Arch Biol Sci. 2022;74(3):251-262 https://doi.org/10.2298/ABS220404024M

Foraging habitat characteristics influence the nest-box occupancy and breeding parameters of European roller (*Coracias garrulus*) in Serbia

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Received: April 4, 2022; **Revised**: June 24; 2022; **Accepted**: August 5, 2022; **Published online**: August 15, 2022

Abstract: The European roller (*Coracias garrulus*) is an endangered species whose breeding in Serbia depends almost entirely on nest boxes. The aim of the present study was to assess the influence of prey availability and foraging habitat characteristics on nest-box occupancy and breeding parameters. Data from 20 roller foraging sites over 5 breeding seasons were used in a set of linear regression models to evaluate which factors affect the diversity and biomass of roller prey, as well as nest-box occupancy and breeding parameters. Our analyses revealed that prey availability parameters were significantly affected by the grazing regime and biophysical parameters. An area under grassland negatively affected nest-box occupancy, clutch size and fledging success. In contrast, grazing intensity showed positive effects. Although grazing negatively affected prey diversity and quantity, it potentially increased the likelihood of a successful hunt by forming short vegetation. These results indicate that the habitat characteristics linked to the ability of the species to hunt successfully should be considered when installing nest boxes as a part of the broader management of roller breeding sites. Furthermore, nest-box installation in open agricultural habitats other than grasslands should be considered in the conservation strategy for the species in Serbia.

Keywords: European roller, *Coracias garrulus*; nest box; prey; perches; grazing

INTRODUCTION

Declines in the populations of farmland bird species in Europe are extensively documented and attributed to the depletion of nesting and feeding resources in intensively farmed landscapes [1]. The amount of prey for insectivorous species is decreasing due to the loss of areas covered by natural or semi-natural vegetation, reduction in the ecological complexity of habitats, and the use of agrotechnical measures. Changes in habitat structure and the removal of certain elements, such as hedges or solitary trees, are considered equally unfavorable factors, resulting in the loss of nesting sites or suitable foraging habitats [2]. Conservation of farmland birds primarily implies management modifications aimed at regulating the key limiting factors for target species [3], which vary with area [4] and across time [5]. Therefore, determination of the key limiting factors is crucial in the development of efficient management strategies [6].

Setting up nest boxes is an efficient conservation measure for bird species for which the lack of suitable and safe nesting sites is considered a key limiting factor [7,8]. Nest boxes can make up for the lack of natural nesting sites and positively influence reproductive parameters such as juvenile survival [9]. Furthermore, as nest boxes enable the monitoring of key species and their ecology, they are important for the popularization of conservation measures [10,11]. Nonetheless, nest boxes can act as ecological traps if they cause higher mortality of individuals that use them, attract species to suboptimal habitats or lead to unwanted adaptation to artificial nesting sites [12,13].

The European roller *Coracias garrulus* (hereafter: roller) is a typical, mostly insectivorous, secondary cavity nester [14], whose population and breeding area are declining in Europe [15]. For breeding, the roller uses tree hollows made by large woodpecker species (e.g. *Picus viridis*) or cavities in sand or loess bank

How to cite this article: Milinski L, Radišić D, Arok M, Nikolić T. Foraging habitat characteristics influence the nest-box occupancy and breeding parameters of European roller (*Coracias garrulus*) in Serbia. Arch Biol Sci. 2022;74(3):251-62.

walls [14,16]. It prefers foraging on terrestrial invertebrates and slow-flying arthropods, while rarely feeding on small vertebrates [14,17]. Throughout Europe, land use intensification and structural homogenization of the landscape have markedly reduced the quality and quantity of suitable habitats and prey resources, as well as the number of available breeding cavities [15,16,18]. Empirical evidence further indicates that the limiting factors differ across the species' range. For example, while southern populations (south of France) are limited by available nesting sites, northern populations (Latvia) are particularly affected by food availability [19,20]. Nest boxes are often used in roller conservation, and tend to yield highly positive results [8,21-23] even though the influence of other factors was found more relevant in some cases [24]. According to the optimal foraging theory, the roller's selection of nesting sites and reproductive success are determined by the availability of optimal foraging habitats, prey abundance within foraging habitats and habitat characteristics that influence the probability of successful hunting strikes [25]. The occupancy of nest boxes and breeding success in different parts of Europe are generally positively influenced by the presence of optimal foraging habitats and the abundance of available prey within them [16,19,21], especially in the close vicinity of the nest, where rollers mostly forage [26]. However, the effect of habitat characteristics that enables rollers to successfully hunt, such as the availability of perches, used by the birds to scan for invertebrate and small vertebrate prey, remains insufficiently explored [26]. Scant evidence suggests that the success of prey spotting and hunting can be influenced by the type and structure of vegetation, shaped in part by management [2].

