

# 1 **Grazing intensity drives a trophic shift in the diet of common alpine birds**

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## 14 **Highlights:**

- 15 • The trophic level of the diet of common insectivorous birds was measured using  
16 stable isotopes along a gradient of grazing pressure by large mammalian  
17 herbivores (LMH).
- 18 • Bird diet shifted from being dominated by herbivorous arthropod species when  
19 LMH pressure was low to being dominated by arthropods species with another  
20 diet (e.g. detritivorous, predator, coprophagous), when LMH pressure was high.

21 • This result highlights a strong trophic interaction mechanism between LMH and  
22 insectivorous birds in open landscapes, and the relevance of investigating those  
23 interactions on large gradients through isotopic analysis.

24

25

26 **Abstract**

27 Large mammalian herbivores (LMH) shape vertebrate communities and structure food webs in  
28 many terrestrial ecosystems. However, the mechanisms that underlie the effects of LMH on  
29 other vertebrates are poorly understood. In France, domestic LMH have grazed alpine and  
30 mountain grasslands for thousands of years, profoundly influencing landscapes and wildlife.  
31 As LMH modify habitat structure, favour coprophagous insects and compete with herbivorous  
32 insects, the diet of insectivorous alpine birds may be deeply influenced by LMH grazing  
33 intensity. To investigate this, we sampled common insectivorous birds faeces (water pipit  
34 *Anthus spinoletta* and wheatear *Oenanthe oenanthe*) in sites characterized by different levels of  
35 grazing intensity by domestic and wild herbivores, in the open landscapes of the southern  
36 French Alps and the western Pyrenees. We used isotopic discrimination based on nitrogen  
37 stable isotope ratios as an indicator of the trophic level of the arthropods found in bird faeces.  
38 From isotopic ratios, we found that bird diets shift from mainly herbivorous arthropods at sites  
39 of low grazing intensity, to one mainly composed of other groups, such as predatory,  
40 detritivorous or coprophagous arthropods, at sites of higher grazing intensity. This result  
41 highlights the strong trophic link between LMH and insectivorous birds in open landscapes,  
42 contributing to a better understanding of interactions between domestic grazing, an activity that  
43 has historically modelled European landscapes, and biodiversity, with particular relevance for  
44 landscape management and bird conservation.

45

46 **Keywords: large mammals, herbivory, trophic interactions, isotopic ecology, alpine**  
47 **meadows, grassland ecosystems**

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## 52 **Introduction**

53 By selectively consuming large quantities of plant biomass, large mammalian herbivores  
54 (LMH, body weight > 2kg. sensu Fritz & Loison, 2006) strongly influence plant traits and  
55 communities (Bardgett & Wardle, 2003; Clay et al., 2005), soil structure and chemistry, and  
56 food webs (Daskin & Pringle, 2016; Foster et al., 2014; Hunter & Price, 2008; Keesing &  
57 Young, 2014; Legagneux et al., 2014; MacSween et al., 2018; McNaughton, 2006). These  
58 grazing animals are known to reduce both the diversity and abundance of many herbivorous  
59 insects, while favouring a higher diversity and abundance of coprophagous insects, which  
60 benefit from their faeces (Bardgett and Wardle, 2003; Mysterud et al., 2010; van Klink et al.,  
61 2015). Together, modifications of vegetation structure and arthropod communities may in turn  
62 affect the diet of insectivorous birds (Goosey et al., 2019). In birds, quality and quantity of the  
63 diet available during breeding season is known to be of major importance for breeding success,  
64 and thus for the dynamics of populations (Lindström, 1999). Modifications of habitat and  
65 arthropod communities by LMH can thus potentially favour some bird species and disfavour  
66 others through trophic links. However, while hundreds of studies have provided evidence of  
67 correlation between LMH grazing and bird species abundance, the mechanisms that underlie  
68 the contrasting effects of LMH on other groups of species, and especially trophic links, are  
69 often lacking (Hunter and Price, 2008; Foster et al., 2014; Daskin and Pringle, 2016).

70 Cold ecosystems such as alpine meadows are places of low primary productivity. Insect and  
71 bird communities living in these ecosystems are thus expected to be particularly influenced by  
72 the indirect impacts of LMH grazing (see e.g. Ims and Henden, 2012). Vegetation structure has  
73 been demonstrated to be a major driver of bird communities worldwide (Jähnig et al., 2018;  
74 Jetz et al., 2012). In alpine meadows, grazing by domestic LMH is considered to have a major  
75 indirect effect on alpine bird diversity and abundance through habitat modification at landscape  
76 scale (Jähnig et al., 2018). This has been shown, for example, by the influence of LMH grazing

77 on the elevation of the treeline (Körner and Paulsen, 2004), or by its influence on woody and  
78 herbaceous vegetation quality and structure on a very local scale (Ims and Henden, 2012; Laiolo  
79 et al., 2004; Loe et al., 2007). However, the indirect influence that domestic LMH may have on  
80 bird communities through the modification of food resources (insects) (recently suggested in  
81 Goosey et al., 2019, on the basis of the available community of arthropods), has not been  
82 previously tested.

83 The aim of this study was to test the existence of an indirect trophic interaction between birds  
84 and LMH in alpine meadows in France. Insectivorous birds living in cold open landscapes are  
85 considered opportunists (Rotenberry, 1980; Wiens and Rotenberry, 1979, 1980), thus we  
86 expected diet to change from herbivorous arthropods to other arthropods (e.g. predatory,  
87 detritivorous and coprophagous insects), according to the relative availability/accessibility of  
88 these resources as grazing intensity increases (Martínez et al., 2021). However, as the diet of  
89 these bird species has not been investigated in detail, we thought it may also be possible that  
90 they select for specific prey among those available, maintaining their preferred type of prey  
91 whatever the latter's relative abundance. Given the significant effort that would be required to  
92 test our hypothesis based on direct observations of predation behaviours, or based on the  
93 dissection of remains (see e.g. Greig-Smith and Quicke, 2009), we used carbon and nitrogen  
94 stable isotope analysis (SIA) of faeces – in particular nitrogen, which allows a robust  
95 quantitative investigation of trophic links between species (Caut et al., 2009; Kelly, 2000;  
96 Layman et al., 2007; Quinby et al., 2020). DNA metabarcoding is another effective method to  
97 investigate changes in birds' diet, however we focused on SIA because metabarcoding was  
98 harder to interpret in a quantitative way, and much more expensive. More specifically, we tested  
99 whether the dietary isotopic signature of the two most common bird species found in the alpine  
100 meadows of the French Alps and Pyrenees, i.e. the water pipit and the wheatear, was influenced  
101 by domestic LMH grazing intensity. As the expected nitrogen stable isotope ratio for

102 herbivorous insects is lower than the expected ratio for coprophagous, detritivorous or  
103 predatory arthropods (e.g. Hyodo, 2015), we expected a strong increase in this ratio in the bird  
104 diet along the grazing intensity gradient.

105 Each summer in the alpine landscapes of the Alps and Pyrenees, more than three million  
106 domesticated mammals (mostly sheep and cattle) are brought to graze for two to five months  
107 (Agreste, 2015). Grazing pressure is highly heterogeneous and dynamic in these landscapes,  
108 due to a variety of social and ecological constraints, including farming practices, domestic herd  
109 behaviour, grassland productivity, and accessibility to humans and animals (Bar Massada et al.,  
110 2008; Hinojosa et al., 2018; Lezama et al., 2014; Steinauer and Collins, 1995). We took  
111 advantage of this heterogeneity to sample bird faeces at sites along a gradient of pasture-grazing  
112 intensity, from sites abandoned by domestic grazing activities for decades to sites with a  
113 permanent presence of thousands of domestic LMH during the summer. In order to provide a  
114 strong test of our main hypothesis, the study was conducted in two contrasting areas in terms  
115 of climate and arthropod community: the Mediterranean Alps and the Atlantic Pyrenees.

116

## 117 **Material & methods**

### 118 **General approach**

119 Due to the limited duration of the period of the year favourable to implement this study, and to  
120 maximize chances to detect the strong response we expected following our main hypothesis,  
121 we focused on sampling the extremities of the grazing intensity gradient found in French  
122 mountains. As many environmental constraints could influence plant productivity, habitat  
123 structure, and finally insect communities, we therefore sampled similar sites in terms of  
124 vegetation structure (herbaceous dominated), and elevation.

### 125 *Study area and grazing intensity*

126 The fieldwork was carried out in two geographical areas in France: the western Pyrenees (within  
127 or next to the Pyrenees National Park), and the southern Alps (Mercantour National Park). The  
128 north-western Pyrenees are characterized by higher moisture levels and colder temperatures on  
129 average than the southern Alps, which are influenced by the Mediterranean climate (see site  
130 mean temperatures in Table 1, calculated following the Kloog et al., 2016, method, which does  
131 not account for precipitation).

