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Article

Ecology and reproductive biology of the European Roller *Coracias garrulus* L., 1758 in Stavropol Region

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Abstract. The results of study of the ecology and biology of the European Roller in the Stavropol Region during the period of agricultural transformation of the environment in 1984–2019 are presented. Favorable conditions for this bird species are found in steppe areas used for grazing animals and on non-irrigated arable land. Rollers nest mainly in holes in natural cliffs (46.9% of the total number of nests) and cliffs of anthropogenic origin (37.4%), as well as in tree hollows (15.7%). The nesting period of the population (the time of pairing, nest building, egg laying, development, and growth of nestlings, and feeding of nestlings) has characteristics that are associated with traditional agriculture. At the same time, the largest clutch size known for European populations, of seven eggs was found, and the eggs were somewhat smaller than in most of the range. The average clutch size (4.43 ± 0.17 eggs) and brood size (3.43 ± 0.13 chicks) correspond to the range optimum. The breeding success is 77.5%. A cautious assumption is made that the increase in clutch size and decrease in egg size may be an adaptive response of the species to changes in habitat in the last 30–50 years.

Key words: adaptation, behavior, problems of biodiversity conservation, rare and endangered species, rate of environmental change

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Научная статья

Особенности экологии и биологии размножения сизоворонки *Coracias garrulus* L., 1758 в Ставропольском крае

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Аннотация. В статье представлены результаты изучения экологии и биологии сизоворонки Ставропольского края в период сельскохозяйственной трансформации среды 1984–2019 гг. Благоприятные условия для жизни птицы находят в степных участках для выпаса животных и на неорошаемых пахотных землях. Сизоворонки селятся преимущественно в норах естественных обрывов (46.9% от общего числа гнезд) и обрывов антропогенного происхождения (37.4%), а также в дуплах (15.7%). Гнездовая жизнь популяции (время образования пар, постройки гнезд, откладки яиц, развития и роста птенцов и питание птенцов) имеет видовые характеристики периода традиционного сельского хозяйства. Одновременно обнаружен самый большой для европейских популяций размер кладки из 7 яиц, а сами яйца несколько мельче, чем на большей части ареала. Средние значения размера кладки (4.43 ± 0.17 яиц) и выводка (3.43 ± 0.13 птенцов) соответствуют оптимуму ареала. Успешность размножения составляет 77.5%. Сделано осторожное предположение о том, что увеличение размера кладки и уменьшение размера яиц может быть адаптивной реакцией вида на изменения среды обитания в последние 30–50 лет.

Ключевые слова: адаптация, поведение, проблемы сохранения биоразнообразия, редкие и угрожаемые виды, скорость изменения среды

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Introduction

To address problems of biodiversity conservation, it is important to manage ecosystems so that the rate of species adaptation corresponds to the rate of environmental change (Candolin and Wong, 2012; Kolomiytsev, 1990; Kolomiytsev and Poddubnaya, 2018). The European Roller *Coracias garrulus* L., 1758 is one of the wide-ranging species included in the list of threatened species in the Russian Federation[1]. It is a Palearctic species that has adapted to agricultural landscapes over millennia of their development and expansion (Catry et al., 2011 and others). A noticeable reduction in roller populations has been recorded in different regions of the European part of Russia. In Central Ciscaucasia (Stavropol Region), in the early 1980s, the number of rollers was estimated at 30000 individuals (Khokhlov, 1984). By the 2010s in the entire European part of Russia, the population of the species reached only 12000–30000 individuals (Otsenka chislennosti..., 2017), and in the 2020s. According to expert estimates, the population of the roller was 10000–22000 individuals (Atlas gnezdyashchikhsya..., 2020; Krasnaya kniga..., 2021). The reason for the continued decline in the population of this species in Russia against a background of its stabilization in Western Europe (Bird Life International, 2020) is not entirely clear. The purpose of this study was to recognize the features of the ecology and reproductive biology of the roller as the key indicators of the adaptability of its populations to different environments.

Materials and methods

The data were collected in the Stavropol Region, in the central part of Ciscaucasia and on the northern slope of the Greater Caucasus (Fig. 1). The area of the region[2] is 66160 km^2 and is comparable to the entire area of many countries. The region is located in the steppe zone (about 82% of the area) and captures a strip of semi-desert in the east (18%), in the south – forest-steppes of foothills and foothill subalpine meadows, as well as mosaic–floodplain forests of the Kuban, Kura and Kuma rivers. Surface waters and swamps occupy 2.4% of the territory (comprising 225 rivers, 38 lakes, 1758 reservoirs, ponds and reservoirs, a developed network of reclamation canals), agricultural land is 87.5%, of which arable land is about 61.1%, pasture is 24%, settlements – 7%[1]. Part of the territory is covered with forests and forest belts (1.7% of the total area), which have been established since the end of the 19th century (mostly after 1948), especially since the late 1960s to fight dust storms. According to the isocline of the amount of precipitation, the territory under study can be conditionally divided into two zones: one with annual precipitation exceeding 400 mm (crop production prevails here) and the other with annual precipitation less than 400 mm per year (animal husbandry predominates).

In the last three decades, the habitat of the European roller in the region has changed markedly: the number of sheep and cattle has decreased by almost a third, and due to the ploughing of pastures in the livestock zone, there has been an increase in the area of agricultural crops, primarily cereals (Malovichko, 1999). It has been shown that the heterogeneity of the territory (the alternation of plots of open farmland with small forest stands or windbreaks of trees and shrubs) also decreased. Such changes in agriculture lead to a deterioration in the food base for the rollers and the destruction of places suitable for breeding and foraging.

Data on the biology and ecology of the roller were collected in 1984–1998 and 2000–2019 using generally accepted methods (Bibby et al., 1998; Malovichko, 1999; Novikov, 1953) throughout the Stavropol Region. More than 250 plots with habitats suitable for rollers, and 568 cliffs of various origins in quarries, banks of water bodies, ravines, gullies, farms, sheep stations, groves, forest belts, and ravine forests were examined. Nesting was studied in 2004 and 2006–2019. The following periodization of the life cycle was adopted: spring migration – April, autumn migration – August and September, nesting period – from late April to late July.

One hundred and thirty nests were described. The nests were examined from 10 a.m. to 12 a.m. (UTC +3). The laid eggs were numbered with a graphite pencil; the inscriptions were updated at subsequent inspections. Breeding success was assessed by the ratio of hatched chicks to laid eggs (46 nests, 204 eggs). Oological analysis was performed on 62 specimens. To assess the characteristics of growth and development, chicks (n = 13) were marked with colored rubber bands 0.8 mm thick. Chicks were weighed on electronic scales in the morning hours – from 7 a.m. to 9 a.m. every day or every other day (depending on weather conditions, the birds were not disturbed in unfavorable weather). The daily activity during the period of feeding three chicks in one nest was studied in the Arzgirsky District in the north of the Stavropol Region, observations were made from shelters from 5 a.m. to 10 p.m. on July 8–14, 2018.

Habitat preferences were determined in buffer zones with a radius of 1000 m around nesting sites, as well as the size of foraging areas (Arslan and Akveran, 2019) in four foraging habitats: sheep station, game reserve, steppe, and coastal shallows.