The roller population in Serbia is considered to be largely dependent on the artificial nest boxes placed on (mostly) grassland patches across the species' historic range [27]. Formerly abundant in the Pannonian part of the country, around the year 2000 the roller disappeared from northern Serbia almost entirely [28]. As a result, the roller is strictly protected in Serbia with a near-threatened status on the Serbian Red List of birds [29]. The lack of suitable cavities for breeding is recognized as the main limiting resource for rollers on the Pannonian plain, which is why extant conservation efforts primarily rely on nest-box installation [27,30]. Subsequent adoption of a nest-box program led to a significant recovery in the national population; a similar observation was made in Hungary [23] for rollers that belong to the same Pannonian population [31]. Even though the roller conservation program in Serbia is considered highly successful, prey availability and foraging habitat characteristics have never been analyzed with the view of steering future conservation programs.

The aim of this study was to assess the role of surrounding habitat characteristics in nest-box performance. For this purpose, influential factors were split into five categories as follows: habitat characteristics, perching structures, biophysical characteristics of habitats, habitat management and prey availability, and their influence on nest-box selection and breeding parameters was examined. We hypothesized that the aforementioned factors determine the abundance of available feeding resources and the possibility of their successful use, thus influencing both nest-box selection and breeding success. Moreover, we analyzed the impact of the biophysical characteristics of habitats and habitat management on prey communities (mass and generic diversity of prey). Based on the findings yielded, we offer practical recommendations for the continuation of the nest-box program and the allocation of conservation measures.

MATERIALS AND METHODS

Ethics statement

Ethics approval was not required for the purpose of our fieldwork campaigns as the localities were distributed within non-protected areas.

Study area

The study area is situated in the lowlands of the Central Banat region in NE Serbia (Novi Bečej, Kumane, Melenci, Taraš, Bašaid and Novo Miloševo municipalities). As the area is located on the Pannonian plain, the climate is continental, characterized by hot and relatively arid summers with less than 400 mm of annual precipitation [32]. Although the area is dominated by agricultural land, a significant portion is covered by semi-natural grasslands, usually located on patches of poor-quality saline soils and used mainly for cattle or sheep grazing. These semi-natural grasslands are of particular conservation interest given that the distribution of remnant salt steppe fragments that are rich in biodiversity is a focus of future conservation spatial programs and will be the backbone for the Serbian Natura 2000 network in the Pannonian part of the country [33]. Grasslands are strongly influenced by the underground water regime and are sometimes flooded during periods of high underground water levels. Trees (poplar, willow and non-native species) are scarce and their numbers are rapidly declining due to illegal logging.

Nest-box occupancy and breeding parameters monitoring

Twenty nest boxes (16 of which were installed on electric pylons and 4 on trees) were monitored for five consecutive breeding seasons from 2015 to 2019. Only nest boxes that were visited at least twice per breeding season (from June 10th to 25th, and from June 25th to July 15th) were included in the analysis. The aim of earlier visits was to determine the nest-box occupancy, while subsequent visits were conducted to ring chicks and assess the number of fledglings. The final number of fledglings was achieved (corrected retrospectively) by checking the nest boxes for dead hatchlings after the fledging period [34]. For each breeding season, (i) nest-box occupancy (1 indicates occupied if at least one egg was laid, 0 designates unoccupied), (ii) clutch size (number of eggs found in nest box) and (iii) fledging success (number of fledglings, chicks old enough for ringing, the clutch size) were recorded. Friedman's test, a nonparametric test allowing for comparisons of repeated measures set at 0.05 significance level, was used to determine possible differences in nest-box occupancy and breeding parameters in different years [35].

Habitat information

Our investigation focused on habitats in the close vicinity of nest boxes, which are used most intensively by breeding rollers as their foraging ground [21,26,36]. Hence, we established buffers with a 200-m radius around each nest box, in which we monitored habitat composition, landscape metrics, perching structures, biophysical parameters, grassland management and available prey. Information on the habitat composition and perching structures was obtained by photo interpretation of orthophoto images sourced from Google Earth Pro version 7.3.3.7786, adjusted by field observations. We calculated the area of landscape patches representing five main land-cover categories: (i) grassland, (ii) cropland, (iii) farmland, (iv) shrubs and (v) urban areas within each nest-box buffer. We estimated the share of linear features that rollers can use for perching and/or hunting as the length of perching structures (fences and electric power lines). Landscape metrics represented by the Shannon diversity index [37], habitat diversity (HDiv) and number of fragments, total number of patches within plot (NumP), were derived from data on habitat composition. The type and intensity of grassland management (categorized as no grazing, non-intensive grazing or intensive grazing) were assessed in the field through observation and recorded using interviews with local herdsmen. To acquire information for biophysical parameters, we derived variables from Landsat 8 satellite images. The averaged values of the Normalized Difference Vegetation Index (NDVI), the Automated Water Excitation Index (AWEI) and Bare Soil Index (BSI) in 20-m resolution within every 200-m nest-box buffer were calculated. All available Sentinel images for the May-July period for five consecutive study seasons (2015-2019) were collected and used to derive selected indices, which were subsequently grouped into biophysical parameters [38,39]. Acquired raw indices derived from time series of Landsat 8 satellite images were then exposed to further selection by choosing a data point closest to the study period and by setting an 80% threshold for pixel quality. NDVI was used as a measure of habitat productivity [40,41], while the BSI was included to distinguish bare soil and dry vegetation [42], and AWEI was adopted for identifying water surfaces [43].

