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Breeding biology of ring ouzel (*Turdus torquatus*) in the West Carpathians, Slovakia

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Abstract. Reproduction is an important life history trait, affecting both parental fitness and population persistence. To contribute to knowledge of breeding ecology of birds living in high mountain ecosystems we monitored reproductive periods of ring ouzel (*Turdus torquatus*) in northern Slovakia. Between May 1985 and July 1989 essential characteristics of breeding biology of this species were recorded. Field data on 40 nests from the West Carpathians were obtained. In 38 complete clutches we observed clutch sizes of three (n = 3), four (n = 24), five (n = 10) and six (n = 1) eggs. The total success rate was recalculated using 34 nests. Out of 146 eggs laid 116 young hatched (79.5 %) and 52 young fledged (35.6 %). We assume that our research caused some increased predation, so if we eliminate (statistically) this impact then the revised numbers are: 115 eggs laid, 90 young hatched (78.3 %) and 63 young fledged (54.8 %). Length of incubation was between 13 and 15 days (n = 14 nests), with an average of 14 days. The main incubation period ran from May 10th-19th. Breeding care for young in the nest lasted between 11 and 15 days, with an average of 13 days (n = 13). Shorter length of breeding care in the nest (11 days) was a result of external disturbances, mainly by raptors. Fledging largely occurred between May 21st and June 9th.

Key words: ring ouzel, Turdus torquatus, breeding biology, the West Carpathians

Introduction

Mountain and high mountain ecosystems are facing increasing threat. Contrary to the lowlands and forest avifauna, sufficient knowledge on the basic ecology of alpine and sub-alpine bird species is still lacking, in both Slovakia as well as the balance of Europe (Lehikonen *et al.* 2019). This is especially true for species that live particularly remote lives outside of human interest. The supramontaneous species, ring ouzel, has been shot in the past for its distinctive black and white coloration (Čaputa *et al.* 1982). This species is generally overlooked by European Union (EU) member states because is not listed on Annex I of the Birds Directive. However, as a migratory species it should be subject to the same conservation measures as Annex I species, under Article 4.2 of the Birds Directive. The EU holds around 60 % of the global population of ring ouzel, and the Carpathians are the highest-density region in the world for this species. After the retreat of the last glaciers, habitat for this species has been reduced to northern Europe and subalpine mountain regions of Europe. We rank the species among typical glacial relics. Subspecies *T. torquatus alpestris* breeds in montane areas from Spain east to Romania, with high densities in the Pyrenees, Massif Central, Alps, Balkan, Greece, Asia Minor and the Carpathians (del Hoyo *et al.* 2005). In Eastern Europe, birds of this species largely winter at lower elevations south of their breeding range (Hagemeijer and Blair 1997). Migration to overwintering grounds in southern Spain and North Africa occurs mostly in September, October and November (White 1907; Glutz von Blotzheim and Bauer 1988; Busche 1993). The ring ouzel is also a good example of a subalpine species for which information on small-scale ecological requirements is still largely lacking across its breeding range (Bocheński 1968; Burfield 2002; D´ Amicis 2002; Holupirek 2004; Beale *et al.* 2006; Ciach and Mrowiec 2013; Bacht *et al.* 2013; Sim *et al.* 2013a, 2015). Breeding areas for British birds are typically comprised of steep slopes with crags, gullies, scree or boulders, as well as more gently sloping or flat areas, and are often dominated by heather, pasture or bracken (Poxton 1986, 1987; Cramp 1988). In Fennoscandia, *T. torquatus torquatus* breeds in similar open areas on fells above pine (*Pinus*) forests, but also nests on the edge of birch (*Betula*) or spruce (*Picea*) stands (Bannerman 1954). In contrast, *T. torquatus alpestris* habitually breeds in open conifer woods close to moist, grassy areas at altitudes of 600-2000 m a.s.l., favouring spruce, fir (*Abies*) and occasionally beech (*Fagus*) forests. The main range of the ring ouzel in the Alps or Caucasus is similar to the upper limits of the coniferous forest and the mountain pine and *Rhododendron* sp. zone (Demetiev and Gladkov 1954; Glutz von Blotzheim 1964). In the northern Carpathians this species is found between 500 and 1700 m a.s.l. (Bocheński 1960; Głowaciński and Profus 1992; Janiga 1992; Janiga and Poxton 1997; Tomiałojć and Stawarczyk 2003).

