter Recreational Activities on Mountain Environments. Bentham Books. https://doi.org/10.2174/97816080548861130101

Robb GN, McDonald RA, Chamberlain D, Bearhop S (2008) Food for thought: supplementary feeding as a driver of ecological change in avian populations. Frontiers in Ecology and the Environment 6: 476–484. https://doi.org/10.1890/060152

Rolando A, Caldoni R, De Sanctis A, Laiolo P (2001) Vigilance and neighbour distance in foraging flocks of Red-billed Choughs, Pyrrhocorax pyrrhocorax. Journal of Zoology 253: 225–232. https://doi.org/10.1017/S095283690100019X

Rolando A, Caprio E, Negro M (2013) The Effect of Ski-Pistes on Birds and Mammals. In Rixen C and Rolando A (eds) The Impacts of Skiing and Related Winter Recreational Activities on Mountain Environments. Bentham Books, pp-101-122.

Rolando A, Laiolo P (1997) A comparative analysis of the diets of the Chough Pyrrhocorax pyrrhocorax and the Alpine Chough Pyrrhocorax graculus coexisting in the Alps. Ibis 139: 388–395. https://doi.org/10.1111/j.1474-919X.1997.tb04639x

Rolando A, Laiolo P (1997) A comparative analysis of the diets of the Chough Pyrrhocorax pyrrhocorax and the Alpine Chough Pyrrhocorax graculus coexisting in the Alps. Ibis 139: 461–467. https://doi.org/10.1111/j.1474-919X.1997.tb04659.x

Rolando A, Laiolo P, Carisio L (2003) Urbanization and the flexibility of the foraging ecology of the Alpine Chough Pyrrhocorax graculus in winter. Revue d’Ecologie (Terre Vie) 58: 337-352.

Rolando A, Laiolo P, Formica M (1997) A comparative analysis of the foraging behaviour of the Chough Pyrrhocorax pyrrhocorax and the Alpine Chough Pyrrhocorax graculus coexisting in the Alps. Ibis 139: 461–467. https://doi.org/10.1111/j.1474-919X.1997.tb04659.x

Rolando A, Patterson IJ (1993a) Foraging behaviour and diet of the Alpine Chough Pyrrhocorax graculus in the Italian Alps in summer. Journal of Ornithology 134: 181–187. https://doi.org/10.1007/BF01640087

Rolando A, Patterson IJ (1993b) Range and movements of the Alpine Chough Pyrrhocorax graculus in relation to human developments in the Italian Alps in summer. Journal of Ornithology 134: 338–344. https://doi.org/10.1007/BF01640430

R Development Core Team (2015) The R foundation for statistical computing, Vienna, Austria.

Schoech SJ, Bowman R, Bridge ES, Boughton RK (2007) Baseline and acute levels of corticosterone in Florida Scrub-Jays (Aphelocoma coerulescens): Effects of food supplementation, suburban habitat, and year. General and
Shochat E (2004) Credit or Debit? Resource Input Changes Population Dynamics of City-Slicker Birds. Oikos, 106: 622-626.

Skaug H, Fournier D, Nielsen A (2006) glmmADMB: generalized linear mixed models using AD Model Builder. R package version 0.3.

Sindaco R, Savoldelli P, Evangelista M (2012) Ortotteri, Mantidi e Fasmidi dell’Italia nord-occidentale (Piemonte, Valle d’Aosta, Liguria) (Insecta: Orthoptera, Mantodea, Phasmatodea). Rivista piemontese di Storia naturale, 33: 111-160.

Støstad HN, Aldwinckle P, Allan A, Arnold KE (2017) Foraging on human-derived foods by urban bird species. Bird Study 64: 178–186. https://doi.org/10.1080/00063657.2017.1311836

Tomasevic JA, Marzluff JM (2017) Cavity nesting birds along an urban-wildland gradient: is human facilitation structuring the bird community? Urban Ecosystems 20:435–448. https://doi.org/10.1007/s11252-016-0605-6

West EH, Peery MZ (2017) Behavioral mechanisms leading to improved fitness in a subsidized predator. Oecologia 184: 787–798. https://doi.org/10.1007/s00442-017-3898-0

Will A, Watanuki Y, Kikuchi DM, Sato N, Ito M, Callahan M, Wynne-Edwards K, Hatch S, Elliott K, Slater L, Takahashi A, Kitaysky A (2015) Feather corticosterone reveals stress associated with dietary changes in a breeding seabird. Ecology and Evolution 5(19): 4221–4232. doi:10.1002/ece3.1694

Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R, Statistics for Biology and Health. Springer-Verlag, New York.