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(Article begins on next page)



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Flocking of foraging Yellow-billed Choughs *Pyrrhocorax graculus* reflects the availability of grasshoppers and the level of human development in high elevation ecosystems

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Summary

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 Yellow-billed (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 that are heavily developed for recreational activities. We tested therefore whether flock size co-varied with grasshopper abundance along an elevational gradient in two alpine areas subject to different levels of human disturbance.

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 performing negative binomial GLMs account for effects of period (i.e. from June to mid-August), site and elevation.

In both study areas, chough flocks were larger at the elevation where grasshoppers were more abundant. This 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 was positive at a natural site and negative at a tourist site. This suggests that where there is a high level of human pressure, other factors, such as the availability of human-provided food, may disturb the natural relationship between choughs and their key prey. Overall, our results indicate that flocking by foraging Yellow-billed Choughs reflects both grasshopper abundance and the degree of anthropogenic influence.

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 al. 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 future of high elevation animal species is of particular concern, because climate change will displace both vegetation and human activities. For instance, it is 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 reduce the 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 Yellow-billed (Alpine) Chough, *Pyrrhocorax graculus*, a gregarious bird that moves in flocks throughout the year, is an excellent target species in this context. It is generally assumed that flocking may be advantageous to detect predators (Rolando et al. 2001; Jiménez et al. 2013), and has additional survival value in relation to food finding (Ward and Zahavi 1973), for instance through sharing information about food localisation (Fernández-Juricic et al. 2004).

The diet of the Yellow-billed 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 have been observed around high altitude touristic areas, where they gather around restaurants when tourists are present (Storch and Leidenberg 2003). In summer, however, grasshoppers (Orthoptera), that are particularly abundant in alpine meadows above the treeline, are the principal chough food (Koch et al. 2015). Grasshopper remnants may be found in over 80% of droppings (Rolando and Patterson 1993a; Rolando & Laiolo 1997; Laiolo & Rolando 1999). Thus Yellow-billed Choughs and grasshoppers represent a predator-prey interaction within 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 grasshopper abundance can drive concomitant suppressions of predatory bird densities (Norelius & Lockwood 1999; Pescador et al. 2019). However, such studies have never involved alpine species.

We tested whether Yellow-billed 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 choughs, we expected flock size to correspond spatially and temporally with prey abundance and biomass. We surveyed two areas differing in human pressure, a relatively undisturbed location and another

characterised by high altitude restaurants and bars where anthropogenic food is available for choughs. Therefore, we expected to find a weaker relationship between choughs and natural key prey in the latter area and a stronger relationship in the natural site, where alternative food sources are absent.

2. MATERIALS AND METHODS

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). Mont Avic Natural Park 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 Cervinia area is a popular tourist destination, characterised by marked anthropisation due to leisure activities, such as skiing and other outdoor pursuits, and the presence of high-altitude ski resorts, bars and restaurants. The Cervinia skiing complex includes 72 ski pistes in Italy (plus 78 pistes on the Swiss side), 200km of tracks covered with artificial snow and a snowpark that reaches as high as 2,800m a.s.l. Tourists can participate in such activities as cross-country skiing, heliskiing on the glacier, trekking and downhill skiing. Consequently, Cervinia is frequented by tourists year-round; 63,000 people visited the area during summer 2017 alone, (Cervino spa, personal communication). Ski developments are particularly concentrated at Plateau Rosà (3,500m asl), where a lot of restaurants and bars around the cable-car station produce garbage all year round.

2.2. Fieldwork

Yellow-billed Chough survey

Direct observations on birds feeding in pastures were carried out almost daily from June to August 2016–2017 from 08.00 to 17.00 hours. We surveyed all the sites potentially frequented by Alpine Choughs, walking along transects or reaching favourable observation points. Observations were made daily, changing the time of day each site was observed to account for possible daily variations in behaviour. For each observation, we recorded flock size and site elevation (for more details see Vallino et al. 2019). Particular individuals could not be distinguished since most birds were unmarked.