The species is usually single-brooded in the Carpathian area, and we assume that this is the most common reproductive strategy in its other central and eastern European mountain habitats (Walter 1995). Nests are built in trees, mostly in larches close to the trunk, at a height from 1.5 to 20 m (Janiga and Višňovská 2004). Females take care of nest building and brooding, with very few exceptions of male assistance in these tasks. Most birds leave the study area immediately after reproduction, (i.e., before the end of June), spending the post-breeding period at higher elevations (Glutz von Blotzheim and Bauer 1988). Because the Carpathians are host to the mose plentiful populations of ouzels, information on the central European population is essential for preservation of this species.

Moreover, due to climate change, a better understanding of the ecology of ring ouzel is a priority. For example, British nest records show that the species currently lays its first clutch approximately eight days earlier than in 1968 (Baillie *et al.* 2005), suggesting that climate change has already affected breeding life of ouzels. During breeding season, adults feed nestlings almost exclusively on invertebrates, particularly earthworms (*Lumbricidae*) (Burfield 2002). *Lumbricidae* availability is largely determined by rainfall and temperature (Askew and Yalden 1985), and thus temperature and rainfall during breeding are determinants of nest survival. In Britain and Iceland, the decline of the species has continued, with perhaps as much as a 58 % decline occurring between 1988 and 1999 (Wotton *et al.* 2002; Buchanan *et al.* 2003; Burfield and Brooke 2005; Sim *et al.* 2010; Mee 2018). In parts of the Scotland the local population remains stable (Rebecca 2001). In Switzerland, the species decreased by 36 % between 1990 – 2018 (Barras *et al.* 2020). Climatic factors have also an indirect impact on the occurrence of the ring ouzel (Beale *et al.* 2006; von dem Bussche *et al.* 2008). Withdrawal of the ring ouzel into higher habitats under the influence of changing rainfall and temperature is predicted in many regions (Gubitz and Spath 2002; von dem Bussche *et al.* 2008). Changes are also probable in terms of population size in the Carpathians region, where an altitudinal shift may occur in the subalpine zone. The aim of this study is to contribute to knowledge on the breeding biology of the ring ouzel, and this historical data also helps to establish a baseline against which current changes should be monitored to determine population trends of the species.

Material and Methods

The area around Veľký Brankov, in the Low Tatra National Park, Slovakia (May 1985 to July 1989) was selected for this study. We recorded essential characteristics of breeding biology of the species, including: nest locations, nest structure, number of eggs laid, number of young hatched, success and length of incubation, number of nestlings and fledglings, and success rate of breeding. Eggs and nestlings were marked with a felt-tipped pen and older nestlings were ringed with a combination of colored plastic rings, so that each individual was identifiable. Field data on 35 nests from Brankov was collected. Additionaly, information from one nest in Choč Hills (1989) and four nests from the West Tatra mountains (1998-1999) was also used (Table 1). The survey of the nests took place in 3 - 4 day intervals. After finding the nests, they were regularly visited during the incubation period in 2 - 3 day intervals.

The real numbers of nests (or number of cases) in the final evaluation of individual statistical characteristics (in the chapter – Results) can differ, because not all nests were equally accessible for gathering all of the characteristics. Following the initial discovery of the nests, basic measurements were carried out. For additional details see Janiga and Višňovská (2004) or Schirutschke (2005). Incubation was regularly watched from a prescribed distance from the nest, (i.e., whether the female was actively brooding or not). The date and order of hatching were determined (hatching scheme) either during hatching afterward based on developmental characteristics of individual birds (Janiga 1992). The total number of eggs in a clutch, the number of chicks hatched from eggs that were laid, and the number of young that flew out of the nest were all recorded. Losses of eggs, losses of chicks and total losses during nesting, as well as the causes of these losses, were determined. During this research, a researcher inadvertently negatively affected the nesting process in several nests, and this problem is discussed under Results. For chicks that successfully left the nest, this date was recorded, as well as the time period of time chicks remained in the nest from hatching to leaving the nest.

During recording of nest care, the activity of parents in defence of the nest, (i.e., the aggressiveness of the nesting pair), was also ascertained. We distinguished four categories of this behaviour:

1 – Very aggressive individual; attacks a researcher while defending the nest.
2 – Aggressive sounds when in close proximity to researcher, but does not attack.
3 – Louds sounds from a distance and/or "whistle" warnings.
4 – Flies away and observes the nest from afar, or is not present.

