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**University College Cork, Ireland**  
Coláiste na hOllscoile Corcaigh

1 **Stopover ecology of autumn-migrating Bluethroats (*Luscinia svecica*) in a highly**  
2 **anthropogenic river basin**

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13  
14 **Short title:** Stopover ecology of Bluethroats

15 **Key words:** *Luscinia svecica*, home range, body condition, habitat selection, corn crop, diet, trophic resources.

16  
17 **Summary**

18 Wetlands are highly productive habitats used by many avian species as stopover sites during their migrations.  
19 However, these habitats are highly threatened by anthropogenic activities, such as land use changes, the  
20 introduction of exotic species and global warming. Further understanding on the spatiotemporal use of wetlands  
21 and their surrounding areas by migrating birds is essential to predict how these changes might affect avian *en*  
22 *route* ecology. We selected a habitat-generalist passerine, the Bluethroat *Luscinia svecica*, as model of how  
23 migratory birds exploit a highly anthropogenic river basin in southwestern France (i.e. Barthes de la Nive)  
24 during autumn migration. We captured and radiotracked 29 young Bluethroats in this region to shed light on  
25 different aspects of their stopover ecology and behaviour, such as stopover duration, habitat selection and home  
26 range size. We also characterized Bluethroat diet and arthropod availability in different habitats. Bluethroats  
27 positively selected pure or mixed reedbeds (associated with sedge), hydrophilous tall grasslands and corn crops.  
28 Birds staying more than just one day 8.4 days on average, used preferably corn crops. Home range sizes were on  
29 average 5.8 ha (fixed kernels K95) and high occupancy area (K50) was 1.36 ha with large individual variation.  
30 Bluethroats stopping over with low fuel loads tended to have larger home ranges and used preferentially corn  
31 crops, wet or mesotrophic grasslands and rural paths. Reedbeds were typically used as roosting habitat for the  
32 majority of birds, being on average 397 m apart from their daytime core areas. Short-staying birds tended to  
33 show higher fuel loads and restricted their activities to a smaller home range (1 ha) in pure and mixed reedbeds.  
34 The diet of Bluethroats was dominated by ants, spiders and beetles that were particularly abundant in corn crops.  
35 The use of corn crops by autumn-migrating Bluethroats in our study site seems a reasonable solution in a highly  
36 altered environment. Reducing the use of insecticides in these crops and delaying the harvesting time after mid-  
37 October are two supplemental measures that, together with a good management of the remaining wetland  
38 patches, could greatly favour Bluethroats and other migratory species in this region.

39  
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48  
49 **Author contributions:** All of the authors contributed to data collection. K.S. prepared the habitat map, F.L. and  
50 C.K. gathered data on bird diet and arthropod availability. P.F., I.H. and C.K. analysed the data, designed the  
51 methods and conducted the research. All of the authors took part in the formulation of the questions and  
52 hypotheses. P.F. wrote the paper in cooperation with I.H. and C.K.

53 **Conflict of interest:** The authors declare that they have no conflicts of interest.

54 **Ethics statement:** All data and information from external sources used for the analyses and preparation of the  
55 manuscript are properly cited. The conclusions are entirely based on our own results. All applicable  
56 international, national, and/or institutional guidelines for the care and use of animals were followed.

## 57 Introduction

58  
59 The global conservation of migratory birds not only relies on the protection of their breeding and wintering  
60 habitats, but also on the presence of suitable stopover sites along their migratory routes (Hutto 2000, Yong 1998  
61 Newton 2008). Coastal marshes, estuaries and other types of wetlands are highly productive habitats largely used  
62 during migration by waterbirds and other avian species, constituting key conservation areas (Czech and Parsons  
63 2002). Wetland habitats experienced a dramatic reduction and an increased fragmentation during the 20th  
64 century, mainly as a consequence of the pressure of human activities, such as urbanization and the drainage for  
65 agricultural use (von Behren 2007; Whited et al 2000; Czech and Parsons 2002). As a result, wetlands usually  
66 remain now embedded in a complex and highly-altered human matrix, where every year migrating birds rest and  
67 search for food to undertake their next flight bout.  
68

69 The wetland remnants that many birds use as stopover sites are normally small and face some common problems  
70 that, in some cases, can be mitigated by human intervention. For example, many wetland managers implement  
71 measures to avoid clogging, which could lead to bush encroachment and the progressive disappearance of marsh  
72 vegetation (Clark and Wilson 2001). The control of invasive and exotic species, that can alter wetland  
73 biodiversity and functioning, is also a common practice (Fontanilles et al. 2014; Arizaga et al. 2013). These  
74 measures would increase the quality and carrying capacity of the wetlands, which would be very beneficial for  
75 migrating birds (e.g. fuel deposition; Delingat and Dierschke 2000). Another aspect that has hitherto received  
76 little attention is the potential management and planning of the areas surrounding the wetland. These adjacent  
77 areas might be intensively used by migrants given the restricted size of wetland patches and the potential high  
78 intra and interspecific competition with other migratory and resident individual birds. This situation could be  
79 particularly exacerbated during the migration peaks, when large number of individuals can co-occur in a single  
80 location (Newton, 2004). Such circumstance predicts that many migrants will be forced to expand their home-  
81 ranges and use alternative habitats out of the wetland. In this context, identifying which alternative habitats are  
82 positively selected by migrating birds during their brief stopovers would be essential to design buffer areas that  
83 best meet the requirements for these migrants *en route*. However, this knowledge is limited in many key  
84 stopover areas..  
85

86 In this study, we analysed the stopover ecology of migrating Bluethroats *Luscinia svecica* in Barthes de la Nive  
87 (France) during autumn migration. Barthes de la Nive is a mosaic of wetlands, riparian woodlands and farmlands  
88 located near the Adour River mouth in the Southwestern Atlantic coast of France. The scattered wetlands in this  
89 region attract a large diversity of both aquatic and non-aquatic birds during migration periods (Fontanilles et al.  
90 2011). The only radiotracking study carried out in this area so far showed that the globally endangered Aquatic  
91 Warbler *Acrocephalus paludicola* had a strong preference for reedbeds but, to a lesser extent, it also made use of  
92 some farmlands (Fontanilles et al. 2014). This highlights the relevance that the surrounding matrix might have  
93 even for a wetland specialist as the Aquatic Warbler. Conversely, Bluethroats are migratory birds that can use a  
94 large range of habitats, mainly reedbeds and marshlands (Arizaga et al. 2006; Musseau et al. 2017), but also  
95 bushlands, woodland and farming habitats (Cramp 1988; Cornulier et al. 1997; Chiron, 2017, Berndt and Hölzel  
96 2012), making it an interesting model to study its stopover ecology and habitat selection during migration.  
97 Arizaga et al. (2011) radiotracked 20 autumn-migrating Bluethroats in Txingudi (North Spain), a wetland located  
98 less than 30km away from Barthes de la Nive. Their results showed a strong selection for reedbeds, low-  
99 halophytic vegetation and tidal flats. However, Txingudi is located in a more urbanized environment that  
100 probably restricts bird movements, and its proximity to the river mouth allows the presence of habitats that are  
101 lacking in Barthes de la Nive (e.g. halophytic vegetation). On the other hand, bird ringing information obtained  
102 for both wetlands during autumn migration showed dramatic differences in the number of within-season  
103 recoveries, which are much more usual in Txingudi than in Barthes de la Nive (Arizaga et al. 2011; Fontanilles  
104 unpublished data). These differences could be a consequence of a longer stopover duration of Bluethroats in  
105 Txingudi than in Barthes de la Nive, but they could also be caused by the existence of larger home ranges in  
106 Barthes de la Nive, something that would be possible in its much less urbanized surrounding. All these aspects  
107 suggest a different stopover ecology and behaviour of Bluethroats between both wetlands in spite of their  
108 geographic proximity that remains still unresolved.  
109