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[1] Order of the Ministry of Natural Resources of Russia dated March 24, 2020 No. 162 “On approval of the List of wildlife objects listed in the Red Book of the Russian Federation”.

[2] Report on the state of the environment and nature management in the Stavropol Territory in 2021. Ministry of Natural Resources and Environmental Protection of the Stavropol.

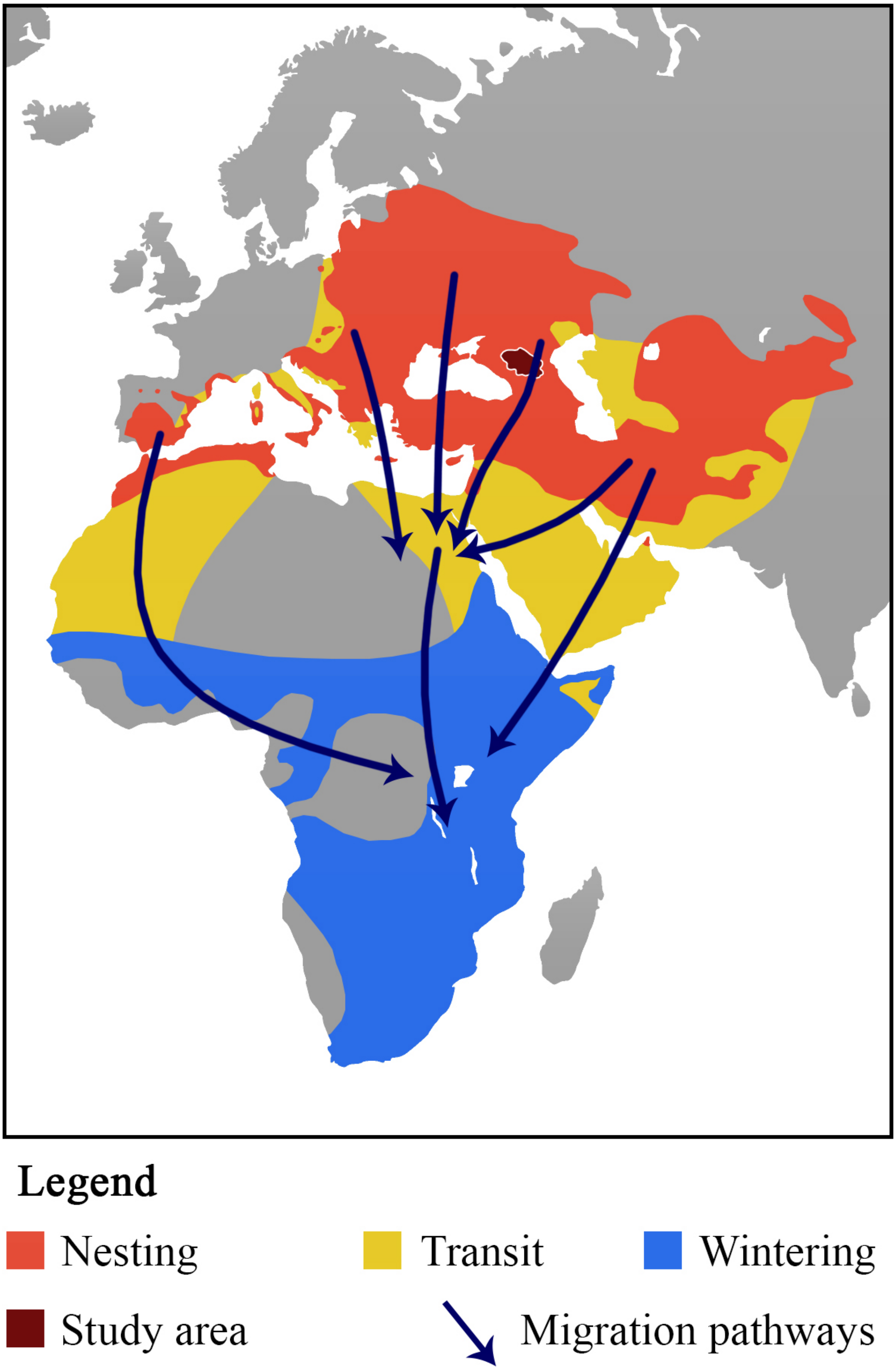

Fig. 1. Research area (Stavropol Region) within the range of the European roller (according to Elphick, 2011 and Bird Life International, 2020)

A large flock of sheep and a herd of cows, haystacks, outbuildings, one elm tree *Ulmus* sp. and water outlet from an artesian well providing a watering hole for domestic and wild animals were in the sheep station with an area of 5 hectares. The sheep station had dung stored in small piles, inhabited by numerous beetles. The entire territory had large populations of locusts *Locusta migratoria* L., 1758, which fed about 1.5 thousand rose starlings *Sturnus roseus* (L., 1758) nesting in the sheep station. The game reserve with an area of about 8 hectares, built in 2012, has two-story buildings, wagons and outbuildings for cows and sheep, an animal station rich in various invertebrates, mainly insects. Fruit trees, elms and acacias *Acacia* sp. about 1.5–2.0 m high were planted around the game reserve. The steppe is represented by areas of fescue-feather grass, sagebrush-fescue, sagebrush and, in depressions, meadow-salt marsh vegetation (with bushes of saltwort and tree-like *Salsola soda* L., *S. dendroides* Pall. and prickly thorn grass *Phlomis pungens* Willd.); the steppe occupies most of the territory where the birds foraged. The coastal swampy shoal of the Chogray reservoir, about 250–300 m wide, is bounded by a cliff with a roller nest. At the water's edge there are reed beds, and in some places single saltworts. Of invertebrates locusts and dragonflies are dominant here.

To study nutrition, we examined the contents of the stomachs of rollers hit by cars on the roads (n = 7) and observed through binoculars the prey brought to the chicks and the incubating female. Information on the enemies of hole-nesting birds was obtained as a result of direct observations of predator attacks on birds, destruction of clutches and chicks (n = 8) and examination of the contents of pellets (n = 24) and feeding tables (n = 16) of the eagle owl *Bubo bubo* (L., 1758).

The roller is not considered a dimorphic species, but females are not as brightly colored as males, and an experienced observer can easily determine the sex (Malovichko et al., 2021).

Statistical analysis was performed using StatSoft Statistica 12.0 and Microsoft Excel 2016 software.

Results

Nesting and nests

The roller has a typical sclerophilous nest hole and settles mainly in holes in clay and sandy cliffs, as well as in the walls of silage pits and small human-built excavations. The latter are usually used by the birds for 1–2 years, then become overgrown with grass. The founders of multispecies colonies of hole-nesting birds are sand martins *Riparia riparia* (L., 1758) and European bee-eaters *Merops apiaster* (L., 1758). These dig new burrows every year, and their disused burrows are occupied by rollers, hoopoes *Upupa epops* L., 1758, common kestrels *Falco tinnunculus* L., 1758, little owls *Athene noctua* (Scopoli, 1769), common starlings *Sturnus vulgaris* L., 1758, field and house sparrows *Passer montanus* (L., 1758), and *P. domesticus* (L., 1758), etc. Rollers settle in the colony after the appearance of various perching places next to it. Usually, nests of different bird species are located at a distance of 2–3 m apart. Kestrels and starlings arriving for nesting earlier than rollers, and occupying available holes, can negatively affect the population of the latter.