Using this scale, the degree of aggression of parents during the incubation period and during the care of the chicks was determined, as well as the ratio of

	1985	1986	1987	1988	1989	1998	1999	Total
Brankov – Low Tatra mountains	2	6	7	8	12	0	0	35
West Tatra mountains	0	0	0	0	0	1	3	4
Choč Hills	0	0	0	0	1	0	0	1
Number of nests	2	6	7	8	13	1	3	40

Table 1. Summary of the number of examined nests of ring ouzel.

the aggressiveness of the female and the male. After fledglings left the nest, some of the nests were taken for analysis of nesting material and some for analysis of parasites that live in nests. The parasites were extracted in photoeclectors at the Zoological Institute of the Faculty of Science, Comenius University. Larvae and images of bird fleas were determined (Dr. Cyprich, Dr. Krumpál).

Results

161 eggs were found in 38 nests. Ring ouzels laid three to six eggs per clutch, but clutches of four were the most frequent (Fig. 1). The average number of eggs in a complete clutch was 4.3. (s = ± 0.6).

In this study, the data is evaluated in two ways. In the first case, the real breeding success of ouzels is calculated, and in the second case, the increased breeding success is calculated that likely would have occurred without the influence of this research. In twelve nests, the birth rate was likely negatively affected in several ways by our presence near the nests. In seven cases, predators were inadvertently attracted to the nest as the breeding pair were defending the nest, or predators were attracted to the nest as a result of human presence (i.e., pine marten followed our footprints in the snow). Three nests were directly affected by humans, where parents abandoned their eggs (once), or abandoned hatchlings (twice), which subsequently died. In one case, a female was trapped in the mist net, and did not return to the nest the following day, resulting in the death of two young. The male stayed with the young near the nest, fed them, defended them and managed to preserve them. The remaining young flew out of the nest at 11 - 12 days after hatching, earlier than is commonly observed. This example shows how dangerous this collection process (netting, ringing and weighing) can be to a breeding pair during this sensitive nesting period.

While human-induced losses were minimal during incubation, when nest visits occurred with similar frequency, nests appear to be more vulnerable during this juvenile stage. Data on breeding biology is presented in Table 2.

Incubation success in ouzels was very high (Fig. 2); in the majority of nests chicks hatched from all laid eggs. 30 nests with nestlings were monitored until the young fledged (Fig. 3). The effect of field research on the mortality of nestlings was highly significant, the difference was approximately 20 % in the young production.

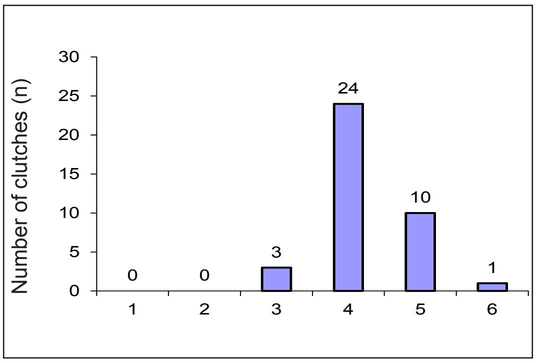

Fig. 1. Number of eggs in a complete clutch.

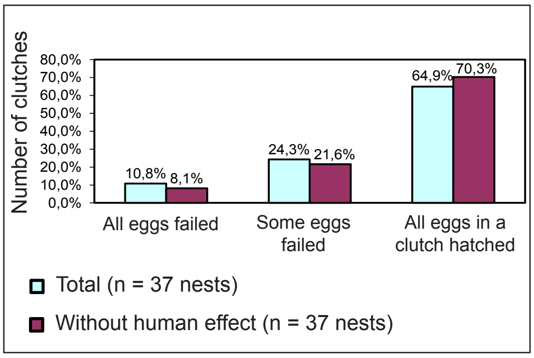

Fig. 2. Success rate of hatching in ring ouzels.