Prey monitoring

Our investigation focused on habitats in the close vicinity of nest boxes, which are used most intensively by breeding rollers as foraging ground [19,25,36]. Hence, we established buffers with a 200-m radius around each nest box, within which we monitored the available prey, habitat composition and structure, grassland management and biophysical parameters. To sample available prey, three 20-m-long transects were randomly selected in each plot using QGIS software (1.8). Prey sampling using pitfall traps and a sweep net was conducted during the first week of July, coinciding with the chick-rearing period. On each transect, five pitfalls filled with preservative were installed 5 m apart and were retained for one week. Parallel to installing traps, sweep net samples were obtained from both sides of each transect. Only prey specimens larger than 1 cm were collected, as rollers are proven to favor them over smaller prey [44]. Samples were stored in 70% ethanol until required for further analyses. Due to cattle disturbance and weather issues, some pitfalls were not retrieved. Consequently, we later used the number of prey specimens per pitfall within one nest box (the total number of specimens found within the plot was divided by the number of found traps). The abundance of specimens from sweep netting was expressed as raw counts. Prey biomass was determined by drying specimens for 24 h at 60°C before weighing them on an analytical balance with ±0.001 g precision. The Shannon index (H') was calculated as a measure of prey diversity [37]. The abundance, mass and H' of the available prey were analyzed separately for pitfall and sweep net samples.

Data analysis

To examine the influence of the environment and landscape features on rollers' prey availability, nest-box occupancy and breeding parameters, we developed a set of linear regression models. All variables were standardized (centered and scaled) and correlations between predictor variables were analyzed using Spearman's correlation coefficient with a threshold set at 0.8 for excluding highly correlated variables [45]. Furthermore, a stepwise function with a "backward" direction was applied for each response variable to remove the least significant variables until the model with the best explanatory power was achieved. While the combination of variables regarding each response variable differed (as a result of previous elimination), model building was uniform for all: (i) response variable ~ single explanatory variable, (ii) response variable ~ interactive variables combination and (iii) response variable ~ interactive variable combinations + a single explanatory variable. Based on the AICc values, the "best" model settings were selected by the function model.avg, whereas models with $\Delta AIC \geq 7$ were considered to result in less explanatory power and were excluded from observations [8,46].

Prey mass and diversity as response variables were fitted by generalized linear mixed models (GLMMs) based on the Gaussian distribution family, separately for pitfall and sweep net samples, with the year as a random effect. We used pitfall sample mass and the Shannon index as response variables with a set of habitats and landscape predictors. The same approach was adopted for sweep net samples. For nest-box occupancy and breeding parameters, we fitted the GLMMs, whereby the year was treated as a random factor. We defined a binary response variable that obtained the value of 0 if the nest box was unoccupied during the research season and 1 otherwise. For breeding parameters, we fitted GLMMs based on the Poisson distribution with a log link function for clutch size, while fledging success was fitted by the Gaussian distribution family. All variables with marks and data sources available for statistical analyses are grouped and listed in Table 1.

All analyses were performed in R software version 3.5.3. [47]. Variables with the best explanatory power were selected by stepAIC function in the R package MASS [48]. Linear regression models were performed by lmer and glmer functions in R package lme4 [49]. We used multi-model inference with the information criterion, corrected for small sample size (AICc) and predictor relative importance to rank our subset models in the package MuMIn (model.avg function) [46,50].

RESULTS

Prey parameters

Available prey sampled using pitfall trapping and sweep netting mainly consisted of Coleoptera and Orthoptera specimens (66.36%), which is in accordance with the composition of prey remains found in the nest boxes (Supplementary Table S1). The grazing regime, biophysical parameters (NDVI and BSI) and interaction between them exerted significant influence on the studied prey parameters (Table 2), whereas the

Table 1. Summary of all variables available for analysis arranged by corresponding subsets.

All available variables	Mark	Data source
Habitat composition		
% of grassland coverage	% grassland	Google Earth orthophoto
% of cropland coverage	% cropland	Google Earth orthophoto
% of farm area coverage	% farmland	Google Earth orthophoto
% of urban area coverage	% urban	Google Earth orthophoto
% of shrub area	% shrub	Google Earth orthophoto
Landscape metrics		
Habitat diversity	HDiv	Derived variable
Number of fragments	NumP	Derived variable
Perching structures – linear elements		
Perching structures (m)	perches	Google Earth orthophoto
Biophysical parameters		
The normalized difference vegetation index	NDVI	Landsat 8 satellite images
Bare Soil Index	BSI	Landsat 8 satellite images
Automated Water Extraction Index	AWEI	Landsat 8 satellite images
Grazing management		
Grazing regime (0–2)	grazing	Field observation and interview
Breeding parameters		
Nest box occupancy (0/1)		Field observations
Clutch size – number of eggs		Field observations
Fledging success		Derived variable
Prey parameters		
Shannon diversity index for net samples	shan_net	Derived variable
Shannon diversity index for pit samples	shan_pit	Derived variable
Total mass of prey from net samples (g)	mass_net	Field observations
Total mass of prey from pit samples (g) *	mass_pit	Field observations
Total abundance of prey from net samples	tot_net	Field observations
Total abundance of prey from pit samples *	tot_pit	Field observations

