The placement and the size and shape of nests of Ring Ouzel (*Turdus torquatus*) reflect the environmental conditions at different altitude

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Abstract. The placement and size and shape of the nests of the Ring Ouzel vary locally in response to variation in environmental conditions such as altitude. Nests at the higher elevations were built on thinner and younger spruce trees than nests located at lower altitudes. Nest at low elevations tended to be smaller but more spacious than their counterparts. In some cases, they tended to be wide with short nest cups. These differences in nests suggest that Ring Ouzels tailor nest structure to the microclimate at the nest site.

Key words: Turdus torquarus, nest location and structure, breeding, the West Carpatians, principal component analysis

Introduction

Pair formation in birds is closely related to nestbuilding behaviour, as evidenced by nest-site choice and the use of nest material by many birds during courtship and pairing.

Selection of an appropriate nest site is a critical aspect of avian reproduction, since it determines the environment to which the adult, the eggs, and nidicolous young will be exposed for extensive and critical portions of the life cycle. Thus, nest placement may affect reproductive success importantly, and it presumably has evolved in relation to various factors, such as predation (Pikula and Beklová 1984), the local availability of resources (Bocheński 1985), and microclimate (Pikula 1979).

The structure an avian nest is also related to environmental condititions. The nest may be an evolutionary compromise between such benefits as insulation from adverse local climate (low temperatures and rain), keeping the eggs and nestlings warm during incubation (depending on the material used in nest building) and other physical factors (Sciurine and Kern 1980, Kern 1984), and such costs as the energy expended in nest building, predation risk during nest building and nest predation due to nest conspicuousness (Slagsvold 1989).

Adaptive variation among species in bird nests has been discussed, i.e., different species coping

with radically different biological and climatic conditions (Soler *et al.* 1998). However, similar variation would be anticipated intraspecifically since species with a wide geographic range are also confronted with a wide variety of nesting conditions. The Ring Ouzel (*Turdus torquatus*) is amenable to such a study since its nests often persist in the late snows in May. The species breeds in the mountains and moors of Scandinavia, north Britain, Ireland, central and southern Europe. In the Western Carpathians it nests reguraly in the spruce forests near subalpine meadows, mainly between 450 and 1,800 m a.s.l. (Janiga and Poxton 1997).

Our study relates intraspecific variation in the placement and structure of the nests of Ring Ouzel to local climatic conditions. The work deals with the following questions: Does plasticity exist in the nest-building behaviour and therefore in the structure of Ouzel nests? Are the birds able to change the structure of the nest to fit the prevailing conditions to which they are exposed?

Material and Methods

The study area in the locality Brankov - Low Tatra mountains (West Carpathians, Slovakia) has been described in Janiga (1992) This site has an elevation ranging from 850 to 2,500 m. The terrain consisted of a relatively steep, south-north running mountain chain surrounded by gentle slopes to the west and east. The vegetation of the study area is the young fragmented spruce forest intermixed with beech. At higher elevations, meadows and other opened areas are common. Field data on 35 nests were obtained from April through June from 1985 to 1989. One nest was collected in Choč Hills in 1989. The next four nests were collected in fragmented spruce forests in the West Tatra mountains during May 1998-1999. Allong the edges of this forest are subalpine and alpine meadows with stands of beech trees.

Nets were placed close to the spruce trunks, one was find on the rocky ground. When the eggs were laid, the following information was recorded for each nest loacation: Diameter of tree near the ground, height of the nest aboved the ground, location of nest in the study area, elevation, and nest dimensions - inner and outer diameter, height and height of the nest cup (see Results). When the young fledged the nests were collected and the horizontal thickness of three distinguishable nest layers were measured **12** M. Janiga & Z. Višňovská

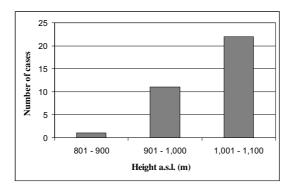


Fig. 1. Distribution of nest locations of *Turdus* torquatus by altitude.