Grasshoppers and their habitat

In 2016 and 2017, two elevational transects were set up in each area to monitor the distribution and phenology of grasshoppers. Each transect comprised seven or eight sampling plots on grasslands, at 100m intervals of elevation. Plots were monitored from June to mid-August and were extended from 2,000m asl (C) or 2,100m asl (MA) to 2,700m asl. These elevations have been demonstrated to be the most frequented by Yellow-billed Choughs at Cervinia in summer (Rolando and Patterson 1993a). Transect locations were based on observations of foraging choughs during a pilot study in 2015. In each plot, we surveyed grasshoppers three times during each visit, each time passing a one metre pole, kept close to the ground, through the vegetation for two metres, therefore sweeping a total area of 6m² per plot. Grasshoppers that flushed were counted to determine their abundance/m² (Rolando and Patterson 1993a). To obtain grasshopper biomass we collected 100 individuals at different developmental stages. These were measured in the laboratory (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,

10–15mm, > 15mm) and determined the relative mean weight of each class. For each plot, we measured the body length of six randomly selected individuals to obtain the mean body length of local grasshoppers. Finally, the global biomass of grasshoppers in a plot was obtained by multiplying the mean weight of the corresponding body length class (i.e. that encompassing the mean 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 10m radius. The presence of a stream, a path or active grazing was also recorded but none of these features proved to be relevant during the analysis. To describe habitat structure, we also measured the height of 20 randomly selected grass stems per plot to determine the mean grass height.

Grasshoppers were collected to establish taxonomic diversity. In 2017, we collected three random individuals from each plot each time that we repeated the transect survey, but only adults could be used for identification. Therefore, in 2019, in late July and August (when most individuals were at the adult stage), we collected additional individuals along the same transects and at the same plots identified in the previous field seasons. Collected grasshoppers were stored in plastic tubes for subsequent identification in the laboratory (species nomenclature and taxonomic order follow Massa et al. 2012).

2.3. Data analysis

Yellow-billed Cough flock size

We modelled chough flock size (i.e. the number of birds observed foraging together) in relation to period, site, elevation and its quadratic term as well as 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 that corresponded to grasshopper sampling sessions: periods 1, 2, 3, 4 and 5 corresponded 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 lme4 R package (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, minimising the effects of multicollinearity and revealing patterns in the data by performing a Principal Component Analysis (PCA: Gauch 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.

Yellow-billed Chough flock size and grasshopper abundance

To assess whether chough flock size was linked to grasshopper abundance, we considered all the flocks observed and grasshoppers counted within 100m 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 mid-point of range of flock size) 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 the median values we obtained were all integers and referred to counts we checked for overdispersion in preliminary Poisson GLMs of median flock size and we finally performed Negative Binomial GLMMs. Given that median values could generate non integer values, we also computed alternative Gaussian GLMs for log-transformed median flock sizes and those models rendered similar results to Negative Binomial GLMs. The results of gaussian GLMs are not discussed but may be consulted in the supplementary material (Supplementary material appendix 1 Table A7-A9).

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 (Supplementary material appendix 1 Table A6, fig. 4), site, elevation and the interaction between residuals and site. Residuals measured whether the 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 greater than expected, given the number of grasshoppers found, while negative values represented sites where biomass was below the expected values given the relationship with abundance.

3. RESULTS

Yellow-billed Chough flock size

Overall, we observed 949 flocking events. The altitudinal belt where the highest numbers of flocks were observed was 2,400–2,500m asl at Cervinia (236 observations) and 2,200–2,300m asl (198 observations) at Mont Avic (Supplementary material appendix 1 Table A1). Flock size was smaller at MA than at C (mean number of individuals \pm 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 3,500m to feed on scraps.

Grasshopper abundance, biomass and habitat

In total, 15 grasshopper species were identified. The most abundant, ubiquitous, species was *Chorthippus biguttulus biguttulus* (Linnaeus, 1758), followed by *Aeropus sibiricus* (Linnaeus, 1767) (Supplementary material appendix 1 Table A2).