*pitfall samples are shown as a number of specimens (mass of specimens) per one pitfall trap

negative impact of intensive grazing affected all prey parameters, except the mass of prey sampled by pitfalls. Habitat diversity has been shown to be important for prey diversity conducted by net, while habitat fragmentation exerted a statistically significant negative impact on pitfall sample diversity (Tables 2,3). The area under bare soil was positively correlated with the prey mass calculated from specimens collected using pitfall traps (Table 3). This outcome was attributed to the case of arthropods frequently falling into stored cups.

Nest-box occupancy

Over the five breeding seasons, 66 successful roller breeding attempts were detected in the observed nest boxes, whereby 55% to 80% of nest boxes were occupied per season (Supplementary Table S2). According to Friedman's test, there was no statistically significant difference in nest-box occupancy across the analyzed seasons (Friedman's test: $\chi^2=7.44$; P=0.1142). As roller breeding pairs change their nesting location between seasons, all nest boxes (with one exception) were inhabited at least once during the research period. Multi-model inference resulted in one significant model ($\Delta AIC<7$) with high explanatory power ($\Delta AIC=0$) for nest-box occupancy. Based on this result, habitat diversity in combination with interaction between the grazing regime and area under the grasslands exerted the strongest influence on nest-box selection. The grazing regime exhibited a significant positive effect, while the area under grassland and habitat diversity had a statistically significant negative effect (Tables 4,5).

Breeding parameters

In all of the studied nest boxes, the number of eggs produced per season varied between 46 and 71, while the average number of eggs per nest box was 4.2±0.79 (Supplementary Table S2). There was no statistically significant difference in clutch size between the seasons (Friedman's test: $\chi^2=4.12$; P=0.3896). Five models showed adequate explanatory power ($\Delta AIC<7$) for clutch size, and the model with the best explanatory power included prey mass (pitfall samples) and interaction between the grazing regime and the area under grasslands (Table 6). According to these findings, grazing management on grasslands was the most influential factor for the number of eggs in a clutch in the nest boxes, with a statistically significant positive effect (grazing and grassland*grazing), while areas under grassland had negative effects (Table 5).

Table 2. Results of GLMM analysis and model selection based on AICc showing combinations of biophysical parameters, landscape metrics and grassland management that influenced prey attributes (Shannon index and mass); the year was used as a random factor. Models with values of ΔAIC<7 were considered appropriate while those with values above were not observed. (HDiv – habitat diversity; NumP – number of fragments in the research plot).

	df	LL	AICc	ΔAIC	*w*
Shannon index – net samples					
HDiv	4	-173.50	355.15	0.00	0.57
grazing	4	-174.14	356.42	1.27	0.30
HDiv + grazing*BSI	7	-172.38	359.17	4.02	0.08
grazing*BSI	6	-173.78	359.86	4.71	0.05
Intercept	3	-190.53	387.15	32.00	0.00
BSI	4	-191.25	390.64	35.49	0.00
Shannon index – pitfall samples					
Nump + grazing*BSI	7	-239.21	492.82	0.00	0.54
Nump + grazing*NDVI	7	-239.64	493.70	0.88	0.35
grazing	4	-244.49	497.12	4.30	0.06
Intercept	3	-246.53	499.15	6.33	0.02
BSI	4	-246.08	500.30	7.48	0.01
grazing*BSI	6	-244.32	500.94	8.12	0.01
NDVI + grazing*BSI	7	-244.24	502.89	10.07	0.00
Nump	4	-247.83	503.81	10.99	0.00
NDVI	4	-248.10	504.34	11.52	0.00
grazing*NDVI	6	-246.34	504.99	12.17	0.00
BSI + grazing*NDVI	7	-245.34	505.09	12.27	0.00
Mass – net samples					
grazing	4	37.04	-65.93	0.00	0.70
NDVI + grazing*BSI	7	38.45	-62.50	3.43	0.13
grazing*BSI	6	36.93	-61.55	4.38	0.08
grazing*NDVI	6	36.73	-61.16	4.77	0.06
BSI + grazing*NDVI	7	36.94	-59.47	6.46	0.03
NDVI	4	25.64	-43.14	22.79	0.00
Intercept	3	22.51	-38.94	26.99	0.00
BSI	4	21.83	-35.51	30.42	0.00
Mass – pitfall samples					
BSI	4	564.67	-1121.20	0.00	1
grazing*BSI	6	559.51	-1106.72	14.47	0
AWEI	4	555.64	-1103.14	18.05	0
Intercept	3	554.07	-1102.06	19.14	0
HDiv + grazing*BSI	7	557.12	-1099.82	21.37	0
grazing	4	553.46	-1098.77	22.42	0
AWEI + grazing*BSI	7	556.54	-1098.68	22.51	0
NDVI + grazing*BSI	7	556.11	-1097.82	23.38	0
BSI + grazing*NDVI	7	554.17	-1093.93	27.26	0
NDVI	4	549.79	-1091.43	29.77	0
HDiv	4	549.02	-1089.89	31.30	0
grazing*NDVI	6	543.70	-1075.10	46.10	0
AWEI + grazing*NDVI	7	542.56	-1070.71	50.49	0
HDiv + grazing*NDVI	7	540.96	-1067.51	53.68	0