110 In order to better understand the stopover ecology of the Bluethroat in Barthes de la Nive, we performed a  
111 radiotracking study during autumn migration that aims to shed light on (1) the stopover duration and the  
112 proximate factors that affect it, (2) habitat selection and home range sizes, and (3) we complemented the study  
113 with an analysis of Bluethroat diet and the availability of food resources. Although Bluethroats are not globally  
114 threatened, some populations have been considered to be under high risk of extinction (Huntley et al. 2007).  
115 Consequently, we expect that the spatial information generated in this study could be valuable for the competent  
116 authorities to design management practices contributing to the conservation of Bluethroats and other birds during  
117 their migrations.  
118

119  
120

121  
122 **MATERIALS AND METHODS**  
123

124 **Study area and vegetation map**

125 Barthes de la Nive (43°27'N; 01°28'W) is a 442-ha mosaic of natural and anthropogenic habitats (Fig. A1),  
126 whose remaining wetlands have been maintained safe from complete drainage due to its role in reducing the risk  
127 of flooding in Bayonne city. The wetlands are connected to the Adour river by channels, so that its hydrology is  
128 influenced by the flow of the river and the tidal regimes. However, its natural influence and ecologic functions in  
129 Adour estuary were drastically affected to urbanize the city, to develop port facilities and dykes, which virtually  
130 destroyed the original mudflats and intertidal areas. Our study site is now a protected area included in the  
131 European Natura 2000 network (FR7200786). The non-urban areas near the river have been widely used for  
132 pasture, as hay meadows and other agricultural purposes, being corn plantations the primary crop nowadays.  
133 Farming in the region uses a reasonably low quantity of fertilizers and no insecticide. Field abandonment and  
134 lack of management is increasing gradually bush and tree encroachment, which is changing dramatically the  
135 landscape. A vegetation map was obtained from photo-interpretation and field validation for summer 2014 and  
136 2015 (see Fig. A1 in Supplementary Material, Table1). This approach showed the relative importance of each  
137 habitat in the region (see Table 1).  
138  
139

140 **Bluethroat trapping and body measurements**

141 Mist-netting sessions were performed from mid-August to late September when migrating Bluethroats stop over  
142 in this region during their post-breeding migratory period. Note that Bluethroats do not breed in Barthes de la  
143 Nive or use it for moulting (Fontanilles et al. 2011). Ringing sessions took place in five different locations across  
144 the study area: four wetlands and one corn crop (see details in Supplementary Material Fig. A1, Ap. 3, Table 2).  
145 These five sites were reasonably distant to each other (see Fig. A1) to reduce potential geographic bias and,  
146 according to previous studies (Fontanilles et al. 2011, Fontanilles 2014), they represent the two main habitats  
147 (i.e. reedbed, corn crops) where Bluethroats occur during their stopover at Barthes de la Nive.  
148

149 To maximize the number of captures, we used one male song playback from 30 minutes before dawn (when  
150 mist-nets were open) until a tagged bird was released (when mist-nets were furled; de la Hera et al. 2017). By  
151 using the tape lures only 30 minutes before sunrise, we reduced the possibilities of forcing the landing of  
152 migrating Bluethroats and we expected to capture only birds that decided voluntarily to stop over in our study  
153 area (Schaub 1999; Arizaga et al. 2015). During our ringing sessions, we captured 58 Bluethroats (28 in 2014  
154 and 30 in 2015).  
155

156 Several morphological measurements were taken from each bird in order to obtain a composite index of bird  
157 body size (Freeman and Jackson 1990, Tellería et al. 2013, see Supplementary Material). We also recorded body  
158 mass ( $\pm 0.1$  g) and standard scores of fat and muscle (Busse 2000). Body size-corrected measurements of body  
159 mass were used to estimate individual fuel loads. This was done using a linear regression of body mass on body  
160 size (see Supplementary Material Ap. 2, Fig. A2), where individuals with higher fuel loads showed more  
161 positive residuals (Salewski et al. 2009).  
162  
163

164 **Radio tracking information**

165 Out of the 58 Bluethroats captured, 29 juveniles were equipped with a radio-transmitter, with a minimum of 4  
166 radiotagged individuals in each of the 5 ringing sites (25 birds were trapped in the reedbeds and 4 in the corn  
167 crops; see details in Supplementary Material, Ap. 3, Table A2). Life expectancy of the emitters is typically more  
168 than 17 days and the average detection distance is 80-300 meters. We only tagged first-year birds because the  
169 study site is mainly used by this age group, and because juveniles face their first autumn migration and,  
170 consequently, their habitat choice cannot be influenced by previous experience (Piper 2011).

171 On the day of capture, monitoring of tagged Bluethroats started at least one hour after the bird was released in  
172 order to avoid bias linked to potential stress behaviour. For birds that stayed in the area the following days after  
173 capture (see below), they were normally monitored 8h per day during, normally, 3-4 days in long-staying  
174 individuals. After this period, we checked their presence every day, but the intensity of the radiotracking  
175 typically got reduced and depended on other duties associated with the project, particularly, the trapping and  
176 monitoring of other individuals (see Supplementary Material Ap.3 for more details).

177 The positions of the birds were obtained normally by triangulation (3 vectors taken consecutively within less  
178 than 10 minutes), but we used bi-angulation in those cases in which landscape barriers (like canals, rivers or  
179 dense vegetation) impeded taking more than two informative vectors, or just one vector plus an estimation of the  
180 actual distance to the bird when this was observed. We used Sika receivers (Biotrack Ltd) and Yagi antennas to  
181 find the birds, and vectors were delimited using a GPS (to determine observer position; Garmin Ltd.) and a  
182 compass (to obtain magnetic Azimuth). All this information was computerized using the software  
183 Cartoexplorateur (Bayo Ltd.), and we considered the centroid of the triangle determined by the three  
184 corresponding vectors as the most likely geographic position of the bird, or the intersections between lines when

185 two vectors were only available. Prior to the start of radiotracking, observers were trained in the study area and  
186 the accuracy of the triangulation method was assessed. The average error found in the estimation of the positions  
187 of transmitters hidden in the study area was  $14.5 \pm 1$  m ( $n=69$ ), which can be considered enough given the  
188 purpose of studying main habitat selection.

