

Grazer density and songbird counts in a restored conservation area

Lilla Lovász ^{Corresp., 1, 2}, Fränzi Korner-Nievergelt ³, Valentin Amrhein ^{1, 2}

¹ Department of Environmental Sciences, Zoology, Universität Basel, Basel, Switzerland

² Research Station Petite Camargue Alsacienne, Saint-Louis, France

³ oikostat GmbH, Ettiswil, Switzerland

Corresponding Author: Lilla Lovász

Email address: lilla.lovasz@unibas.ch

Grazing by large herbivores is increasingly used as a management tool in European nature reserves. The aim is usually to support an open but heterogeneous habitat and its corresponding plant and animal communities. Previous studies showed that birds may profit from grazing but that the effect varies among bird species. Such studies often compared bird counts among grazed areas with different stocking rates of herbivores. Here, we investigated how space use of Konik horses and Highland cattle is related to bird counts in a recently restored conservation area with a year-round natural grazing management. We equipped five horses and five cattle with GPS collars and correlated the density of their GPS positions on the grazed area with the density of bird observations from winter through the breeding season. We found that of the eight most common songbird species observed in our study area, the Eurasian Skylark and the Common Starling had the clearest positive correlations with grazer density, while the Blackbird showed a negative correlation. Skylarks and Starlings in our study area thus seem to profit from year-round natural grazing by a mixed group of horses and cattle.

1

2 **Grazer density and songbird counts in a restored** 3 **conservation area**

4

5

6 Lilla Lovász^{1,2}, Fränzi Korner-Nievergelt³, Valentin Amrhein^{1,2}

7

8 ¹ Department of Environmental Sciences, Zoology, University of Basel, Basel, Switzerland9 ² Research Station Petite Camargue Alsacienne, Saint-Louis, France10 ³ oikostat GmbH, Ettiswil, Switzerland

11

12 Corresponding Author:

13 Lilla Lovász¹

14

15 Email address: lilla.lovasz@unibas.ch

16

17

18 **Abstract**

19

20 Grazing by large herbivores is increasingly used as a management tool in European nature
21 reserves. The aim is usually to support an open but heterogeneous habitat and its corresponding
22 plant and animal communities. Previous studies showed that birds may profit from grazing but
23 that the effect varies among bird species. Such studies often compared bird counts among grazed
24 areas with different stocking rates of herbivores. Here, we investigated how space use of Konik
25 horses and Highland cattle is related to bird counts in a recently restored conservation area with a
26 year-round natural grazing management. We equipped five horses and five cattle with GPS
27 collars and correlated the density of their GPS positions on the grazed area with the density of
28 bird observations from winter through the breeding season. We found that of the eight most
29 common songbird species observed in our study area, the Eurasian Skylark and the Common
30 Starling had the clearest positive correlations with grazer density, while the Blackbird showed a
31 negative correlation. Skylarks and Starlings in our study area thus seem to profit from year-round
32 natural grazing by a mixed group of horses and cattle.

33

34 **Introduction**

35

36 Bird communities in open landscapes are often positively influenced by ungulate grazing,
37 due to the heterogeneous, structure-rich environment created by the grazers (Roth 1976; van Klink
38 et al. 2016; VanWieren 1995; Vera 2000). Therefore, grazing by one or more species of large
39 herbivores is increasingly used as a management tool in European nature conservation areas
40 (Henning et al. 2017; Loucougaray et al. 2004; Rosenthal et al. 2012).

41 The extent to which bird species react to grazing likely depends on how much they rely on
42 the particular niches affected by grazing (Milchunas et al. 1988). For example, shortened
43 vegetation may provide suitable nesting habitat and higher food availability for some bird
44 species, while others may be impeded by the effect of trampling (Leal et al. 2019; Sharps et al.
45 2017; Toepfer & Stubbe 2001). The Eurasian Skylarks *Alauda arvensis* is one example of a
46 species that was shown to require open and structurally diverse habitat mosaics with relatively
47 short vegetation to maximize their nesting attempts (Wilson et al. 1997). In contrast, trampling
48 was reported to be the main cause of nest loss of Skylarks and Meadow Pipits on meadows
49 grazed by livestock at high densities (Pavel 2004).

50 Studies so far mainly compared how the impact of grazing on bird communities differs
51 between enclosures with different stocking rates of large herbivores (Baldi et al. 2005; Dross et
52 al. 2018). For example, (Batary et al. 2007) found that grassland birds were more abundant on
53 extensively grazed areas compared to intensively grazed areas, while this was not the case in
54 non-grassland birds.