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 1). 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 a maximum at about 2,300m in period 2 (figures 1.1 and 1.2). As shown in table 2, 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 2,000 and 2,600m and reaching a maximum value at 2,300m.

Results of grasshopper biomass models indicated that prey biomass was related to period and included PC1 (table 3). 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 cover and height of grass, and decreased in plots with a higher percentage of rocks and mosses.

Relationship between Yellow-billed Choughs and grasshoppers

The median flock size per 100m elevational belt was positively related to the abundance of grasshoppers; thus the number of choughs in the flocks and the number of prey increased in tandem (figure 2a). The median flock size was lower in site MA (figure 2c) and had a quadratic relationship with elevation (figure 2b, Supplementary material appendix 1 Table A3), with maximum median flock size at 2,500m. The median number of 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 3a). The model included a quadratic relationship with elevation with maximum median flock size at 2,500m (figure 3b, Supplementary material appendix 1 Table A4). This contrasting result was further confirmed by modelling the residuals of the relationship between grasshopper abundance and biomass and median chough count. Our results showed an interaction between the residuals and site, meaning that flock sizes were 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 4, Supplementary material appendix 1 Table A5).

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 Leidenberg (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.

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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SUPPLEMENTARY ELECTRONIC MATERIAL

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Appendix 1. Table A1. Distribution of flock observations per belt and per site.
Table A2. List of grasshopper species identified *a posteriori*.
Table A3, A4, A5, A6, A7, A8, A9 Model summaries (Tablas A3-A6: resumen de los modelos).

Table 1. 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	<i>-0.401</i>	0.358	0.338	-0.146
VHSD	-0.386	0.352	0.357	-0.069
Shrub cover	0.030	<i>-0.564</i>	0.332	-0.094
Trail presence	-0.097	<i>-0.504</i>	0.345	-0.176
Ski-piste cover	-0.006	0.035	-0.044	<i>0.842</i>
Snow cover	0.140	-0.033	-0.317	-0.121
Bare ground cover	0.077	-0.002	<i>-0.436</i>	-0.345
Rock cover	<i>0.462</i>	0.329	0.201	-0.172
Moss cover	<i>0.445</i>	0.253	0.190	-0.153
Grass cover	<i>-0.493</i>	0.024	<i>-0.401</i>	-0.195
Eigenvalues	1.567	1.407	1.295	1.104
Variance explained	24.57	19.8	16.78	12

Table 2. 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 3. GLMM of grasshopper biomass according to period, PC1 and site (MA = Mont Avic). For the categorical variables Period and Site, reference levels were Period 1 and site C (Cervinia) respectively.

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 1. 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.