189

### 190 **Stopover duration and its determinants**

191 We used the number of days spent by each Bluethroat after being tagged (assessed by the radiotracking survey)  
192 as a proxy of stopover duration. This approach is expected to provide a better idea than ringing recaptures on  
193 how long Bluethroats stopover in Barthes de la Nive, since ring-recovery data are spatially restricted, have a  
194 lower detection probability and strongly depend on a good sampling strategy (Chernetsov 2012). According to  
195 the non-Gaussian distribution of stopover durations (see Fig. A3), we performed non parametric tests (Wilcoxon  
196 tests, Kruskal-Wallis tests and Spearman correlations) to evaluate which factors (year, sex, site, date of capture,  
197 muscle development, fat accumulation and body condition) better correlated with the observed variation in  
198 stopover duration.

199

### 200 **Habitat selection**

201 Initially, we tested whether Bluethroat locations were randomly distributed across habitats. We applied the  
202 quadrats method (Zaminetti 2005) by defining a grid of  $K$  squares  $100 \times 100$  m enveloping all the radio-tracking  
203 points. The theoretical distribution  $K_{th}(n)$  was obtained following the Poisson's law:  $K_{th} = [K \cdot (D^n/n!)] \cdot \exp(-D)$   
204 where  $n$  is the number of points per mesh,  $K(n)$  the number of stitches having  $n$  points,  $N$  is the total number of  
205 locations and  $D$  is the average density of locations by cell that is defined as  $N$  divided by  $K$ . The existence of  
206 significant differences between the two distributions (i.e.  $K(n)$  and  $K_{th}(n)$ ) was assessed using a Kolmogorov-  
207 Smirnov test.

208 Secondly, for assessing habitat selection, we calculated for each habitat the electivity index of Jacobs (1974)  $I_h =$   
209  $U - D / (U + D - 2U \cdot D)$  where  $U$  is the proportion of locations in habitat  $h$  and  $D$  the proportion of this habitat in  
210 the study area. The index ranges between -1 (strong rejection of a particular habitat) and 1 (strong selection). We  
211 used the proportion of locations instead of the proportion of areas in core areas to take into account the edge  
212 effects and to be more precise with the actual habitat used. We excluded habitats poorly represented showing  
213 less than 5 locations.

214

### 215 **Home range estimates**

216 The overall home range size of each individual Bluethroat was estimated by the model of 95% kernel (K95;  
217 Worton 1989). The K95 approach is usually used in this type of studies, which would allow between study  
218 comparisons (Börger *et al.* 2006). Areas of high occupancy were also estimated using the 50% kernel (K50),  
219 considered as a good estimator of core areas (Börger *et al.* 2006). We calculated the overall home range with all  
220 the locations for each bird and also for each day when there was a minimum of 10 positions. Home range sizes  
221 were processed using the Ranges 8v2.10 software (Anatrack Ltd).

222

### 223 **Home range analysis**

224 We explored whether overall home range size varied in relation to the proportion of habitats contained within it  
225 (10 habitat variables, see Table 1), several metrics of heterogeneity (mean patch size, number of habitat or  
226 Shannon index perform of patch size distribution) and individual-associated variables (body condition, sex and  
227 stopover duration). For this purpose, we performed General Linear Models (GLM) using the home range size  
228 (K50 and K95) as a response variable, while habitat cover and individual-associated variables were included as  
229 explanatory variables. According to the distribution of home range size (positive long tail distribution), we  
230 applied a negative binomial error distribution to the GLM in order to minimize issues related to the over-  
231 dispersion ratio in the models (i.e. as close as possible to 1; Zuur *et al.* 2009). Following a multi model inference  
232 (Burnham *et al.* 2011; Grueber *et al.* 2011), we generated a set of candidate models containing all possible  
233 variable combinations and ranked them by corrected Akaike information criterion (AICc) using the dredge  
234 function (R package MuMIn; Barton 2019). We only integrated the models complying with the following  
235 conditions: (i) models do not include simultaneously correlated covariates ( $R^2 > 0.7$ ) and (ii) models do not  
236 include more than three variables to avoid over-parameterization due to the limited data set. Since the  
237 simultaneous inclusion of habitat cover and measures of habitat heterogeneity generated important multi-  
238 collinearity problems, we decided to perform two separate modelling: one with habitat cover within the home  
239 range and individual-associated variables; and a second one, with measures of habitat heterogeneity and  
240 individual-associated variables (results of this second modelling are shown in Appendix 5). We restricted this set  
241 of models using a cut-off of 2 AICc. The modelling with habitat cover resulted in 4 and 3 top models for K50  
242 and K95, respectively (see Supplementary Material Ap. 5, Table A3). The modelling with measures of habitat  
243 heterogeneity resulted in 4 and 2 top models for K50 and K95, respectively (see Supplementary Material Ap. 5).  
244 Following the same approach, we explored whether daily home range size (with a minimum of 10 positions)  
245 varied in relation to habitat cover within home range and individual-associated variables. According to the  
246 hierarchical structure of this data set (radio-tagged individuals survey each day), we treated the variable  
247 "individual identity" as a random effect, while considering the other explanatory variables (home range and  
248 individual-associated variables) as fixed effects (Zuur *et al.* 2009). Following a multi model inference using

249 General Linear Mixed Models with a negative binomial error distribution, the daily home range analyses resulted  
250 in a total of 2 and 3 top models for the K50 and K95, respectively (see Supplementary Material Ap. 5, Table A).  
251 We also used a secondary method based on PCA analysis detailed in Supplementary Material Ap. 6.

252

### 253 **Roosting habitat selection**

254 To provide information on roosting behaviour, we identified the habitats used between sunset and sunrise  
255 (roosting locations) and also estimated their distance to the daytime areas where birds were potentially foraging.  
256 We identified the habitat of all those locations on the vegetation map. We compared the proportions of roosting  
257 locations occurring in each habitat to identify the most used by *a posteriori* Wilcoxon test. For birds flying to a  
258 roosting location far away from the area used during daytime hours, we calculated the distance between the  
259 centroid of the home range exploited during daytime hours and the core of roosting locations. We then compared  
260 the proportions of habitats between these two areas (home range during daytime hours vs. roosting locations  
261 core) by *a posteriori* Wilcoxon test.