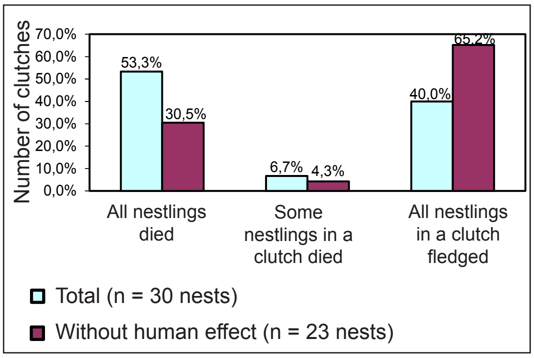

Fig. 3. Success rate of fledging in ring ouzel.

Total success rate – number of young fledged from number of eggs laid was recalculated from 34 nests (Fig. 4). Out of 146 eggs laid, 116 young hatched (79.5 %), and 52 young fledged (35.6 %). If we eliminate the impact of our research then the adjusted numbers are: 115 eggs laid, 90 young hatched (78.3

Variable	Variant	x (n)	S	min – max
Number of eggs in complete clutch	Total	4.2 (38)	0.62	3 – 6
	Without human effect	4.2 (38)	0.62	3 – 6
Number of hatchlings per clutch	Total	3.5 (37)	1.37	0 – 5
	Without human effect	3.6 (37)	1.24	0 – 5
Number of fledglings per clutch*	Total	1.7 (30)	1.93	0 – 5
	Without human effect	2.7 (23)	1.94	0 – 5

* at least one young successfully hatched

Table 2. Breeding biology characteristics of ring ouzel (x – mean; n – number of nests; S – standard deviation).

%), and 63 young fledged (54.8 %). In general, females must lay two eggs to rear one fledgling.

Losses caused by field research were described earlier. Other causes of failed eggs were mainly strong storms, snowstorms, deceased parents or abandonment (22 eggs or 68.7 % of failed eggs). Three eggs (9.4 % of failed eggs) were destroyed by a squirrel or bird of prey. Seven sterile eggs (21.9 % of failed eggs) were found in seven nests; four in four-egg nests, two in five-egg nests and one in a six-egg clutch. Mortality of nestlings was higher than mortality of eggs. Cold weather or abandonment of nestlings caused the death of 13 young in a nest (20.3 % of all dead nestlings). 51 chicks were killed by predators; nine nests were impacted by a bird of prey, two by a mustelid, and two by a squirrel.

The dates of the laying of the first egg are summarized in ten day inverals in Fig. 5. The average days to lay the first eggs, hatch the first nestlings and fledging of the first young are summarized in Table 3. It was found that 92 per cent of eggs were laid between April 22nd and May 10th.

The incubation period lasted between 13 and 15 days (n = 14 nests), and the average was 14 days. More detailed account of the hatching scheme of chicks is presented in Fig. 6. The primary period was between 10th and 19th May. The pattern of hatching in a given nest was very variable and often depended on the number of eggs in a clutch (Table 4). The chicks in the nest usually did not hatch at once, but at intervals of half a day to one day. Hatching asynchrony of two days was observed only twice (7.1 % of 28 exactly observed nests).

Breeding care for young in the nest lasted between 11 and 15 days, (13 days on average) in the 13 nests observed. We can assume that shorter length of breeding care (11 days) was a result of external disturbance – generally predation by raptors. The date of fledging was commonly between May 21st and June 9th, though in one nest the fledging of young occurred on May 7th (Table 3).

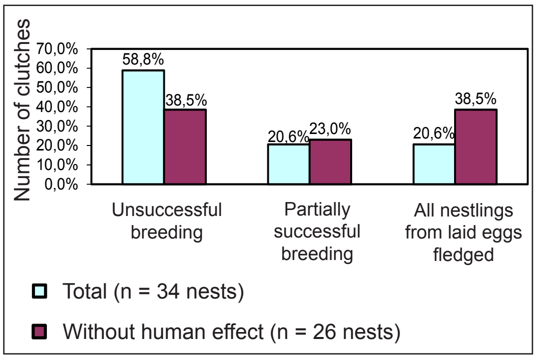

Fig. 4. Overall success rate of breeding of ring ouzel.

