

1 **High breeding performance of European Rollers *Coracias***
2 ***garrulus* in a heterogeneous farmland habitat of southern**
3 **Hungary**

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15 Short title: Rollers' breeding in farmland

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17 Keywords: farmland birds, nest-box, food availability, nestling diet

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20 Word count: 6,382

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30 Summary

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32 **Capsule** Rollers showed slightly higher breeding performance in farmland mosaics than in
33 natural grasslands in southern Hungary, where both habitats were supplied with nest-boxes.

34 **Aim** To establish which factors affect Rollers' breeding success in agricultural and their more
35 traditional grassland habitats.

36 **Methods** Rollers' reproductive success in farmland mosaics and grassland habitats were
37 compared. Laying date, clutch size, feeding rate, as well as prey abundance and diversity, as
38 estimated by sweep netting and pitfall trappings, were evaluated. Their effects on breeding
39 performance were analysed by generalized linear models.

40 **Results** In the agricultural habitat Rollers showed an even higher reproductive output than in
41 their traditional habitat of natural grassland. Prey composition showed differences between
42 the two habitats, with the lower abundance of orthopterans in farmland mosaics being
43 substituted by the higher abundance of coleopterans and the diversity of arthropods
44 (Orthoptera, Coleoptera, Heteroptera, Arachnida, Hymenoptera, Lepidoptera, Diptera,
45 Homoptera, Mantidae, Myrmeleonidae and Odonata) .

46 **Conclusions** This species can thrive where good quality resources are available, even outside
47 of their typical habitat, where nest box erection schemes may benefit this threatened species.

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51 **Introduction**

52

53 In the last three decades, the populations of many farmland and grassland bird species have
54 declined throughout Europe (Siriwardena *et al.* 1998a; Donald *et al.* 2001; Donald *et al.*
55 2002; BirdLife International 2004). This trend has been attributed to widespread
56 intensification of agricultural practices (Tucker & Heath 1994; Donald *et al.* 2001), such as
57 reduction and fragmentation of semi-natural grasslands (Söderström *et al.* 2001). Large areas
58 of meadows and pastures have been abandoned or transferred to arable fields (Vickery *et al.*
59 2001), and the use of insecticides have increased (Boatman *et al.* 2004; Hart *et al.* 2006).
60 Donald *et al.* (2006) showed that among 58 avian species classed by an independent
61 assessment as being primary birds of farmland, 41 showed negative trends across Europe
62 between 1990 and 2000, of which 19 proved to be significant. Agricultural intensification
63 may negatively affect birds' survival rate (Siriwardena *et al.* 1998b), and their reproductive
64 output (Siriwardena *et al.* 2000; Hart *et al.* 2006). In insectivorous species, one of the reasons
65 for these changes is a decline in food supply. For example, arthropod diversity and abundance
66 can be lower on intensively managed areas and this may result in less diverse nestling diet
67 (Britschigi *et al.* 2006).

68 Variation in the abundance and quality of food supply is thought to be an important
69 determinant of life-history traits of birds. As an ultimate factor, food availability may affect
70 breeding time, clutch size, offspring quality (Martin 1987; Tortosa *et al.* 2003) and
71 reproductive success (Goławski & Meissner 2008). Consequently, the composition of food
72 resources and the annual fluctuation of prey are some of the main factors determining
73 population breeding parameters and density (Korpimäki 1984; Korpimäki & Norrdahl 1991;
74 Arroyo & Garcia 2006).

75 The European Roller (*Coracias garrulus*) is a threatened bird species in Europe. It
76 suffered from a serious population decline during the 1970's, disappearing as breeding
77 species from Finland, Denmark, Germany and the Czech Republic (Cramp *et al.* 1993). The
78 Hungarian population was also affected by this process, Rollers disappeared from the western
79 part of the country, and the larger population of the eastern region also showed a serious
80 decline (Hungarian Checklist and Rarities Committee 1998). The likely reasons for this
81 decline are the lack of nest-sites and food availability due to changing agricultural practices
82 (Tucker & Heath 1994). Nest-box installation proved to be an efficient method to replace
83 natural nesting places (Avilés *et al.* 2000). Other studies reported less success with nest-box
84 programs for Rollers (Sosnowski and Chmielewski 1996), or even identified that nest-boxes
85 may serve as ecological traps and reduce reproductive success of Rollers having lower
86 individual quality (Rodríguez *et al.* 2011). Decreases in the extent and/or quality of feeding
87 sites (grasslands) still cause conservation problems for Rollers and other insectivore avian
88 species, such as Lesser Grey Shrikes (*Lanius minor*) (Giralt *et al.* 2008) and Red-backed
89 Shrikes (*Lanius collurio*) (Golawski & Golawski 2008). According to Donald *et al.* (2001)
90 the Roller was one of the 19 primary farmland species which showed negative trend as a
91 consequence of agricultural intensification in Europe. Furthermore, its breeding success and
92 egg productivity are affected by farming practices (Avilés & Parejo 2004).