* df – degrees of freedom; LL – log likelihood; AICc – score; ΔAIC – delta AIC; *w* – weighted AIC score

High fledgling survival rates resulted in 78% fledging success in the least successful breeding season, while 92% was the highest registered success (Supplementary Table S2). However, the difference in reproductive success between the seasons was not statistically significant (Friedman's test: χ^2=7.56; P=0.1091). Seven models exhibited an adequate explanatory power (ΔAIC<7). The model that included only linear element length had the lowest ΔAIC value, followed by the null model (Table 7). Statistically significant effects of selected variables were not found, but linear element length, grazing regime and the area under cropland showed a positive effect, while the area under grassland and habitat diversity had a negative effect (Table 5).

DISCUSSION

The results yielded by this study show that prey availability, habitat characteristics and structures in close vicinity of nest boxes exert different influences on nest-box occupancy and breeding parameters of roller pairs. Grassland coverage around the nest boxes had a significant negative effect on nest-box occupancy and clutch size, while the effect on fledging success was not significant but it was still negative. This is a surprising result, considering that grasslands are recognized as key habitats for the survival of several farmland birds, especially insectivores, including the roller [51], as they provide a rich source of diverse and numerous insect fauna [52]. Our study area was relatively uniform in terms of habitat diversity (grasslands were the dominant land-cover type around nest boxes); moreover, the breeding season coincided with a period of dry weather resulting in sparse vegetation. Thus, the presence of other land-use types within the study area indicated an increase in habitat heterogeneity. A positive effect of habitat heterogeneity within some parts of the breeding range has been reported by other authors [21,53], who have suggested that patch margins could represent particularly significant foraging areas. A positive effect of arable land covered with cereal crops on nest-box occupancy and roller breeding success has also been shown in southern Europe [8,21,54]. It is possible that they benefit from the abundance of insects found on these crops (e.g. genera *Anisoplia, Cetonia, Mecinus*, etc.), especially at the beginning of the breeding season, considering that rollers are prone to shift foraging preferences based on prey availability [53,55]. As the remains of the insect genera were frequently found in the nest boxes, rollers either forage on arable land or prey on insects attracted by a specific crop in midflight. Furthermore, arable land after harvest or land covered by underdeveloped maize or sunflowers represent a suitable foraging ground for dwelling invertebrates such as *Pentodon* sp, also detected in roller diet. Even though the presence of other land-use types (including non-irrigated crops) in close vicinity of nests had a positive effect on nest-box occupancy, the influence of grasslands on a wider spatial scale (entire breeding territories and the landscape level) could be different [16,21,26].

According to the models developed as part of this investigation, nest-box occupancy and clutch size are positively affected by the grazing regime, while fledging success is positively affected both by the grazing regime and the length of linear elements, which can be attributed to improved foraging conditions [26]. Intensive grazing has negative effects on both prey diversity and prey biomass. However, intensively grazed grassland patches with short vegetation appear to be suitable for hunting large insects that are more exposed than in tall grass that could be found on grasslands with a low intensity grazing regime. Thus, it seems that the ability to successfully spot and catch prey in ground vegetation could be more important than the number of potential food resources. As the roller hunts using perches [14], a greater availability of power lines, fences and other linear structures in the vicinity of nest boxes significantly increases the area that can be scouted effectively, while decreasing

Table 3. Model coefficients of selected variables used in GLMMs to distinguish which one significantly influenced the response variables and prey parameters (Shannon index and mass).