262

### 263 **Diet of Bluethroat**

264 To elucidate why birds tend to select specific habitats, we analysed their diet and the invertebrate availability.  
265 We collected 105 faecal samples during ringing operations for all sites in 2015 (n=52) and 2014 (n=30) and only  
266 in Urdains in 2012 (n=23). All remains identified in faeces were used to estimate the minimum number of prey  
267 items and the occurrence of each taxonomic group within each sample. While some bias in diet analyses was  
268 possible because small or soft-bodied preys are less easily detected, a strong correlation has been found between  
269 prey remains in droppings and the actual composition of the diet (Davies 1977a, 1977b). We also assessed prey  
270 biomass using predictive models based on the relationship between body length and mass of terrestrial  
271 arthropods (Hodar 1996; see Supplementary Material Ap. 7 for additional details). We explored which factors  
272 influenced prey abundance, testing explicitly the effects of age (young vs adult birds), sex and day using a  
273 Generalized Linear Model (GLM) with a Poisson error distribution. P-values were corrected for over-dispersion.  
274 Only taxa representing more than 2% of the prey abundance were considered

275

### 276 **Invertebrate availability between habitats**

277 We estimated the variation in the abundance of (near) ground invertebrates (the main feeding substrate of  
278 Bluethroats) between the two main habitats occupied by Bluethroats (corn crops and reedbeds). Given the large  
279 extension of the study area, we decided to focus our invertebrate sampling on three of the five trapping areas: the  
280 corn crop area, and Villefranque and Urdains reedbeds (Fig. A1). The corn crops in the other bank of the Nive  
281 River had similar management practices, so they are expected to have a similar invertebrate availability. We  
282 used 3 standardized coloured (yellow, white, blue) bowl traps and a pitfall glass per station (for a total of 12  
283 stations, 6 in the corn crops, 3 in each reedbed). All stations were sampled simultaneously at 3 temporal stages in  
284 August 2015. Traps were deployed for four days. For more details, see Supplementary Material Ap. 8. For  
285 subsequent analyses, we pooled together the data of the three bowl traps of each station. We focused the analyses  
286 on those taxa whose remains had been found in faeces of trapped Bluethroats. We compared invertebrate  
287 availability, abundance and biomass between the two reedbeds and the corn crop using General Linear Models  
288 with a Poisson error distribution.

289 Unless specified, mean values are given  $\pm$  se (standard error).

290

291

## 292 **RESULTS**

293

### 294 **Stopover duration and body condition effect**

295 Tagged Bluethroats stayed on average  $5 \pm 1$  (range 1-20) days upon capture in Barthes de la Nive, but showing a  
296 clearly non-Gaussian distribution where up to 13 individuals left the study area the next night after being  
297 captured (Fig. A3). The remaining 16 Bluethroats stayed on average  $8.4 \pm 1.3$  days (see Table A1, Fig. A3).

298 Observed variation in stopover duration did not differ significantly between years ( $W=91$ ,  $p=0.536$ ), sites  
299 (Kruskal-Wallis  $H(3, 29) = 1.11$ ,  $p=0.774$ ), sex ( $W=133$ ,  $p=0.189$ ), date of capture ( $r$  Spearman = -0.11,  $t_{27} = -$   
300  $0.59$ ,  $p=0.558$ ) or muscle development ( $r$  Spearman = -0.17,  $t_{27} = -0.92$ ,  $p=0.365$ ). The fat score was significantly  
301 associated with stopover duration ( $r$  Spearman = -0.40,  $t_{27} = -2.24$ ,  $p=0.034$ ). However, the individual trait that  
302 better explained stopover duration was fuel load, which was estimated from the residuals of body mass on body  
303 size (effects of body size on body mass:  $\beta=0.888$ ,  $F_{1,27}=100.9$ ,  $p < 0.001$ ). Thus, Bluethroats with larger size-  
304 corrected fuel loads left the Nive basin earlier on average ( $r$  Spearman = -0.59,  $t_{27} = -3.78$ ,  $p < 0.001$ ; Fig. 1) than  
305 birds with smaller fuel stores. Additionally, we analysed whether stopover duration differed between habitats  
306 used. Irrespective of where they were trapped, birds that used corn crops remained significantly ( $W=23$ ,  
307  $p < 0.001$ ) longer ( $10$  days  $\pm 1.1$ se,  $n=10$ ) in the area than those not using this habitat type ( $2.7$ days  $\pm 0.6$ se,  $n=19$ ;  
308 see Fig. 2).

309

### 310 **Habitat selection**

311 The 29 radiotracked juvenile Bluethroats provided 1718 positions during their stay. Bluethroat locations were  
312 not randomly distributed among habitats. Their distributions differed significantly from the theoretical null

distributions (Kolmogorov-Smirnov test  $D = 0.896$ ,  $p < 0.0001$ ). The main habitats used by all birds were corn crops and reedbeds, either pure or mixed (Fig. 3). The distribution differed between birds staying one day, which preferred pure reedbed ( $W=55.5$ ,  $p=0.034$ ), and the remaining, which positively selected the corn crops ( $W=162$ ,  $p=0.013$ ). Birds stopping over for just one day made use of less habitat types ( $2.2 \pm 0.3$  [1-4] habitats) than birds staying longer ( $4.7 \pm 0.5$  [2-10];  $W=180.5$ ,  $p < 0.001$ ). However, during the first day of stay, there were no differences between them in the preferred habitat and number of them (tests Wilcoxon,  $p > 0.05$ , Fig.A4). Bluethroats positively selected pure and mixed reedbeds, corn crops and hydrophilous tall grasslands (Fig. 4). They moderately selected paths, wooded reedbeds and mesophic grasslands, while they avoided water, railways, ferns, wet grasslands, houses, woodlands and hay meadows.

### Home range analysis

The average number of locations per individual was  $59.2 \pm 9$  ( $22.5 \pm 1.6$  for birds staying one day, and  $89 \pm 12$  for birds staying longer). The average overall K95 home range was  $5.8 \pm 1.8$  ha with a large variation between individuals (range 0.016-46.5). The core area (i.e. K50) was on average  $1.36 \pm 0.35$  ha (range 0.004-7.6). K95 areas were larger in birds staying more than one day ( $9.72 \pm 3$  ha) than in birds stopping over just one day ( $1.07 \pm 0.46$  ha;  $W = 23$ ,  $p < 0.001$ ). Similar results were obtained for the K50 core area:  $0.28 \pm 0.12$  ha for long-staying birds, and  $2.24 \pm 0.53$  ha for birds staying only 1 day ( $W = 18$ ,  $p < 0.001$ ).