93 In Hungary, extended pastures and meadows were the most typical historic habitats
94 for Rollers (Sziij 1958), where they mainly bred in old patches of white poplars (*Populus*
95 *alba*) and oak (*Quercus robur*) woods, in the holes of the Green Woodpecker (*Picus viridis*)
96 and also in the holes of the rarer Black Woodpecker (*Dryocopus martius*) (Kalotás 1998). In
97 southern Hungary the breeding population of Rollers decreased rapidly in the second half of
98 the 20th century, parallel with the reduction of the natural oak forests and the disappearance
99 of old poplar woodland patches. In the second half of the 20th century the disappearance of

100 cottages with old orchards also reduced suitable breeding sites, and the remaining young and
101 premature black-locust (*Robinia pseudoacacia*) woodlands had no suitable nesting holes for
102 Rollers. Fig. 1 shows population changes of Rollers in the last three decades in Hungary.
103 Rollers totally disappeared from southern Hungary in the 1980's and in the 1990's they
104 gradually disappeared from ca. 1/3 of the country, mainly from the western parts
105 (Transdanubia) (Kalotás 1998). After installation of nest-boxes, Rollers recolonized dry
106 grasslands in southern Hungary and became a relatively frequent breeding species in
107 grasslands and the mosaics of agricultural areas as well.

108 In the present study we aimed to compare breeding performance of Rollers in two
109 presently favoured breeding habitats of this species, where the missing natural holes are
110 provided artificially. One of these habitats is the farmland mosaics, which seems to be
111 dominant in the countryside of southern Hungary. The other habitat is the traditional Roller
112 habitat in Hungary, the dry grassland ("steppe") with scattered trees or woodland patches. As
113 the breeding population of Rollers has increased recently in both habitat types, we
114 hypothesized that breeding performance of Rollers would be similar in these habitats, and
115 predict similar values in clutch size, hatching success fledging success and reproductive
116 success. We also hypothesized that food supply was also similar in these habitats, which is a
117 critical factor for reproductive success. We also compared the main types of food that Rollers
118 delivered to their nestlings, and also surveyed the abundance and diversity of these main prey
119 items available in the field. We predicted similar food supply and similar prey selection of
120 rollers in the two habitats, if our hypothesis is true. Alternatively, these habitats differ for
121 Rollers, which may have consequences on their reproductive performance.

122

123 **Methods**

124

125 Study area

126

127 The study was conducted near the town of Szeged, southern Hungary, in two sites (Fig. 2): (i)
128 "Natural grassland" habitat at the village Baks (46°32'N; 20°03'E). This habitat was alkaline
129 natural grassland (often called "steppe"), which was characterized by salt and dry grassland
130 patches. Due to the lack of natural holes available for breeding, nest-boxes (approx. height:
131 30 cm, width: 20 x 20 cm, diameter of the entrance hole: 6-6.5 cm) were installed in the area
132 in previous years. With the help of this nest-box program we made dry grasslands available
133 for Rollers. Originally, they used to occupy grassland areas with scattered trees or where
134 nearby woodland patches were available with natural tree holes (Szijj 1958). The installation
135 of nest-boxes started in 1990 (Molnár 1998) and continued until 2008. Altogether 80 nest-
136 boxes were placed into this area, from which about 57-61% of them were occupied by Rollers
137 during any one year of the study. All nest-boxes were fixed on trees, mostly on black locusts
138 or poplars (*Populus* sp.). In this habitat breeding density of Rollers was about 0.255-0.235
139 pairs/10 ha in 2009 and 2010, respectively. (ii) "Farmland mosaics" at the village Szatymaz
140 (46°24'N; 19°57'E). The second site is an agricultural area, which is the mosaic of salt
141 grassland patches (23% of the whole area) and extensive cereal cultures (3%), arable fields
142 (53%) and artificial forest monocultures (4% of the whole area). The size of the grassland
143 patches within this habitat was about 14 ha. Nest-boxes were placed into the grassland
144 patches, from the year of 1988 (Molnár 1998). During the study period 65 nest-boxes were
145 available for Rollers and about 45% of them were occupied. We placed the next-boxes on
146 trees (lone trees and treelines) and electric pylons. In this habitat density of the breeding
147 Roller population was about 0.32-0.362 pairs/10 ha in 2009 and 2010, respectively.