55 However, it was so far rarely examined how the effect of space use patterns of grazers on
56 particular birds varies within a given grazed area. One example is Kohler et al. (2016) who

57 investigated space use of horses in relation to a bird assemblage in a German nature reserve by
58 using a GPS collar on one of the horses. The authors found that the density of bird observations,
59 especially of the Skylark, was higher where the density of horse GPS positions was higher.

60 Here, we studied how counts of songbirds are related to the space use of a mixed
61 assemblage of five Konik horses and five Highland cattle in a French nature reserve that was
62 recently ecologically restored. The applied management approach is natural grazing, a low
63 intensity (<0.5 animal units per hectare) year-round grazing regime with the aim of substituting
64 extinct wild herbivores such as the wild horse (*Equus ferus*) or the aurochs (*Bos primigenius*)
65 with domestic breeds kept in semi-wild conditions, i.e. without systematic winter feeding and
66 with minimal human intervention (Linnell et al. 2015; Vermeulen 2015). We thus investigated
67 how counts of the different bird species from winter through the breeding season correlate with
68 the density of GPS positions of the horses and cattle equipped with GPS collars in a natural
69 grazing regime.

70

71 **Materials & Methods**

72

73 Study site

74

75 Our study site is located on the Rhine Island of the nature reserve Petite Camargue
76 Alsacienne in France, north of Basel, Switzerland. About 100 ha of the island has been part of an
77 ecosystem restoration project since 2014. The former crop fields on the area have been turned
78 into an alluvial environment. A mixed habitat of grassland scattered with bushes (hawthorn, dog
79 rose) and gravel sites was constructed, surrounded by patches of old forests (oak, ash). Since the
80 beginning of the restoration project, saplings of willow and poplar are increasingly growing on
81 some parts of the area. The water of the Rhine is led through the island in small creeks, and
82 several ground-water ponds have been created.

83 The study was done with permission of the national nature reserve Petite Camargue
84 Alsacienne.

85

86 Grazer data

87

88 Konik horses and Highland cattle were gradually introduced into a 32-ha test enclosure on
89 the island between September 2018 and March 2019 to contribute to the maintenance of the
90 heterogenous and open habitat. We equipped all horses (n=5) and cattle (n=5) with GPS collars
91 (Followit, type Pellego) recording their positions once per hour, starting from the time of their
92 arrival to the area. We used data starting from January 2019 when three cattle and all five horses
93 were present on the area; two additional cattle arrived in March 2019. The data were downloaded
94 through satellite processing from the interface of the GPS collar provider (Followit), therefore no
95 contact to the animals was necessary to access the data. Since decades, GPS collars have been
96 widely used on cattle without causing harm or disturbance (e.g. Turner et al. 2000; Ungar et al.

97 2005), and as recently discussed by Collins et al. (2014), GPS collars also comply with animal
98 welfare requirements for horses.

99 GPS accuracy may be affected by atmospheric conditions, satellite or receiver errors (Hurn
100 1993), satellite geometry (Dussault et al. 2001), topography, overhead canopies, or adjacent
101 structures (Di Orio et al. 2003; Moen et al. 1996); therefore the GPS fixes in our dataset likely
102 had some imprecision. Our applied GPS collars did not record HDOP (horizontal dilution of
103 precision) data and we therefore did not correct for inaccuracy of the fixes. However, since only
104 3.32% of all grazer positions fell outside the fenced area (those fixes were not included into the
105 analysis), we assumed that this rate would not strongly influence our results (see also Ganskopp
106 & Johnson (2007).

107 For statistical analysis, we pooled all grazer positions; we considered the hourly GPS fixes
108 positions of horses and cattle as describing their space use (i.e., the density distribution of all
109 horses and cattle over the study area).

110

111 Bird data

112

113 In 2019, we made 22 bird surveys between 31 January and 24 July. Visits were carried out
114 in favorable weather conditions, on days without rain and with little or no wind.