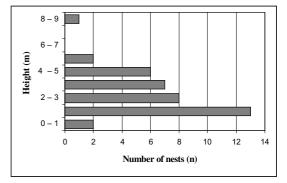


Fig. 2. Height above ground of Ring Ouzel nests.

and weighed (after drying). The study sites were visited three – four times a week during the reproductive months.

The relation between elevation, nest height above the ground and nest dimensions was analyzed using a principal component analysis (Schaefer 1976), where character loadings were computed from a correlation matrix. The data were standardized.

Results

The mean height above the sea level of nests at the locality Brankov was 1,032 m (Fig. 1), in the West Tatra moutains the height ranged from 1,320 to 1,480 m. At Brankov, 20 nests were placed at eastern slopes of the mountain chain, and 15 on western parts. Height of the nests above the ground was ascertained in 39 cases. Only a small proportion of birds nested on the ground (2 nests). The mean height was 2.8 m (s = 1.6 M, max. = 8.5 m). The number of nests in categories at one meter intervals is shown in figure 2. All ouzel nests were in living spruce trees. The width of the trunk near groud was measured in 37 of such trees; and of these 31 had the trunk diameter from 3 to 20 cm. The birds preferred young spruce trees.

The nest of ouzels is structured from three distinguishable layers. Blades of grass were the

most common material of the inner lining layer. The middle layer was mainly structured from the mud, and the outer ftom the twigs. Table 1 and figure 3 summarize the data on dimensions of ouzel nests.

The results of the principal component analysis for the Ring Ouzel nest placement are shown in table 2. Component 1 (PC1) has high correlations with the distance of the nest above the ground, with width of the trunk, and also with the nest height. The variables are negatively correlated to the height above the sea level. Those birds, which nested at lower altitude, built their nests at higher distances above the ground and used older spruce trees than birds nesting at higher altitude. At low elevations, ouzels tended to build high nests. PC-2 summarizes 23 per cent of the overall variance explaining the trends in the width of nests. At higher elevations, the nests tended to be wider than the nests placed at lower altitude. PC -3summarizes 19 per cent of variance, the three variables in this component are of high values of the same sign (+), and the axis fairly represents the trends in the general size of nests. PC-4 tracks a contrast between the narrower nest with high nest cup (but not higher nest) at higher elevations and relatively wider nests with shorter nest cup which tended to occur at lower altitudes. PC -5 desribes the contrast between the size of the nest and size of the nest cup. There were large nests with smaller nest hollows, and smaller nests

Variable	х	(n)	min-max	S
Height of the nest cup (HH)	7.3 cm	(35)	5.3 - 8.7 cm	0.79
Inner diameter (ID)	10.4 cm	(36)	8.0 - 12.0 cm	0.79
Height of nest (H)	13.7 cm	(36)	11.0 - 19.0 cm	1.82
Outer diameter (OD)	17.8 cm	(37)	14.3 - 23.0 cm	2.18
Height of the 1 st layer	2.4 cm	(14)	0.4 - 3.5 cm	0.94
Height of the 2 nd layer	1.5 cm	(15)	1.0 - 2.0 cm	0.30
Height of the 3 th layer	2.2 cm	(13)	0.5 - 4.0 cm	1.18
Depth of floor (sum of the three	layers) 6.4 cm	(35)	3.0 - 11.5 cm	1.82
Total weight of nest	171.4 g	(27)	86.0 - 328.0 g	55.34
Weight of the 1 st layer	20.5 g	(22)	11.5 - 29.0 g	5.24
Weight of the 2 nd layer	116.1 g	(22)	58.5 - 234.5 g	47.54
Weight of the 3 th layer	44.9 g	(22)	18.0 - 79.0 g	16.84

Table 1. Characteristics of Ring Ouzel nests in the West Carpathians.



