

Why dark plumage of the European Blackbirds *Turdus merula*?

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Abstract

Why does the European Blackbird's dark coloration match the ground color of the less widespread of its breeding habitats, the riparian forest, although its main European population occurs in the pale-litter woodland? It is argued that crypsis of all the age stages was more necessary in riparian stands, as this habitat is more risky for the species owing to a high ground vegetation surrounding a foraging bird. Poorer crypsis of Blackbird plumage in pale-litter habitats may be a neutral feature, being compensated by easier scanning of the surroundings over the lower and sparser herb vegetation and by a tendency to remain in dark sites. The black plumage of the Blackbird male, perhaps reinforced by sexual selection in pristine forest conditions may also retain its cryptic function.

Keywords: Dark/black plumage, crypsis, primeval habitat, European Blackbird *Turdus merula*

Introduction

When seen on a suburban lawn a Blackbird, especially a male, is both strongly contrasting with the background coloration and unusually fearless in comparison with the behaviour of the same and other thrush species in natural woodland. The Blackbird is the only European *Turdus* species of lowland forests which has a dark plumage. In this paper we attempt to find an explanation for this unique coloration of all the Blackbird age classes. An additional point is, why this coloration appears especially cryptic when under riparian woodland conditions, and why poorer crypticity does not prevent the species from occurring in pale-litter woodland?

The material and ideas used for this analysis originate from observations carried out in remnants of the close-to-pristine forests (Tomiałoć, 1993; Bursell & Dyck, 2003), which is in line with D. Lack's (1965) suggestion that "*Evolutionary ecology should be studied primarily in the natural habitat of the species, where its present adaptations have evolved*". The European Blackbird is thought to have occurred originally in moist or marshy deciduous and mixed woodland (Tomiałoć, 1993), a habitat not unlike the primeval tree-stands still preserved in the Białowieża National Park, Poland (hereafter referred to as BNP). Another ancestral habitat may be montane, mainly along rivers

and streams, as is recently known from the east-Palaearctic mountains (Snow, 1958; Clement & Hathway, 2000).

This paper is a by-product of other field studies of forest birds (Bursell & Dyck, 2003; Tomiałoć & Wesolowski, 2005). Difficult to collect (hence, scarce) observations of the extremely secretive forest Blackbirds (Tomiałoć, 1993, 1994) allow us to offer only a suggestive explanation for the species' unusual plumage coloration and for a behavior connected to this. In secondary, chiefly urban populations some of these pristine features have been lost entirely (e.g. preference for forested and wet sites), or they lost their pristine function (e.g. crypticity in plumage and behaviour); thus, our observations from the close-to-pristine habitats are the only source of "original" data.

Primeval habitat of European forest thrushes

The pristine habitat of two common forest thrushes (the Blackbird and the Song Thrush, *T. philomelos*) must have been quite different physically and structurally from the secondary woodland or parkland they often inhabit recently. The BNP close-to-pristine tree stands reflect an "original" state of the optimal habitat: it is structurally very patchy at the ground level, abounds in light and dark, dry and moist sites (see photographs in British Birds 98:181-184), all contributing to a mosaic of microhabitats best exemplified in riparian woodland, but present also in other forest types (Faliński, 1986; Bobiec et al., 2000). Of importance is the high number of dark patches produced by the deep shadows of a tall forest, the bare dark soil exposed by uprooted trees or by big game, and a scarcity of open glades (limited edge-effect) amidst extensive forest tracts.

Received: 18-VIII-05

Accepted: 27-XII-06

Distributed: 28.VI.07

However, even for so well studied a species as the Blackbird it is not clear (Snow, 1958; Cramp, 1988; Glutz v. Blotzheim & Bauer, 1988) precisely which type of woodland was its ancestral habitat. Across the European Lowland its strong preference for dark humid stands was emphasised by early researchers (Gloger, 1833; Naumann, 1905; Tischler, 1941), who barely knew the human-adapted populations of the species. Even today, such a narrow habitat spectrum remains typical of the east-European populations (Malchevskiy & Pukinskiy, 1983; own obs.), while the widest array of (secondarily?) occupied habitats is reported from heavily transformed Western Europe. The latter feature is thought to result from its recently increased population and ecological expansion (Glutz v. Blotzheim & Bauer, 1988), which finds support in the data from the BNP, where the Blackbird is almost three times more numerous now than it was 30 years ago (Tomiałojć & Wesolowski, 2005). Studies classifying this species as an inhabitant of bushy formations or of dry-ground woodland seem to describe secondary situations.

It has been documented (Tomiałojć et al., 1984; Tomiałojć 1993) that riparian ash-alder *Circaeo-Alnetum* stands in BNP harbour the highest Blackbird density of 2.5-2.7 p/10 ha. Yet, the dry-ground oak-lime-hornbeam *Quercus-Tilio-Carpinetum* stands, once widespread across our continent, are also well populated, perhaps only recently. Although in the latter habitat the Blackbird density remained lower for 15 years (1.8-2.3 p/10 ha), its breeding success, confusingly, was consistently higher (Tomiałojć 1993, 1994). There are at least two potential reasons for the former habitat to be preferred originally: (a) better food resources or (b) greater safety owing to a more complex structure, offering more refuges. These hypotheses should be investigated.