132 Bird faeces and insects were sampled at 5 sites in the Pyrenees and 8 sites in the Mercantour  
133 (Table 1). In both regions, we selected sites at homogeneously grazed spatial units that were  
134 large enough to host many bird territories (93 to 1177 hectares, sites are very different in size  
135 as very large sites with homogeneous grazing pressure were very scarcely found). We pre-  
136 selected sites with contrasting grazing intensity based on information from local municipalities,  
137 local managers, and national park rangers. Grazing pressure varied from sites with no domestic  
138 grazing (domestic grazing activities were abandoned 20 years ago) to sites with very intensive  
139 grazing (the permanent presence of thousands of domestic and/or wild LMH during summer)  
140 (Table 1). Based on information on domestic LMH numbers provided by local stakeholders



141 (documents called “pasture grazing plans”), we calculated an expected stocking rate ( $\text{AUM}\cdot\text{ha}^{-1}$   
142 <sup>1</sup> for Animal Unit Months per hectare) (Table 1). Due to the temporal dynamic of domestic  
143 grazing activity, it was impossible to correctly evaluate stocking rate from field counts: Herds  
144 can be absent, or not detected at the time of sampling, for various reasons like topology,  
145 movements of the herd, last minute change in shepherd calendar, veterinary interventions, etc.  
146 However, we needed to adjust for the difference between expected stocking rate and effective  
147 LMH pressure at the time of field sampling. This field observation was not dedicated to provide  
148 another evaluation of stocking rate, but to test for the effect of presence or absence of LMH at  
149 the time of sampling. We thus noticed presence or absence of LMH clues based on direct  
150 information or proxies of LMH presence (animal sightings or fresh dung, see column “LMH  
151 clues” in Table 1) during sample collection. We also measured vegetation height based on an  
152 average of twenty measures per site at “random” locations. We obtained this randomness by  
153 performing vegetation measures at regular time intervals (half an hour or one hour depending  
154 on the number of operators). If location of the operator at measurement time was not  
155 independent from habitat structure due to faeces collection, the operator chose a random,  
156 perpendicular direction from his path with a coin, and moved fifty steps in that direction (see  
157 the result on figure 1). At each of the random locations, vegetation height was measured five  
158 times in a quadrat of one squared meter using marked sticks and following a systematic grid  
159 (one next from the middle and four at the four corners). We estimated the height with maximum  
160 density of vegetation in contact with the stick location (Table 1), vegetation category was  
161 noticed as herbaceous, ligneous, mosses or bare ground, but only height was accounted here  
162 (height = 0 for bare ground). As wild ungulate densities were difficult to estimate at the time of  
163 sampling and on small areas, and were not available from monitoring programs at this scale  
164 (Maillard et al., 2010), we noted them as absent (1 site), present (10 sites), or “high” (2 sites)  
165 when high abundances of wild ungulates were observed during field sampling (more than 50

166 individuals observed in the site during the one to three days of sampling). Finally, due to limited  
167 number of sites sampled, and covariation between descriptors like vegetation height and AUM  
168 principally (see statistical analysis for values), we needed to summarize grazing intensity in a  
169 single variable for the analysis. Thus, we decided to classify the sites in four categories for  
170 further analysis: the two first categories for sites with low or very low grazing pressure: (1) >15  
171 years without domestic grazing (N=1); (2) <15 years without domestic grazing, or with low  
172 domestic grazing intensity (N=4). The categories 3 and 4 are sites with high or very high grazing  
173 pressure: (3) regular grazing by large numbers of livestock (N=6); (4) regular grazing at very  
174 high density (N=2) (see Table 1).

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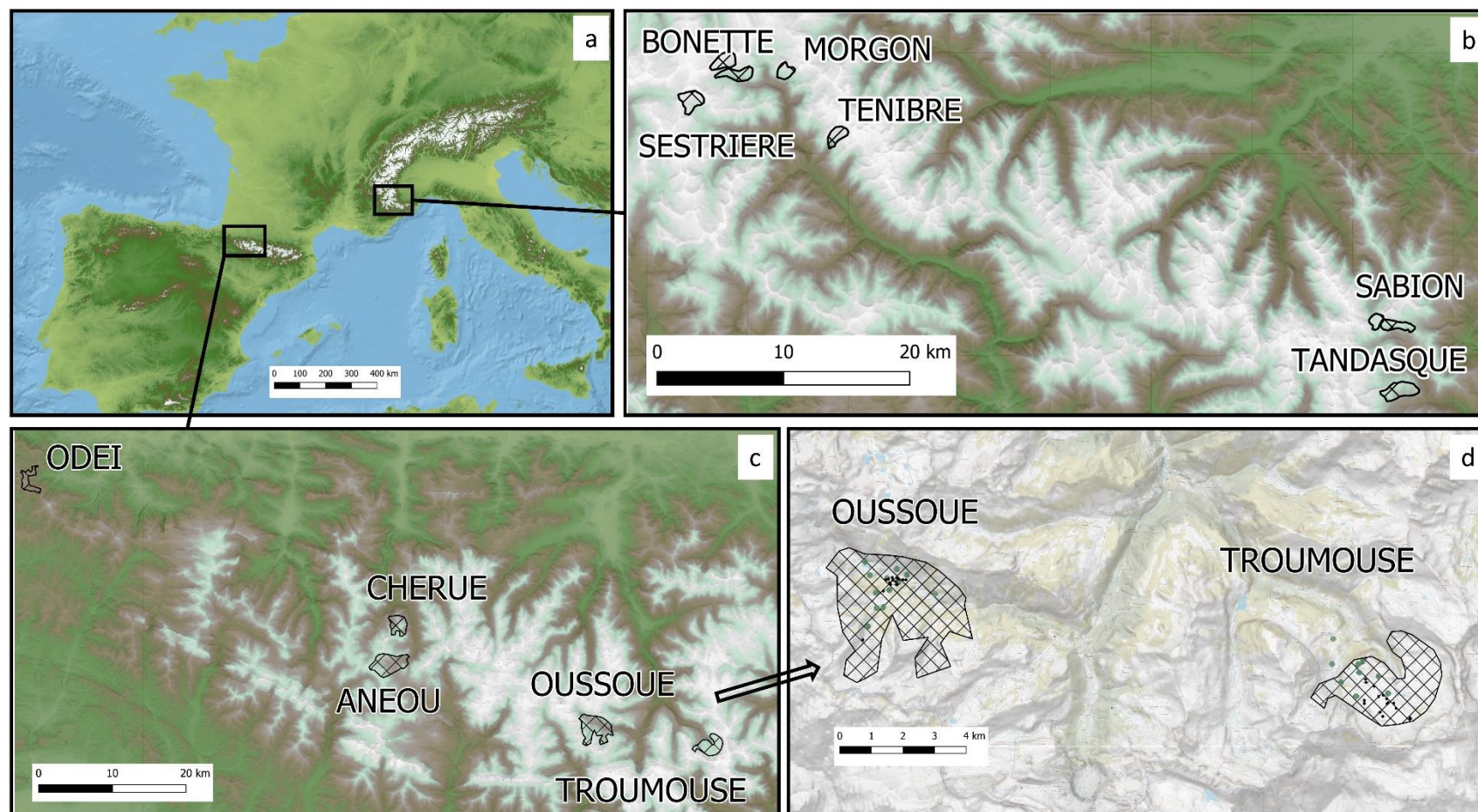


Figure 1: Map of the study sites in southern French Alps and western Pyrenees (a). Black dots on the (d) panel are collection locations for faeces and insects, and each green dot represent an aggregate of 5 random habitat measurements. Background colours depend on elevation in all but (d) panel, which background is local topographic map with forests in dark green and moors in light grey (IGN, SCAN25®, see Lafay et al., 2015). Sabion and Bonette sites were divided in two locations due to contrasted grazing conditions locally (see table 1), thus two polygons are represented but detailed names are not shown to help with reading.

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CAT	DETAILS	REGION	YEAR	SITE	N	AREA (h)	ELEVATION	T°C	AUM PER HECTARE	LMH CLUES	WILD LMH	HERBACEOUS HIGHT (cm)
1	Abandoned for 20 years. colonization by ligneous ongoing	MERCANTOUR	2017	TENIBRES	20	159	2230	9.04	0	NO	present	30
2	Abandoned since 10 years, colonization by ligneous ongoing	MERCANTOUR	2017	MORGON	32	120	2300	9.21	0	NO	present	25
2	No domestic grazing. Wild chamois are abundant	MERCANTOUR	2017	SABION	50	164	2110	9.85	0	NO	<b>high</b>	40
2	Sheep barely graze this high elevation area	MERCANTOUR	2017	BONETTE(HIGH)	15	190	2440	8.61	0,2	NO	present	15
2	Late grazing (August - September), only by cows (60)	PYRENEES	2016	OSSOUE	29	1177	1770	9.79	0,2	NO	present	50
2	Abandoned since 10 years in theory but 25 cows are present	PYRENEES	2016	CHERUE	7	514	1960	10.99	0,2	YES	present	30
3	Sheep, Cow	MERCANTOUR	2017	TANDASQUE	26	287	2040	11.36	0,9	YES	present	20
3	Sheep	MERCANTOUR	2017	BONETTE	15	202	2030	9.93	1,7	YES	present	20
3	Sheep	MERCANTOUR	2017	SESTRIERE	28	224	2290	8.36	1,5	NO	present	25
3	Sheep, Cow	PYRENEES	2016	ODEI	21	417	1510	13.95	1,6	YES	absent	10
3	Sheep, Cow, Horse	PYRENEES	2016	ANEOU	15	1094	1840	10.12	3,4	NO	present	15
4	Sheep, Cow, high density of chamois and ibex	MERCANTOUR	2017	SABION (HIGH)	76	93	2230	9.5	3	YES	<b>high</b>	5
4	Sheep, Cow	PYRENEES	2016	TROUMOUSE	20	667	2130	9.57	1,9	YES	present	5