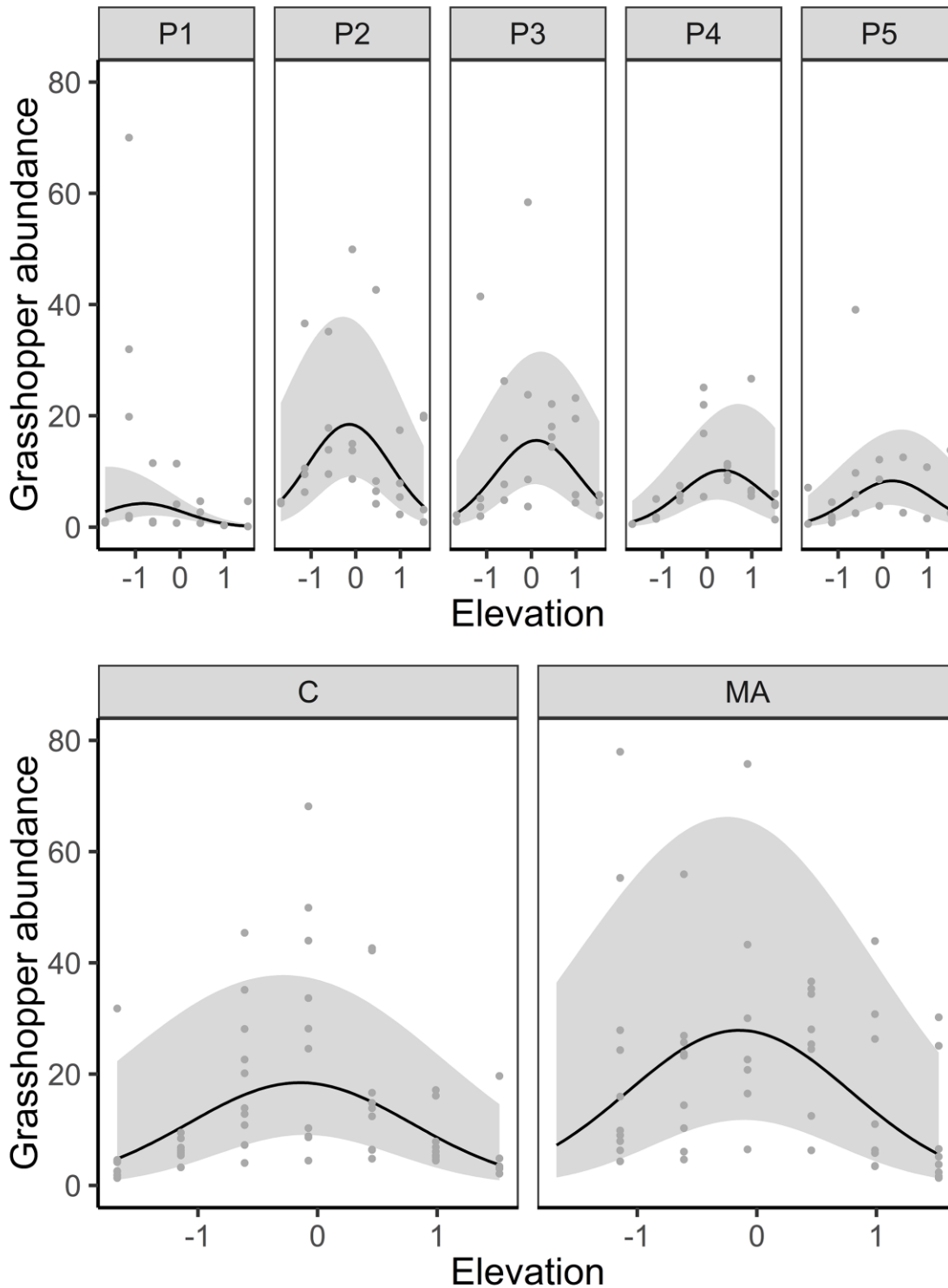


Figure 2. Relationship between median flock size and grasshopper abundance (centred and scaled) (a), site (b) and elevation (centred and scaled) (c). Shaded areas represent 95% confidence limits.