115 We surveyed bird abundance by transect walking on the grazed meadows; we did not
116 include a 10.6-ha-area of old forests that was part of the enclosure, so that the final size of the
117 studied area was 21.4 ha. We selected three line transects (Gregory et al. 2004; Laiolo 2005)
118 over the meadow area, each of about 700 m length, so that all parts of the grazed meadow were
119 in visual and/or auditory distance from a transect. A trained observer (L.L.) walked along the
120 transects with a slow pace and marked the position of the observed birds on a digital map (Map
121 Marker 2.11_1442). Every identified bird species was recorded; birds flying higher than 20 m
122 above the ground without showing connection to the area were excluded (e.g., skylarks that
123 made territorial songflights at >20 m elevation were counted, but raptors crossing >20 m over the
124 meadows were not). Surveys were conducted in the mornings until noon, avoiding dawn hours to
125 minimize detectability differences due to rapid changes in birds' conspicuousness and activity
126 (Dawson (1981). The order of visits of the three transects per morning were alternated
127 systematically. Differences in bird detectability between transects were probably rather small,
128 due to the similar open habitat of the surveyed areas. To minimize the risk of double counts, we
129 used a cut-off distance of 60 m to either side of the transects so that transects would not overlap
130 but cover the entire grazed area, and followed the recommendation of Dawson & Bull (1975):
131 unless it is reasonably sure that the same individual is observed, observations are counted as
132 different individuals.

133 Eight bird species had sufficient sample sizes ($n > 20$ counts) for statistical analysis: Barn
134 Swallow (*Hirundo rustica*), Common Blackbird (*Turdus merula*), Common Starling (*Sturnus*
135 *vulgaris*), Eurasian Skylark (*Alauda arvensis*), Great Tit (*Parus major*), Meadow/Water Pipit

136 (*Anthus pratensis/spinoletta*; these two species were merged for analysis), Red-backed Shrike
137 (*Lanius collurio*) and White Wagtail (*Motacilla alba*).

138

139 Statistical analysis

140

141 For analysis, the study area was divided into 113 50x50 m grid cells using the corner points
142 of the UTM grid. Numbers of bird counts and of recorded grazer positions were summed up per
143 grid cell, resulting in measures of bird density and of grazer density. Grazer GPS positions per
144 grid cell were summed over the last 30 days prior to a bird survey; we assumed that grazer space
145 use patterns earlier than 30 days before the respective bird survey did not substantially influence
146 bird space use. Because we assumed detectability of bird species to be relatively homogeneous
147 across the study area and we were not interested in estimating the total number of birds present
148 in the study area, we did not take detectability into account in our analyses (as e.g. Buckland et
149 al. 2001). Due to the migratory behaviour of some bird species, species composition changed
150 over the course of the study. For the analyses, we excluded periods when a migratory bird
151 species was not regularly present in our study site, which was from the 9th survey session (17th
152 April) for the Pipits; until the 7th survey session (23rd March) for the Barn Swallow; and until the
153 12th survey session (4th May) for the Red-backed Shrike. The surveys were distributed between
154 winter, spring and summer in order to capture a large variety of environmental conditions (e.g.
155 temperature, vegetation) as well as different bird behaviours (wintering, migrating, breeding).

156 We used a negative binomial mixed model with a logarithm link function to measure
157 species-specific correlations between bird counts and grazer density. The logarithm of the size of
158 grid cells was used as an offset in the linear predictor in order to make counts comparable
159 between grid cells of different sizes (at the edges of the study area some parts of the grid cells
160 fell outside of the fenced area). We log-transformed grazer densities and therefore replaced
161 values of zero (i.e. zero observations in a grid cell) with half of the minimal non-zero value. The
162 log-transformed grazer density was used as covariate and bird species was included as a random
163 factor. Both random intercepts and random slopes were used to model species-specific
164 correlations between bird and grazer density.

165 We fitted the model using Bayesian methods as implemented in Stan
166 (StanDevelopmentTeam 2014) via the function `brm` from the package `brms` (Bürkner 2017) in R
167 3.6.1 (RCoreTeam 2016). The default flat prior distributions over the reals were used for the
168 average correlation between bird and grazer density. Half-student $t(3,0,10)$ was used for the
169 variance parameters and $\text{Gamma}(0.01, 0.01)$ was used as prior distribution for the shape
170 parameter of the negative binomial distribution.

171 We assessed model fit by residual analyses and posterior predictive model checking. From
172 the residuals we calculated a semi-variogram in order to check for spatial correlation, and we
173 calculated the autocorrelations in order to check for temporal correlation. The semi-variance
174 ranged between 2.5 and 3.5 over the distances 0 to 200 m and it did not increase with distance.
175 Temporal autocorrelations measured within species and within the 50x50 m grid cell ranged

176 from -0.002 to 0.004 for the lag of 1 to 10 weeks, and thus we judged these temporal correlations
177 to be small enough to be ignored. We further simulated 2000 different virtual replicated data sets
178 from the model (posterior predictive distribution) and compared the proportion of zero values as
179 well as the variance between the replicated and the real data in order to check for zero-inflation
180 and overdispersion. The proportion of zero values in the replicated data ranged from 0.97 to 0.98
181 (1 and 99% quantiles), which included the proportion of zero values in the data (0.98). Also, the
182 standard deviation of the data (1.89) fell within the range of standard deviations of the replicated
183 data from the model (0.80 to 8.21). Therefore, we concluded that the model described the
184 variance and the proportion of counts of zero of our data well and did not suffer from apparent
185 spatial and temporal correlation.