148

149 Number of nest-boxes did not change in the years of our study. No pairs of Rollers
150 bred in natural holes in our study areas. In nest-boxes no competitors were observed, except a
pair of Western Jackdaws (*Corvus monedula*) bred in a nest-box. A few attempts at nest-box

151 occupation were observed by Eurasian Scops Owls (*Otus scops*) and Starlings (*Sturnus*
152 *vulgaris*), but Rollers won in these cases. Previously we also observed a few successful
153 nesting attempts of Red-footed Falcons (*Falco vespertinus*) in Rollers' nest-boxes, but not in
154 the years of the study.

155 The study was conducted in 2009 and 2010, during the breeding season of Rollers
156 (from late April to early August). We also sampled prey of Rollers in the first year of the
157 study.

158

159 Arthropod abundance

160

161 We studied the availability of prey on 12 and 14 plots at the Baks and Szatymaz sites
162 respectively, in 2009. At both sites plots were established in grassland patches of the habitat,
163 within the breeding territories of Rollers (average territory size was 4.83 ha, Molnár 1998).
164 Rollers preferred to collect food from grassland patches (our unpubl. results). The dry short-
165 grass steppe habitat offers high visibility of prey for sit-and-wait predators, like Rollers and
166 Lesser Grey Shrikes (Lovászi et al. 2000), when they are perching on trees or power lines.
167 Only one plot per Rollers' territory was used to avoid pseudoreplication in data. Our sampling
168 plots were established within 150 m radius around the nest-boxes, because Avilés et al.
169 (2000) reported about 165-170 m foraging radius of Rollers in the nesting period.

170 Although Rollers sometimes catch small vertebrates, they typically forage on
171 terrestrial invertebrates and slowly flying arthropods (Cramp *et al.* 1993; Avilés & Parejo
172 2002). We used pitfall traps and sweep-net sampling to estimate arthropod abundance and
173 potential prey species diversity. In each study plot we randomly placed five pitfall traps of
174 plastic cups with the diameter of 65 mm in a line, 1 m apart from each other. Ethylene glycol
175 (30-50%) was used as killing-preservative solution. We also sampled potential prey by sweep

176 netting in three transects within a territory, under good weather conditions (above 15 Celsius
177 degree temperature on a windless day, e.g. below 2 on the Beaufort scale). Pitfall-traps were
178 active for two weeks between 16 June and 20 July, which overlapped the feeding period of
179 nestlings. This resulted in two samples from pitfall traps and three samples from sweep
180 netting. Rollers usually feed on arthropods larger than 1 cm (Cramp et al. 1993) hence we
181 selected the food items larger than 1 cm from the collected samples for further analyses. We
182 identified arthropods to families, then dried (72 hours, 60 °C) and their biomass was
183 measured (accuracy: 0.001g) (see Table 2a for main taxa of arthropods determined).

184

185 Breeding parameters and feeding behaviour

186

187 From the end of April to August we checked nest-boxes weekly to monitor the breeding
188 attempts of Rollers. Nest-boxes were monitored weekly through all the breeding cycle, but in
189 the case when we found a clutch larger than one or two eggs, we rechecked it in the next 1-2
190 days during the egg laying period or if the clutch was considered complete we monitored it
191 every 4-5 days until the first egg hatched. Incubation begins before clutch completion,
192 usually just after the third egg has been laid, and the mean clutch size is 3.8 (Cramp *et al.*
193 1993). Start of laying was estimated by backward calculation, assuming that an egg was laid
194 in every second day and the incubation period was about 18 days (Cramp *et al.* 1993). We
195 calculated hatching success as the percentage of hatched eggs in a clutch and fledging success
196 as the percentage of hatchlings that fledged. The number of 20-23 days old nestlings was
197 accepted as the number of fledglings produced by a pair, because fledging time is 26–27 (25–
198 30) days (Cramp *et al.* 1993). Reproductive success was calculated as the number of
199 fledglings per pair that laid at least one egg. We documented feeding rates and prey
200 composition delivered by Rollers to their nestlings by video recordings (Sony DCR-HC53E