Out of 568 surveyed cliffs, 196 cliffs of natural origin and 164 cliffs of anthropogenic origin were inhabited by different species of hole-nesting birds. In natural cliffs (high banks of rivers and lakes, walls of ravines), 78 colonies of rollers (46.9% of the total number of nests of this species) were noted; in cliffs of anthropogenic origin (quarries, silage pits, temporary excavations) – 67 settlements (37.4%). In the last 15 years, as a result of demand for building materials, many sand and clay pits have appeared, resulting in slightly larger colonies of hole-nesting birds in the region, but their numbers are dynamic and change with habitat change. Thus, out of 83 new quarries surveyed in 2015–2019, bird colonies were noted in 27 (32.5%), and roller nest holes were found in only 9 (10.8%), which had trees and shrubs nearby.

The average height of populated cliffs is 6.4 ± 0.4 m (n = 44). In this case, the distance from the upper edge of the cliff to the nest hole varies from 0.4 to 3.0 m (1.8 ± 0.2 m on average), and the distance from the bottom of the cliff to the nest hole varies from 1.6 to 6.0 m (4.6 ± 0.3 m on average). An increase in the height of the cliffs is accompanied by an observed increase in the distance from the bases and from the edges of the cliffs to the holes (Fig. 2). The depth of the holes studied was small, averaging 0.7 m (n = 4), varying from 0.4 to 1 m. Some of the nests were located in old (last year's) haystacks and metal pipes (19.6% in the period 1984–1998).

Birds occupy the same nest for several years (from 2 to 7, on average 3.5 years), however, after the death of a clutch or brood, the rollers stop using the shelter for a long time (for 3–7 years (maximum observation period), on average 5.3 years; possibly longer). Observations of 11 nests in which the clutch or brood died showed that only one nest (9%) was repopulated three years after unsuccessful breeding.

In the last 10 years, due to the appearance of old trees, rollers began to nest in hollows made mainly by the green woodpecker *Picus viridis* L., 1758. In the presence of hollow trees, birds willingly occupy them (26 hollows or 15.7% of the total number of roller nests). For example, in 2007–2018 we found rollers nesting in groves of *Robinia pseudoacacia* L. (n = 19)

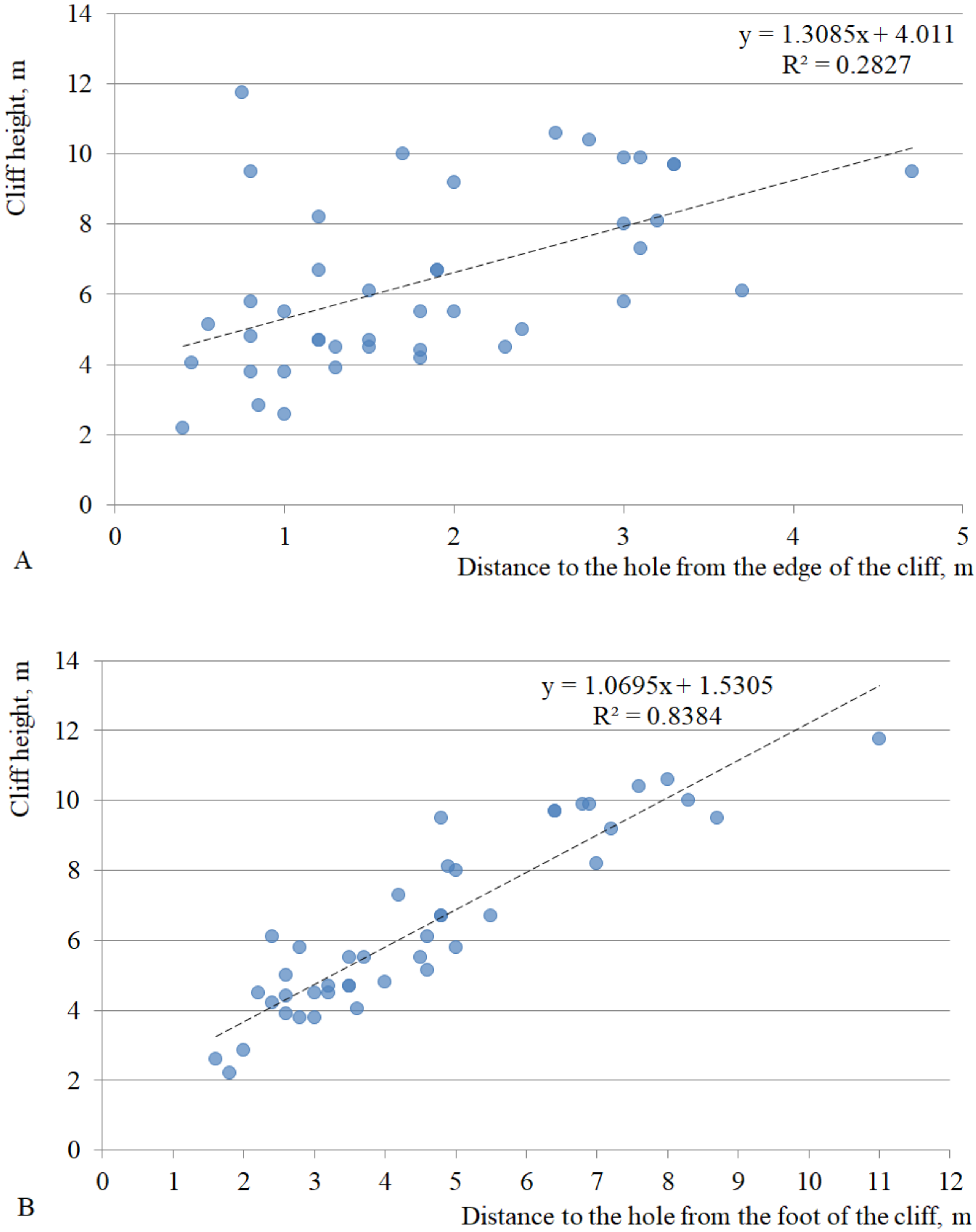

Fig. 2. Dependence of the location of the roller nest holes (n = 100) on the height of the cliff: **A** – taking into account the distance from the edge of the cliff to the hole; **B** – taking into account the distance from the base of the cliff to the nest hole.

and elms (n = 7): in the Irgaklinsky reserve (n = 6), near lake Zunkar (n = 3), in the floodplain forest along the Kuma River near the villages of Urozhaynoye (n = 7) and Velichayevsky (n = 3), villages of Novokumskoe (n = 3) and Terkum (n = 4).

Reproduction

Birds arrive in the region in the middle or at the end of April and almost immediately occupy the nesting territory. Already during the courtship period, they use the nesting territory with a radius of about 50 m, which is guarded mainly by the male. Birds indicate their territory to other males by air tumbling. This behavior occurs during courtship and pair formation, sometimes in the later stages of reproduction. These flights are followed by ritual feeding. Feeding of the female by the male begins a few days before egg laying and continues until it is completed (Malovichko et al., 2021). Mating begins 3–5 days before the start of egg laying and occurs before the completion of laying on a perch next to the nest. During this period, the birds show pair bonding and mutual care (Malovichko et al., 2021).