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181

182 *Table 1: Sampling and grazing conditions at each site where bird faeces and insects were collected. YEAR: year during which sampling was*  
183 *carried out. N: number of samples collected; ; h: hectares ; AUM : Animal Unit Months ; LMH : Large Mammalian herbivores ; CAT: Category*  
184 *of grazing intensity.*

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186

187 ***Sample collection and recorded parameters***

188 The sampling of bird faeces and insects took place in June and July 2016 in the Pyrenees, and  
189 in June and July 2017 in the Mercantour (number of samples per site in Table 1). To collect  
190 faeces, we observed birds standing on rocks until they defecated or flew away. In the second  
191 case, the location of the bird was recorded and faeces were only collected if fresh (small bird  
192 faeces dry in less than 10 minutes even when not exposed to sunshine in these conditions, *pers.*  
193 *obs.*). We targeted the water pipit (*Anthus spinoletta*) and wheatear (*Oenanthe oenanthe*), but  
194 also collected faeces of the common linnet (*Linaria cannabina*) as a control, as this latter  
195 species is known to mostly eat flowers and seeds (Moorcroft et al., 2006), thus the nitrogen  
196 isotope ratio of its diet is expected to be below the ratio of insectivorous birds. We collected  
197 130, 137 and 23 faeces for the water pipit, wheatear and common linnet respectively.

198 We sampled arthropods specimens to provide a baseline of isotopic signature found in potential  
199 birds' prey depending on their diet, but not to identify with precision the taxonomic group of  
200 each individual caught. During insect sampling (sweep net and by hand), we collected 33  
201 individuals in both regions and across both the grazing and elevation gradients (from 1560 to  
202 2450 m.) (Supplementary material 1). We chose insects of the taxonomic and trophic groups  
203 found at most sites: of herbivorous insects we mainly collected juvenile grasshoppers  
204 (Orthoptera: Acrididae, n=8; other groups of herbivorous: n=4), which didn't need to be  
205 identified to species level to be sure of their phytophagous diet. For coprophagous insects, we  
206 collected Coleopteran larvae found in cow dungs (n= 5, not identified), and adults, which  
207 needed to be identified (n=3, identified as *Sphaeridium scarabeoides*, *Onthophagus facticornis*,  
208 and *Aphodius fimetarius*). We also collected Dipterans larvae, all found in dungs (n=5, not  
209 identified) and adults (n=3, all identified as *Scatophaga stercoraria*). Sample size was too small  
210 to include in the analysis insects identified as detritivorous/omnivorous based on field  
211 observations (n=3, 1 Chironomidae sp., 1 Tenebrionidae sp., 1 Forficulidae sp.), and predatory

212 insects (*Rhynocoris* sp., n=2).  $\delta^{15}\text{N}$  values are however reported for these two last groups in the  
213 results. For non-herbivorous insects, we focused on coprophagous insects as we considered  
214 isotopic signature to be the most uncertain for this group, also the diet of larvae living in dungs  
215 is easy to infer. All these groups of insects are expected to be a potentially significant part of  
216 grassland birds' diet (Kaspari & Joern, 2006).

217 The sampling locations and elevations were recorded using a GPS device (precision to about  
218 10 m, GPS position was used to extract elevation from a raster at sampling location when this  
219 information was lacking). All faeces and insect samples were stocked in 96° alcohol for 3 to 4  
220 months. Potential conservation shifts are induced by conservation in 96° alcohol, they are not  
221 problematic for the interpretation of model results, as they are not time dependent (Sweeting et  
222 al., 2004). However, any other interpretation of the data, e.g. visual comparisons between  
223 isotope ratios found in arthropods tissues and those found in bird faeces, should be considered  
224 carefully due to inconsistent conservation shifts among tissues (maximum value 1.1‰ for  
225 nitrogen and 2‰ for carbon, Sweeting et al., 2004).

226

### 227 *Isotope analysis*

228 After sample collection, we measured carbon and nitrogen stable isotope ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ )  
229 and the C and N contents of bird faeces and insects. Samples were rinsed with Milli-Q water,  
230 dried and ground using an agate mortar and sieved through a 125 $\mu\text{m}$  mesh. About 1mg of each  
231 sample of faeces and insect matter were weighed with a 1 $\mu\text{g}$  precision balance, and packaged  
232 into tin capsules (all body parts except for the digestive system, extracted before grinding).  
233 Simultaneous determinations of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were carried out using a Pyrocube Elemental  
234 Analyser (EA, Elementar GmbH) connected online in continuous flow mode to an isotopic-  
235 ratio mass spectrometer. The SIA technique we used was derived from Fourel et al. (2014). The

236 precision for replicate analyses was 0.1‰ for both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ . The data was calibrated based  
237 on international reference material IAEA-600, IAEA-CH6 and IAEA-N2. The  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$   
238 values are expressed in  $\delta$  notation, deviation from standards in parts per thousand (‰), relative  
239 to V-PDB belemnite and atmospheric  $\text{N}_2$  (air), respectively:  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N} = (\text{R}_{\text{sample}}/\text{R}_{\text{standard}} - 1)$   
240  $\times 1000$  (1) where  $\text{R} = {}^{13}\text{C}/{}^{12}\text{C}$  or  ${}^{15}\text{N}/{}^{14}\text{N}$ . The terminology to report isotope ratios follows the  
241 guidelines of Bond and Hobson (2019): the “ $\delta$ ” symbol is used for isotope ratios, and the “ $\Delta$ ”  
242 symbol is used for isotopic differences.

243

#### 244 *Statistical analysis*

245 For modelling  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  variations in insects, we only tested variables expected to have a  
246 strong effect on isotope ratios found in insects (sample size are much smaller than for birds).  
247 For  $\delta^{15}\text{N}$  these variables were insect diet (categorical with two levels: herbivorous and  
248 coprophagous), elevation (linear), and grazing intensity (either linear or four classes). In  
249 addition to these variables, region was added for  $\delta^{13}\text{C}$  models, as  $\delta^{13}\text{C}$  is a good marker of  
250 location and elevation (Körner et al., 1991; Gerschlauer et al., 2019).

251 To test for the presence of an effect of the intensity of grazing by LMH on the isotopic ratios  
252 measured in birds’ diet, we modelled variation in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  in insectivorous bird faeces, as  
253 well as in herbivorous and coprophagous insect tissues, with linear mixed models, including  
254 the site identity as a random factor to account for repeated measurements at each site (Bolker  
255 et al., 2009). For modelling  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  variations in bird faeces (response variable), we  
256 included as covariates the elevation (linear), bird species (categorical), region (categorical), and  
257 presence of mammals during field work (categorical with two levels: presence/absence). To  
258 explore whether change in bird diet was more abrupt in some part of the grazing intensity  
259 gradient (based on the four classes described above, see also table 1), this variable was included

260 as a categorical variable, or as a continuous variable, in two different models. As expected,  
261 stocking charge (AUM) and vegetation height were strongly correlated with this grazing  
262 intensity gradient ( $r=0.84$ , and  $r=-0.84$  respectively). Due to low number of sites sampled, and  
263 due to the absence of a specific sampling design dedicated to separate the effect of vegetation  
264 structure from the effect of grazing intensity on bird diet, we didn't include those covariables  
265 in the analysis (see e.g. Dormann et al., 2018).

266 All analysis were implemented in R (R Development Core Team, 2018) with the package  
267 "lme4" (Bates et al., 2014).

268

269

## 270 **Results**

271 Estimates for the effects of covariates on  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  variation in insects are shown in Table  
272 2. We found that herbivorous and coprophagous insects showed significant nitrogen isotope  
273 difference, with a higher  $\delta^{15}\text{N}$  level in coprophagous insects ( $\Delta^{15}\text{N}_{\text{C-H}} = \delta^{15}\text{N}_{\text{C}} - \delta^{15}\text{N}_{\text{H}} = 6.1$  [CI  
274 95% 4.5, 7.6],  $\chi^2(1) = 31.4$ ,  $p < 0.001$ , Figure 2&3). Among coprophagous arthropods,  $\delta^{15}\text{N}$   
275 values for dipterans ( $n=8$ ) varied between 4.11 and 10.45 (mean 7.47), and  $\delta^{15}\text{N}$  values for  
276 coleopterans ( $n=8$ ) varied between 1.86 and 4.96 (mean 3.62).  $\delta^{15}\text{N}$  values for detritivorous  
277 insects ( $n=3$ ) were 2.18, 2.13, and 0.92;  $\delta^{15}\text{N}$  values for predatory insects ( $n=2$ ) were 2.66 and  
278 4.15. The  $\delta^{15}\text{N}$  values of insect tissues decreased with elevation for both herbivorous and  
279 coprophagous insects (slope = -0.9 [CI 95% -0.2, -1.6],  $\chi^2(1) = 4.6$ ,  $p=0.03$ , Figure 2 left panel),  
280 and no effect of grazing intensity was detected (slope = -0.1 [CI 95% -0.8., 0.7],  $\chi^2(1) = 0.09$ ,  
281  $p=0.89$ ).