Bluethroats with greater overall home range included more wet grassland, woodland and mesophilic grassland within their range, and also exhibited a longer stopover duration. On the other hand, Bluethroats with smaller overall home range exhibited larger quantities of body reserves and occupied areas with a higher proportion of reedbed (Table 2). Analyses performed for daily home ranges highlighted that Bluethroats with greater home range included more hay grasslands, open water, and woodlands; while Bluethroat with smaller daily home range occupied areas with a higher proportion of crop fields, natural paths and pure reedbeds (Table 2). In addition, analyses performed with measures of habitat heterogeneity, showed that Bluethroats with greater overall home range exhibited a more diversified home range (Appendix 5). According to AICc, measures of habitat heterogeneity performed better than habitat cover variables for K95, while it was the opposite for K50 (Appendix 5). A second analytical method based on PCA analysis gave similar results (see Supplementary Material Ap. 6).

### Roosting habitat selection

We identified the overnight habitat ( $n= 103$  nights) in 26 Bluethroats. Pure reedbed was the main roosting habitat, with 44.2% of the nights (Fig. 5). Mixed or wooded reedbeds were also well-represented within the roosting habitats, representing 17.5% and 16.8 %, respectively. So, reedbeds (pure, mixed and wood reedbed) were the preferred habitats for roosting ( $80.1 \pm 8\%$  of nights) in 23 birds that stayed for at least one night. Corn crops were also used by 5 birds but less frequently than reedbeds:  $13.1 \pm 6\%$  of nights.

83% of the birds that spent the night in reedbeds (pure, mixed and wood reedbed) occupied the same reedbed during the day. This took place in  $59 \pm 9\%$  of the nights (Fig. 6). This particularly concerned the 13 Bluethroats which stopped over for just one day. Individuals staying for at least 2 days showed relatively predictable movements and selected repeatedly the same areas during the night. 27% of the birds (7) spent the night in a reedbed (Urdains or Villefranque) and normally moved during the day to a corn crop. This was noticed for  $12.5 \pm 5\%$  of the nights. We calculated the distance between roosting core areas and daytime (foraging) core areas. Birds flew on average  $397 \pm 33$  m to reach its roosting location ( $n=10$ , range 80- 692 m). Five birds also used corn crops to stay during the night after using it also during the daytime (19 nights).

**Diet analysis and habitat-specific invertebrate availability** We obtained 105 faecal samples: 84 faecal samples from first year birds and 21 from adults, 55 from males and 47 from females. A total of 431 prey items were identified,  $4.1 \pm 0.8$  on average per dropping. We found 14 orders of invertebrates ( $2.2 \pm 0.3$  on average per sample). The diet of Bluethroats was dominated by ants (Hymenoptera Formicidae), representing 45.5 % of prey items and occurring in 54% of the samples (Table 3). Spiders (Araneidae) were the second most abundant group (20.4%) with a similar occurrence to ants (53%); and beetles (Coleoptera) were the third most common group (10.2% of all prey items and 31% of the samples). These two last taxa were the main contributors to the consumed biomass, representing 64.7 % and 14.9%, respectively. We did not detect any significant effects of Bluethroat age and sex on prey abundance (Table 3). We did also observe that leafhoppers (Cicadellidae) were less consumed over time (Table 3).

Corn crops hosted significantly more invertebrates and biomass than reedbeds for beetles, flies(Diptera) and spiders in pitfalls, and for leafhoppers in bowls (Table 4). Corn crops also had higher availability of non-Formicidae hymenopterans than Urdains in bowls, but less than Villefranque. Finally, ants were more abundant in Urdains than in the other two sites.

## DISCUSSION

### Variation in stopover duration and home range size

377 Bluethroats showed large variation in their stopover duration and home range size in Barthes de la Nive. The  
378 observed mean differed from that obtained by Arizaga et al. (2013). Thus, stopover duration was shorter and  
379 home range larger in Barthes de la Nive (mean stopover duration of 5 days and mean home range size of 5.8 ha)  
380 than in Txingudi (9.6 days and 2 ha, respectively). Differences in stopover duration between these two sites were  
381 mediated by the fact that 45% of the radiotracked Bluethroats in Barthes de la Nive apparently departed the  
382 following night after capture, a circumstance that never took place in Txingudi (Fig. A3). If these short-staying  
383 individuals were excluded from the calculations, the stopover duration in Barthes de la Nive (i.e. 8.4 days) would  
384 conform better to the values obtained in Txingudi. After the signal of a bird disappeared from the place it was  
385 last detected, we carefully explored the whole study area by car the following day in its search, and sporadically  
386 during subsequent days. This makes us very confident that the stopover duration estimates obtained in Barthes de  
387 la Nive are reliable. Likewise, the fact that only one of the 29 radiotracked Bluethroats stayed longer than the  
388 life-expectancy of the transmitter would not alter these between-site differences or the general conclusions of our  
389 study (see below). The number of Bluethroats whose stay reached the expected functional life of the transmitters  
390 in Txingudi was slightly higher (3 out of 20) than in Barthes de la Nive, supporting the longer stopover duration  
391 of Bluethroats in the former site.

392  
393 It could be argued that the higher number of short-staying Bluethroats in Barthes de la Nive was caused by the  
394 use of playbacks during the trapping sessions, which were not implemented in Txingudi. Although we cannot  
395 rule out completely this confounding factor as an alternative explanation to observed results, current evidence  
396 does not support this idea. Thus, the use of playbacks typically attracts Bluethroats with lower body reserves  
397 (Arizaga et al. 2015) and, as our results show, birds with less fuel loads would tend to have longer stopover  
398 durations (Alerstam and Lindström 1990; Salewski and Schaub 2007). This impact of playback on fuel loads of  
399 autumn migrating Bluethroats was consistent in the three wetlands on the Bay of Biscay (Gironde, Txingudi,  
400 Urdaibai) analysed by Arizaga et al. (2015) that are geographically very close to Barthes de la Nive. If  
401 Bluethroats do show transient vs. non-transient divergent behaviours during migration as have been described for  
402 other migratory species (Rappole and Warner 1976), playbacks might have also biased stopover duration  
403 estimates if they do preferentially attract transient individuals. However, a study of stopover duration using tape  
404 lures did not detect these transient Bluethroats during autumn migration (Arizaga et al. 2010). Likewise, neither  
405 the results obtained by Arizaga et al. (2015) would support this possibility, since playbacks do not seem to affect  
406 the number of Bluethroat recaptures, and this would be an expected outcome if playbacks promoted the capture  
407 of more transient individuals that would have less recapture prospects. Likewise, and contrary to what would be  
408 expected for their transient condition, these short-staying individuals did not move as much as would be  
409 expected after being trapped in Barthes de la Nive, and their first-day home range did not differ significantly  
410 from that observed for long-staying conspecifics.