Most pairs breed in mid-May – mid-July. The egg-laying period usually lasts from May 20–25 to June 15–20. There may be later periods associated with repeated clutches and individuals that arrived later than the main mass of birds. Incubation begins mainly from the last 10 days of May to the end of June.

Incubation continues for 17–19 days. At night, the female incubates the clutch; during the day, partners often change. At the beginning of incubation, the female flies out of the hole to feed, at this time the male feeds the female very rarely, on average once a day. After laying is completed, intense incubation begins, and the male feeds the female up to 6–8 times a day near the nest. After feeding, the female returns to the nest or is replaced by the male. During the incubation period, the male can incubate the clutch from 22 to 52% of the daytime. He replaces the female at different times of the day for 15–35 minutes, the female leaves for half an hour in the early morning (from 7 to 8 a.m.), in the afternoon (from 3 to 4 p.m.) and late in the evening (from 8 to 9 p.m.). During the incubation period, the male actively protects the nesting territory and drives away not only other rollers, but also other bird species: rooks *Corvus frugilegus* L., 1758, marsh harriers *Circus aeruginosus* (L., 1758), cuckoos *Cuculus* sp., hoopoes, little owls, hooded crows *Corvus cornix* L., 1758 and turtle doves *Streptopelia turtur* (L., 1758). The incubation regime can be significantly violated. Thus, in one pair, the female was normally in the nest 54% of the daytime, and the following year, when a

Fig. 3. Roller chicks (left to right: two 22–23 days old and a 25–26 day old) in a nest hole.

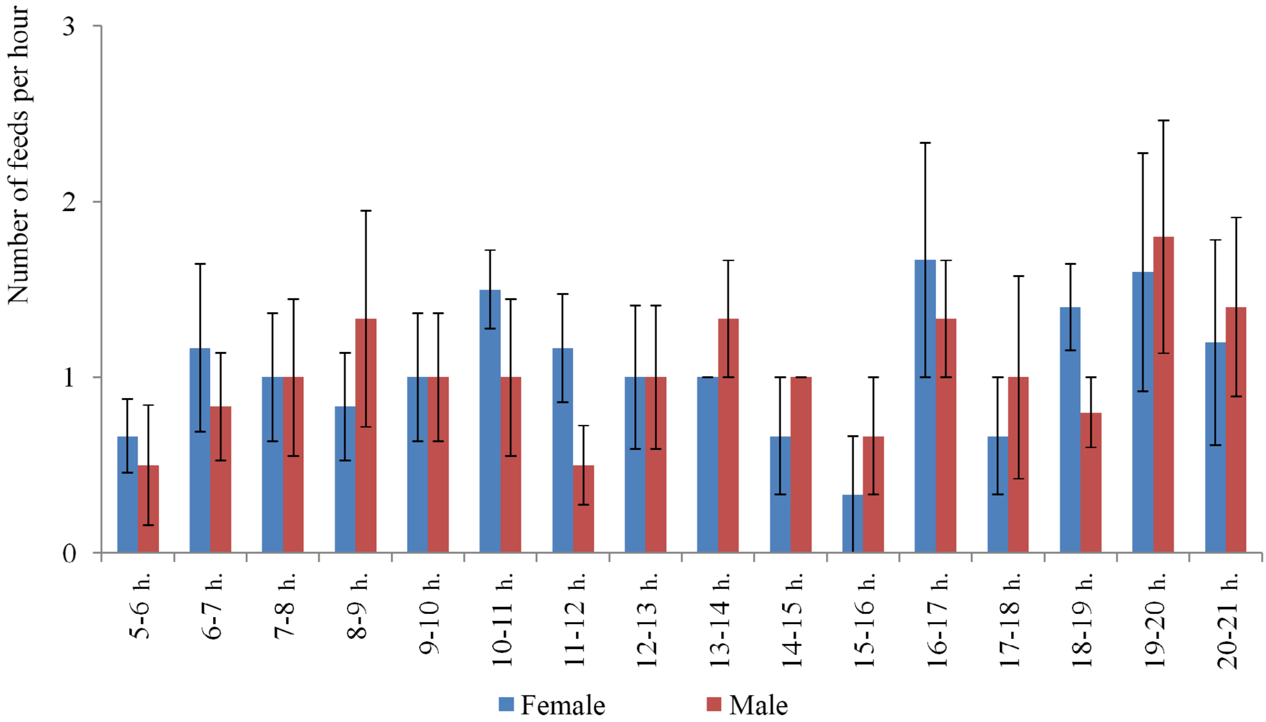

Fig. 4. Feeding intensity of the roller chicks on average for 1 hour in the period of July 8–11, 13, 14, 2018 (n = 6 days).

bulldozer was working near the nest, the male was in the nest 72% of the daytime. The female began to fly up to the hole during the operation of the bulldozer only two weeks after the beginning of this disturbance.

The clutch contains from 3 to 7 (4.43 ± 0.17) eggs (n = 204). The eggs are almost regular, round or ellipsoid in shape, with a smooth, dense and shiny white shell. Egg sizes average 32.97 ± 0.19 mm (31.50–34.90 mm) × 26.81 ± 0.89 mm (25.90–27.93 mm), weight 13.77 ± 0.11 g (12.70–14.20 g) (n = 62).

The appearance of the first chicks of the roller in the nests (n = 38) in the north and northeast of the Stavropol Region occurs in the second ten days of June: June 06.10.2016 and 06.10.2019; 06.11.2014; 06.13.2012; 06.15.2018; 06.18.2013; 06.19.2017. Most chicks appear in the second ten days of June – in early July; sometimes they hatch only at the end of the first ten days of August. The duration of hatching of the chicks depends on the size of the clutch and can take from 2 to 4 days.

Two days before hatching, cracks appear on the egg, and a day before hatching, a rounded hole 4–5 mm in diameter is formed in the central part of the egg, from which the beak of the nestling protrudes with a clearly visible egg tooth. After 5–6 hours, the chick breaks the shell into approximately two equal halves and leaves it on its own. The shell remains in the nest; rollers, unlike passerines, do not take it out.

The hatchling is naked, blind, the oral cavity is whitish. The weight of the body of a newly hatched chick (n = 13) is on average 14.77 ± 0.33 g (13.0–17.5 g), the wing length is on average 11.25 ± 0.04 mm (10.9–11.38 mm), the beak length is 17.00 ± 0.04 mm (16.7–17.2 mm), tarsus length 12.00 ± 0.06 mm (11.6–12.3 mm), calcaneal callus well developed, with whitish-pink tubercles. On the 2nd or 3rd day of life, pigmentation in the places of pterylae becomes clearly visible, the auditory canals are open. On days 4–5, the tubes of flight and tail feathers break through. The eyes open on the 7th day. On the 6–7th day, stumps break through on the pterylae. On the 11th day of life, the pinfeather of the tail feathers reaches 19 mm. The opening of the fans of the flight feathers occurs on the 12th day, the tail feathers – on the 13th day. In 23–24-day-old chicks, the body is covered with contour feathers, they are colored similarly to adults, but duller. From this age, the chick can make small, forced flights of up to 100 m without landing.