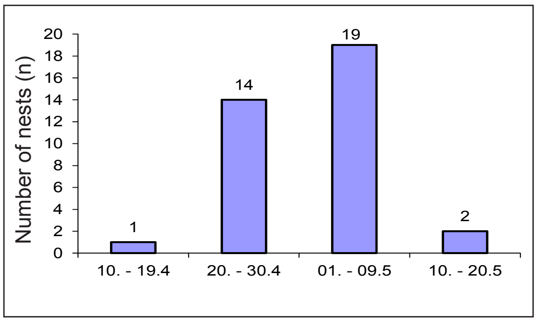

Fig. 5. The breeding season of the ring ouzel as shown by the number of first-egg laying dates in „third-month" periods.

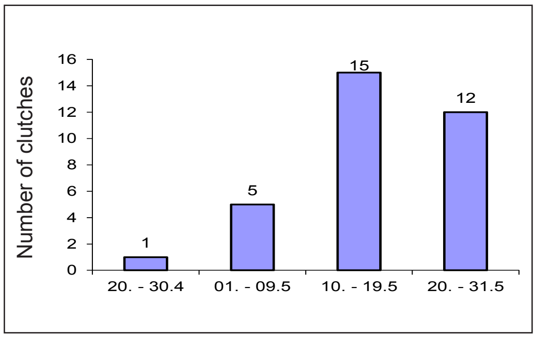

Fig. 6. Dates of chick hatching divided into decades of days in April and May.

Variable	x (n)	min - max	S
Date of the laying of the first egg	1st – 2nd May (36)	10th April– 17th May	7.31
Date of the first chick hatched	16th May (33)	24th April – 30th May	7.13
Date of the first young fledged	28th – 29th May (13)	7th May – 9th June	8.21

Table 3. The date of laying, hatching and fledging of young (n – number of nests measured; S – standard deviation).

Nests with three young (5)		Nests with four young (18)		Nests with five young (5)	
Hatching asynchrony pattern	**Number of cases**	**Hatching asynchrony pattern**	**Number of cases**	**Hatching asynchrony pattern**	**Number of cases**
3 + 0	2	4 + 0	2	5 + 0	0
2 + 1	2	3 + 1	13	4 + 1	2
1 + 2	1	2 + 2	3	3 + 2	3

Table 4. Pattern of hatching asynchrony in ring ouzel nests. The eggs did not hatch all at once, in a given day, the first group of nestlings usually hatched (for example, three chicks in the pattern 3 + 1) , followed by the second group of eggs, which hatched from 0.5 to 1 day after the first hatch (for exemple when one chick hatched later, the scheme is 3 + 1).

Despite being more itmid and elusive than other European thrushes, ring ouzels are highly territorial during breeding season, and often very actively defend the nesting area against both intra – and interspecific intruders. During incubation (23 nests observed), in 19 cases (82.6 %) the degree of aggression was the same in both sexes (whether aggressive or non-aggressive); a slightly higher to definitely higher rate of aggression was observed in females in three cases (13 %), and in one case (4.4 %), the male was more aggressive than the female in defence of the clutch. In nests with young (n = 28), the parent pair participated in the defense of the nest to the same extent in 20 cases (71.4 %). The female was more aggressive than male in three nests (10.7 %), and the male was more active in defense than female in five nests. In females (n = 15), in eight cases (53.3 %) the degree of aggression was the same during the incubation period and during the rearing of the young in the nest, (i.e., they behaved more or less the same during the entirety of the nesting period). Only one female (6.7 %) was more aggressive during incubation than during the care period for nestlings, but up to six females (40 %) showed increased aggression in nests with young. Males (n = 15) behaved in the same way in seven cases (46.7 %), throughout the nesting period. Similarly to females, only one male (6.7 %) showed an increased degree of aggression during incubation, but up to seven males (46.7 %) were more aggressive when there were young present in the nest.

In 1986, six nests were collected: three immediately after successfully fledging, two after predation of nestlings, and one in which the eggs failed. The presence of different groups of invertebrates was also examined. There were larvae and adults of Diptera, Coleoptera, Hymenoptera, Acarina, Heteroptera, Psocoptera, Colembola, Araneae, Chilopoda and Siphonaptera. Extreme numbers of flea larvae were found in three nests, in two from which young fledged (1200 and 28) and in one where the nestlings were killed by a predator (500 larvae and 2 imagos).