282 Estimates for the effects of covariates on  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  variation in bird faeces are shown in  
283 Table 2. For nitrogen isotope ratios measured in bird faeces, we found no evidence of isotope



284 difference between the two focal species (mean  $\Delta^{15}\text{N}_{\text{P-W}} = 0.16$  [CI 95% -0.2, 0.5],  $\chi^2(1) = 0.12$ ,  
285  $p=0.42$ , Table 2). The mean nitrogen isotope difference between the linnet and the water pipit  
286 was  $\Delta^{15}\text{N}_{\text{W-L}} = -3.67\text{‰}$  [CI 95% -2.9, -4.4],  $p<0.001$ , (Figure 2, Figure 3,  $\chi^2(1) = 21.45$ ,  
287  $p<0.001$ ). The Alps and Pyrenees had similar values for  $\delta^{15}\text{N}$  measured in faeces ( $\Delta^{15}\text{N}_{\text{Al-Py}} =$   
288  $0.02\text{‰}$  [CI 95% -0.8, 0.8],  $\chi^2(1) = 0.07$ ,  $p=0.95$ ). There was some evidence that  $\delta^{15}\text{N}$  decreased  
289 with elevation (slope= -0.3 [CI 95% -0.6, -0.1],  $\chi^2(1) = 3.28$ ,  $p=0.03$ ). We found that  $\delta^{15}\text{N}$  was  
290 positively correlated to grazing intensity: the slope of  $\delta^{15}\text{N}$  variation along the grazing intensity  
291 gradient was 0.84 [CI 95% 0.5, 1.2],  $\chi^2(1) = 10.72$ ,  $p<0.001$ , and the mean isotope difference  
292 between sites without grazing activity for 15 years (category 1) and intensively grazed sites  
293 (category 4) was estimated to be 2.4‰ [CI 95% 1.2, 3.6] (Table 2, Figure 3). In the raw data  
294 (boxplots Figure 3), it is clear that not any of the bird faeces collected in sites of the first  
295 category of grazing intensity had a higher signature than those of herbivorous arthropods. Then,  
296 the proportion of individual faeces signature found above the maximum value for insectivorous  
297 arthropods increases along grazing intensity categories, and is maximal in grazing category 4  
298 with more than 75% of the individual bird faeces signatures being superior to maximum  
299 herbivorous arthropods' signature. When using grazing categories in the model, the results  
300 showed that all sites significantly differed from those with the lowest value for grazing  
301 category, in terms of  $\delta^{15}\text{N}$  found in bird faeces (stars on Figure 3). Finally, the presence of  
302 mammals during field sampling was slightly correlated to the  $\delta^{15}\text{N}$  measured in bird diet, with  
303 estimated 0.35‰ higher  $\delta^{15}\text{N}$  on average when mammals or fresh dung were present [CI 95%  
304 -0.4, 1.1] ( $\chi^2(1) = 1.82$ ,  $p=0.35$ ), this effect was not statistically significant.

305 For the variation of  $\delta^{13}\text{C}$  in faeces, we found no mean difference between the two focal bird  
306 species,  $\Delta^{13}\text{C}_{\text{P-W}} = -0.09\text{‰}$  [CI 95% -0.3, 0.1] ( $\chi^2(1) = 0.31$ ,  $p=0.24$ , Table 2), but the mean  
307 difference between the linnet and both focal species was  $\Delta^{13}\text{C}_{\text{P-L}} = 1.0\text{‰}$  [CI 95% 0.6, 1.4] ( $\chi^2(1)$   
308  $= 89.64$ ,  $p<0.001$ ). As expected, the regions differed in the  $\delta^{13}\text{C}$  measured in bird faeces, with

309 a mean difference of 0.9‰ [CI 95% 0.4, 1.4] ( $\chi^2(1) = 8.54$ ,  $p=0.004$ ), between Pyrenees and  
310 Alps samples. The slope of  $\delta^{13}\text{C}$  variation along the grazing intensity gradient was 0.3‰ [CI  
311 95% 0.1, 0.6],  $\chi^2(1) = 5.13$ ,  $p=0.02$ , and the mean  $\delta^{13}\text{C}$  isotope difference between sites without  
312 grazing in the last 15 years and intensively grazed sites was 1.45‰ [CI 95% 0.76, 2.15]. When  
313 using grazing categories, the results showed that only the most intensively grazed sites were  
314 significantly different from other sites in terms of  $\delta^{13}\text{C}$  found in bird faeces (stars on Figure 4).

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Table 1: Estimates (and their standard errors) of the effects of covariates on nitrogen and carbon isotope ratios found in bird faeces and insects collected in the French Alps and Pyrenees. Estimates in bold differ significantly from 0 at the 95% level of confidence. N.T.: Not tested; Oe. Oe.: *Oenanthe oenanthe* (Wheatear); Li. Ca. *Linaria cannabina* (Common Linnet); Pyr. Pyrenees.

	Estimate (SE)			
	BIRDS		INSECTS	
	$\delta^{15}\text{N}$	p-value	$\delta^{15}\text{N}$	p-value
Insect type	--- N.T. ---		<b>-6.05 (0.78)</b>	<b>&lt;0.001</b>
Elevation	<b>-0.32 (0.13)</b>	<b>0.03</b>	<b>-0.89 (0.39)</b>	<b>0.03</b>
Grazing intensity	<b>0.84 (0.19)</b>	<b>&lt;0.001</b>	<i>-0.05 (0.38)</i>	<i>0.89</i>
Bird species (Oe. oe.)	0.15 (0.18)	0.42	--- N.T. ---	
Bird species (Li. ca.)	<b>-3.67 (0.38)</b>	<b>&lt;0.001</b>	--- N.T. ---	
LMH presence	0.35 (0.38)	0.35	--- N.T. ---	
Region (Pyr.)	0.02 (0.40)	0.95	--- N.T. ---	
	$\delta^{13}\text{C}$		$\delta^{13}\text{C}$	
		p-value		p-value
Insect type	--- N.T. ---		-0.60 (0.50)	0.23
Elevation	0.18 (0.11)	0.45	0.61 (0.49)	0.23
Grazing intensity	<b>0.30 (0.12)</b>	<b>0.02</b>	<i>-0.25 (0.27)</i>	<i>0.35</i>
Bird species (Oe. oe.)	-0.09 (0.11)	0.24	--- N.T. ---	
Bird species (Li. ca.)	<b>1.02 (0.24)</b>	<b>&lt;0.001</b>	--- N.T. ---	
LMH presence	0.07 (0.23)	0.65	--- N.T. ---	
Region (Pyr.)	<b>0.89 (0.24)</b>	<b>0.002</b>	<i>0.95 (1.08)</i>	<i>0.38</i>

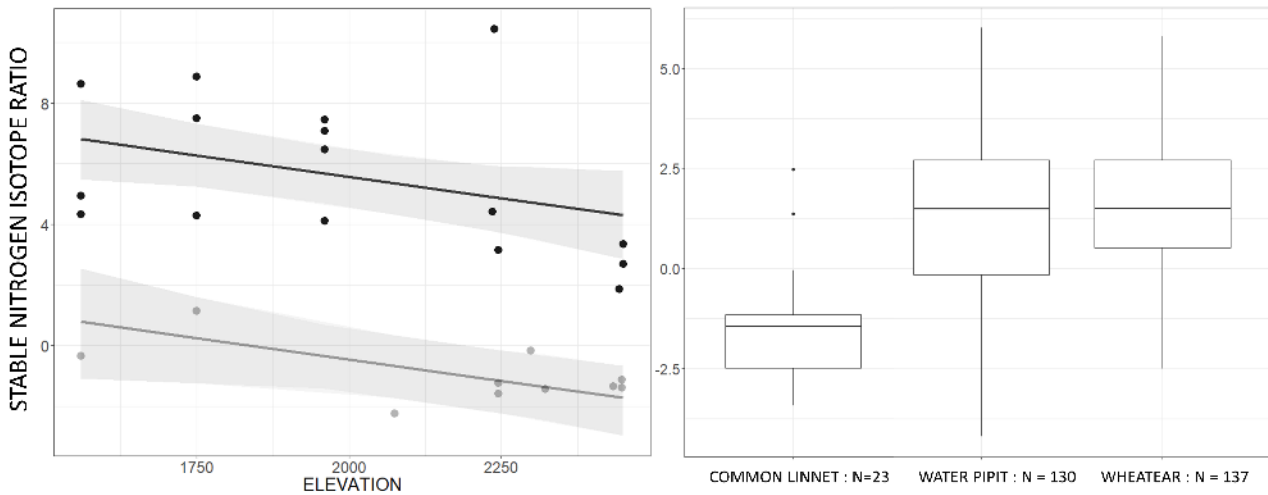


Figure 2: Left: Nitrogen isotope ratios measured in the two groups of insects (coprophagous insects: dark grey line; herbivorous insects: light grey line), as a function of elevation. Lines show the estimated effect and the shaded areas their 95% confident intervals of elevation on the variation of  $\delta^{15}\text{N}$  in each insect group. Right: Raw nitrogen isotope ratios in the three bird species' faeces. Central lines in boxplots show the median values, and edges are the 25<sup>th</sup> and 75<sup>th</sup> percentiles. Whiskers lengths are 1.5 interquartile range. N: sample size.