201 camera). We positioned the video camera about 5 m from the nest-boxes on a tripod, and left
202 it in place for 5-10 minutes, before recording started to allow habituation of the parents.
203 Recording sessions typically lasted one hour (mean 64.7 min \pm 1.1 SE). We recorded Rollers
204 between 0600 and 1200 hours in the morning, because Poole (2006) reported the frequency
205 of Rollers' feeding activity was similar within this period. We recorded Rollers' chick feeding
206 twice at each nest, first during the first week of the nestling period and the second recording
207 during the third week of the nestling stage in 2009; Roller nestling period is at least 3 weeks
208 long (Cramp *et al.* 1993).

209

210 Statistical analyses

211

212 We tested three sets of models to determine if there were differences across habitats.

213 (1) How reproductive success (number of hatchlings per clutch size, expressed as percentage;
214 the response variable in the model) was affected by the nesting parameters, such as feeding
215 rate, date of the first egg laid and clutch size, prey availability as covariates, including habitat
216 type as a fixed factor. Two model derivatives were compared by multi-model inference (see
217 details below): the first variant was the simple effect model where only the main effects
218 among the studied variables were considered, while in the second variant, clutch size was
219 added as a correction term for dispersion parameter (Bolker *et al.* 2009) due to control the
220 effects of different clutch sizes on the response variable. This means that the arc sine
221 transformed clutch size was added as a known coefficient to the linear predictor to avoid any
222 potential biases in the model estimates caused by the difference in clutch sizes.

223 (2) How feeding rate was affected by the nesting parameters, such as date of the first egg laid,
224 clutch size and prey availability, and including habitat types as a fixed factor. Two model
225 derivatives were compared by multi-model inference: the first model was the simple effect

226 model, while in the second variant the linear predictor was corrected by clutch size, similarly
227 to model (1).

228 (3) Three models were built (to avoid collinearity) to describe how food resources (mean for
229 orthopterans, coleopterans and the total abundance of prey as response variables) vary
230 between habitat types and collection methods (including their interactions).

231 For models (1) and (2) we used information criterion (AICc) to rank the models in
232 terms of their ability to explain the responses (Burnham and Anderson 2002). In this way
233 parameters of the “best approximating” model were selected for the most parsimonious
234 explanation of the data.

235 We used generalized linear models to reveal the relationships between the assumed
236 explanatory and response variables using Gaussian error term. The response variable
237 reproductive success was arc sine transformed, while feeding rate and food resources
238 variables were $\log(x+1)$ transformed to allow linear fitting of the models (c.f. Bolker 2009).
239 We applied multi-model inference to select the most parsimonious model in the case of
240 models 1 and 2. The analyses were carried out in R 3.0.1 (R development team 2013), using
241 the package MuMIn for multi-model inference (Barton 2013). Box-and-whisker plots were
242 generated by SPSS ver. 17.

243

244 **Results**

245

246 We found similar clutch sizes of Rollers in the two study sites (mean clutch sizes were $3.94 \pm$
247 0.98 SE and 3.72 ± 1.22 SE in the grassland and mosaic habitats, respectively; Mann-
248 Whitney U-test, $U_{83,54} = 2030.0$, $P = 0.42$). Hatching success (81% in the grassland and 85%
249 in the mosaic habitats; $U_{72,51} = 2065.0$, $P = 0.95$) and number of hatchlings was also similar
250 between the two habitats (mean number of hatchlings was 3.27 ± 1.57 SE in the grassland

251 and 3.26 ± 1.59 SE in the mosaic habitats; $U_{77,54} = 1661.0$, $P = 0.35$). Fledging success
252 (percentage ratio of hatchlings that fledged) also showed similar values in both of the habitats
253 (82.9% and 90% in the grassland and mosaic habitats, respectively; $U_{68,49} = 1428.5$, $P =$
254 0.16). The only habitat-related difference in reproductive performance was found in breeding
255 success (percentage of eggs that fledge per pair that laid at least one egg) that proved to be
256 higher in the mosaic than in the grassland habitat (64.2% and 77% in the steppe and mosaic
257 habitats, respectively; $U_{76,52} = 1487.5$, $P = 0.019$; Table 1).