	Estimate	**SE**	**Ad SE**	**z**	**P(>|z|)**	
Shannon index – net samples						
(Intercept)	0.7848	0.0344	0.0345	22.7380	0.0000	***
BSI	-0.0125	0.0340	0.0340	0.3680	0.7130	
HDiv	0.1041	0.0823	0.0823	1.2640	0.2060	
grazing	-0.0694	0.0834	0.0834	0.8320	0.4060	
grazing*BSI	0.0034	0.0158	0.0159	0.2170	0.8280	
Shannon index – pitfall samples						
(Intercept)	1.3265	0.0509	0.0511	25.9580	0.0000	***
BSI	0.0397	0.0448	0.0449	0.8850	0.3763	
NDVI	0.0213	0.0400	0.0401	0.5310	0.5957	
NumP	-0.1487	0.0664	0.0665	2.2350	0.0254	*
grazing	-0.1773	0.0595	0.0596	2.9750	0.0029	**
grazing*BSI	0.0245	0.0422	0.0423	0.5800	0.5622	
grazing*NDVI	0.0237	0.0378	0.0379	0.6260	0.5313	
Mass – net samples						
(Intercept)	0.2566	0.0286	0.0287	8.9360	0.0000	***
BSI	-0.0104	0.0202	0.0202	0.5160	0.6060	
NDVI	0.0141	0.0284	0.0285	0.4970	0.6190	
grazing	-0.0774	0.0125	0.0125	6.1890	0.0000	***
grazing*BSI	0.0052	0.0127	0.0128	0.4050	0.6850	
grazing*NDVI	-0.0005	0.0040	0.0041	0.1150	0.9080	
Mass – pitfall samples						
(Intercept)	0.0399	0.0083	0.0083	4.8040	0.0000	***
BSI	0.0116	0.0020	0.0020	5.7530	0.0000	***
NDVI	0.0000	0.0000	0.0000	0.0030	0.9980	
AWEI	0.0000	0.0001	0.0001	0.0110	0.9910	
HDiv	0.0000	0.0000	0.0000	0.0040	0.9970	
grazing	0.0000	0.0002	0.0002	0.0260	0.9790	
grazing*BSI	0.0000	0.0002	0.0002	0.0250	0.9800	
grazing*NDVI	0.0000	0.0000	0.0000	0.0000	1.0000	

* P<0.05, ** P<0.001, *** P<0.000, SE – standard error, Ad SE – adjusted SE

Table 4. Results of GLMM analysis and model selection based on AICc showing which variables and their combinations influenced nest box occupancy (the year was used as a random factor). Models with values of ΔAIC<7 were considered appropriate while those with values above were not observed. The model with the lowest ΔAIC value had the highest impact on nest box occupancy. (HDiv – habitat diversity; NumP – Number of fragments within research plot; mass_pit – pitfall samples).

Nest box occupancy	**df**	**logLik**	**AICc**	**ΔAIC**	**w**
HDiv + grazing*grassland	6	-46.59	106.12	0.00	0.98
mass_pit + grazing*grassland	6	-50.63	114.19	8.07	0.02
NumP + grazing*grassland	6	-52.53	118.00	11.88	0.00
mass_p	3	-56.42	119.10	12.98	0.00
%cropland	3	-57.37	121.00	14.88	0.00
(Intercept)	2	-59.56	123.25	17.13	0.00
%grassland	3	-58.54	123.33	17.21	0.00
mass_pit + grazing*NDVI	6	-55.29	123.53	17.40	0.00
NDVI	3	-58.92	124.11	17.98	0.00
%urban	3	-59.20	124.67	18.54	0.00

Table 4. continued

Nest box occupancy	df	logLik	AICc	ΔAIC	w
grazing	3	-59.30	124.86	18.74	0.00
NumP	3	-59.43	125.12	19.00	0.00
HDiv	3	-59.53	125.31	19.19	0.00
grazing*NDVI	5	-58.71	128.09	21.96	0.00
NumP + grazing*NDVI	6	-58.06	129.07	22.95	0.00
HDiv + grazing*NDVI	6	-58.14	129.22	23.09	0.00

* df – degrees of freedom; LL – log likelihood; AICc – score; ΔAIC – delta AIC; *w* – weighted AIC score

Table 5. Model coefficients of selected variables used in GLMMs to distinguish which one of them significantly influenced the response variables: a) nest box occupancy, b) clutch size and fledging success of roller. (HDiv – habitat diversity; NumP – number of fragments within research plot; mass_pit – pitfall samples; tot_pit – quantity of pitfall samples).