Discussion

Ecotones or environmental discontinuities with a median cover of forest, with open canopy cover consisting of spruce, stone-pine and larch, characterise the optimal habitat of ring ouzel in the Alps or Carpathian mountains. The altitudinal extent of the ring ouzel in the Carpathians is lower than that in the Alps. An increase in abundance of ouzels occurs between 900–1500 m a.s.l., in the subalpine vegetation zone. Nutrient-poor grasslands, forbs and coppice of the high-elevation sites are additional characteristics of preferred habitats. The proximity of clearcuts and young tree stands may also create a landscape, temporarily suitable for the occurrence of ouzels, especially in lower mountain locations (Marisova and Vladyshevskii 1961; Oberwalder *et al.* 2002; Karaska 2002; Janiga and Višňovská 2004; Bashta 2005; Kajtoch 2011). However, nutrient-rich valley grassland and farmlands may have a negative effect on ring ouzel existence, as do large amounts of debris and settlements. Climate change has also proven to be an important indicator of ring ouzel occurrence (Beale *et al.* 2006; von dem Bussche *et al.* 2008), predicting the most suitable ring ouzel habitats in the subalpine temperature range. Snowpack plays a crucial role for the occurrence of birds in spring, when its melt provides much of the water supply in subalpine and alpine ecosystems (Resano – Mayor *et al.* 2019). The water supply resulting from snow highly influences soil moisture and penetrability during breeding season, as well as increases ouzels' access to their primary foodsource – earthworms (Marisova and Vlayshevskii 1961; Glutz von Blotzheim and Bauer 1988; Tyller and Green 1994; Burfield 2002). Earthworms are more active in the upper ground layers and hence more accessible when soil is humid and soft, (i.e., in the mountains during or shortly after rainfall or during the snowmelt period). Since they are considered climate-sensitive invertebrates, ouzels that rely on them as a food source are significantly vulnerable in the face of climate change (von dem Bussche *et al.* 2008). The positive effect that wet and penetrable soils have on the availability of earthworms is thus key for ouzels and some other species of birds in alpine ecosystems (Resano-Mayor *et al.* 2019, Barras *et al.* 2020). When ouzels arrive at the alpine breeding grounds in April, their habitats are still characterized by a dense snowpack. Birds perform daily elevational movements, and overnight in breeding sites, but during the rest of the day, they visit snow-free meadows at lower elevations to forage. An earlier spring snowmelt can accentuate the risk of a phenological mismatch for migratory ouzels, with negative consequences for their population dynamics (Barras et *al.* 2021a, b). Beale *et al.* (2006), suggest that once the trend in climatic variables is taken into account, the ring ouzel territory occupancy will decline by an average of 3 - 6 % per year, as a direct consequence of the recent trend towards warmer summers. In the mid and western European mountains, Alpine ring ouzels have shown a negative population trend since 1990, with a local retreat to higher altitudes (Kronshage 2003). Withdrawal of the ring ouzel to higher ground under the influence of climate change is predicted in the Alps (von dem Bussche *et al.* 2008) and changes are also probable in the distribution of this species in the Carpathians, where an altitudinal shifting of the extent of the lower subalpine zone may occur (Ciach and Mrowiec 2013).

Laying dates for ouzels from the Carpathians or Alps are highly dependent on snowcover and snowmelt. Birds begin breeding at one year of age, and all the evidence points toward a monogamous mating system. Within our research area, 92 per cent of eggs were laid between April 22nd and May 10th. Thus, ouzels reproduce particularly early compared to other sympatric mountain bird species (Barras *et al.* 2020, 2021a). In the Carpathians, females began breeding earlier in the season than in Fennoscandia (Pulliainen *et al.* 1981, Hudec *et al.* 1983). Although there is evidence for the occurrence of second broods in the mid and western European mountains (Walter 1995; Gubitz and Spath 2002), ouzels are generally single-brooded. In the Alps, Carpathians or Fennoscandia, breeding conditions are only suitable for a short time (Barras *et al.* 2020). In some cases, second clutches are in fact substitute layings. For example, at our locality, one female laid the first egg and then was disturbed by a squirrel. The bird was subsequently located in a nearby vacant Song Thrush nest, and laid her next eggs in this new nest. An additional substitute clutch was found in mid-May. However, if breeding conditions remain suitable for longer periods, it is possible that the species may become multi-brooded. In Great Britain, for example, 62 % of females made second breeding attempts. These females usually often laid their first eggs in April, earlier than the mean laying date for all ouzels. Triple-brooded females likely begin breeding the earliest in the season, and have shorter inter-brood intervals than other females (Sim *et al.* 2012, 2013a). The extent of double-brooding is unclear, but likely varies with latitude throughout Britain (Cramp 1988). Tyller and Green (1994) summarized the data from nest records for Wales, Scotland and England, where the laying peak occurred during the first 10 days of May; slightly later than described by Flegg and Glue (1975), and continued until early July. In England and Scotland there was no clear relationship between altitude and laying date, while in Wales, laying was delayed by four days on average for every 100 m in altitude gain. Circumstantial evidence that the extent of double-brooding in ouzels is associated with rainfall, was provided by Appleyard (1994). The number of second clutches was highly influenced by rainfall in June. In the Alps and Carpathians, ouzel are mainly single brooders, and we assume that effective natality is compensated by larger clutch size than in the British Isles (Table 5).