An increase in body weight of chicks occurs until the age of 14 days; by this time, they gain up to 91% of the body weight of fledglings. The maximum weight gain occurs on the 13th day, when the average weight gain is 13.6 ± 0.12 g (12.2–15.1 g). Over the next nine days, the growth decreases and becomes negative 2–4 days before departure – the body weight of the chicks decreases. By the time of departure, the weight of the chick is 140–150 g which corresponds to the weight of adult birds. Roller chicks (Fig. 3) leave the nest at the age of 26–27 days (by the end of July); first, the older chicks fly out, then the younger ones,

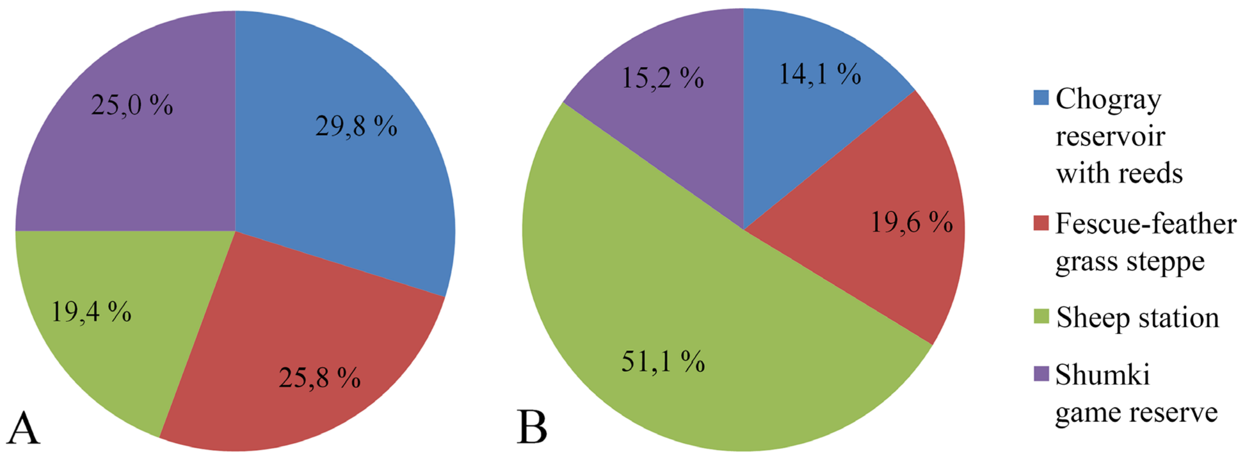

Fig. 5. Use of feeding stations by female (**A**) and male (**B**) rollers (average over 6 days: 8–11, 13, 14 July 2018).

which fly to the older ones, guided by their cry. Parents feed the chicks 6–10 times a day for another 2–3 days after leaving the nest. The family keeps at a distance of 300–700 m from the abandoned nest for about two weeks. At this time, the chicks acquire the skills of independently searching for and obtaining food. The brood size varies from 2 to 5 (3.43 ± 0.13) chicks (n = 46). The breeding success in 46 nests was 77.5%.

The male usually performs the main task of feeding the chicks in the first days after they hatch (when the female is still busy warming them) and before the last chicks leave the nest (when the female feeds and guards the fledglings). Observations of the feeding activity of chicks in the northeastern part of the region on the shore of the Chogray Reservoir in 2018 for six days before the chicks leave the nest showed that both parents take part in feeding the chicks, as well as incubation. They most often hunt close to the nest, but they may make flights of 1 km or further. During this period, a pair of birds made 159 feedings (for 76 hours of observations). The shares of the female and male in feeding the chicks are approximately the same: the female fed the chicks 82 times (51.6% of the total number of feedings), and the male 77 times (48.4%) (Fig. 4). On average, each parent fed the chicks once per hour. During the period when the chicks were in the nest, the female fed them a little more often than the male, and on the last two days, when the chicks began to leave the nest and feeding became irregular, the male fed them somewhat more often. Sometimes a pair has an assistant in breeding offspring. For example, in 1990, a ringed male from the brood of 1989 helped the parents. The assistant flew to the nest even during the incubation period, after the appearance of the chicks, he brought food, but the father drove him away. Only eight days after the appearance of the chicks, he managed to feed them, when an adult male was not near the nesting site. The adult male began to tolerate the assistant and allowed it to participate in feeding only just before the final departure of the chicks from the nest. Only eight days after the appearance of the chicks, he managed to feed them, when an adult male was not near the nesting site.

Weather conditions, apparently, have little effect on the intensity of feeding of chicks, with the exception of very heavy rain, during which parents usually sit on the perch.

Observations on the use of different biotopes for gathering food were carried out in the northeastern part of the region on the shore of the Chogray reservoir from 5 a.m. to 10 p.m. (parents finished feeding the chicks at 8:40–8:50 p.m.) for six days before the chicks first flew. Adult birds foraged in four main habitats (Fig. 5): in the steppe, anthropogenic areas (on the sheepfold and near the game reserve, using power lines as perches) and in the shallows of the reservoir. If the female hunted in all habitats for approximately the same time, then the male clearly preferred the territory of the sheep station. It is possible that the longer flights of the female were associated with the need for faster recovery of muscles after a period of incubation, or because of her greater caution. In case of obvious danger to herself or the brood, she sat down on a perch, looked around and waited for the threat to pass, and only after that she flew into the hole with food. The male carried food directly to the hole, despite the danger.

Nutrition and hunting

During the six days before the departure of the chicks, their diet was dominated by locusts (50.0%), butterflies and moths (18.6%), grasshoppers (8.8%), small snakes (6.8%), earthworms (6.8%), sand lizards (2.0%), dragonflies (2.0%), mole crickets (2.0%), beetles (2.0%), and mouse-like rodents (1.0%).

The composition of the food brought by the male and the female to feed the chicks was different (Fig. 6). Butterflies and moths (34.1%), locusts (31.8%), grasshoppers (18.2%), and earthworms (11.4%) formed the basis of food objects taken by the female. In contrast to the female, the male brought the chicks mainly locusts (63.8%), less frequently snakes (12.1%) and butterflies and moths (6.9%). Vertebrates (reptiles and rodents) were only brought to the chicks by the male

The roller is a trophic generalist, or omnivore: these birds eat any available invertebrates (mostly insects) and small vertebrates, including lizards, snakes, rodents, young birds. Sometimes they eat dead animals, more often on the roads. Rollers often use energy-efficient hunting methods. Where a large number of sheep are pastured, birds often prey on insects that are scared by domestic animals. During the harvesting of grain crops, rollers hunt over the fields, as do small falcons: common kestrel *Falco tinnunculus* L., 1758 and red footed falcon *F. vespertinus* L., 1766, as well as corvids: rook, magpie *Pica pica* (L., 1758) and hooded crow. If the roller nest is close to such fields, then adult rollers can hunt all day next to working combine harvesters and other agricultural machinery, catching mainly large insects and small mouse-like rodents. Rollers use four main methods of hunting: a long lookout for the victim, sitting on a perch, and then diving from a perch to the ground or grass (without landing); looking out for prey from a perch, flying and grabbing prey in flight from the ground or grass surface; flying and trapping insects in flight close to the ground; moving on the ground in or after rain and collecting earthworms.