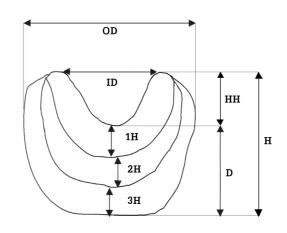


Fig. 3. Definition of nest measurements. OD - outer diameter, ID - inner diameter, H - height of the nest, HH - height of the nest hollow, 1H - height of the 1st layer, 2H - height of the 2nd layer, 3H - height of the 3rd layer, D - depth of the nest floor (sum of three layers)

with large nest hollows. The large nests tended to be located at lower altitudes, and placed at young spruce trees (compare PC1). PC – 6 is probably a measure of general shape of nests. Some nests were narrow and high with wide and short nest hollow and their counterparts were wide and short but of narrow and high nest cup. The first six components explained more than 95 per cent of data variance.

Discussion

Adaptations to habitat - nest placement (PC1)

Factors affecting the choice of a suitable nesting site by birds are under strong selective pressures that favor individuals who choose sites where the chance of rearing a brood is greatest (Smith 1974, Gibo *et al.* 1976). In Eurasia, Ring Ouzels breed in upper and middle latitudes, from oceanic upland in Great Britain to continental montane in Alps, Carpathians, and Caucasus (Cramp 1983). In the mountains, it breeds normally in conifere woodlands on shady and moist slopes, preffering margins near moist open grass or moors near woods, among which spruce (Korodi Gál 1970, Glutz von Blotzheim 1988, Janiga 1992) Nest sites used in Europe are summarized in Table 3. Although the nest placement of the Ring Ouzel varies geographically, this can be explained mostly by differences in climate. The placement of bird nests is often believed to be adaptive in minimizing adverse climatic effects. The nests of certain species are placed to maintain an amenable microclimate and to reduce wind stress (Collias and Collias 1964). The nest placement of the Ring Ouzels also reflects the local climatic conditions. The nests from mountain chain tended to be lower in the young spruce tree than the nest from lower elevations (see PC1 - nest placement component in results). Nest placement comparably varies in other species of nidicolous birds. For example, the nests of the Common Amakihi (Hemignathus virens virens) from a warm rain forest on Kohala Mountain were significantly higher in the canopy of trees than the nests from Mauna Kea, a cold upland savannah (Kern and Riper 1984). Because the ouzels are able to tolerate exposure to high winds and rainfall, the important thermal factor favoring selection of a nest site with a dense branch and leaf spruce canopy (small trees at higher elevations, older - higher trees at lower altitude) is probably amelioration of heat stress during the afternoon by maximizing the time that the nest is shaded. This may be a relatively common thermoregulatory mechanism used by many other species of birds (Pikula 1979, Walsberg 1981, Pikula and Beklová 1983, 1984).

The size and shape of nests have also been said in some cases to conserve warmth (Schaefer 1953), and to protect young from intense sunlight in birds (Collias and Collias 1964). Palmgren and Palmgren (1939) documented differences in the nests of several European songbirds relative to climatic variations between breeding areas. Watt and Dimberio (1990) and Lent (1992) suggested that the relationships of bird nest structure to individual fitness may vary with species and with temporal and spatial variation in the environment. Schaefer (1980) reported differences in the nests of Northern Orioles (Icterus gulbula) as a function of latitude, and Kern and Riper (1984) described differences in the nests of Common Amakihi (Hemignathus virens virens) as a function of elevation. Our data complement these and illustrate that altitudinal differences also occur in the nests of at least one Turdidae species.

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Width of spruce trunk on the ground	0.60	0.20	-0.21	0.16	0.42	-0.12	0.58
Inner diameter	-0.08	0.62	0.18	-0.20	0.49	0.48	-0.26
Height of the nest hollow	-0.0007	7 -0.15	0.68	0.48	0.38	-0.33	-0.17
Outer diameter	0.03	0.55	0.33	-0.37	-0.34	-0.56	0.13
Height of nest	0.38	-0.18	0.57	-0.12	-0.35	0.54	0.27
Height above the ground	0.63	0.18	-0.15	0.25	-0.28	-0.03	-0.64
Height above the sea level	-0.30	0.43	-0.04	0.70	-0.36	0.20	0.26
Variation (%)	25.4	23.3	18.8	12. 1	9.0	7.5	3.9

Table 2. Loadings of the original variables on the principal components of variation of nest placement and structure measurements.