	Estimate	SE	Ad SE	z value	P(>|z|)	
a) Nest box occupancy						
(Intercept)	-0.9102	1.1470	1.1630	0.7830	0.4337	
NDVI	0.0001	0.0100	0.0101	0.0080	0.9938	
% cropland	0.0003	0.0150	0.0151	0.0210	0.9832	
% grassland	-7.2460	2.2410	2.2670	3.1950	0.0014	**
% urban area	0.0000	0.0033	0.0033	0.0060	0.9953	
HDiv	-6.1570	2.4200	2.4480	2.5150	0.0119	*
NumP	-0.0006	0.0228	0.0230	0.0260	0.9792	
grazing	1.9170	0.8591	0.8706	2.2020	0.0277	*
Mass_pit	-0.0098	0.0798	0.0800	0.1230	0.9024	
grazing*NDVI	0.0000	0.0052	0.0053	0.0030	0.9974	
grazing*grassland	-0.9839	1.1570	1.1710	0.8400	0.4009	
b) Clutch size						
(Intercept)	0.0843	0.3434	0.3472	0.2430	0.8082	
BSI	-0.0023	0.0230	0.0232	0.1000	0.9207	
% cropland	0.0002	0.0057	0.0057	0.0360	0.9710	
% grassland	-0.5932	0.1797	0.1816	3.2670	0.0011	**
% urban area	0.0000	0.0011	0.0011	0.0100	0.9922	
% shrub	-0.0005	0.0102	0.0102	0.0480	0.9616	
HDiv	-0.0178	0.0783	0.0788	0.2260	0.8212	
grazing	0.5462	0.1916	0.1936	2.8210	0.0048	**
mass_pit	-0.1015	0.0992	0.0997	1.0180	0.3087	
tot_pit	0.0040	0.0229	0.0231	0.1750	0.8614	
grazing*BSI	-0.0002	0.0084	0.0084	0.0270	0.9782	
grazing*grassland	0.2218	0.0980	0.0992	2.2370	0.0253	*
c) Fledging success						
(Intercept)	0.5894	0.0900	0.0907	6.4970	0.0000	***
% cropland	0.0005	0.0068	0.0069	0.0710	0.9430	
% grassland	-0.0022	0.0267	0.0267	0.0820	0.9350	
% urban area	0.0004	0.0063	0.0063	0.0630	0.9490	
% shrub	-0.0045	0.0220	0.0220	0.2060	0.8370	
HDiv	-0.0006	0.0114	0.0114	0.0520	0.9590	
perches	0.0489	0.0672	0.0674	0.7250	0.4680	
grazing	0.0082	0.0410	0.0411	0.2000	0.8410	
mass_pit	-0.0258	0.0532	0.0533	0.4840	0.6280	
grazing*grassland	0.0006	0.0095	0.0095	0.0630	0.9500	

* P<0.05, ** P<0.001, *** P<0.000, SE – standard error, Ad SE – adjusted SE

the distance to the nearest perch reduces the individual's energy consumption [26,56]. A significant portion of linear structures in our study area was comprised of power lines that proved to be especially convenient as perches. As they are located at a considerable height above ground, power lines enable rollers to easily scout the terrain across large continuous areas. Available evidence shows that rollers are often quicker to inhabit nest boxes set on electric pylons compared to those set on trees, probably because they are easier to find [20,21]. Our results indicate that rollers might benefit from a greater number of perches, especially on intensively grazed grassland patches, which increases significantly with the length of power lines in close vicinity of the nest box. This might also explain the preference rollers have for nest boxes set on electric pylons, even though electrocution presents a significant threat for species that use such perches to scan the area for prey [57]. During this study, no cases of roller electrocution were recorded, probably because this species perches on power lines, where the probability of electrocution is smaller. Nonetheless, the presence of electric pylons should be considered when selecting new nest-box sites.

The roller conservation program in Serbia focuses mostly on the remaining grassland patches in Vojvodina. The main reason for the adoption of this strategy is the assumption that, compared to other habitat types, grasslands are more suitable to roller dietary requirements due to the lower risk of pesticide poisoning. Also, there is a greater chance that occupied nest boxes will be included in protected areas or the ecological network if they are in natural or semi-natural habitats, most of which are already incorporated into the ecological network in Vojvodina [33]. As the program has yielded positive outcomes, the present practice that focuses on grasslands should be continued, but agricultural land should also be considered in nest-box programs because it can act as a habitat for at least a part of the roller population. In addition, as grasslands on the Pannonian plain are severely fragmented [58], nest boxes set in arable land can act as steppingstone corridors to uninhabited yet potentially protected grasslands. Finally, the installation of new nest boxes in grasslands is currently limited by the lack of suitable sites such as solitary trees, electric pylons and other tall structures, which in turn limits population growth in Vojvodina. Landscape improvement through tree planting and setting up specific nest-box-carrying structures is, therefore, a viable long-term conservation strategy that can be supported by setting up nest boxes on unused structures on agricultural land, as this would benefit population expansion and recolonization of former habitats.

Habitat composition and structure are important in nesting site selection and should be considered when allocating conservation measures in the future. The individual and mutual effects of grassland management type (grazing and mowing), biophysical parameters and prey availability on rollers are complex and require further detailed investigations involving larger samples, as well as consideration of specific environmental conditions during different breeding seasons. On the other hand, to successfully plan conservation measures, the effect of studied parameters should be tested on other spatial scales, such as entire foraging territories or areas populated by a larger number of breeding pairs. Given that factors affecting chick survival were not examined in the present study, it would be beneficial to investigate the role of different types of parasites, including the mites and flies that are often found in nest boxes. Considering their possible cross-effects with the amount and type of available prey, the potential for parasitic infection should be the subject of future recolonization effort plans [59].