258 We collected a total number of 8816 arthropods larger than 1 cm (67.6 g dry biomass)
259 were collected by pitfall trapping and sweep-net sampling (Table 2a). Sweep-netting proved
260 to be sensitive for orthopterans, as about 87% of the caught specimens and 82.2% of the dry
261 biomass belonged to this prey type. Beetles were represented in only 1.8% of specimens and
262 4.3% of the dry biomass. Conversely, pitfall traps caught similar proportion of orthopterans
263 (47.2% of specimens and 58.4% of the dry biomass) and coleopterans (31.8% of specimens
264 and 30.6% of the dry biomass). The total amount of dry biomass of orthopterans collected by
265 sweep-netting was highest in the natural grassland than in the mosaic habitat ($U_{12,13} = 39000$,
266 $P = 0.035$). For pitfall trapping we found no difference in the arthropods collected in the two
267 habitats ($U_{24,30} = 317.5$, $P = 0.46$). Shannon's diversity of the arthropod families, when it was
268 calculated from sweep-net samplings, was significantly higher in the mosaics than in the
269 grassland ($U_{12,14} = 162000$, $P = 0.001$; Fig. 3a), but these values were similar in the two
270 habitats if it was calculated from pitfall traps ($U_{12,14} = 58000$, $P = 0.19$; Fig. 3b). We video-
271 recorded Rollers when they were delivering food for their nestlings in the nest-boxes (Table
272 2b). These videos revealed that rollers typically fed their nestlings insects, mainly
273 orthopterans (in 40.1% of feeding) and coleopterans (23.3%), but other insects were also
274 important (25.3%). Although the frequency of delivered vertebrates was only 9.3%, their
275 contribution to nestling diet by mass was more important. No difference was found between

276 the two habitats regarding some of the prey types (coleopterans: $U_{28,39} = 489.5$, $P = 0.46$;
277 vertebrates: $U_{28,39} = 440.5$, $P = 0.13$), but rollers delivered more orthopterans in the grassland
278 ($U_{28,39} = 358.0$, $P = 0.015$) and more prey from small mammals (rodents and shrew-mice)
279 ($U_{28,39} = 452.0$, $P = 0.044$) in the farmland mosaics.

280 Reproductive success of Rollers was affected by egg laying date and habitat type,
281 showing higher reproductive success in the farmland mosaics (Table 3). However, feeding
282 frequency did not affect reproductive success. Including clutch size in the model improved it
283 (weight=0.624, AICc=27.6, logLik=-5.128, df =8) suggesting that differences due to habitat
284 were probably not restricted to adult quality and reflected the quantity or quality of food
285 provided to the chicks. Feeding rate was however the same across habitats and only depended
286 on clutch size (Table 4) suggesting that differences across habitats were likely to reflect
287 quality of food provided. The simple effect model provided the better fit than the model
288 including clutch size as offsetting factor (Table 3). Clutch size affected the feeding rate of
289 Rollers, as individuals with larger clutches showed higher feeding rate.

290 Food availability varied significantly across habitats controlling for collection method
291 (Table 5). Orthopterans seems to be the most important group in prey availability, as shown
292 by the sweep netting methods. Coleopterans have more importance in the farmland mosaics
293 (Table 5).

294

295

296 **Discussion**

297

298 Our results showed that Rollers' reproductive success in southern Hungary was higher in
299 mosaic farmland habitats than in the dry natural grassland ("steppe") habitat. This habitat
300 type is known as the most important original habitat for Rollers in this area (Szijj 1958;