The female alone builds an open-cup nest, lays one egg per day, and performs most, if not all, incubation and brooding (Marisova and Vladyshevskii 1961; Korodi Gál 1970; Durman 1977). However, there is rare evidence of male participation in incubation (Flegg and Glue 1975), usually at night (Gubitz and Spath 2002). The average complete clutch size from the Carpathians and Alps is between 4.24 to 4.6 eggs, and is larger than in Britain (3.7 to 4.2 eggs) (Table 5). Ring ouzel clutches in Welsh and Scotish/English samples are generally similar, and clutches of four predominate (Tyller and Green 1994; Burfield 2002). Durman (1977) and Poxton (1986) recorded more clutches of five eggs in Great Britain during wet years, due to an abundant supply of earthworms for adults during the laying period. Many such clutches were also found in Northumberland (Galloway and Meek 1984). Occasionally, clutches of six were recorded (Flegg and Glue 1975).

During incubation, adult ouzels often fly long distances from the nest to feed. However following the hatch at 12-14 days of incubation, it is advantageous for parents to have a good food source nearby, as both parents provision their nestlings until they fledge at 11-15 days of age (Marisova and Vladyshevskii 1961). During nesting, ouzels largely forage in very short grass swards, with 90 % of the selected foraging sites offering ground vegetation shorter than 10 cm. In the mid-European mountains, grass usually exceeds this height in the first half of of June. Because ring ouzel use the brief window between snowmelt and the growth of ground vegetation for their breeding period, they elect to forage at sites with predominantly short grass (Barras *et al.* 2020). This strong selection preference for short grass indicates that prey accessibility may be the

Sub-sp.	Country	n	Clutch size (%)					x	References
			2 eggs	3 eggs	4 eggs	5 eggs	6 eggs		
torq.	England	79		10 (12.7 %)	56 (70.9 %)	12 (15.2 %)	1 (1.3 %)	4.05	Flegg and Glue (1975)
torq.	Scotland	38		1 (2.6 %)	30 (78.9 %)	7 (18.4 %)	0	4.16	Poxton (1986)
torq.	Scotland	99		(7-15 %)	(76-88 %)	(4-11 %)	0	3.75-4.17	Burfield (2002)
torq.	Scotland	75		7 (9.3 %)	60 (80 %)	8 (10.7 %)	0	4.01	Arthur and White (2001)
torq.	Wales	89	2 (2.2 %)	13 (14.6 %)	63 (70.8 %)	11 (12.4 %)		3.93	Tyller and Green (1994)
torq.	Scotland, England	301	3 (0.9 %)	32 (10.6 %)	228 (75.7 %)	38 (12.6 %)		4.00	Tyler and Green (1994)
alp.	Swiss	92		8 (8.7 %)	38 (41.3 %)	43 (46.7 %)	3 (3.3 %)	4.45	Glutz von Blotzheim (1964)
alp.	Czecho-Slovakia	24		3 (12.5 %)	11 (45.8 %)	10 (41.7 %)	0	4.29	Hudec *et al.* (1983)
alp.	Slovakia	38		3 (7.9 %)	24 (63.2 %)	10 (26.3 %)	1 (2.6 %)	4.24	This study
alp.	Ukraine	17		0	mostly	mostly	rarely	?	Marisova and Vladyshevskii (1961)
alp.	Romania	39		0	12 (30.7 %)	27 (69.3 %)	0	4.6	Korodi Gál (1970)

Table 5. Clutch size of ring ouzels from different regions of Europe (n = number of nests examined, x average clutch size).

main cause drawing ouzels toward higher ground, as a result of the influence of climate change (as predicted in the Alps and Carpathians) (Beale *et al.* 2006; von dem Bussche *et al.* 2008). The transition to more dense vegetation at lower altitude sites formerly inhabited by ring ouzels, is followed by the shift of ring ouzel to sites at higher elevation, and the movement of blackbirds and fieldfares into the newly-suitable lower elevation habitats (Kronshage 2003; Janiga´ s personal observations).