186 We used 2000 simulated random values from the joint posterior distribution of the model
187 parameters to describe parameter estimates and their uncertainty. We used the median of the
188 marginal posterior distribution as point estimate and the 2.5% and 97.5% quantiles as lower and
189 upper limits of the 95% Bayesian compatibility intervals (Amrhein et al. 2019b).

190

191

192 **Results**

193

194 In total, we observed 2125 individuals from 64 bird species. From the eight species included
195 in the analysis, we made a total of 1424 observations. The only species that certainly bred on the
196 grazed area were the Skylark and the Red-Backed Shrike. The White Wagtail likely bred on the
197 meadows in the study area. The Great Tit, Common Starling and Common Blackbird bred in the
198 bushes and patches of forest in and around the fenced area. Barn Swallows were observed
199 foraging in flight and Pipits mainly in flocks on the ground.

200 Median grazer density per grid cell did not change markedly over the course of the study
201 (figure 1). Variance in grazer density increased in May, indicating that grazing occurred
202 homogeneously on all cells in winter, while during spring and summer some cells were grazed
203 with a higher intensity whereas others were largely avoided by the grazers.

204 Bird species that showed a relatively clear positive correlation with grazer density ($P(\beta > 0)$ is
205 relatively high; table 1, figure 2), given our statistical model, were Starlings and Skylarks. In the
206 Starling, our data are most compatible with slopes between 0.28 and 1.02 and in the Skylark with
207 slopes between -0.18 and 0.63 (table 1). Species with the clearest negative correlations were
208 Blackbirds and Barn Swallows ($P(\beta > 0)$ is relatively low): the data on the Blackbird are most
209 compatible with slopes between -0.92 and 0.07, and in the Barn Swallow with slopes between
210 -1.33 and 0.29 (table 1). Apart from the Starling, however, the patterns are quite uncertain, given
211 the wide compatibility intervals (table 1, figure 2).

212

213

214 **Discussion**

215

216 We investigated responses of birds to natural grazing in a newly restored nature
217 conservation area by using GPS collars on individual cattle or horses. We studied grazing
218 pressure on a continuous scale, which differs from earlier studies that categorized grazing
219 pressure, e.g., as "high" or "low" (e.g. Batary et al. 2007). Further, unlike previous studies that
220 investigated either the breeding season or winter (e.g. Hartel et al. 2014; Leal et al. 2019), we
221 considered bird observations starting from winter through the breeding season, with year-round
222 presence of semi-wild grazers. The resulting correlations therefore describe not only territorial
223 behaviour of breeding birds but average relationships between bird and grazer densities over
224 many different environmental conditions and life-cycle stages of birds.

225 Among the eight investigated bird species, the density of Starling observations showed the
226 clearest positive correlation with density of grazer GPS positions in our study site. This was to be
227 expected, given that Starlings usually prefer grazed pastures rather than arable farmlands
228 (Heldbjerg et al. 2017) and often follow grazing herds, profiting from flushed insects (Källander
229 2004). We also found a relatively clear positive correlation in the Skylark (although also slight
230 negative correlations would be compatible with our data, given our model (Amrhein et al.
231 2019a). Skylarks have been suggested to both benefit from and be impeded by grazing (see
232 reviewed by Donald 2010). This is because trampling by large herbivores may destroy nests
233 (Pavel 2004), while the shortened vegetation height benefits Skylarks in terms of food
234 availability and suitable nesting habitat (Odderskær et al. 1997; Wilson et al. 1997). In our study
235 site, both Starlings and Skylarks bred on or around the grazed area and were present throughout
236 the study period, i.e. also outside the breeding season.

237 Those results do not necessarily imply a causal relationship; in general, correlations between
238 grazers and birds could arise because both prefer the same habitat. In our study site, however, the
239 habitat was completely restored and ecological succession started from bare ground in 2014.
240 Although in the meantime, some of the growing saplings were removed manually, horses and
241 cattle contribute to keeping the vegetation short and to re-creating areas with bare soil (e.g. at
242 resting areas) since autumn 2018. Although the degree of causality is hard to quantify, we think
243 it is probably correct to say that Starlings and Skylarks seem to profit from the presence of
244 horses and cattle by using habitat that is kept open by the grazers.