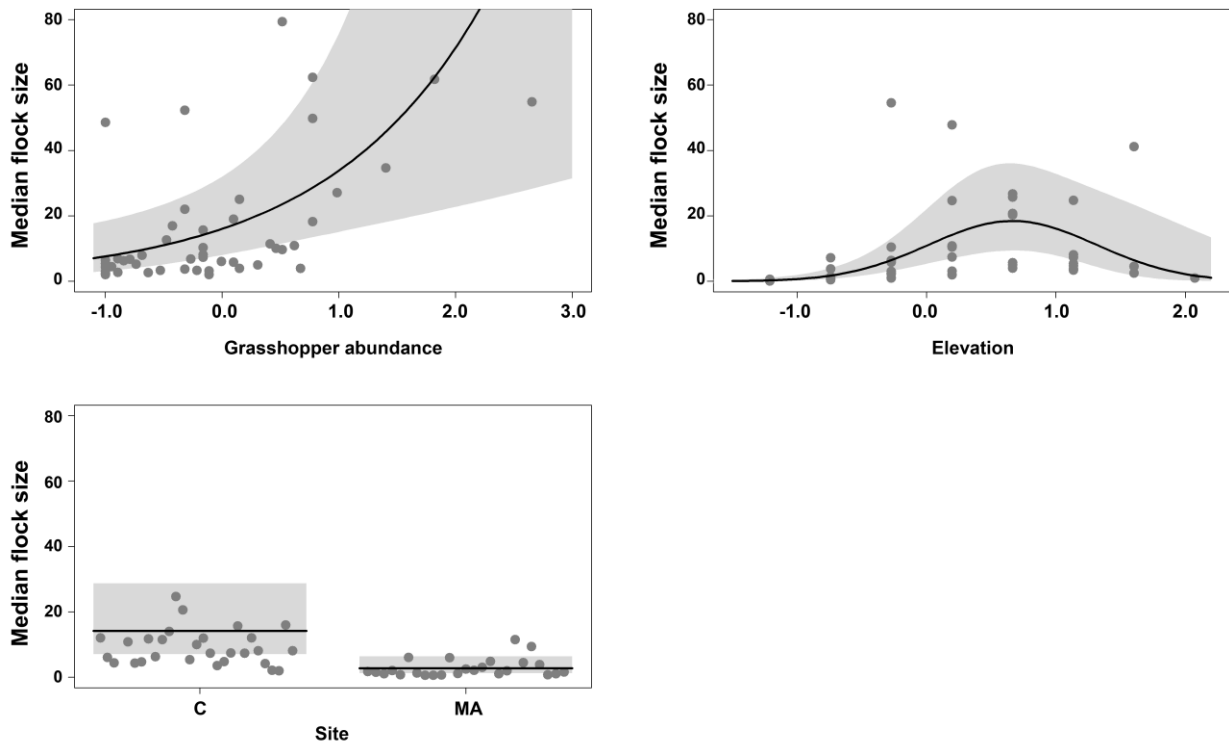


Figure 3. Relationship between median flock size and grasshopper biomass (mg) (a), and median flock size and elevation (b) for each site. Shaded areas represent 95% confidence limits.