301 Molnár 1998), although this species cannot be regarded as a specialist on grasslands (Batáry
302 *et al.* 2007). The decrease in the availability of natural nesting holes for this species in the
303 second half of the last century drove this breeding population close to extinction (Kalotás
304 1998; Molnár 1998), but offering suitable nest boxes for Rollers seems to be an effective way
305 to help their survival. Our study revealed high diversity of potential prey types in both
306 habitats, and the dominance of orthopterans when preys were collected by sweep netting.
307 Sweep netting revealed higher abundances of orthopterans and more taxa than pitfall
308 trappings, suggesting the usability of this method for surveying prey availability for Rollers.
309 Reproductive performance of this species in farmland mosaics was slightly higher in the
310 farmlands than in natural grasslands. Although the main prey type of this species, the
311 orthopterans were less numerous in farmland mosaics than in grasslands, Rollers
312 compensated for this by collecting other insects and small vertebrates in the mosaic habitat.
313 Although the abundance of the main prey types somewhat differed in these two habitats,
314 Rollers were able to compensate this difference with the preference for coleopterans in
315 farmlands. This shift did not reduce their breeding success, even it was higher in farmland
316 mosaics than in grasslands. Despite of the difference in food supply in the two habitats, video
317 records revealed that orthopterans dominated in their prey selection when Rollers fed their
318 nestlings. We suggest that Rollers utilized the available resources successfully in both
319 habitats and so both of them seem to be suitable for this species.

320 Original breeding habitats of Rollers have also changed in Spain, and there they now
321 use different agricultural habitats for breeding sites such as cereal fields, irrigated crops,
322 pastures, holm oaks, olive groves or scrub fields, as well as more traditional habitats (Avilés
323 *et al.* 1999; Avilés *et al.* 2000; Avilés & Parejo 2004). Though Avilés & Parejo (2004)
324 revealed that farming practices had a negative effects on Rollers' breeding performance, they
325 also suggested that the decrease in natural nest-sites that resulted from agricultural

326 intensification is probably the main effect responsible for the decline of Roller populations. In
327 France, Rollers also breed in farmland mosaics, but prefer sites with higher density of
328 orthopterans (Bouvier et al. 2014).

329 Although the food composition of Rollers in our study site appears to be similar to
330 that of in their European range (Cramp *et al.* 1993; Avilés & Parejo 2002), our study revealed
331 differences in nestling food composition in different habitat types. Fragmentation may have
332 complex effects on insect density and movement (Hunter 2002) and probably provides
333 variable hunting possibilities for insectivorous species. Hunting success of the sit-and-wait
334 predator Roller is affected by several factors besides food availability, such as perch type and
335 vegetation (Cramp *et al.* 1993). The Roller is a polyphagous species, foraging on a wide range
336 of prey (Szijj 1958), and our findings showed that Rollers can effectively switch between
337 prey species based on their availability. We also found higher frequencies of small mammals
338 and lizards in the mosaic site than in the natural grasslands. Avilés & Parejo (2002) showed
339 that small mammals significantly contributed to the biomass of the nestling diet in Rollers,
340 therefore their abundance may have a positive effect on breeding success. Video-recordings
341 revealed that Rollers fed their nestlings with easily-available large insects, mainly
342 orthopterans, but when availability of this prey was reduced in the farmland habitat they
343 collected more coelopterans. Other studies have pointed to the potential importance of
344 vertebrates in Rollers' food, but vertebrates never dominate as prey, and can best be regarded
345 as only occasional elements (Szijj 1958; Sosnowski & Chamielski 1996). Only one
346 exceptional case is known where anurans comprised 70% of Roller diet (Barthos 1906).
347 Small mammals, birds, snakes, lizards, and anurans might represent valuable food types
348 because of their higher biomass, but in Hungarian samples small mammals and reptiles were
349 detected only at a relatively low frequency.

350 In the present study we show an example where a new man-made habitat type can be
351 suitable for breeding and survival for a vulnerable bird species as long as critical limiting
352 factors are addressed (i.e. nest site availability). The farmland mosaics in southern Hungary
353 seem to be offering a high-quality breeding habitat for Rollers, if supplied with artificial nest
354 boxes. These large-sized nest boxes are also necessary in the traditional breeding habitat of
355 this species, where there is now a shortage of natural holes for breeding. In southern Spain
356 nest boxes had a negative impact on Rollers' reproduction (Rodríguez et al. 2011). The
357 variation in the importance of nest boxes in helping Roller populations clearly needs further
358 research in different parts of Rollers' breeding range, as several factors may influence their
359 usability. For example, snake predation is an important factor which reduces the applicability
360 of nest boxes for Rollers in Spain (Parejo & Avilés 2011), but no snake predation was
361 observed in Hungary. These results suggest that geographical variations may possible be
362 explained by regional factors affecting nest-box suitability, and the importance of evaluating
363 population effects of conservation actions on a case by case basis. Our study probably
364 provides an example of how nature conservation practices – provision of nest boxes - may
365 help in the survival of a threatened generalist species in new habitats, if there is sufficient
366 food availability.