245 We observed the clearest negative correlations in Blackbirds and Barn Swallows. Possible
246 explanations may be that Blackbirds are often found next to areas with more dense vegetation
247 that may not be preferred by grazers, while Barn Swallows were often observed flying over the
248 water ponds that naturally had low or zero densities of grazer GPS positions. The uncertainty in
249 the correlations found for Pipits, Red-Backed Shrikes, White Wagtails and Great Tits seems too
250 high to allow interpretation, although the slightly positive correlations in Red-Backed Shrikes
251 and Pipits would fit what we would expect given that those species are often found on or next to
252 areas with bare ground.

253 It will be interesting to investigate in future studies how the space use of birds and grazers
254 varies depending on season and how this affects the correlations between bird and grazer
255 densities. It would also be interesting to study the influence of vegetation and ecological

256 succession on spatial behaviour of grazers and birds, although here again it would be difficult to
257 disentangle cause and effect.

258 Similar to our study, (Kohler et al. 2016) found that associations between bird abundance and
259 grazer density varies greatly among bird species. Also Neilly & Schwarzkopf (2019) described
260 that responses of birds to grazing are often complex and will reflect habitat requirements of the
261 individual bird species. Whether a possible effect of natural grazing in a nature reserve is
262 meeting conservation goals thus depends on which species one aims to protect. Among the eight
263 most often observed birds in this study, the two species that are most threatened are the Skylark
264 and the Red-Backed Shrike (according to the IUCN Red List (BirdLife 2018; BirdLife
265 International 2017)). The observed positive correlations with grazer densities in those species are
266 encouraging from a conservational point of view, given that natural grazing with horses and
267 cattle is usually implemented to enhance habitat diversity and to support species of conservation
268 concern.

269

270

271 **Acknowledgements**

272

273 We thank the team of the Réserve Naturelle Petite Camargue Alsacienne to have made it
274 possible to conduct the research in the nature reserve.

275

276

277 **References**

278

- 279 Amrhein V, Greenland S, and McShane B. 2019a. Retire statistical significance. *Nature* 567:
280 305-307. 10.1038/d41586-019-00857-9
- 281 Amrhein V, Trafimow D, and Greenland S. 2019b. Inferential Statistics as Descriptive Statistics:
282 There Is No Replication Crisis if We Don't Expect Replication. *American Statistician*
283 73:262-270. 10.1080/00031305.2019.1543137
- 284 Baldi A, Batary P, and Erdos S. 2005. Effects of grazing intensity on bird assemblages and
285 populations of Hungarian grasslands. *Agriculture Ecosystems & Environment* 108:251-
286 263. 10.1016/j.agee.2005.02.006
- 287 Batary P, Baldi A, and Erdos S. 2007. Grassland versus non-grassland bird abundance and
288 diversity in managed grasslands: local, landscape and regional scale effects. *Biodiversity*
289 *and Conservation* 16:871-881. 10.1007/s10531-006-9135-5
- 290 BirdLife. 2018. *Alauda arvensis*. The IUCN Red List of Threatened Species 2018:
291 e.T102998555A132039889. Available at [https://dx.doi.org/10.2305/IUCN.UK.2018-](https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T102998555A132039889.en)
292 2.RLTS.T102998555A132039889.en. (accessed 31 July 2020).
- 293 BirdLife International. 2017. *Lanius collurio* (amended version of 2016 assessment). The IUCN
294 Red List of Threatened Species 2017.
- 295 Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, and Thomas L. 2001.
296 Introduction to distance sampling: estimating abundance of biological populations.
- 297 Bürkner P-C. 2017. brms: An R package for Bayesian multilevel models using Stan. *Journal of*
298 *statistical software* 80:1-28.
- 299 Collins GH, Petersen SL, Carr CA, and Pielstick L. 2014. Testing VHF/GPS collar design and
300 safety in the study of free-roaming horses. *Plos One* 9.
- 301 Dawson D, and Bull P. 1975. Counting birds in New Zealand forests. *Notornis* 22:101-109.
- 302 Dawson DG. 1981. Counting birds for a relative measure (index) of density. *Studies in avian*
303 *biology* 6:12-16.
- 304 Di Orio AP, Callas R, and Schaefer RJ. 2003. Performance of two GPS telemetry collars under
305 different habitat conditions. *Wildlife Society Bulletin*:372-379.
- 306 Donald P. 2010. *The skylark*. Bloomsbury Publishing.
- 307 Dross C, Princé K, Jiguet F, and Tichit M. 2018. Contrasting bird communities along production
308 gradients of crops and livestock in French farmlands. *Agriculture, Ecosystems &*
309 *Environment* 253:55-61.
- 310 Dussault C, Courtois R, Ouellet J-P, and Huot J. 2001. Influence of satellite geometry and
311 differential correction on GPS location accuracy. *Wildlife Society Bulletin*:171-179.
- 312 Ganskopp DC, and Johnson DD. 2007. GPS error in studies addressing animal movements and
313 activities. *Rangeland Ecology & Management* 60:350-358.
- 314 Gregory RD, Gibbons DW, and Donald PF. 2004. Bird census and survey techniques. *Bird*
315 *ecology and conservation*:17-56.
- 316 Hartel T, Hanspach J, Abson DJ, Mathe O, Moga CI, and Fischer J. 2014. Bird communities in
317 traditional wood-pastures with changing management in Eastern Europe. *Basic and*
318 *Applied Ecology* 15:385-395.
- 319 Heldbjerg H, Fox AD, Thellessen PV, Dalby L, and Sunde P. 2017. Common Starlings (*Sturnus*
320 *vulgaris*) increasingly select for grazed areas with increasing distance-to-nest. *Plos One*
321 12:17. 10.1371/journal.pone.0182504