After the chicks leave the nest, the rollers hunt mainly from perches, most often from power lines and telegraph poles. During this period, adult birds teach young ones the technique of hunting in places with large numbers of insects. Often one of the adult birds, having caught the prey, demonstrates it to the fledglings. Brood members take turns flying off their perches and perched next to the parent. Often, young birds, after an unsuccessful hunt, actively beg or take food from their parents. Birds hunt during the day, at dusk and sometimes at night for insects attracted by the light of a street lamp.

As observations (Fig. 6) and analysis of the contents of the stomachs of birds (Table 1) show, the composition of feed depends on the abundance and availability of food objects. In Ciscaucasia, the rollers feed on various large beetles: the forest cockchafer *Melolontha hippocastani* Fabricius, 1801, longhorn beetle *Dorcadion carinatum* (Pallas, 1771),

Table 1. Composition of food objects of rollers (road-killed) from analysis of stomach contents (n = 7) in the Stavropol Region in August – early September 2013–2019.

Food objects		Number of specimens	% of total number of specimens	Occurrence of objects in stomachs	
				n of stomachs with objects	%
Order Orthoptera		49	41.1	7	100
	Family Acrididae	31	26.0	5	71.1
	Family Tettigoniidae	15	12.6	3	42.9
	Family Gryllotalpidae	3	2.5	1	14.3
Order Coleoptera		62	52.2	7	100
Lizards (Lacertilia)		3	2.5	3	42.9
Unidentified objects		5	4.2	5	71.1
Total		119	100		

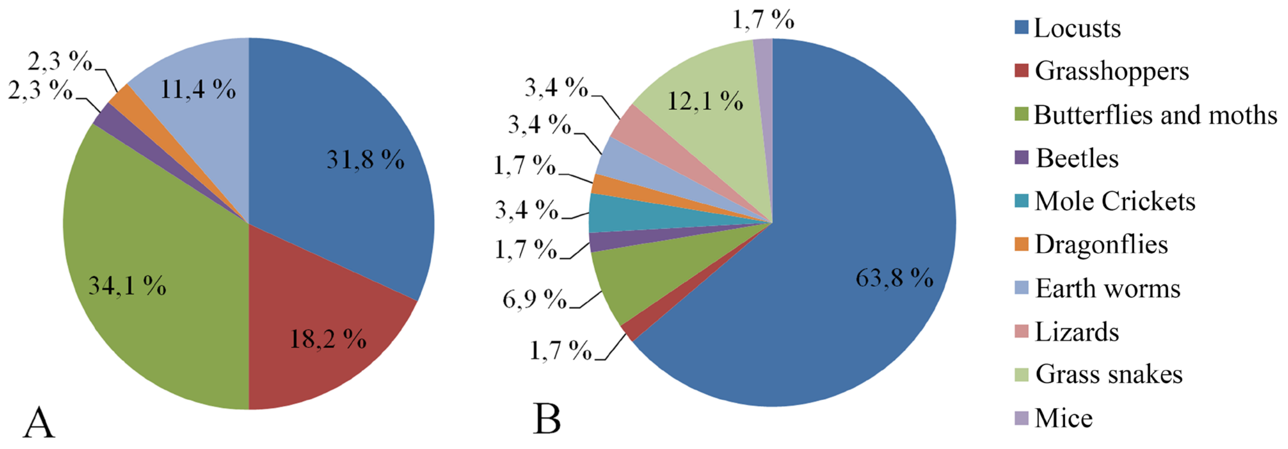

Fig. 6. The composition of the feed brought by the female (**A**) and male (**B**) rollers (average over 6 days: July 8–11, 13, 14, 2018).

ground beetle *Zabrus tenebrioides* (Goeze, 1777) and other large insects: the shield bug *Eurygaster integriceps* Puton, 1881, dragonfly Corduliidae, blue-winged grasshopper *Oedipoda caerulescens* (L., 1758), bush crickets (Tettigonioidea), desert cricket *Melanogryllus desertus* (Pallas, 1771), butterflies and their caterpillars, as well as earthworms, sand lizard *Lacerta agilis* L., 1758, grass snake *Natrix natrix* (L., 1758), dice snake *N. tessellata* (Laurenti, 1768), and mouse-like rodents.

Limiting factors

The roller population in southern Russia may decline for many reasons. Local population reductions can occur under the influence of extreme natural conditions. Thus, after heavy rains, as a result of the collapse of cliffs, four out of four broods under observation died (1987); five out of five broods died as a result of flooding of silage trenches (1988). At the end of June 1989, after a sharp cold snap and prolonged rain, a dead brood of two chicks and an exhausted adult bird were found. High temperatures up to 45–50 °C in July 1997 led to the death of an adult bird with three chicks.

Predators can cause noticeable damage to the population. The main enemies of rollers are eagle owl, goshawk *Accipiter gentilis* (L., 1758), sparrowhawk *A. nisus* (L., 1758), weasel *Mustela nivalis* L., 1766, stray cats *Felis catus* L., 1758, and sometimes snakes. The most dangerous predator for the rollers is the eagle owl, which in the Stavropol Region nests along coastal cliffs. For example, at the nest of an eagle owl in a cliff on the Chogray Canal on July 26, 2007, in pellets (n = 20), many feathers and bones of rollers were found along with the remains of hedgehogs and jerboas. Three eagle owl pellets collected near the same canal on July 19, 2007 contained feathers and bones of rollers, and another one contained the remains of the greater jerboa *Allactaga major* (Kerr, 1792) (Fedosov and Malovichko, 2006). Every year in July, when still inexperienced young rollers move to an independent life, remains of rollers were found on the feeding sites of this owl in the cliffs of the Aigurka River and the high bank of Manych-Gudilo Lake. We recorded goshawk hunting for rollers on Left Island on Manych Lake in June 2011 (2 cases) and June 2014 (4 cases). Brown rats *Rattus norvegicus* (Berkenhout, 1769) can prey on colonies of hole-nesting birds, which was recorded on May 29, 2008 in a sheep station, 500 m from the Kuma River. Here the shepherds observed how a common fox *Vulpes vulpes* (L., 1758) dug out a nest of rollers.

The death of birds can be caused by the direct effect of anthropogenic factors: in the vicinity of almost every settlement, young hunters kill 3–4 birds during the autumn season. Rollers are killed on roads: for example, in 1985–1990, on only a 20 km stretch of the Solnechnodolsk – Filimonovskaya highway, 4–5 rollers were found annually killed by cars. In the period 2001–2019 we observed 12 deaths of rollers in collision with cars. Most often this happens in the middle of summer and autumn, when inexperienced fledglings dominate in the population. At this time, the birds concentrate on power lines near the roadsides and, while hunting, fall under the wheels of cars or collide with the windshield. Unintentional actions, such as walling up nests in silage pit walls during cattle foraging, resulted in the deaths of 20% of nests in 1983–1998.

In the early 1990s the number of rollers had decreased to about a third of the population at the beginning of the 1980s (Malovichko, 1999), which, apparently, was caused by the widespread use of chemicals (herbicides, insecticides, etc.) in the 1980s. Unfortunately, there were no special studies on this problem at that time. In the 2000s factors limiting the growth of the population of rollers include a reduction in the area for grazing animals and non-irrigated arable land and an increase in the sown area of monocultures with intensive use of chemicals and the destruction of all ecotone biotopes along fields, roads, and water bodies (Atlas of nesting birds..., 2020).