14

M. Janiga &

Z. Višňovská

Species	Country	Height a.s.l. (m)	Height above the ground	References	
		(n)	(n)		
torq.	Great Britain	225 - 525m, min-max= 30 - 1125m (408)	0 - 0.45m (94%), 0.45 - 3m (6%) (297)	Flegg and Glue, 1975	
torq.	Scotland	260 - 350m (52)	0m, rarely higher (52)	Poxton, 1986	
	Scotland	209 - 533m, x=352 (22)	0m, rarely to 1.5m (22)	Poxton, 1987	
alp.	<i>Swizerland</i> (Alps, Jura)	from 1,000 to upper forest level (180?)	2.5 - 3m, min-max = 0-10m	Glutz von Blotzheim, 1964	
alp.	<i>Germany</i> (Schwarzwald)	1,100 - 1,350m (?)	(?) (?)	Knoch, 1970	
alp.	Poland (Tatras)	900 - 1,600m, locally from 700m (?)	3.5m, min-max = 1 - 16m (26)	Bocheński, 1968	
alp.	Czechoslovakia	locally from 400m, mainly 800 - 1500m (?)	2.9m, min-max = 0 - 8m (16)	Hudec <i>et al.</i> , 1983	
alp.	<i>Slovakia</i> (Low Tatras, West Tatras)	900 - 1,100m, 1,320 - 1,480m (37)	2.8 m, min-max = 0 - 8.5m (39)	Janiga and Višňovská, this study	
alp.	<i>Ukraine</i> (Carpathian Mountains)	to 1,400m, to upper forest level (17)	0.5 - 10m (17)	Marisova and Vladishevskii, 1961	
alp.	Romania (West Mountains)	app. 1,430m (39)	6.03m, min-max = 0.8 - 18m (39)	Korodi Gál. 1970	
amic.	Armenia (Caucasus)	upper forest level (?)	on the ground mainly (?)	Dementiev <i>et al.</i> , 1954	

Table 3. Location of Ring Ouzel nests in Europe.

Nest width in relation to altitude (PC2)

In ouzels, nests built at higher altitudes are relatively wider than nests placed at lower elevations. The differences in the width of the nest may be due to differences in phenotypes of breeding pairs. Owners of such nests tended to lay larger eggs than birds from narrower nests (Višňovská 2000). Intraspecific correlations between size of birds and shape of the nest are well documented in Schaefer (1976).

Size of nest independent on altitude (PC3)

It has recently been shown for the black wheatear (Oenanthe leucura – Moreno *et al.* 1994) and the magpie (*Pica pica*, Soler *et al.* 1995) that individual with better parental qualities build larger nests. Trends of variation in the general size of nest in ouzels (PC3) did not relate to elevation, and the height of nest from the ground. From this point of view, we may assume that parental quality of ouzel does not differ in pairs breeding at different altitudes. Table 4 gives details on nest size for a number of ring ouzel populations in Europe. Size of nests generally does not differ between the localities. Additionaly, variation in size of nests seems to occur independently of altitude or latitude of ouzel breeding sites.