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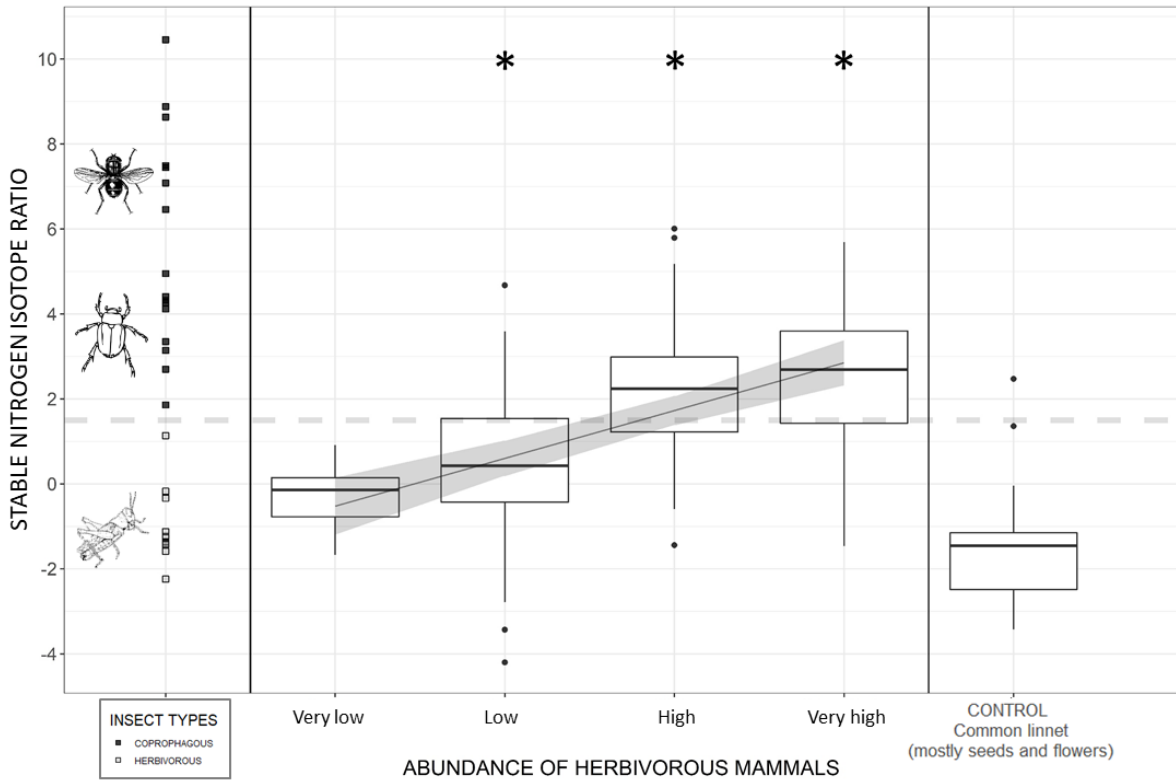


Figure 3: Central panel is the effect of grazing intensity on  $\delta^{15}\text{N}$  found in bird faeces. Nitrogen isotope ratios in insect tissues are shown in the left panel of the figure, with different shades for herbivorous and coprophagous insects, which are clearly separated. In the middle panel, stable nitrogen isotope ratios found in the faeces of insectivorous birds are shown as a function of the gradient of LHM grazing intensity in 4 discrete categories. The solid line represents the predicted effect of grazing intensity based on the  $\delta^{15}\text{N}$  model, continuous grazing intensity, and the grey area the 95% CI). Prediction was made holding elevation at the mean value for this study: 2170 m. The right panel shows  $\delta^{15}\text{N}$  values found in the control: the common linnet, which mostly consumes plants. The dotted horizontal line is equidistant from the maximum  $\delta^{15}\text{N}$  value for herbivorous insects and the minimum  $\delta^{15}\text{N}$  value for coprophagous insects. Central lines in boxplots show the median values, and edges are the 25<sup>th</sup> and 75<sup>th</sup> percentiles. Whiskers lengths are 1.5 interquartile range. Stars show the categories that differ from the first one in the model including grazing intensity as a categorical variable.

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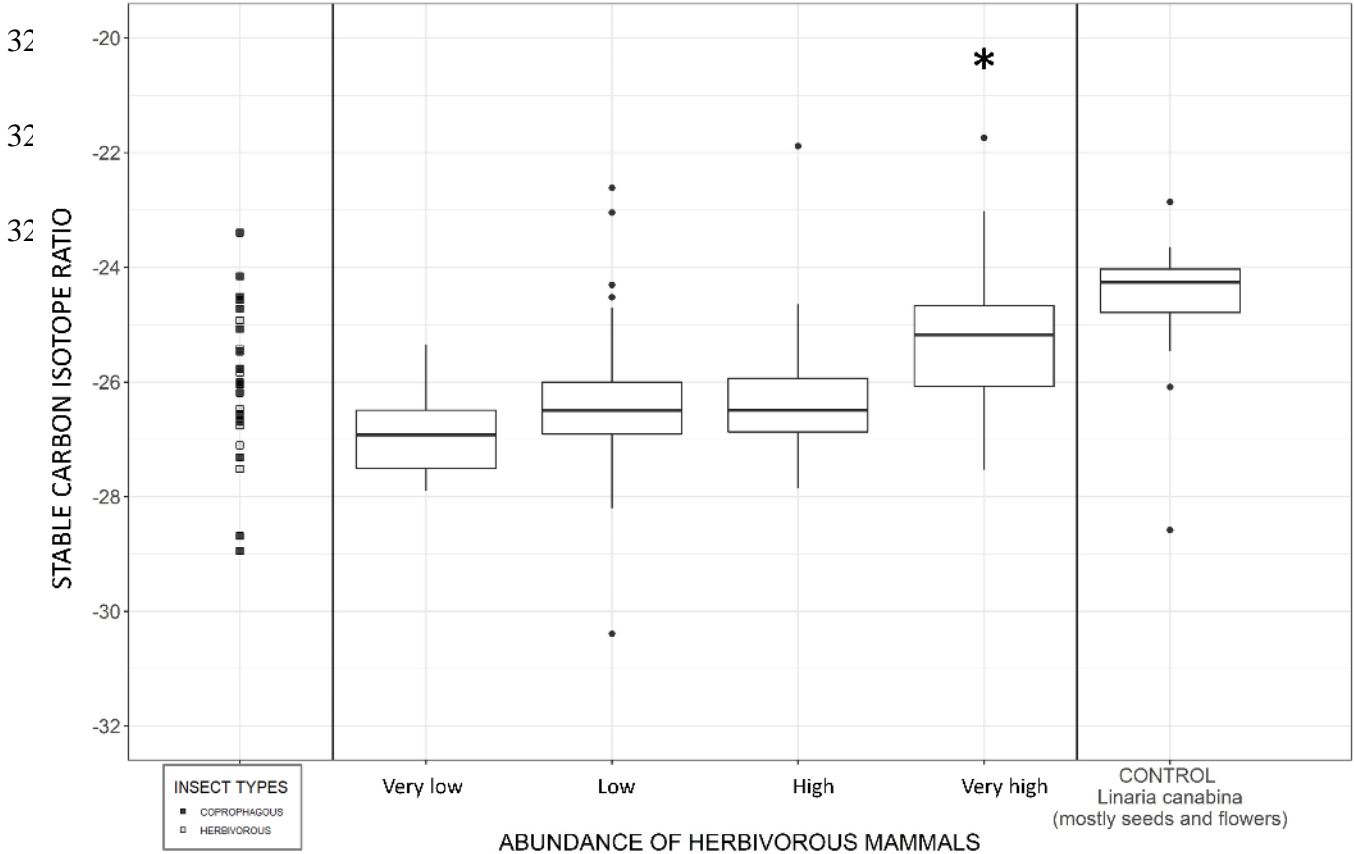


Figure 4: The effect of grazing intensity on  $\delta^{13}\text{C}$  found in bird faeces. In the left panel, carbon isotope ratios in insect tissues are shown with different shades for herbivorous and coprophagous insects. In the middle panel, stable carbon isotope ratios measured in insectivorous bird faeces are shown as a function of a gradient of LMH grazing in 4 discrete categories. The right panel shows the  $\delta^{13}\text{C}$  values for the control: the faeces of the common linnet. The star indicates the grazing category that significantly differs from category 1 (Very low) in terms of carbon isotope ratios found in bird faeces. Central lines in boxplots show the median values, and edges are the 25<sup>th</sup> and 75<sup>th</sup> percentiles. Whiskers lengths are 1.5 interquartile range. Stars show the categories that differ from the first one in the model including grazing intensity as a categorical variable.