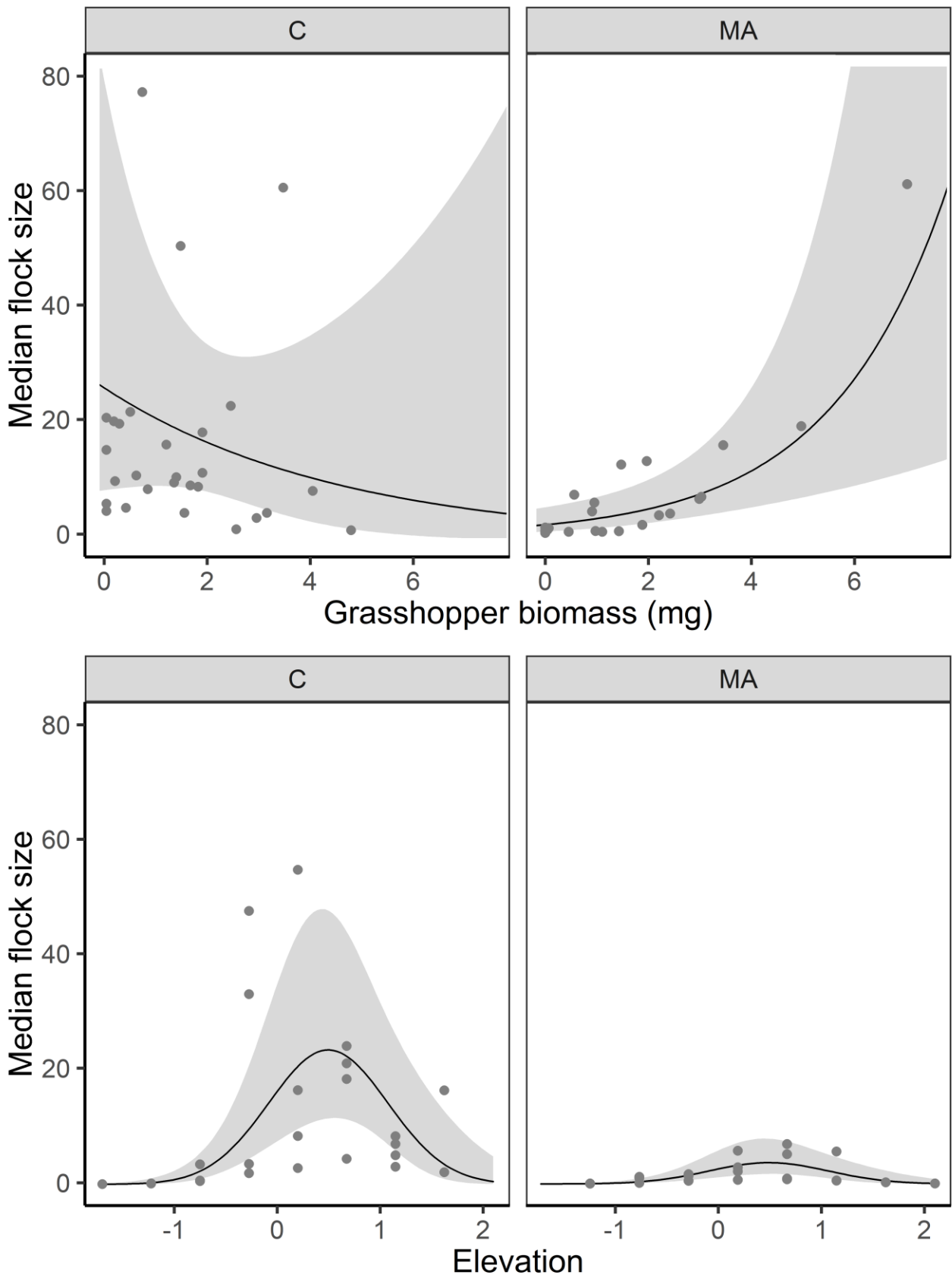
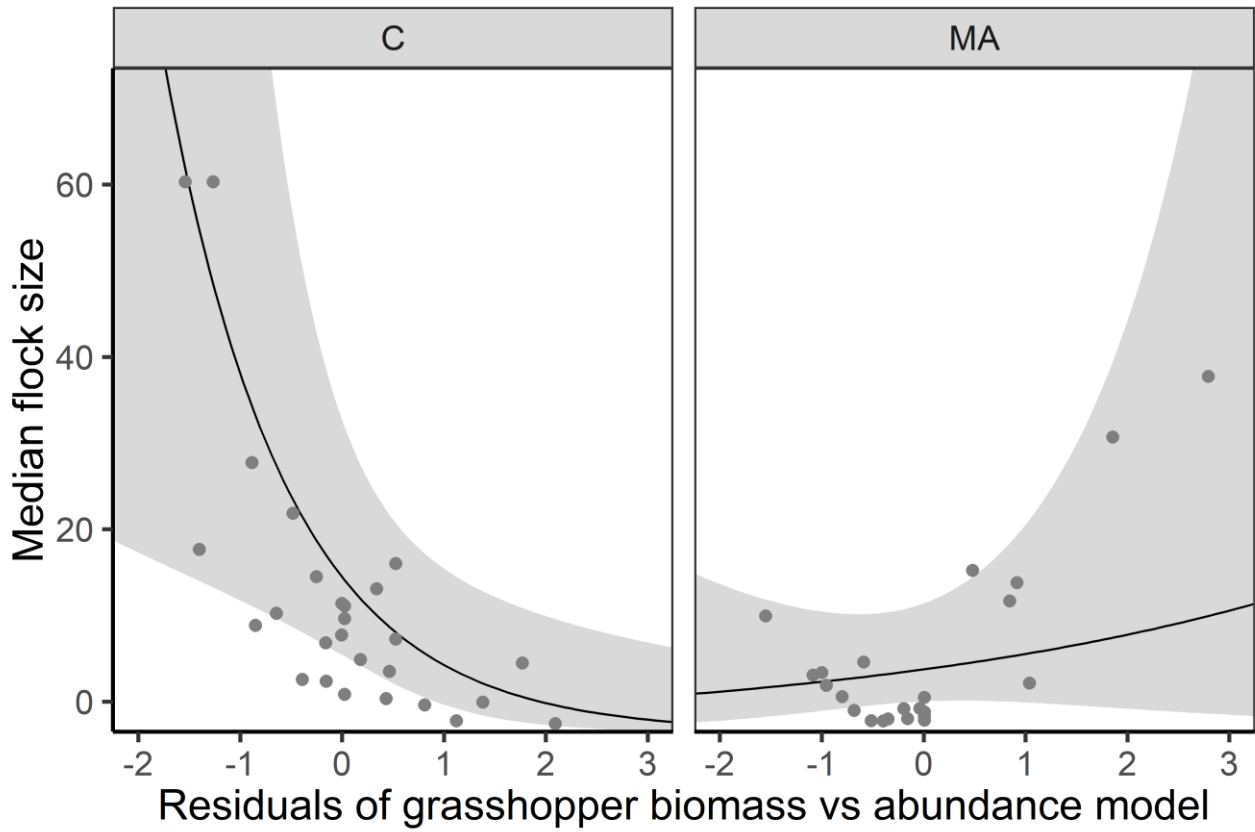