411  
412 Observed differences in stopover duration between Barthes de la Nive and Txingudi might explain the relatively  
413 low number of recaptures obtained in Barthes de la Nive when compared to Txingudi and also other nearby sites  
414 for which there is no radiotracking information so far (i.e. Gironde and Urdaibai; Arizaga et al. 2015).  
415 Additionally, these differences in recapture rates could be also promoted by the existence of overall home ranges  
416 that are nearly twice to three times larger in Barthes de la Nive than in Txingudi (Arizaga et al. 2013) and in  
417 Gironde (Musseau et al. 2017). These contrasting differences between Txingudi and Barthes de la Nive are  
418 potentially mediated by the strong differences in the degree of urbanization and habitat composition that seem to  
419 have profound consequences in the stopover behaviour of Bluethroats between two relatively close locations.

#### 420 421 422 **Habitat and roosting site selection**

423 Migrating Bluethroats in Barthes de la Nive strongly selected reedbeds (pure and mixed) and other hydrophilic  
424 natural grasslands, which concurs with the favourite habitat that Arizaga et al. (2013) and Musseau et al. (2017)  
425 found for migrating and moulting conspecifics, respectively. Much less known was the preference of migrating  
426 Bluethroats for corn crops, although one study had detected this species in this crop type during migration  
427 (Gottschalk & Cover 2016) and some populations of Bluethroats seem to thrive and even breed successfully in  
428 some agricultural fields, such as oilseed rape crops (Cornulier et al. 1997; Berndt and Hölzel 2012, Chiron  
429 2017). We did not find the preference of Bluethroats for tidal mudflats or low-halophytic vegetation described in  
430 other studies (Arizaga et al. 2013; Godet et al. 2015; Musseau et al 2017), but the representation of these habitats  
431 in Barthes de la Nive is relatively limited, which could explain this lack of use.

432  
433 Our results showed that home-range size is smaller when birds occupied reedbeds (for overall home ranges) and  
434 corn crops (for daily home ranges). A potential explanation for this result is that these habitats might offer more  
435 trophic resources, which would prevent birds from making long foraging trips (Bibby and Green 1980;  
436 Chernetsov et al. 2004). Another complementary hypothesis for the higher occurrence of Bluethroats in these  
437 two habitat is that, given their dense structure, they could also provide a suitable shelter, not only for roosting  
438 during the night but also to rest during daytime between migration flight bouts. The use of reedbeds as roosting  
439 habitat has been described before in Bluethroats (Eybert et al. 2004; Harmange et al. 2016) and our study  
440 confirmed this preference and suggested that corn crops might occasionally play a similar role. In contrast, long-



441 staying Bluethroats seem to expand their home range probably because they are in high demand of food for  
442 refueling and, perhaps, because of the competition with conspecifics and other species (Chernetsov and Titov  
443 2001; Fransson et al. 2008).

444 If home-range size is considered a proxy of habitat quality, inland reedbeds could be interpreted as a refuge or a  
445 more optimal habitat than corn crops, which might represent the most-commonly available substitution habitat  
446 (Godet et al. 2018), where birds needing to refuel would move due to competition and the limited availability of  
447 reedbeds.

448 In our site, Bluethroats encounter also some potentially unsuitable habitats such as woodlands, open water,  
449 mown grasslands and infrastructures (house, road, railway) that would explain why they had to fly away a  
450 relatively long distance from their preferred roosts (Harmange et al. 2016), expanding their home range size.  
451 Similar patterns have been shown in Briere for breeding Bluethroats (Godet et al. 2015).

452  
453 We did not detect any difference between males and females in home range size, flight distance or stopover  
454 duration. Typically, small-sized, young and female Bluethroats are subordinated to large, adult and male  
455 conspecifics, respectively (Lindström et al. 1990, Moore et al. 2003). Our results suggest that Barthes de la Nive  
456 was occupied, not under an ideal despotic distribution, but under an ideal free distribution, where home range  
457 size would be determined by its habitat composition.

#### 458 **Diet of birds and invertebrate availability**

460 The diet description for our study site fitted well with the trophic characterization made in other Bluethroat  
461 studies (Allano et al. 1998; Orłowski *et al.* 2014; Musseau et al. 2017). In decreasing order of importance, our  
462 study showed the relevance of ants (40.6% of prey; 8.7% of biomass), flies (resp. 14% and 6.5%), beetles  
463 (13.7%, 40%) and spiders (9.4%, 22.5%). Bluethroats typically forage on the ground (Orłowski et al. 2014,  
464 Allano et al. 1998, Cramp 1988) where ants are particularly abundant. As in other agricultural farms (Cornouiller  
465 et al. 1997), corn crops showed a relatively high insect abundance and biomass, which could explain why  
466 Bluethroats positively selected this habitat. Again and as a consequence of the relative scarcity of intertidal  
467 habitats, arthropods such as amphipods (Malacostraca Amphipoda) were absent from the diet of Bluethroat in  
468 Barthes de la Nive, although they have been found in other studies (Musseau et al. 2017; Allano et al. 1998).

469  
470

#### 471 **Habitat management implications**

472 Our study confirmed the importance of wetlands and their associated reedbeds in Barthes de la Nive for  
473 migrating Bluethroats, as it was also shown for other bird species stopping over in the region (Fontanilles et al.  
474 2014). This reaffirms the need to conserve and potentially expand these valuable habitats, whose largest  
475 remnants in Southwestern France persist in the Nive/Adour river basin. These wetlands are mainly threatened by  
476 clogging and bush encroachment, particularly by invasive exotic tree species (i.e. *Acer negundo*, *Baccharis*  
477 *halimifolia*), so regular intervention is needed to maintain their characteristic aquatic vegetation.

478 Likewise, our results unexpectedly revealed a positive selection of corn crops by Bluethroats. The tall and dense  
479 arrangement of corn plants resemble the habitat structure of reedbeds. However, corn crops do not seem to  
480 constitute an ecological trap but a substitution habitat (Godet et al. 2018), a human-induced opportunity for  
481 migrating birds. Anyway, further research would be required to further understand this selection process and  
482 whether it also takes place in other sites. Our preliminary results suggest that corn crops would provide plenty of  
483 food resources and a suitable shelter for birds stopping over in Barthes de la Nive. Our study using the  
484 Bluethroat as model species raises the question of how other bird species respond to the presence of corn crops  
485 during their stopovers. The corn crops of Barthes de la Nive are used by a large group of migratory species  
486 (Fontanilles not published), so that measures to maintain or increase the suitability of this common crop for birds  
487 around the limited wetland remnants should be encouraged. Among them, promoting organic farming and  
488 postponing the harvesting time after mid-October, when most insectivorous migrants are in or near their southern  
489 wintering quarters, would be relatively easy to implement and might have immediate payoff (Dänhardt et al.  
490 2010).

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727 **Table 1:** Abbreviations for the different habitats available in Barthes de la Nive with its corresponding  
728 percentage of cover in the study area.