## 327 **Discussion**

328 Our results showed that in two distinct geographic areas, the  $\delta^{15}\text{N}$  values measured in bird  
329 faeces increased along the grazing intensity gradient (Figure 3). This result demonstrates a clear  
330 trophic relationship between LMH and insectivorous birds. The  $\Delta^{15}\text{N}$  isotopic discrimination  
331 between trophic levels in the trophic networks of European alpine meadows is about +3‰,  
332 ranging from +1.5‰ to +4.5‰, (see e.g. Sponheimer et al., 2003; Männel et al., 2007), which  
333 is consistent with the differences we found in insects (see the difference in  $\delta^{15}\text{N}$  between the  
334 faeces of the common linnet and those of insectivorous birds, and the difference in  $\delta^{15}\text{N}$  between  
335 herbivorous insects and coprophagous insects). The +2.4‰ [CI 95% 1.2, 3.6] shift we estimated  
336 along sites on the gradient of grazing intensity is thus a strong signal of trophic shift. This signal  
337 is consistent with the hypothesis that birds' diets shift, under increasing grazing pressure, from  
338 mainly herbivorous arthropods to one mainly composed (>75% from raw data see Figure 3) of  
339 other arthropods with another diet, (i.e. detritivorous, predatory, or coprophagous see e.g.  
340 Brodmann et al., 1997; Freyroos et al., 1995; Goosey et al., 2019; Greig-Smith and Quicke,  
341 2009).

342 The main hypothesis to explain the change in  $\delta^{15}\text{N}$  along the grazing intensity gradient (Figure  
343 3) is that LMH influence the arthropod communities available for birds through direct impacts  
344 and habitat change. The direct impact of LMH on arthropod community is mostly to lower the  
345 abundance of herbivorous insects through competition for resources, and to increase the  
346 abundance of coprophagous arthropods. Due to habitat structure modification, they can also  
347 increase the availability of predatory and detritivorous arthropods for birds (Tschardtke, 1995).

348 An alternative explanatory mechanism might be that the  $\delta^{15}\text{N}$  variation observed in bird faeces  
349 is the result of increased  $\delta^{15}\text{N}$  in plant tissues along the grazing intensity gradient (due to the  
350 more intense use of animal nitrogen by soil microorganisms and in some plants), which may  
351 have been transferred to birds through the trophic levels (see e.g. Laiolo et al., 2015). However,

352 previous studies investigating the effect of grazing intensity on the  $\delta^{15}\text{N}$  of plants and soils have  
353 found that soil  $\delta^{15}\text{N}$  was generally not correlated with grazing intensity, especially at high  
354 elevation (Du et al., 2017; Frank and David Evans, 1997; Han et al., 2008; Tonn et al., 2019).

355 Considering that the shift we identified is representative of a shift in common insectivorous  
356 birds' diet along the gradient of grazing intensity we sampled, this result could be explained by  
357 multiple mechanisms of prey selection by birds: (1) birds forage randomly, size of the prey and  
358 effort to catch it being more important than the prey species, so the shift we found in  $\delta^{15}\text{N}$   
359 measured in bird faeces could be representative of a shift in the insect community/availability,  
360 (2) birds prefer herbivorous insects, but the lower abundance of these in highly grazed areas  
361 constrains birds to prey on other arthropods, (3) birds prefer other arthropods like detritivorous,  
362 predatory, or coprophagous species over herbivorous ones, and more intensively grazed areas  
363 are where the former are more abundant and/or more accessible. As open mountain landscapes  
364 are considered highly variable, they are generally occupied by opportunistic species in terms of  
365 diet (Rotenberry, 1980; Wiens and Rotenberry, 1979, 1980), so the first hypothesis is supported  
366 by the empiric literature on open grassland birds. In grassland ecosystems, being able to cope  
367 with changes in the availability of food induced by LMH and other factors may be a huge  
368 advantage for insectivorous birds in adapting to the unpredictable nature of food resources  
369 (Wiens and Rotenberry, 1979). In alpine meadows, the surface area of homogeneous habitats  
370 shrinks with elevation, thus it may be of even greater importance to be able to take advantage  
371 of very diverse prey potentially available in order to maintain large, connected, and thus more  
372 resilient populations. However, our results also strongly suggest selection mechanisms, as put  
373 forward in the second and third hypotheses. For example, there is no sample in bird diets  
374 showing as high  $\delta^{15}\text{N}$  signature as can be found in most coprophagous dipterans (Figure 3),  
375 which suggests that those insects are not a usual prey for insectivorous birds sampled in this  
376 study. Another example can be inferred from the increase of the  $\delta^{15}\text{N}$  signature found in bird

377 faeces for each category of grazing: In category one, all isotopic signatures in bird faeces are  
378 below the higher herbivorous arthropod signature, and below the lower value for non-  
379 herbivorous arthropods (Figure 3), but it is not the case anymore as soon as sites are in grazing  
380 category 2 (low intensity of grazing, AUM <0.3). This result seems to corroborate the third  
381 hypothesis: An intuitive explanation could be that modifications in vegetation structure due to  
382 grazing, even at low intensity, may provide birds an opportunity to catch insects that are hidden  
383 by vegetation in absence of grazing, which is obviously the case for detritivorous insects, and  
384 for many predatory arthropods like ground spiders (preferred prey for a similar species see  
385 Douglas et al., 2008, similar expected isotopic shift, see e.g. Bennett et al., 2009). It is also  
386 possible that the three mechanisms coexist through variations in individual strategies of prey  
387 selection (Bolnick et al., 2011, see e.g. Hodar, 1998).

388 To extend this study, it would be of particular interest to investigate bird diets with isotopic  
389 methods and complementary methods allowing for more precise taxonomic investigation of  
390 birds' diet (DNA metabarcoding, Cabodevilla et al., 2021, Rytönen et al., 2018, direct  
391 observations at nest sites see e.g. Douglas et al., 2008). In parallel to a quantitative description  
392 of the local insect community, such data would allow to further identifying the mechanisms of  
393 prey selection by birds in different contexts in terms of available arthropod community. Also,  
394 it would be very relevant to design a sampling plan that would allow to separate effects of  
395 vegetation height, and grazing pressure, in a same analytical process. Finally, monitoring  
396 breeding success in contrasted sites in terms of diet, would also be needed to infer the  
397 consequences of changes in diets on population sizes of different grassland bird species.

398 We checked for  $\delta^{13}\text{C}$  ratios in insects and bird faeces mainly because  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  tend to  
399 covary. We found that only the most intensively grazed sites stood out from the others with a  
400 higher  $\delta^{13}\text{C}$  ratio. The general pattern of variation found in  $\delta^{13}\text{C}$  in southern European  
401 ecosystems is mostly explained by the photosynthesis strategies of the primary producers (C3,



402 C4 or CAM, Kelly, 2000). However, alternatives to C3 photosynthesis are rarely found in the  
403 herbaceous systems of this region, so this is unlikely to explain the increase in mean  $\delta^{13}\text{C}$  we  
404 found in bird faeces at the most intensively grazed sites, and in insects along the vegetation  
405 height gradient. It is more likely that grazing reduced the local availability of soil moisture and  
406 increased plant evapotranspiration, causing grazed plants to reduce water loss by closing their  
407 stomata. This would lead to a reduction in the  $\text{CO}_2$  diffusion inside the leaf intracellular space  
408 (Cernusak et al., 2013; Liancourt et al., 2020). Hydo et al. (2015) found similar differences in  
409 the  $\delta^{13}\text{C}$  ratio of insects that fed in the canopy versus understory leaves, which seems consistent  
410 with this our results on  $\delta^{13}\text{C}_{\text{INSECTS}}$  and in  $\delta^{13}\text{C}_{\text{LINNET}}$ , as this species is known to feed on the  
411 ground on very low vegetation. However, our results on  $\delta^{13}\text{C}_{\text{BIRDS}}$ , model including vegetation  
412 height, similarly to some results of Laiolo et al, (2015) in a similar environment, suggests poor  
413 baseline effect.

414

## 415 **Conclusion**

416 We found a strong and consistent pattern of covariation between the diet of insectivorous birds  
417 and grazing by domestic and wild herds. This study opens to many other possible sampling  
418 designs to contribute to a better understanding of the interactions between birds and domestic  
419 grazing: Which arthropods are selected by birds depending on availability of the different  
420 arthropods groups in the community, and their respective size? Do isotopic signatures match  
421 the baselines effects expected when focusing on the arthropods that are effectively the prey of  
422 birds? As species with lower dietary flexibility may be more impacted in their diet and  
423 reproduction success by the profound changes in insect communities induced by LMH (Goosey  
424 et al., 2019), an interesting perspective could also be to test the generality of these results by  
425 analysing the dietary response of birds to grazing with a larger sample of species. Domestic  
426 grazing has historically shaped Europe's landscapes and biodiversity (Sartorello et al., 2020).