Figure 4. Relationship between median flock size and interaction between residuals of the model of grasshopper biomass and abundance (both centred and scaled) for each site. Shaded areas represent 95% confidence limits.



Supplementary material

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

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SHORT TITLE: Alpine Chough flocking and grasshopper availability

Appendix 1.

Table A1. Distribution of flock observations per belt and per site. Note that observations at 3500m asl have not been included in the model analysis.

Elevation	Cervinia	Mont Avic
2000 – 2100	2	1
2100 – 2200	43	82
2200 – 2300	42	63
2300 – 2400	45	198
2400 – 2500	109	24
2500 – 2600	236	27
2600 – 2700	9	7
2700 - 2800	3	3
3500 *	55	

Table A2. List of grasshopper species identified *a posteriori* and their abundance in 2019

(see Methods for details) in the two study areas. Species nomenclature and taxonomic order follow Massa et al. 2012.

Species	N in C	N in MA	Total N
<i>Anonconotus alpinus</i> (Yersin, 1858)	2	16	18
<i>Anonconotus baracunensis</i> Nadig, 1987		1	1
<i>Anonconotus ghiliani</i> (Camerano, 1878)	2	4	6
<i>Anonconotus alpinus/ghiliani</i> -		4	4
<i>Platycleis grisea</i> (Fabricius, 1781)	5		5
<i>Bohemanella frigida frigida</i> (Boheman, 1846)	4	5	9
<i>Epipodisma pedemontana</i> (Brunner von Wattenwyl, 1882)		8	8
<i>Omocestus haemorrhoidalis</i> (Charpentier, 1825)	21		21
<i>Omocestus rufipes</i> (Zetterstedt, 1821)	4	1	5
<i>Omocestus viridulus</i> (Linnaeus, 1758)	37	2	39
<i>Stenobothrus lineatus lineatus</i> (Panzer, 1796)	32		32
<i>Aeropus sibiricus</i> (Linnaeus, 1767)	20	33	53
<i>Aeropedellus variegatus</i> (Fischer de Waldheim, 1846)	1	4	5
<i>Chorthippus apricarius apricarius</i> (Linnaeus, 1758)	14		14
<i>Chorthippus biguttulus biguttulus</i> (Linnaeus, 1758)	69	80	147
Juvenile forms	24	50	74
TOTAL ABUNDANCE	235	208	443

Table A3. Negative binomial GLM of the median flock size in relation to grasshopper abundance, elevation and site. For the categorical variable Site, the reference level was site C (Cervinia).