The study area of this investigation represents part of the historic range of rollers where recolonization was highly successful owing to the use of nest boxes in the context of the larger program of roller population recovery in Serbia [27] and the wider Pannonian plain

Table 6. Results of GLMM analysis and model selection based on AICc showing which variables and their combinations influenced clutch size (the year was used as a random factor). Models with values of ΔAIC<7 were considered appropriate while those with values above were not observed. The model with the lowest ΔAIC value had the highest impact on nest box occupancy. (HDiv – habitat diversity; NumP – number of fragments in the research plot; mass_pit – pitfall samples; tot_pit – quantity of pitfall samples).

Clutch size	**df**	**logLik**	**AICc**	**ΔAIC**	**w**
mass_pit + grazing*grassland	6	-205.75	424.45	0.00	0.61
grazing*grassland	5	-208.29	427.26	2.81	0.15
HDiv + grazing*grassland	6	-207.68	428.31	3.86	0.09
tot_pit + grazing*grassland	6	-207.92	428.78	4.33	0.07
BSI + grazing*grassland	6	-208.05	429.04	4.59	0.06
mass_pit	3	-213.17	432.60	8.15	0.01
% shrub	3	-214.51	435.28	10.83	0.00
% grassland + grazing*BSI	6	-211.64	436.21	11.76	0.00
% cropland	3	-215.07	436.41	11.96	0.00
mass_pit + grazing*BSI	6	-212.39	437.73	13.28	0.00
% grassland	3	-216.36	438.99	14.54	0.00
(Intercept)	2	-217.94	440.01	15.56	0.00
% urban area	3	-217.29	440.85	16.40	0.00
BSI	3	-217.49	441.25	16.80	0.00
grazing	3	-217.51	441.29	16.84	0.00
HDiv	3	-217.88	442.01	17.56	0.00
tot_pit	3	-217.91	442.08	17.63	0.00
grazing*BSI	5	-216.76	444.19	19.74	0.00
HDiv + grazing*BSI	6	-215.79	444.53	20.08	0.00
tot_pit + grazing*BSI	6	-216.68	446.30	21.85	0.00

* df – degrees of freedom; LL – log likelihood; AICc – score; ΔAIC – delta AIC; *w* – weighted AIC score

Table 7. Results of GLMM analysis and model selection based on AICc showing which variables and its combinations influenced fledging success (the year was used as a random factor). Models with values of ΔAIC<7 were considered appropriate while those with values above were not observed. The model with the lowest ΔAIC value had the highest impact on nest box occupancy. (HDiv – habitat diversity; NumP – number of fragments in the research plot; mass_pit – pitfall samples).

Fledging success	**df**	**logLik**	**AICc**	**ΔAIC**	**w**
perches	3	-61.35	131.13	0.00	0.39
(Intercept)	2	-62.94	132.14	1.01	0.24
mass_pit	3	-61.93	132.29	1.16	0.22
% shrub	3	-63.35	135.14	4.01	0.05
grazing	3	-63.37	135.18	4.04	0.05
% cropland	3	-64.75	137.95	6.82	0.01
% urban area	3	-64.83	138.10	6.97	0.01
HDiv	3	-64.94	138.32	7.18	0.01
% grassland	3	-65.01	138.46	7.33	0.01
grazing*grassland	5	-63.59	140.13	9.00	0.00
HDiv + grazing*grassland	6	-63.51	142.29	11.16	0.00
mass_pit + grazing*grassland	6	-63.84	142.95	11.82	0.00

* df – degrees of freedom; LL – log likelihood; AICc – score; ΔAIC – delta AIC; *w* – weighted AIC score

[20,30]. Our results confirm that setting up nest boxes is a successful conservation measure that enables rollers to recolonize their historic habitats. Nevertheless, habitat characteristics in the close vicinity of nest boxes should be considered when planning future conservation activities.

Funding: This work was financially supported by the Ministry of Education, Science and Technological Development of the Republic of Serbia, Grant No. 173002, 451-03-9/2021-14/200358, 451-03-9/2021-14/200125, and the ROLLER LIFE+ project (LIFE13 NAT/HU/000081).

Acknowledgments: The authors are sincerely grateful to Radulović I, Batinić D, Palalić S, Gorunović M, Arsenović N, Tošić V, Ilić M, Jovanović S, Kurtek L, Damnjanović D, Rajkov S, Mora A, Šimončik S, Mojzeš M, Matić I, Šumanović S, Rajković D, Rakić R, Veljković N, who helped in the field investigations. We are very thankful for the expert consultation provided by HabiProt association members. The authors are grateful to the Bird Protection and Study Society of Serbia who kindly provided some logistic support during the field campaigns.

Author contributions: All authors participated in collecting data in the research area. LM and DR prepared the database. LM and TN performed the statistical analysis and prepared the results. The interpretation was done by all authors. LM and DR wrote the manuscript. MA and TN reviewed several drafts of the manuscript.

Conflict of interest disclosure: The authors confirm no actual or potential conflicts of interest, including financial, personal or other relationships with individuals or organizations.

Data availability: Data underlying the reported findings have been provided as part of the submitted article and are available at: https://www.serbiosoc.org.rs/NewUploads/Uploads/Milinski%20et%20al_7628_Data%20Report.pdf

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