427 Testing the pattern we found locally at a macro ecological scale may help to highlight the past  
428 and present influence of domestic and wild LMH on the evolution of the dietary ecology of  
429 insectivorous birds in open landscapes (Bråthen et al., 2018; Legagneux et al., 2014).

430

431 **Data accessibility: DRYAD**

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438 **Authors' contributions:** JC and AB conceived the idea and designed the methodology and IB  
439 supervised the isotopic methodology and discussion for sample preservation; JC and EB  
440 collected the data; IB, FF, JC and AB analysed the data; JC led the writing of the manuscript.  
441 All authors contributed critically to the drafts and gave final approval for publication.

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445 **References**

446 Agreste, 2015. L'agriculture en montagne - Évolutions 1988-2010 d'après les recensements  
447 agricoles [WWW Document]. Publ. Natl.

448 Bar Massada, A., Gabay, O., Perevolotsky, A., Carmel, Y., 2008. Quantifying the effect of  
449 grazing and shrub-clearing on small scale spatial pattern of vegetation. *Landsc. Ecol.*

450 <https://doi.org/10.1007/s10980-007-9189-0>

451 Bardgett, R.D., Wardle, D.A., 2003. Herbivore-mediated linkages between aboveground and  
452 belowground communities. *Ecology*. <https://doi.org/10.1890/02-0274>

453 Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B.,  
454 Eigen, C., 2014. Package “lme4.” *Compr. R Arch. Netw.*

455 Bennett, P. M., & Hobson, K. A. (2009). Trophic structure of a boreal forest arthropod  
456 community revealed by stable isotope (d13C, d15N) analyses. *Entomological Science*,  
457 *12*(1), 17–24. <https://doi.org/10.1111/J.1479-8298.2009.00308.X>

458 Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White,  
459 J.-S.S., 2009. Generalized linear mixed models: a practical guide for ecology and  
460 evolution. *Trends Ecol. Evol.* <https://doi.org/10.1016/j.tree.2008.10.008>

461 Bond, A.A.L., Hobson, K.A., 2019. Reporting Stable-Isotope Ratios in Ecology :  
462 Recommended Terminology , Guidelines and Best Practices. *Waterbirds* *35*, 324–331.

463 Bråthen, K.A., Gonzalez, V.T., Yoccoz, N.G., 2018. Gatekeepers to the effects of climate  
464 warming? Niche construction restricts plant community changes along a temperature  
465 gradient. *Perspect. Plant Ecol. Evol. Syst.* <https://doi.org/10.1016/j.ppees.2017.06.005>

466 Brodmann, P.A., Reyer, H.U., Bollmann, K., Schläpfer, A.R., Rauter, C., 1997. The importance  
467 of food quantity and quality for reproductive performance in alpine water pipits (*Anthus*  
468 *spinoletta*). *Oecologia*. <https://doi.org/10.1007/s004420050074>

469 Cabodevilla, X., Mougeot, F., Bota, G., Mañosa, S., Cuscó, F., Martínez-García, J., Arroyo, B.,  
470 & Madeira, M. J. (2021). Metabarcoding insights into the diet and trophic diversity of six  
471 declining farmland birds. *Scientific Reports* *2021 11:1*, *11*(1), 1–13.  
472 <https://doi.org/10.1038/s41598-021-00519-9>

- 473 Caut, S., Angulo, E., Courchamp, F., 2009. Variation in discrimination factors ( $\Delta^{15}\text{N}$  and  
474  $\Delta^{13}\text{C}$ ): The effect of diet isotopic values and applications for diet reconstruction. *J. Appl.*  
475 *Ecol.* <https://doi.org/10.1111/j.1365-2664.2009.01620.x>
- 476 Clay, K., Holah, J., Rudgers, J.A., 2005. Herbivores cause a rapid increase in hereditary  
477 symbiosis and alter plant community composition. *Proc. Natl. Acad. Sci.*  
478 <https://doi.org/10.1073/pnas.0503059102>
- 479 Daskin, J.H., Pringle, R.M., 2016. Does primary productivity modulate the indirect effects of  
480 large herbivores? A global meta-analysis. *J. Anim. Ecol.* 85, 857–868.  
481 <https://doi.org/10.1111/1365-2656.12522>
- 482 Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G.,  
483 Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E.,  
484 Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013).  
485 Collinearity: A review of methods to deal with it and a simulation study evaluating their  
486 performance. *Ecography*, 36(1), 027–046. <https://doi.org/10.1111/j.1600->  
487 [0587.2012.07348.x](https://doi.org/10.1111/j.1600-0587.2012.07348.x)
- 488 Douglas, D., Evans, D., & Redpath, S. (2008). Selection of foraging habitat and nestling diet  
489 by Meadow Pipits *Anthus pratensis* breeding on intensively grazed moorland. *Bird Study*,  
490 55(3), 290–296. <https://doi.org/10.1080/00063650809461534>
- 491 Du, Y., Guo, X., Zhou, G., Cao, G., Li, Y., 2017. Effect of Grazing Intensity on Soil and Plant  
492  $\delta^{15}\text{N}$  of an Alpine Meadow. *Polish J. Environ. Stud.* 26, 1071–1075.  
493 <https://doi.org/10.15244/pjoes/67977>
- 494 Foster, C.N., Barton, P.S., Lindenmayer, D.B., 2014. Effects of large native herbivores on other  
495 animals. *J. Appl. Ecol.* 51, 929–938. <https://doi.org/10.1111/1365-2664.12268>

- 496 Fourel, F., Martineau, F., Seris, M., Lécuyer, C., 2014. Simultaneous N, C, S stable isotope  
497 analyses using a new purge and trap elemental analyzer and an isotope ratio mass  
498 spectrometer. *Rapid Commun. Mass Spectrom.* <https://doi.org/10.1002/rcm.7048>
- 499 Frank, D.A., David Evans, R., 1997. Effects of native grazers on grassland N cycling in  
500 Yellowstone National Park. *Ecology.* [https://doi.org/10.1890/0012-9658\(1997\)078\[2238:EONGOG\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[2238:EONGOG]2.0.CO;2)
- 502 Freyroos, F., Brodmann, P. a, Reyer, H.U., 1995. Relationships Between Food Resources,  
503 Foraging Patterns, and Reproductive Success in the Water Pipit, *Anthus Sp-Spinoletta.*  
504 *Behav. Ecol.* 6, 287–295. <https://doi.org/10.1093/beheco/6.3.287>
- 505 Fritz, H., & Loison, A. (2006). Large herbivores across biomes. In K. Danell, R. Duncan, B.  
506 Pastor, & J. Pastor (Eds.), *Large Herbivore Ecology, Ecosystem Dynamics and*  
507 *Conservation.* Cambridge University Press.  
508 <https://doi.org/10.1017/CBO9780511617461.003>
- 509 Goosey, H.B., Smith, J.T., O’Neill, K.M., Naugle, D.E., 2019. Ground-Dwelling Arthropod  
510 Community Response to Livestock Grazing: Implications for Avian Conservation.  
511 *Environ. Entomol.* 48, 856–866. <https://doi.org/10.1093/ee/nvz074>
- 512 Greig-Smith, P.W., Quicke, D.L.J., 2009. The diet of nestling Stonechats. *Bird Study.*  
513 <https://doi.org/10.1080/00063658309476774>
- 514 Han, G., Hao, X., Zhao, M., Wang, Mingjun, Ellert, B.H., Willms, W., Wang, Mingjiu, 2008.  
515 Effect of grazing intensity on carbon and nitrogen in soil and vegetation in a meadow  
516 steppe in Inner Mongolia. *Agric. Ecosyst. Environ.*  
517 <https://doi.org/10.1016/j.agee.2007.11.009>
- 518 Hinojosa, L., Lambin, E.F., Mzoughi, N., Napoléone, C., 2018. Constraints to farming in the

519 Mediterranean Alps: Reconciling environmental and agricultural policies. Land use  
520 policy. <https://doi.org/10.1016/j.landusepol.2017.11.047>

521 Hunter, M. D., & Price, P. W. (1992). Playing Chutes and Ladders : Heterogeneity and the  
522 Relative Roles of Bottom-Up and Top- Down Forces in Natural Communities. *Ecology*,  
523 73(3), 724–732. <https://doi.org/10.2307/1940152>

524 Hyodo, F., 2015. Use of stable carbon and nitrogen isotopes in insect trophic ecology. *Entomol.*  
525 *Sci.* <https://doi.org/10.1111/ens.12128>

526 Ims, R.A., Henden, J.A., 2012. Collapse of an arctic bird community resulting from ungulate-  
527 induced loss of erect shrubs. *Biol. Conserv.* <https://doi.org/10.1016/j.biocon.2012.02.008>

528 Jähnig, S., Alba, R., Vallino, C., Rosselli, D., Pittarello, M., Rolando, A., Chamberlain, D.,  
529 2018. The contribution of broadscale and finescale habitat structure to the distribution and  
530 diversity of birds in an Alpine forest-shrub ecotone. *J. Ornithol.*  
531 <https://doi.org/10.1007/s10336-018-1549-9>

532 Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K., Mooers, A.O., 2012. The global diversity of  
533 birds in space and time. *Nature.* <https://doi.org/10.1038/nature11631>