Cup depth and altitude (PC4)

This may again reflect size differences in birds

because depth of the nest cup highly and positively correlates to altitude. But there was found correlation between shape of eggs and depth of nest cups. Long and narrow eggs tended to occur in the nests of deep cups. Variation in microclimate is likely to cause variation in eggs shape in birds. Additionaly, such variation in shape seems to occur independently of variation in food supply before laving (Johnston and Janiga 1995). In general, eggs laved in colder conditions are elongate (long and thin) and eggs produced under warmer conditions are fat (short and wide). The trends in the shape reflect the physiological characteristics of eggs (e.g. proportional amount of albument, yolk, water, etc. - Bolotnikov et al. 1985). The differences in nests suggest that ring ouzels tailor nest structure to the microclimate at the nest site. This is also suggested by the fact that in cool subalpine mountain chain and meadow there is a positive relationship between the height above the sea level and depth of nest cup.

Nest size versus cup size (PC5)

Bocheński (1968) emphasizes two important characteristics of nests in *Turdus philomelos* - the height of nest from the ground and the depth of the nest cup. He says that nests situated nearer the ground and those with a deeper cup have a more stable microclimate than those located at higher up. We found similar trends at PC5 component (see results). Nests located near the ground tended to have larger cup than nests placed 15

Nest structure

of Ring Ouzels

Species	Country	Locality (n)	Variable	References
torq.	Great Britain	Wales (2)	OD- 14.0cm H- 6.0 - 6.6cm ID- 9.0 - 9.3cm HH- 4.0 - 4.5cm	Bocheński, 1968
torq.	Finland	(?) (?)	OD- 14.8 - 22.0cm H-? ID- 9.0 - 10.6cm HH- 4.5 - 6.5cm	Pulliainen <i>et al.</i> , 1981
alp.	Poland	(?) (20)	OD- 17.6cm (15.5-20.5) H- 12.2cm (9.5-20.2) ID- 10.2cm (9.3-11.3) HH- 6.2cm (5.0-7.5)	Bocheński, 1968
alp.	Czechoslovakia	(?) (5)	OD- 17.6cm (15.5-20.5) H- 10.8cm (10.0-11.0) ID- 9.2cm (8.5-10.0) HH- 6.8cm (5.0-8.5)	Hudec <i>et al.,</i> 1983
alp.	Slovakia	Low Tatras, Tatra Mountains (37)	OD- 17.8cm (14.3-23.0) H- 13.7cm (11-19) ID- 10.4cm (8-12) HH- 7.3cm (5.3-8.7) nest weight- 171.4g (86.0-328.0)	Janiga and Višňovská, this study
alp.	Ukraine	Carpathian Mountains (6)	OD- 18.12 - 18.37cm H- 10.57cm ID- 9.57 - 9.87cm HH- 4.47cm	Marisova and Vladishevskii 1961
alp.	Romania	West Mountains (10)	OD- 15.0 - 20.0cm H- 12.0 - 13.0cm ID- 9.0 - 10.0cm HH- 5.0 - 6.0cm nest weight- 191 g	Korodi Gál. 1970

Table 4. Variation in dimensions of Ring Ouzel nests from European localities.

more highly but they were relatively smaller than elevated nests. Such ground nests mainly occured at lower altitudes (compare PC1). Kern (1984) compared the nests of different races of Zonotrichia leucophrys. The races are about the same size, but their nests are not. Mountain race ssp. oriantha build its nests on and above the ground: their elevated nests were much larger than their ground nests. The elevated were significantly heavier, and had a thicker floor than ground nests. Moreover, nests of Z. l. nuttalli and oriantha, which were built on or above ground, generally had much thicker walls and floors than those of Z. l. leucophrys, which were built in the ground. All nests blocked out 96-99% of air currents to which they were exposed. This characteristic is particularly well-suited to the windy conditions that prevail on the breeding grounds.

Shape of nest independent on its location (PC6)

Some ouzel nests are short and wide, some long and thin. We assume that nest shape may be a result of individual nesting abilities of breeding birds.

Our results suggest that the nest placement and structure may vary with temporal and spatial variation in the environment. More data are needed to elucidate these relationships. Such data would be of interest for other bird species, particularly if combined with data on genetic variability. Some trends in size and shape of nests indicate that bird nest morphology should be also viewed as a phenotypic trait subject to natural selection.

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16