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Code	Area (ha)	Habitats
WAT	32.91	open water
PRB	19.35	pure reedbed <i>Phragmites australis</i> > 75%
MRB	11.89	reedbed mixture <i>Phragmites australis</i> (>25%) + <i>Carex sp</i>
WOR	14.63	wooded reedbed (wood < 50%)
WGR	21.37	wet grassland
MGR	64.04	mown grassland
CGR	10.79	mesophilic grassland
CRO	69.4	crop field
FER	0.84	fern
TAL	3.79	hydrophilous tall herb
WOL	171.5	wood land
PAT	12.05	natural path
HOU	7.64	house
RAW	1.54	railway

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734 **Table 2:** Conditional average of estimates ( $\beta_{cond.}$ ), adjusted SE ( $SE_{adj.}$ ) and *P-value* for the variables included in  
735 the model set for daily and global home ranges (K50 & K95), (-) indicated a variable unselected. Abbreviations:  
736 crop field (CRO), mesophilic grassland (CGR), mown grassland (MGR), natural path (PAT), pure reedbed  
737 (PRB), open water (WAT), wet grassland (WGR), wood land (WOL), stopover duration (SOD), fuel loads  
738 (FUEL).  
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Home range	50 % kernel			95% kernel		
	$\beta_{cond.}$	$SE_{adj.}$	<i>P-value</i>	$\beta_{cond.}$	$SE_{adj.}$	<i>P-value</i>
<i>Global home range</i>						
CGR	0.485	0.151	0.001	-	-	-
PRB	-0.362	0.208	0.081	-0.876	0.250	<0.001
WGR	0.404	0.163	0.008	0.683	0.278	0.014
WOL	0.325	0.162	0.045	0.694	0.224	0.002
FUEL	-	-	-	-0.664	0.210	0.002
SOD	0.337	0.182	0.061	0.895	0.289	<0.001
<i>Daily home range</i>						
CRO	-	-	-	-1.532	0.278	<0.001
MGR	0.8355	0.2645	0.002	1.509	0.286	<0.001
PAT	-	-	-	-1.883	0.365	<0.001
PRB	-1.3473	0.3181	<0.001	-2.027	0.585	<0.001
WAT	0.6355	0.2279	0.005	-	-	-
WGR	-	-	-	0.683	0.269	0.014
WOL	0.6010	0.2229	0.007	-	-	-

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742 **Table 3:** Percentage of each arthropod group in the faecal samples of 105 Bluethroats, occurrence frequency,  
 743 proportion of total biomass and factors influencing the relative prey abundance (age: yearlings vs adults; sex and  
 744 day). The number of prey items are given between brackets. "--" indicates no data available.  
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Order	Family	Abundance %	Occurrence %	Biomass %	Age effect		Sex effect		Day effect	
					z	p	z	p	z	p
Hymenoptera	Formicidae	45.48 (196)	54.29	8.34	0.998	0.318	-1.218	0.223	0.868	0.386
Arachnida	Araneidae	20.42 (88)	53.33	14.92	-0.986	0.324	0.373	0.709	-1.326	0.185
Coleoptera		10.21 (44)	31.43	64.70	-0.466	0.641	0.385	0.700	-0.614	0.539
Diptera		7.42 (36)	28.57	2.39	-0.010	0.992	0.462	0.644	0.281	0.779
Hymenoptera	non Formicidae	4.41 (19)	15.24	4.73	-0.193	0.847	0.803	0.422	-0.705	0.481
Hemiptera	Cicadellidae	3.25 (14)	13.33	2.45	-1.388	0.165	0.549	0.583	-1.993	<b>0.046</b>
Crustacea		3.32 (10)	9.52	2.48	0.008	0.993	-0.872	0.383	-0.772	0.440
Gastropoda		1.62 (7)	5.71	--						
Lepidoptera		1.62 (7)	6.67	--						
Neuroptera	Myrmeleontidae	1.16 (5)	3.81	--						
Arachnida	Acarina	0.93 (4)	3.81	--						
Heteroptera		0.7 (3)	2.86	--						
Malacostraca		0.23 (1)	0.95	--						
Amphipoda		0.23 (1)	0.95	--						
Odonata		0.23 (1)	0.95	--						

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 748 **Table 4:** Abundance and biomass (mean ± SE) of the most consumed invertebrates by Bluethroats in corn crops  
 749 (Crop), Villefranque reedbed (Rv) and Urdains reedbed (Ru), which were trapped in pitfall and coloured bowls.  
 750 Numbers in bold indicate the site for which the abundance or biomass was significantly higher than one of the  
 751 other sites (site shown after a slash symbol) or the other two sites. . Two hyphens represent no data available.  
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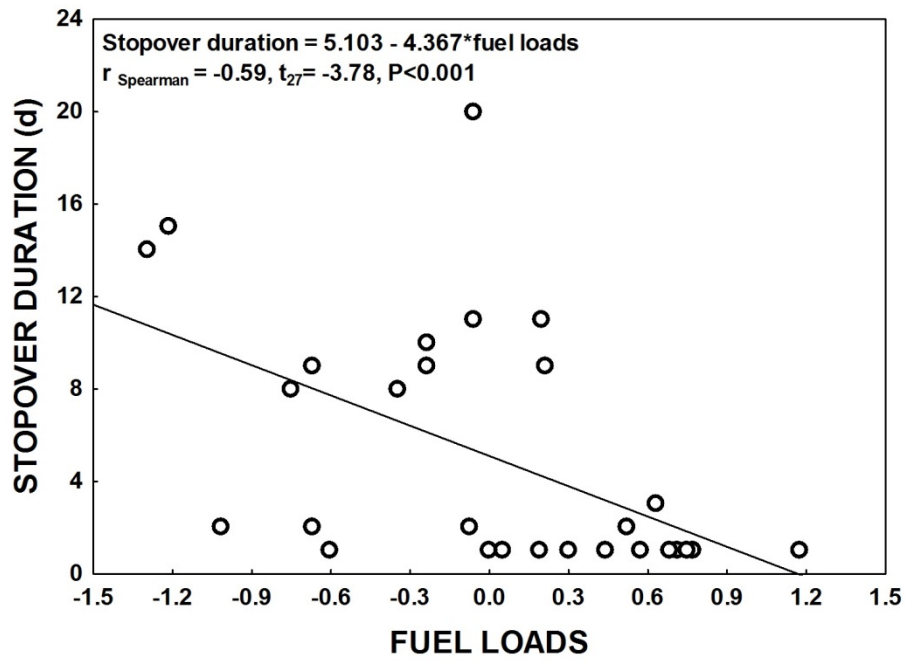
Order	Family	Trap	Abundance			Biomass (mg)		
			Crop	Ru	Rv	Crop	Ru	Rv
Hymenoptera	Formicidae	pitfall	0.2 ±0.1	<b>1.1 ±0.3</b>	0.2 ±0.1	0.04 ±0.02	<b>0.6 ±0.2 /Crop</b>	0.2 ±0.1
		bowl	0.3 ±0.1	--	0.6 ±0.2	0.03 ±0.02	0 ±0	0.2 ±0.1
Arachnida	Araneidae	pitfall	<b>3.5 ±1</b>	0.8 ±0.3	1.3 ±0.4	<b>7.5 ±2</b>	2.5 ±1	4.8 ±2.3
		bowl	1.9 ±0.4	1.2 ±0.5	2 ±0.6	3.4 ±0.8	5.9 ±2.9	<b>9.4 ±3.7</b>
Coleoptera		pitfall	<b>52.8 ±12.2</b>	0.1 ±0.1	2.1 ±0.5	<b>2006.9 ±449.1</b>	1.9 ±1.8	12.4 ±4.2
		bowl	<b>5.5 ±1.4</b>	0.7 ±0.3	<b>3.8 ±1.1</b>	<b>49.2 ±40.7</b>	0.9 ±0.6	8.2 ±3.7
Diptera		pitfall	<b>10.3 ±5.1</b>	0.3 ±0.2	1.1 ±0.3	<b>17.9 ±7.1</b>	0.8 ±0.8	1.1 ±0.5
		bowl	<b>24.5 ±6</b>	1.4 ±0.5	12.3 ±2.5	<b>42.2 ±8.8</b>	1.8 ±0.7	24.1 ±5
Hymenoptera	not Formicidae	pitfall	0.9 ±0.3	0.2 ±0.1	<b>1.4 ±0.5 /Ru</b>	0.7 ±0.3	0.1 ±0.1	<b>2.7 ±1.3</b>
		bowl	4.5 ±1	0.6 ±0.4	<b>8.9 ±1.6</b>	14.4 ±4.5	1.2 ±1.1	<b>43.6 ±8.2</b>
Hemiptera	Cicadellidae	pitfall	0.3 ±0.1	--	0.1 ±0.1	0.2 ±0.2	0 ±0	0 ±0
		bowl	<b>2.7 ±0.7</b>	0.1 ±0.1	0.7 ±0.3	<b>4 ±1.9 /Ru</b>	0 ±0	0.8 ±0.4