Median Alpine Chough flock size	Estimate ± Std. Error	z value	Pr(> z)
(Intercept)	1.337 ± 0.314	-7.14	9.13e-13 ***
Grasshopper abundance	0.746 ± 0.251	2.97	0.003 **
Elevation	11.140 ± 2.429	4.70	0.00027 ***
Elevation^2	-8.790 ± 2.395	-3.67	0.00024 ***
Site MA	-1.631 ± 0.451	-3.61	0.0003 ***

Table A4. Negative binomial GLM of the median flock size in relation to grasshopper biomass, elevation and site. For the categorical variable Site, the reference level was site C (Cervinia).

Median Alpine Chough flock size	Estimate ± Std. Error	z value	Pr(> z)
(Intercept)	1.531 ± 0.463	3.304	0.0009***
Grasshopper biomass	-0.233 ± 0.245	-0.95	0.34
Elevation	10.363 ± 2.353	4.40	0.00257 ***
Elevation^2	-11.307 ± 2.530	-4.47	1.06e-05 ***
Site MA	-2.636 ± 0.617	-4.28	1.91e-05 ***
Grasshopper biomass x Site MA	0.711 ± 0.265	2.68	0.00731 **

Table A5. Negative binomial GLM of the median flock size in relation to grasshopper abundance residuals, elevation and site. For the categorical variable Site, the reference level was site C (Cervinia).

Median Alpine Chough flock size	Estimate ± Std. Error	z value	Pr(> z)
(Intercept)	1.130 ± 0.316	0.34	9.14e-16 ***
Grasshopper residuals	-0.927 ± 0.361	-256	0.01034 *
Elevation	10.148 ± 2.239	4.67	0.00068 ***
Elevation^2	-10.601 ± 2.300	-4.61	4.06e_06 ***
Site MA	-0.944 ± 0.428	--2.21	0.02727 *
Grasshopper residuals x Site MA	1.171 ± 0.494	2.37	0.01779 *

Table A6. Gaussian 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 ***

Table A7. Gaussian GLM of the log median flock size in relation to grasshopper abundance, elevation, and site. For the categorical variable Site, the reference level was site C (Cervinia).

Median Alpine Chough flock size	Estimate ± Std. Error	t value	Pr(> z)
(Intercept)	1.454 ± 0.179	8.130	1.05e-10 ***
Grasshopper abundance	0.525 ± 0.154	3.399	0.002 **
Elevation	4.150 ± 1.019	4.072	0.000166 ***
Elevation ²	-2.309 ± 1.066	-2.166	0.035 *
Site MA	-0.880 ± 0.272	-2.87	0.00597 **

Table A8. Gaussian GLM of the median flock size in relation to grasshopper biomass, elevation, and site. For the categorical variable Site, the reference level was site C (Cervinia).

Median Alpine Chough flock size	Estimate ± Std. Error	t value	Pr(> z)
(Intercept)	1.604 ± 0.269	5.954	2.76e-07 ***
Grasshopper biomass	-0.185 ± 0.157	-1.177	0.24
Elevation	4.085 ± 1.002	4.075	0.00017 ***
Elevation ²	-3.808 ± 1.072	-3.552	0.00086 ***
Site MA	-1.481 ± 0.367	-4.037	0.00019 ***
Grasshopper biomass x Site MA	0.494 ± 0.173	2.846	0.0361 **

Table A9. Gaussian GLM of the median flock size in relation to grasshopper abundance residuals, elevation, and site. For the categorical variable Site, the reference level was site C (Cervinia).

Median Alpine Chough flock size	Estimate ± Std. Error	t value	Pr(> z)
(Intercept)	1.408 ± 0.182	7.736	4.86e-10 ***
Grasshopper residuals	-0.662 ± 0.241	-2.748	0.00836 **
Elevation	3.368 ± 1.002	3.362	0.00151 **
Elevation ²	-4.356 ± 0.999	-4.358	6.70e-05 ***
Site MA	-0.698 ± 0.272	-2.566	0.0134 *
Grasshopper residuals x Site MA	0.932 ± 0.312	2.988	0.00437 **