367

368 **Acknowledgements**

369 We are grateful to the authority of the Kiskunság National Park for allowing us to work in the
370 Pusztaszeri Landscape Protection area. We would like to thank Béla Tokody and the local
371 group of BirdLife Hungary for their assistance in the field. We thank Róbert Gallé and Attila
372 Torma for their help in insect collection and determination. We are grateful to Guillam E.
373 McIvor (University of Exeter) for improving the English. We thank Dr. Will Cresswell, Dr.
374 Gavin Siriwardena and an anonymous reviewer for their comments on the manuscript. The

375 Ministry of Agriculture (former Ministry of Environment and Water) provided permissions
376 for research.

377

378

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490
491

492 Table 1. Clutch size, hatching success, fledging success and breeding success of Rollers,
 493 observed in natural grasslands and farmland mosaics in southern Hungary (means \pm SE;
 494 sample sizes are in parentheses).

495
 496

	Clutch size	Hatching success	Fledging success	Breeding success
Natural grassland				
2009	4.27 \pm 0.129 (51)	95.8 \pm 1.70 (40)	80.4 \pm 5.05 (41)	73.4 \pm 5.06 (44)
2010	3.41 \pm 0.148 (32)	62.6 \pm 7.74 (32)	86.7 \pm 5.09 (27)	51.4 \pm 7.43 (32)
Farmland mosaics				
2009	4.26 \pm 0.169 (23)	92.5 \pm 4.87 (22)	82.3 \pm 6.4 (22)	77.7 \pm 7.02 (23)
2010	3.32 \pm 0.234 (31)	79.8 \pm 6.85 (29)	97.5 \pm 1.71 (27)	78.7 \pm 6.8 (29)

497
 498

499 Table 2. Potential prey supply in Rollers' territories and prey selected for chick feeding in
 500 natural grasslands and farmland mosaics in southern Hungary. (a) Mass of dry biomass (g) of
 501 the main groups of arthropods collected by sweep-netting and pitfall traps (means \pm SE). (b)
 502 Frequency of main prey types in Roller nestling diet identified from video recordings
 503 (number of observations and percentages of all feedings).

504

505

506 (a)

	Natural grassland		Farmland mosaics	
	Sweep-netting	Pitfall traps	Sweep-netting	Pitfall traps
Orthoptera	0.691 \pm 0.66	0.135 \pm 0.17	0.43 \pm 0.044	0.141 \pm 0.152
Coleoptera	0.05 \pm 0.22	0.061 \pm 0.068	0.011 \pm 0.003	0.079 \pm 0.128
Heteroptera	0.0389 \pm 0.17	0.0004 \pm 0.001	0.037 \pm 0.006	0.002 \pm 0.0035
Arachnida	0.0108 \pm 0.037	0.0822 \pm 0.1	0.0095 \pm 0.002	0.017 \pm 0.025
Hymenoptera	0.0104 \pm 0.05	0.0009 \pm 0.002	0.004 \pm 0.001	0.0036 \pm 0.006
Lepidoptera	0.036 \pm 0.17	0.0005 \pm 0.0015	0.0054 \pm 0.0015	0.0001 \pm 0.0001
Diptera	0.01 \pm 0.04	0.0003 \pm 0.0009	0.01 \pm 0.002	0.0015 \pm 0.0027
Homoptera	0.0002 \pm 0.0009	-	0.0005 \pm 0.0003	-
Mantidae	0.0011 \pm 0.006	-	0.064 \pm 0.036	-
Myrmeleonidae	-	-	0.0016 \pm 0.0007	-
Odonata	0.0001 \pm 0.0004	-	0.02 \pm 0.00018	-

507

508

509 (b)

	Natural grassland	Farmland mosaics
Orthoptera	77 (41.62%)	56 (35.44%)
Coleoptera	32 (17.3%)	43 (27.22%)
Other insects	68 (36.76%)	36 (22.78%)
Reptiles	7 (3.78%)	16 (10.13%)
Mammals	1 (0.54%)	4 (4.43%)

510

511

512

513 Table 3. Results of the best model for the reproductive success of Rollers (i.e. the number of
 514 fledglings per pair that laid at least one egg; dependent variable) in southern Hungary with
 515 habitat (fixed factor), feeding rate, laying date, abundance of coleopterans and orthopterans
 516 (covariates) and clutch size (as offset).