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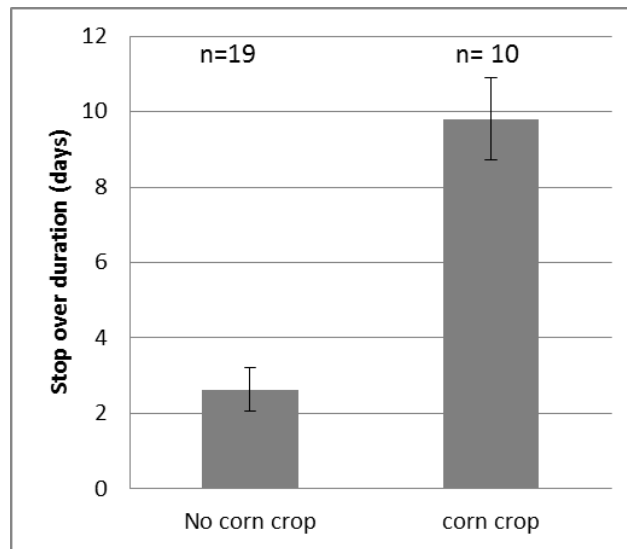
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**Fig. 1.** Relationship between size-corrected fuel loads and stopover duration in Barthes de la Nive, n=29.



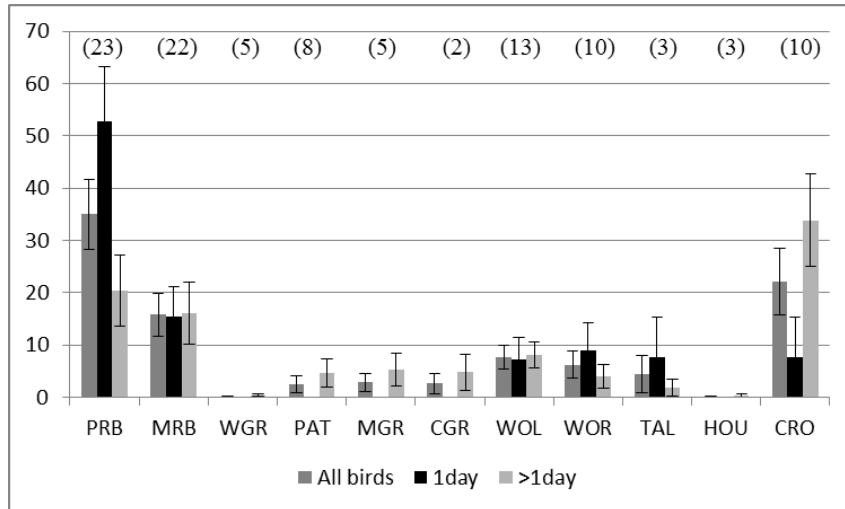
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**Fig. 2.** Variation in stopover duration between bluethroats that used corn crops and birds that did not in Barthes de la Nive, mean  $\pm$  SE.

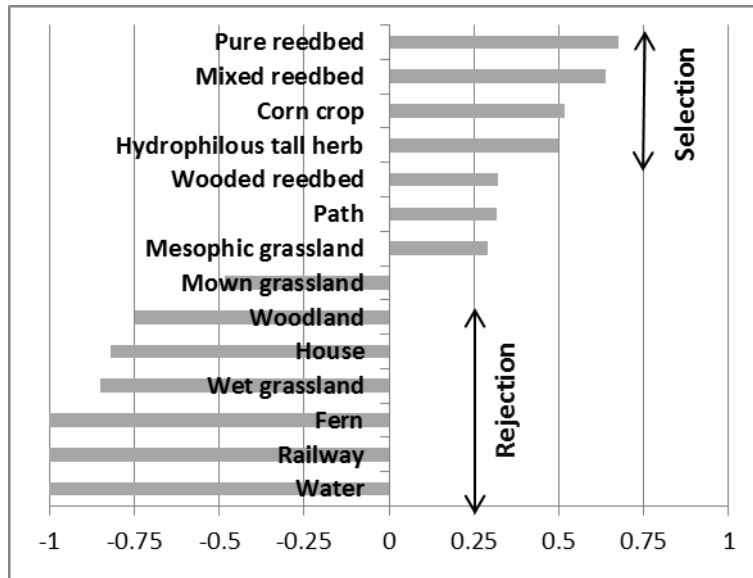


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763 **Fig. 3.** Proportion (mean  $\pm$  SE) of positions occurring in each habitat type of Barthes de la Nive for all  
 764 Bluethroats, those staying one day and those staying more than one day. Abbreviations as in Table 1. The  
 765 number of individual home ranges in which each habitat type was found is shown between brackets.  
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 770 **Fig. 4.** Jacobs index values for each habitat in the Bluethroats radiotracked in Barthes de la Nive. Values below 0  
 771 represent habitat rejection, while values above 0 represent positive selection.



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