534 Kaspari, M., Joern, A., 2006. Prey Choice by Three Insectivorous Grassland Birds:  
535 Reevaluating Opportunism. *Oikos.* <https://doi.org/10.2307/3544909>

536 Keesing, F., Young, T.P., 2014. Cascading consequences of the loss of large mammals in an  
537 African Savanna. *Bioscience* 64, 487–495. <https://doi.org/10.1093/biosci/biu059>

538 Kelly, J.F., 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian  
539 trophic ecology. *Can. J. Zool.* <https://doi.org/10.1139/z99-165>

540 Kloog, I., Nordio, F., Lepeule, J., Padoan, A., Lee, M., 2016. Modelling spatio-temporally  
541 resolved air temperature across the complex geo-climate area of France using satellite-

542 derived land surface temperature data. *International journal of climatology*.  
543 <https://doi.org/10.1002/joc.4705>

544 Körner, C., Paulsen, J., 2004. A world-wide study of high altitude treeline temperatures. *J.*  
545 *Biogeogr.* 31, 713–732. <https://doi.org/10.1111/j.1365-2699.2003.01043.x>

546 Lafay, S., Braun, A., Chandler, D., Michaud, M., Ricaud, L., & Mustière, S. (2015). Automatic  
547 mapping and innovative on-demand mapping services at IGN France. *Cartography and*  
548 *Geographic Information Science*, 42(1), 54–68.  
549 <https://doi.org/10.1080/15230406.2014.980442>

550 Laiolo, P., Dondero, F., Ciliento, E., Rolando, A., 2004. Consequences of pastoral abandonment  
551 for the structure and diversity of the alpine avifauna. *J. Appl. Ecol.* 41, 294–304.  
552 <https://doi.org/10.1111/j.0021-8901.2004.00893.x>

553 Laiolo, P., Illera, J.C., Mele, L., Segura, A., 2015. Abiotic , Biotic , and Evolutionary Control  
554 of the Distribution of C and N Isotopes in Food Webs 185. *The American Naturalist*.  
555 <https://doi.org/10.1086/679348>

556 Layman, C.A., Arrington, D.A., Montaña, C.G., Post, D.M., 2007. Can stable isotope ratios  
557 provide for community-wide measures of trophic structure? *Ecology*.  
558 [https://doi.org/10.1890/0012-9658\(2007\)88\[42:CSIRPF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2)

559 Legagneux, P., Gauthier, G., Lecomte, N., Schmidt, N.M., Reid, D., Cadieux, M.C., Berteaux,  
560 D., Bêty, J., Krebs, C.J., Ims, R.A., Yoccoz, N.G., Morrison, R.I.G., Leroux, S.J., Loreau,  
561 M., Gravel, D., 2014. Arctic ecosystem structure and functioning shaped by climate and  
562 herbivore body size. *Nat. Clim. Chang.* <https://doi.org/10.1038/nclimate2168>

563 Lezama, F., Baeza, S., Altesor, A., Cesa, A., Chaneton, E.J., Paruelo, J.M., 2014. Variation of  
564 grazing-induced vegetation changes across a large-scale productivity gradient. *J. Veg. Sci.*

565 <https://doi.org/10.1111/jvs.12053>

566 Lindström, J. (1999). Early development and fitness in birds and mammals. *Trends in Ecology*  
567 *& Evolution*, 14(9), 343–348. [https://doi.org/10.1016/S0169-5347\(99\)01639-0](https://doi.org/10.1016/S0169-5347(99)01639-0)

568 Loe, L.E., Mysterud, A., Stien, A., Steen, H., Evans, D.M., Austrheim, G., 2007. Positive short-  
569 term effects of sheep grazing on the alpine avifauna. *Biol. Lett.* 3, 109–111.  
570 <https://doi.org/10.1098/rsbl.2006.0571>

571 MacSween, J., Leroux, S.J., Oakes, K.D., 2018. Cross-ecosystem effects of a large terrestrial  
572 herbivore on stream ecosystem functioning. *Oikos* 135–145.  
573 <https://doi.org/10.1111/oik.05331>

574 Männel, T.T., Auerswald, K., Schnyder, H., 2007. Altitudinal gradients of grassland carbon and  
575 nitrogen isotope composition are recorded in the hair of grazers. *Glob. Ecol. Biogeogr.*  
576 <https://doi.org/10.1111/j.1466-8238.2007.00322.x>

577 Martínez, F., Dellapé, P., ... A.B.-J. of A., 2021, U., 2021. Shrub-dwelling arthropod  
578 assemblages respond differently to grazing disturbance in the southern Monte, Argentina.  
579 *J. Arid Environ.* 188. <https://doi.org/https://doi.org/10.1016/j.jaridenv.2020.104384>

580 McNaughton, S.J., 2006. Ecology of a Grazing Ecosystem: The Serengeti. *Ecol. Monogr.*  
581 <https://doi.org/10.2307/1942578>

582 Moorcroft, D., Wilson, J.D., Bradbury, R.B., 2006. Diet of nestling Linnets *Carduelis cannabina*  
583 on lowland farmland before and after agricultural intensification. *Bird Study.*  
584 <https://doi.org/10.1080/00063650609461428>

585 Mysterud, A., Aaserud, R., Hansen, L.O., Åkra, K., Olberg, S., Austrheim, G., 2010. Large  
586 herbivore grazing and invertebrates in an alpine ecosystem. *Basic Appl. Ecol.*  
587 <https://doi.org/10.1016/j.baae.2010.02.009>



588 Quinby, B. M., Creighton, J. C., & Flaherty, E. A. (2020). Stable isotope ecology in insects: a  
589 review. *Ecological Entomology*, 45(6), 1231–1246. <https://doi.org/10.1111/een.12934>

590 R Development Core Team, 2016. R: A Language and Environment for Statistical Computing.  
591 R Found. Stat. Comput. <https://doi.org/10.1007/978-3-540-74686-7>

592 Rotenberry, J.T., 1980. Dietary Relationships among Shrubsteppe Passerine Birds: Competition  
593 or Opportunism in a Variable Environment. *Wiley Online Libr.* 50, 93–110.  
594 <https://doi.org/10.2307/2937248>

595 Rytönen, S., Vesterinen, E., Westerduin, C., Leviäkangas, T., Vatka, E., Mutanen, M.,  
596 Välimäki, P., Hukkanen, M., Suokas, M., & Orell, M. (2018). From feces to data: A  
597 metabarcoding method for analyzing consumed and available prey in a bird-insect food  
598 web. *Ecology and Evolution*, 9(1), 631–639. <https://doi.org/10.1002/ece3.4787>

599 Sartorello, Y., Pastorino, A., Bogliani, G., ... S.G.-J. for N., 2020, U., 2020. The impact of  
600 pastoral activities on animal biodiversity in Europe: A systematic review and meta-  
601 analysis. *J. Nat. Conserv.* 56. <https://doi.org/https://doi.org/10.1016/j.jnc.2020.125863>

602 Sponheimer, M., Robinson, T., Ayliffe, L., Passey, B., Roeder, B., Shipley, L., Lopez, E.,  
603 Cerling, T., Dearing, D., Ehleringer, J., 2003. An experimental study of carbon-isotope  
604 fractionation between diet, hair, and feces of mammalian herbivores. *Can. J. Zool.*  
605 <https://doi.org/10.1139/z03-066>

606 Steinauer, E.M., Collins, S.L., 1995. Effects of urine deposition on small-scale patch structure  
607 in prairie vegetation. *Ecology*. <https://doi.org/10.2307/1940926>

608 Sweeting, C. J., Polunin, N. V. C., & Jennings, S. (2004). Tissue and fixative dependent shifts  
609 of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in preserved ecological material. *Rapid Communications in Mass*  
610 *Spectrometry*, 18(21), 2587–2592. <https://doi.org/10.1002/RCM.1661>

611 Tonn, B., Porath, I., Lattanzi, F.A., Isselstein, J., 2019. Urine effects on grass and legume  
612 nitrogen isotopic composition: Pronounced short-term dynamics of  $\delta^{15}\text{N}$ . PLoS One.  
613 <https://doi.org/10.1371/journal.pone.0210623>

614 Tschardtke, T., 1995. Insect Communities, Grasses, and Grasslands. *Annu. Rev. Entomol.*  
615 <https://doi.org/10.1146/annurev.ento.40.1.535>

616 van Klink, R., van der Plas, F., van Noordwijk, C.G.E.T., Wallisdevries, M.F., Olf, H., 2015.  
617 Effects of large herbivores on grassland arthropod diversity. *Biol. Rev.*  
618 <https://doi.org/10.1111/brv.12113>

619 Wiens, J., Rotenberry, J.T., 1979. Diet niche relationships among North American grassland  
620 and shrubsteppe birds. *Oecologia*. <https://doi.org/10.1007/BF00346594>

621 Wiens, J.A., Rotenberry, J.T., 1980. Patterns of Morphology and Ecology in Grassland and  
622 Shrubsteppe Bird Populations. *Ecol. Monogr.* 50. <https://doi.org/10.2307/2937253>

623