Discussion

In the Stavropol Region, until recently, the roller was an exclusively hole-nesting bird, in contrast to most of its European range, where it lives in sparse tall oak, pine and floodplain forests, old parks and tree avenues (Avilés and Parejo, 2004; Butler, 2001; Kovacs et al., 2008; Rodríguez et al., 2011; Rodríguez-Ruiz, 2016). In the Mediterranean, in the absence of trees, nests are often located in human buildings (Catry et al., 2011; Rodríguez et al., 2011), nest boxes (Catry et al., 2011; Rodríguez et al., 2011), or in the cavities of power transmission poles (Cramp and Simmons, 1988); up to 44% of the population's clutches can be on poles (Tinarelli et al., 2015); in the Stavropol Region, such nest sites have been recorded, but rarely. In the study area, birds sometimes nest in old (last year's) haystacks and metal pipes (Khokhlov, 1984; Malovichko, 1999). Unlike in Northern Anatolia (Arslan and Akveran, 2019), Belarus and the Urals (Poslavsky, 2013; Tarantovich, 2012), rollers in the Stavropol Region do not use old magpie nests, concrete building openings, or rock ledges. This may indirectly suggest that there are enough natural cavities in the region for nesting birds. With an increase in human activity related to agricultural practices, rollers may be forced to use these likely safer nesting sites higher above the ground.

As in most of their range (Cramp and Simmons, 1988), in Stavropol Region, rollers nest in sandy and clayey shores of various water bodies on an area of about 2.4% of the entire territory of the region. A distinctive feature of the study area is also the arrangement of nests in the clay walls of silage trenches and small extraction pit. This adds another 1–2% of the populated territory of the Stavropol Region. The low inhabitance by rollers of new quarries (10.8%) is explained by the fact that most of the quarries are located in open areas, devoid of any woody vegetation, and, consequently, lacking perches for gathering food, resting and spending the night.

Rollers need abandoned burrows of sand martins and European bee-eaters. These birds nest both separately from other species (single pairs and groups) and together with other hole-nesting birds (Ilyukh, 2014; Malovichko, 1999). The average height of inhabited cliffs is 6.4 ± 0.4 m, which is approximately the same as the data obtained in Northern Anatolia (Arslan and Akveran, 2019). In connection with the increase in the number of hollow trees in the region, as well as with the construction of holes in small excavations of the earth, in recent decades there has been a tendency towards an increase in single pairs. Greater coloniality of the species was noted in the past in Italy and Northern Anatolia (Arslan and Akveran, 2019; Ianiro and Norante, 2015). The distance between breeding territories, according to various sources, can be 0.13–5.5 km, 1.2 km on average (Arslan and Akveran, 2019), 98–375 m (215.3 ± 93.7 m) (Sackl et al., 2004), at least 140 m and an average of 600 m (Tarantovich, 2012). Rollers are sometimes known to form groups of 3–5 pairs (Sosnowski and Chmielewski, 1996), of 11.75 pairs in cavities of artificial structures such as bridges (Vaclav et al., 2011), and 15 pairs/km^2 in the area of nest boxes (Finch et al., 2019). The extent to which colonial breeding is favorable for rollers is not known (Poole, 2007). However, the range of foraging flights of rollers during the breeding season, although it may be up to 1 km and further (Prokofieva, 2008; own data), is more often 50–150 m from the nest (Avilés and Parejo, 2002; own data), 274.2 ± 77.9 m (Catry et al., 2011) or 165.0 ± 171.2 m; 66.7% of flights are within a 100 m radius zone (Aviles et al., 1999; own data); family plots occupy from 15.0 to 196.5 ha (average 119.4 ± 59.51 ha) (Bohuš, 2007). Based on this, it can be concluded that in the presence of a sufficient food supply, a high density of nests is natural. This is exactly what we found near Lake Manych-Gudilo and the lower reaches of the Kuma River, and in places poorer in food, single pairs prevailed.

Rollers can occupy the same nest hole for several years in a row (7 or more), although nests in nest boxes are changed every three or four years (Václav et al., 2011). New holes are often located not far from last year's ones. Roller holes are usually 30–50 cm deep, so that eggs and chicks (Fig. 3) are often clearly visible from the outside (Ilyukh, 2014; pers. data).

Birds breed in trees in which there are hollows. In the study area, as well as in other parts of the range (Tarantovich 2012), rollers occupy hollows in pine trees, black locust and elms. In other regions, nests were found in oaks *Quercus* sp. and beeches *Carpinus betulus* L. (Mastronardi et al., 2014), as well as (in order of decreasing frequency of occurrence) in willow *Salix* sp., common ash *Fraxinus excelsior* L., oak, common beech *Fagus sylvatica* L., birch *Betula* sp. and wild cherry *Prunus avium* L. (Sackl et al., 2004). Nests have been recorded in pines (especially *Pinus sylvestris* L.), white poplars *Populus alba* L., less frequently in willows and in natural cavities of plane trees *Platanus orientalis* L. (Avilés and Parejo, 2004).

Rollers usually use abandoned woodpecker holes (Bouvier et al., 2014; Sackl et al., 2004): black woodpecker *Dryocopus martius* (L., 1758), green woodpecker (Sackl et al., 2004; Tarantovich, 2012), grey-headed woodpecker *Picus canus* Gmelin, 1788 (Sackl et al., 2004). All nesting cavities were found in the main trunk of nesting trees at a height comparable to the height of holes in cliffs: 4.5–10.2 m above the ground (Sackl et al., 2004), 4–10 m (Butler, 2001; Fry et al., 2010; Poole, 2007), 1.3–15 m (Mastronardi et al., 2014), at an average height of 11 m (Bohuš, 2002). Some authors noted that rollers use trees with several hollows for nesting, which are occupied by other animals: black swifts *Apus apus* (L., 1758) or bats (Tarantovich, 2012), as well as common starlings and jackdaws *Corvus monedula* L., 1758 (Casadei and Ceccarelli, 2015). This indicates that rollers are fairly tolerant of other animal species in their nesting territory.

The annual cycle of the roller consists of periods of breeding (April–August), wintering (November–February) and migration (August–November for autumn and February–April for spring migration) (Finch et al., 2019; Rodriguez-Ruiz et al., 2019). According to other data, spring migration occurs from March to June (mainly in April–May), and autumn migration takes place from August to November (mainly in September–October) (Kovacs et al., 2008). In the Stavropol Region, these cycles are somewhat shorter: birds arrive in the region in the middle or at the end of April and almost immediately occupy the nesting territory (Ilyukh, 2014; Malovichko, 1999). Pairing on the breeding grounds occurs, as in the Mediterranean, from late April to early May (Casadei and Ceccarelli, 2015), more often from mid-May.