- 322 Henning K, Lorenz A, von Oheimb G, Hardtle W, and Tischew S. 2017. Year-round cattle and
323 horse grazing supports the restoration of abandoned, dry sandy grassland and heathland
324 communities by suppressing *Calamagrostis epigejos* and enhancing species richness.
325 *Journal for Nature Conservation* 40:120-130. 10.1016/j.jnc.2017.10.009
- 326 Hurn J. 1993. *Differential GPS explained : an exposé of the surprisingly simple principles*
327 *behind today's most advanced positioning technology*. Sunnyvale, CA: Trimble
328 Navigation.
- 329 Källander H. 2004. Starlings *Sturnus vulgaris* and cattle—a widespread feeding association. *Ornis*
330 *svecica* 14:11-20.
- 331 Kohler M, Hiller G, and Tischew S. 2016. Year-round horse grazing supports typical vascular
332 plant species, orchids and rare bird communities in a dry calcareous grassland.
333 *Agriculture Ecosystems & Environment* 234:48-57. 10.1016/j.agee.2016.03.020
- 334 Laiolo P. 2005. Spatial and seasonal patterns of bird communities in Italian agroecosystems.
335 *Conservation Biology* 19:1547-1556.
- 336 Leal AI, Acácio M, Meyer CF, Rainho A, and Palmeirim JM. 2019. Grazing improves habitat
337 suitability for many ground foraging birds in Mediterranean wooded grasslands.
338 *Agriculture, Ecosystems & Environment* 270:1-8.
- 339 Linnell JD, Kaczensky P, Wotschikowsky U, Lescureux N, and Boitani L. 2015. Framing the
340 relationship between people and nature in the context of European conservation.
341 *Conservation Biology* 29:978-985.
- 342 Loucougaray G, Bonis A, and Bouzille JB. 2004. Effects of grazing by horses and/or cattle on
343 the diversity of coastal grasslands in western France. *Biological Conservation* 116:59-71.
344 10.1016/s0006-3207(03)00177-0
- 345 Milchunas D, Sala O, and Lauenroth WK. 1988. A generalized model of the effects of grazing by
346 large herbivores on grassland community structure. *The American Naturalist* 132:87-106.
- 347 Moen R, Pastor J, Cohen Y, and Schwartz CC. 1996. Effects of moose movement and habitat use
348 on GPS collar performance. *The Journal of wildlife management*:659-668.
- 349 Neilly H, and Schwarzkopf L. 2019. The impact of cattle grazing regimes on tropical savanna
350 bird assemblages. *Austral Ecology* 44:187-198.
- 351 Odderskær P, Prang A, Poulsen JG, Andersen PN, and Elmegaard N. 1997. Skylark (*Alauda*
352 *arvensis*) utilisation of micro-habitats in spring barley fields. *Agriculture, Ecosystems &*
353 *Environment* 62:21-29.
- 354 Pavel V. 2004. The impact of grazing animals on nesting success of grassland passerines in
355 farmland and natural habitats: a field experiment. *Folia Zoologica* 53:171-178.
- 356 RCoreTeam. 2016. A language and environment for statistical computing. Vienna, Austria: R
357 Foundation for Statistical Computing.
- 358 Rosenthal G, Schrautzer J, and Eichberg C. 2012. Low-intensity grazing with domestic
359 herbivores: A tool for maintaining and restoring plant diversity in temperate Europe.
360 *Tuexenia*:167-205.
- 361 Roth RR. 1976. Spatial heterogeneity and bird species diversity. *Ecology* 57:773-782.
- 362 Sharps E, Smart J, Mason LR, Jones K, Skov MW, Garbutt A, and Hiddink JG. 2017. Nest
363 trampling and ground nesting birds: Quantifying temporal and spatial overlap between
364 cattle activity and breeding redshank. *Ecology and Evolution* 7:6622-6633.
365 10.1002/ece3.3271
- 366 Stan Development Team. 2014. Stan Modeling Language Users Guide and Reference Manual.
367 Version 2.2. ed.