Parameters	d.f.	Estimate s	S.E.	t	P
Intercept (farmland)		-1.79	0.37	-4.77	<0.001
Habitat (grassland)	1,112	-0.54	0.06	-8.53	<0.001
Feeding rate	1,111	0.00	0.00	0.22	0.82
Laying date	1,110	0.06	0.00	8.39	<0.001
Coleoptera mean abundance	3,113	-0.11	0.42	-0.25	0.79
Orthoptera mean abundance	3,107	0.08	0.1	0.78	0.43
Total mean abundance	3,107	0.04	0.07	0.53	0.59

517

518 Table 4. Results of best generalized linear models for the feeding rate of Rollers (dependent
 519 variable) in southern Hungary with habitat (fixed factor), laying date, clutch size, and
 520 abundance of coleopterans and orthopterans (covariates).

Parameters	d.f.	Estimates	S.E.	t	P
Intercept (farmland)		-2.84	1.2	-2.37	0.01
Habitat (grassland)	1,112	0.09	0.1	0.62	0.53
Laying date	1,111	0.06	0.0	3.4	<0.001
Clutch size	1,110	0.39	0.95	4.12	<0.001
Coleoptera mean abundance	3,113	-1.26	0.96	-1.3	0.19
Orthoptera mean abundance	3,107	-0.38	0.23	-1.64	0.1
Total mean abundance	3,107	-0.31	0.18	-1.74	<0.001

521

522

523 Table 5. Results of generalized linear models describing how food resources (abundance of
 524 orthopterans, coleopterans and total abundance of prey as response variables) may vary
 525 between habitat types and collection methods (including their interactions).

526

527 (a) Shannon's diversity of prey

528

Parameters	d.f.	Estimate	S.E.	t	P
Intercept (farmland, pitfall, farmland: pitfall)		0.69	0.04	14.12	<0.0001
Habitat (grassland)	1,36	0.17	0.06	2.62	0.01
Source (sweepnet)	1,35	0.035	0.06	0.51	0.61
Grassland: sweepnet	1,34	-0.532	0.09	-5.56	<0.0001

529

530 (b) Orthopterans

531

Parameters	d.f.	Estimate	S.E.	t	P
Intercept (farmland, pitfall, farmland: pitfall)		0.16	0.04	3.54	0.001
Habitat (grassland)	1,36	-0.06	0.06	-1	0.32
Source (sweepnet)	1,35	0.19	0.06	2.91	0.0006
Grassland: sweepnet	1,34	0.24	0.09	2.74	0.0009

532

533 (c) Coleopterans

534

Parameters	d.f.	Estimate	S.E.	t	P
Intercept (farmland, pitfall, farmland: pitfall)		0.08	0.02	3.28	0.002
Habitat (grassland)	1,36	-0.02	0.03	-0.58	0.56
Source (sweepnet)	1,35	-0.07	0.03	-2.07	0.04
Grassland: sweepnet	1,34	0.05	0.05	1.16	0.25

535

536 (d) Total abundance

537

Parameters	d.f.	Estimate	S.E.	t	P
Intercept (farmland, pitfall, farmland: pitfall)		0.25	0.05	4.341	0.0001
Habitat (grassland)	1,36	-0.02	0.08	-0.336	0.73
Source (sweepnet)	1,35	0.16	0.08	1.93	0.06
Grassland: sweepnet	1,34	0.23	0.11	2.022	0.05

538

539 Legends to figures

540

541 Figure 1 Changes in the number of breeding pairs of Rollers between 1985 and 2013 in

542 Hungary.

543

544 Figure 2 A map to show the location of the two study sites in Hungary.

545

546 Figure 3 Shannon' diversity of arthropods collected three times by sweep nettings (a), or

547 twice by pitfall trappings (b) from Rollers' territories. (white boxes: natural grassland, grey

548 boxes: farmland mosaics; box-and-whisker plots show median, minimum and maximum

549 values, and quartiles)

550

551