Incubation in the Stavropol Region lasts 17–19 days (Malovichko, 1999) as in other parts of the range (Ianiro and Norante, 2015). Roller chicks leave the nest at the age of 26–27 days, which is consistent with the observations of other authors (Fry et al., 2010). The eggs are incubated mainly by the female, who begins incubation while the eggs are being laid (Avilés et al., 1999; Cramp and Simmons, 1988; Fry et al., 2010; Malovichko et al., 2021). A full clutch is from three to seven eggs, in other areas it may be up to six in Mari El and Tatarstan (Popov and Lukin, 1972), up to five in the Pskov Region (Malchevsky and Pukinsky, 1983) and in Italy (Ianiro and Norante, 2015), up to four in the Leningrad region (Malchevsky and Pukinsky, 1983), Belarus (Fedyushin and Dolbik, 1967) and Georgia (Zhordania, 1962). The average clutch size varies from 3.59 in Poland (Sosnowski and Chmielewski, 1996) to 5.07 in Spain (Avilés et al., 1999), compared to 4.43 ± 0.17 eggs in Stavropol Region.

Comparing the size of the roller eggs in the Stavropol Region with those in other parts of the range, it can be noted that here the eggs are smaller than in Western Europe (Makatsch, 1974), Lithuania (Aleksonis, 2008; Antanas, 1987), Belarus (Nikiforov et al., 1989) and Cherkasy Region of Ukraine (Seliverstov, 2007), but larger than in the Sumy Region of Ukraine (Knysh, 2014) and Turkmenistan (Belskaya, 2014). The chicks hatch from mid-June and leave the nest by the end of July (Fig. 7) (Ilyukh, 2014). The first three chicks usually hatch after 1–2 days, while the others hatch on subsequent days, creating a small size hierarchy between chicks (Expósito-Granados et al., 2016; Parejo et al., 2010). Such a pattern appears to take place throughout the range.

Fig. 7. A 25–26 day old roller chick before leaving the nest.

Both parents take part in feeding the chicks, as well as in incubating the eggs. With regard to the frequency of nest visits during the entire feeding period of the chicks, visiting schedules can be very different, even when comparing two days of sampling the same nest (Low et al., 2008). The average number of feedings per hour by a pair of rollers in different regions ranged from 2.8 to 14.5, more often 6–8 (Afanasova et al., 1991; Belskaya, 1964; Prokofieva, 2008; Tarantovich, 2016). The number of visits may depend on several factors, but mainly on the availability and size of the preferred food, and the age of the chicks; before departure, the number of feedings is reduced (Malovichko and Konstantinov, 2000; Tarantovich, 2016). We recorded such a reduced feeding regime, when, on average, parents fed the chicks only twice per hour (Fig. 4).

Reproductive success in the declining populations of Poland (Sosnowski and Chmielewski, 1996) and Germany (Creutz, 1979) is 1.5–1.8 chicks per pair, in Italy – 2.3 (Mastronardi et al., 2014); in growing populations, this figure reaches 3.74 in southwestern Spain (Avilés et al., 1999), 3.7 in Slovakia (Bohuš, 2007), and 4.0–5.4 in France (Poole, 2007). In our observations, the number of chicks per successful nest varied from 2 to 5 (average 3.43 ± 0.13), which corresponded to the level of growing European populations. There is also evidence that differences in reproductive success can be explained by the foraging environment (Avilés and Parejo, 2004; Kiss et al., 2014 and others), although this is not always the case (Rodríguez et al., 2011 and others). The observed isolated cases of assistance in breeding offspring (Afanasova et al. 1991; pers. data) so far cannot be considered evidence of its promoting reproductive success.

Rollers mainly feed on large invertebrates (grasshoppers, crickets, beetles), as well as small vertebrates: lizards, snakes, rodents, young birds and, opportunistically, slugs (Prekopov, 1940), shrews (Vahi, 1962), ramshorn snails *Anisus* sp. (Prokofieva, 2008), small insects (e.g., winged ants) (Avilés and Parejo, 2002; Kiss et al., 2014; Sosnowski and Chmielewski, 1996), amphibians (Meschini et al., 2009; Pettavino, 2015; Tarantovich, 2012), and even fruit (Cramp and Simmons, 1988). As observations and analysis of the contents of the stomachs of birds and the contents of the hollows of the rollers show, the food composition depends on the abundance and availability of food objects.

Sampaio (2018) showed that there is a difference in diet between adults and chicks, whose diet is dominated by beetles and orthopterans, respectively. Dividing food between age groups may be due to locusts being more numerous during juvenile development and/or adults preferring larger prey and higher energy content for their juveniles, helping to reduce nest visits. In the same work, using isotopic analysis, it was demonstrated that females can have a more varied diet, since they have a wider isotopic niche than males.

The destruction of clutches and broods as a result of filling silo trenches with silage mass (Afanasova et al., 1991; Malovichko, 1999) and the death of birds on roads (Ilyukh, 2014; Malovichko, 1999; Shevtsov et al., 2012) are common. The loss of old trees with hollows for roller nests is a major problem (Tinarelli et al., 2015) and the lack of suitable nest sites has become the most significant limiting factor in several regions (Kovács et al., 2008). For Stavropol Region, this is not relevant. Electric shocks from non-insulated voltage poles are dangerous for all kinds of birds. Rollers usually hunt from a perch up to 10 m above the ground, so electrical wires and pylons are ideal. Deaths of rollers on power lines have been reported (Ambrus, 1992; Csibràny, 2016; Demerdzhiev et al., 2009), but we did not observe this.

In the study area, as well as throughout the range (e.g., Arslan and Akveran, 2019; Catry et al., 2011; Cramp and Simmons, 1988), Rollers prefer large areas of pasture and a mosaic of arable land interspersed with meadows and fallows along roads and ditches. The areas of such biotopes are shrinking, and only in the eastern part of the Stavropol Region there are still enough pastures. In all such places, it is important for this bird species to have hunting perches (telegraph poles, trees, shrubs, fences, etc.) and cavities (nest holes in cliffs or hollows in trees) for nesting, as well as large insects (mainly Orthoptera) for feeding (Cramp and Simmons, 1988; Sackl et al., 2004). In Western Europe, nesting density is closely related to the presence of natural cavities (Avilés et al., 1999; Avilés and Parejo, 2004), so the widespread removal of old hollow trees is a key threat to rollers. In the Stavropol Region, such trees appear to have increased in number.

Rollers demonstrate complex biocommunication and behavioral ecology: foraging economy (versatility in feeding, hunting insects scared by animals or agricultural machinery), economical basis of territoriality, advantages of joint feeding of offspring, distribution of parental roles and high coordination of partners' actions that increase reproductive success (Malovichko et al., 2021).

Conclusions

This study investigated the effect of the period of agricultural transformation of the environment in 1984–2019. In the Stavropol Region, the nesting life of the European Roller (the time of pair formation, nest building, egg laying, development and growth of chicks, as well as the feeding of chicks) had the same characteristics as in the period of traditional agriculture. At the same time, the largest clutch size for any European population, of 7 eggs, was discovered for the first time, and the eggs themselves were found to be somewhat smaller than in most of the range. The average clutch size (4.43 ± 0.17 eggs) and brood size (3.43 ± 0.13 chicks) correspond to the level of growing South European populations. The breeding success was 77.5%. The analysis showed that the rollers have become tolerant of busy highways, often with working agricultural machinery. All this, along with the omnivory of the species, makes it competitive in a changing environment and gives grounds for a cautious assumption about the rate of adaptation of the species to the rate of environmental change. More research is needed to test the hypothesis of an increase in clutch size and a decrease in egg size as an adaptive response of the species to habitat changes in the last 30–50 years.

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