- 368 Toepfer S, and Stubbe M. 2001. Territory density of the Skylark (*Alauda arvensis*) in relation to
369 field vegetation in central Germany. *Journal für Ornithologie* 142:184-194.
- 370 Turner L, Udal M, Larson B, and Shearer S. 2000. Monitoring cattle behavior and pasture use
371 with GPS and GIS. *Canadian Journal of Animal Science* 80:405-413.
- 372 Ungar ED, Henkin Z, Gutman M, Dolev A, Genizi A, and Ganskopp D. 2005. Inference of
373 animal activity from GPS collar data on free-ranging cattle. *Rangeland Ecology &*
374 *Management* 58:256-266.
- 375 van Klink R, Nolte S, Mandema FS, Legendijk DDG, WallisDeVries MF, Bakker JP, Esselink P,
376 and Smit C. 2016. Effects of grazing management on biodiversity across trophic levels-
377 The importance of livestock species and stocking density in salt marshes. *Agriculture*
378 *Ecosystems & Environment* 235:329-339. 10.1016/j.agee.2016.11.001
- 379 VanWieren SE. 1995. The potential role of large herbivores in nature conservation and extensive
380 land use in Europe. *Biological Journal of the Linnean Society* 56:11-23.
- 381 Vera FWM. 2000. Grazing ecology and forest history. CABI publishing.
- 382 Vermeulen R. 2015. Natural Grazing. Practices in the rewilding of cattle and horses. Nijmegen:
383 Rewilding Europe.
- 384 Wilson JD, Evans J, Browne SJ, and King JR. 1997. Territory distribution and breeding success
385 of skylarks *Alauda arvensis* on organic and intensive farmland in southern England.
386 *Journal of Applied Ecology* 34:1462-1478. 10.2307/2405262
387

Table 1 (on next page)

Characteristics of the marginal posterior distribution of the model parameters: medians, 2.5 and 97.5% quantiles (limits of the 95% compatibility interval) and proportions of posterior mass above zero ($P(\beta > 0)$).

The posterior mass corresponds to the posterior probability of the hypothesis that the parameter value is positive; values close to 1 indicate strong evidence for a positive relationship, values close to zero indicate strong evidence for a negative relationship.

1 **Table 1. Characteristics of the marginal posterior distribution of the model parameters:**
 2 **medians, 2.5 and 97.5% quantiles (limits of the 95% compatibility interval) and**
 3 **proportions of posterior mass above zero ($P(\beta > 0)$).**

4 The posterior mass corresponds to the posterior probability of the hypothesis that the parameter
 5 value is positive; values close to 1 indicate strong evidence for a positive relationship, values
 6 close to zero indicate strong evidence for a negative relationship.

7
 8

Parameter	Median of posterior	2.5% quantile	97.5% quantile	$P(\beta > 0)$
Intercept	-10.5	-11.7	-9.2	-
grazer density average	0.02	-0.44	0.48	0.53
grazer density Skylark	0.21	-0.18	0.63	0.86
grazer density Pipits	0.12	-0.60	0.86	0.65
grazer density Barn Swallow	-0.48	-1.33	0.29	0.12
grazer density Red-backed Shrike	0.13	-0.35	0.67	0.71
grazer density Wagtail	-0.16	-0.74	0.38	0.26
grazer density Great Tit	0.03	-0.40	0.45	0.56
grazer density Starling	0.62	0.28	1.02	>0.99
grazer density Blackbird	-0.38	-0.92	0.07	0.06
sd species intercept	1.47	0.86	3.13	-
sd species grazer density	0.51	0.21	1.22	-
negative binomial shape	0.013	0.011	0.015	-

9
 10

Figure 1

Grazer density during 22 surveys in the course of the study period (January to July).