Eggs may be at considerable risk during incubation. While losses during incubation are usually lower than losses among nestlings (Korodi Gál 1970; Durman 1977; this study), other studies suggest that more losses may occur during incubation (Poxton 1986). The main causes of loss are infertile or failed eggs, cold weather, egg predation (in our case by squirrels), and nest and parent predation by raptors and mammals (Poxton 1986,; this study). Several studies have reported nest predation by fox, mustelids and corvids, in which case ouzels may disappear from the breeding area (Thompson *et al.* 1997). Losses of nestlings are usually as a result of an unspecified cause (Barras *et al.* 2021a), although wet weather (Flegg and Glue 1975), limited food (Barras *et al.* 2021a) or predation (this study) are the main causes of brood reduction. Our study showed that while ouzels are not common prey for some raptors, the conspicuous behaviour of ring ouzels may make them vulnerable to predation, and even limited predation may adversely affect their numbers. Repeated visitation of nests by humans may attract the attention of raptors during aggressive defence of nests by ouzels, and may reduce breeding success. We found that ring ouzels are highly territorial, and interactions between parents and intruders were often recorded (60 % of nests). From this point of view, potential disturbances must be minimized during ornithological research. The average number of chicks fledged per nest is usually between three and four (Tyller and Green 1994; Burfield 2002; Sim *et al.* 2010, 2012; Barras *et al.* 2021a), but in our case, only two young per nest successfully fledged. Poor reproductive success, (1.6 fledglings/nest) was also reported by Walter (1995) in the Alps. Thus, an important element in the protection of this single brooding species in the mid- European mountains is to reduce disturbance of breeding birds. Fledglings usually remain dependent on parents for a further 2-3 weeks (Cramp 1988). If the females re-nest, the male often provides most post-fledging care (Appleyard 1994). However, in the Alps and Carpathians, parents leave the breeding grounds to move towards higher elevations as soon as the brood have fledged, most probably to track suitable feeding grounds. At many study areas, food sources procured for fledglings included earthworms, tipulids, green caterpillars, coleopterans, spiders, dipterans, geometrid larvae, millipedes, and lizzards (Marisova and Vladyshevskii 1961; Korodi Gál 1970; Tyller and Green 1994). Blueberries may also be an important food source for the survival of juveniles, as the birds change their diet from invertebrates, (potentially highly invaded by helminths) (Sitko and Okulewicz 2010), to fruits. Blueberries and other fruits may flush and reduce the amount of helminths in the gastrointestinal tract of hosts (Sitko in verb). In the late summer, when worms may be inaccessible, ring ouzels feed predominantly on fruit; notably blueberries, rowan, and yew berries (Marisova and Vladyshevskii 1961). This period is crucial for ouzels because most estimated first-year mortality occurs in this species in the first five weeks post-fledging (Sim *et al.* 2011). An ouzel juvenile's survival may depend on its mobility within its habitate in order to locate suitable habitat for foraging (Sim and Rebbeca 2003; Sim *et al.* 2007), remain concealed from predators (Sim *et al.* 2013b; this study), and avoid endo and ectoparasites (e.g., Sitko *et al.* 2006; Sitko and Okuliewicz 2010; Sitko 2011; Bush *et al.* 2018).

This research provides baseline data on breeding ecology of ring ouzel in Slovakian mountains. It would be interesting to compare this historic data to recent samples from the same locality to assess the impact of afforestation, climate change and the increase in tourism on breeding behaviors within this species. An important element in the protection of ouzels may be the maintenance of extensive forms of land-use which are conducive to the short, grassy vegetation responsible for generating a sufficient food source in mountain areas. Important context may also be offered through the comparison of potential differences between mountain and lowland populations, and the different land-use pressures experienced by both habitats.

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