Day of year corresponds to the dates of bird surveys (1 = 1st January) and box plots give the distribution of grazer density per grid cell ($n = 113$) on the log scale. The blue line indicates the standard deviation of grazer densities for each survey.

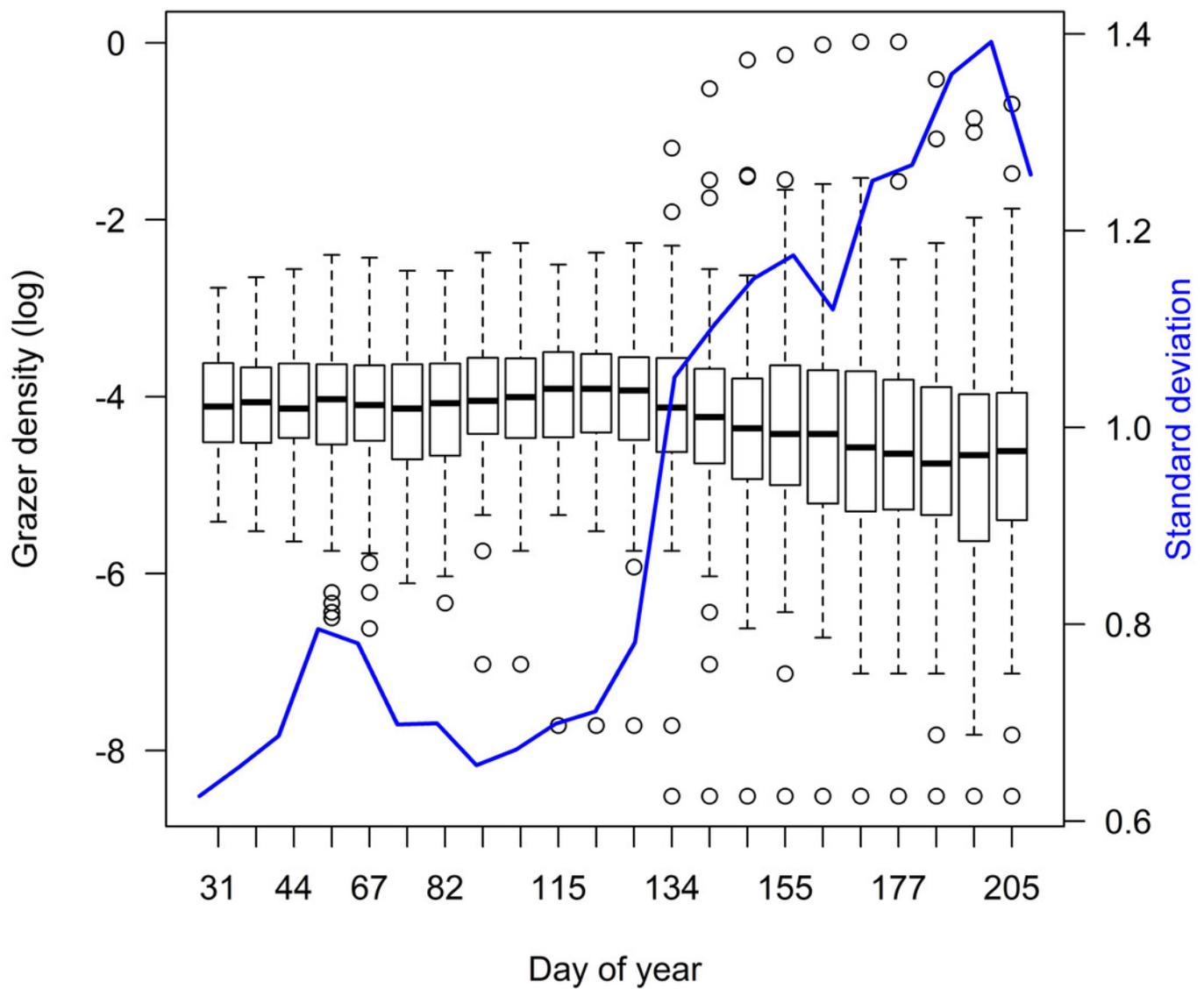


Figure 2

Correlations between bird count density (numbers of bird counts per survey per grid cell) and grazer density (numbers of GPS positions of horses and cattle per grid cell for the last 30 days prior to a bird survey).

Given are medians (solid lines) and 95% Bayesian compatibility intervals (dotted lines) of model predictions. Sample sizes (n) refer to the total number of birds counted in 113 grid cells during 22 surveys.