Food resources in deciduous forests. During the breeding season, the Blackbird's food consists mainly of earthworms, but also of insects and snails (Snow, 1958; Glutz v. Blotzheim & Bauer, 1988; Tomiałojć, 1993). Yet, contrary to expectations, the studies in BNP have shown that the macro-invertebrates in the litter and soil (down to 40 cm deep) are less numerous in the ash-alder stands than in most variants of the oak-lime-hornbeam forest (307 versus 349-401 indiv./m² – Kozulko, 1999). The earthworms alone are also less abundant in the ash-alder (310 kg/ha) than in the oak-lime-hornbeam (422 kg/ha) stands (Kozulko 1999, Kowalczyk et al. 2003), although such a small (biologically insignificant?) difference might be compensated by a reversed proportion in the abundance of saproxylic invertebrates and *Succinea* snails which are more numerous in the ash-alder stands (Wallwork, 1976; Tomiałojć et al., 1984; Speight, 1989; Fog, in Møller, 1997). The difference was more pronounced during the drought conditions when the numbers of invertebrates in the soil and litter of riparian stand were clearly lower (Tomiałojć, 1993). A lack of consistency in BNP between the food abundance and Blackbird densities, the latter parameter also in other European riparian stands being by 25-75% higher not lower (Cramp, 1988; Glutz v. Blotzheim & Bauer, 1988; Flade, 1994), is unexplainable in terms of food resources. There seems to be also barely any other thrush/bird species competitively (excluding predators) superior to the Blackbird under European conditions.

Difference in safety depends on the presence of dark patches. Higher Blackbird densities in wetter sites may be due

to them being safer, because the riparian stands are more complex structurally, contain numerous dark patches, have more decaying fallen trunks and exposed earthy root systems (Faliński, 1986; Møller, 1997; Tomiałojć & Wesolowski, 2005). These sites have a more complex structure of their herb-, bush- and undergrowth-layers (Faliński, 1986). The soil in riparian stands remains partly deprived of the vegetation cover, because of water pools and fresh uprooted windfalls. Finally, they have more trees (*Fraxinus excelsior*, *Alnus glutinosa*) which produce blackish decaying litter. Against such a mosaic combination of background colours all the age categories of Blackbirds may be better camouflaged. Conversely, the dry-land stands, such as deciduous or mixed deciduous-coniferous, which are more extensive both in BNP and in Europe generally, have mostly pale litter with fewer dark sites. Consequently, in such stands and even more in managed woodland and in urban parks the Blackbirds should be much more conspicuous.

Material and methods

The field data originate from the 1975-95 study of Blackbird and Song Thrush breeding ecology carried out in primeval forest of the BNP (Tomiałojć, 1993, 1994, unpubl.), as well as from the work in managed and close-to-pristine forests (Suserup, Strødam) of Denmark (Bursell & Dyck, 2003). In BNP, except for casual observations collected during 25 breeding seasons, the detailed 6-year study was carried out on the Blackbirds (18 pairs, 33 colour-ringed adults) occurring within two sample plots (33 ha and 50.5 ha), one in the old-growth of the riparian forest, the other in the drier oak-lime-hornbeam stand (Tomiałojć, 1993, 1994). The behavior was registered during 140 hours spent in blinds at 17 Blackbird nests in both habitats.

In the Danish forests (Suserup and Strødam) the field-work was conducted during the snowless winter of 1997/98 in an attempt to estimate the degree of background colour matching in selected passerines (Bursell & Dyck, 2003). In 36 days, the investigations took place in natural old-growth forests, where the Blackbird density index was 6.0 times higher than in younger managed stands.

Results and discussion

A majority of Blackbirds flushed from the ground had been staying along the base of decomposed dead trunks (in BNP as well), where the color mosaic was formed by reddish brown litter, brown dead wood and fungus-covered black wood. As elsewhere, the Blackbirds showed a strong preference for ground foraging ($p < 0.0001$, χ^2 -test, 94.6% of observations). Out of 102 foraging records (one record per bird), 55.8% concerned individuals remaining under cover (dense thickets protecting against an avian predator). Individuals more than two meters away from dense cover showed a significant preference for the pooled group of color backgrounds: reddish brown-warm brown-black ($p < 0.001$, χ^2 -test). Therefore, separate notes were taken on reddish brown, warm brown and black backgrounds (Bursell & Dyck, 2003). Given that less than 1% of the ground was covered with black patches (bare soil, decomposing ash leaves and trunks), it was striking that 44%

(20 out of 45) foraging observations more than two meters from cover were on completely black background. Even if the number of observations is too low to be conclusive it strongly suggests that away from cover the matching background color is very pronounced.

Is plumage coloration of thrushes cryptic?

Almost 90% of world thrushes have a buff or pale brown back with more or less mottled breast (Clement & Hathway, 2000). Such a pattern is thought to be primitive in this group (del Hoyo et al., 2005) and apparently cryptic against the prevailing color of the usual forest litter and against the background of arboreal nests. For instance, the Eurasian species originally inhabiting the dry and grey lichen-covered coniferous forests (*Turdus viscivorus*, *T. atrogularis*) have the palest mantle, the eurytopic Song Thrush is somewhat darker, whereas the Redwing, *T. iliacus*, the Ring Ouzel, *T. torquatus*, the Siberian Thrush, *Zoothera sibirica* and the Blackbird, nesting in wet sites, are the darkest.

The Blackbird is the only European *Turdus* species of lowland forests which has a very dark plumage. In Eurasia, there are not only some *merula*-like forms in the southern part of the supercontinent, but also the Siberian Thrush and the Ring Ouzel. These largely dark-colored species, inhabit either flood-plain thickets or montane conifer stands. In other continents there are also some species dark or black-plumaged, e.g. *T. olivaceus* (dark forms), *T. poliocephalus hades*, *T. nigriceps*, *T. infuscatus*, *T. nigrescens*, *Platycichla leucops* and *P. serranus*. Almost all of them occur in humid rain or cloud forest (Clement & Hathway, 2000; del Hoyo et al., 2005), apparently corresponding to BNP riparian stands.

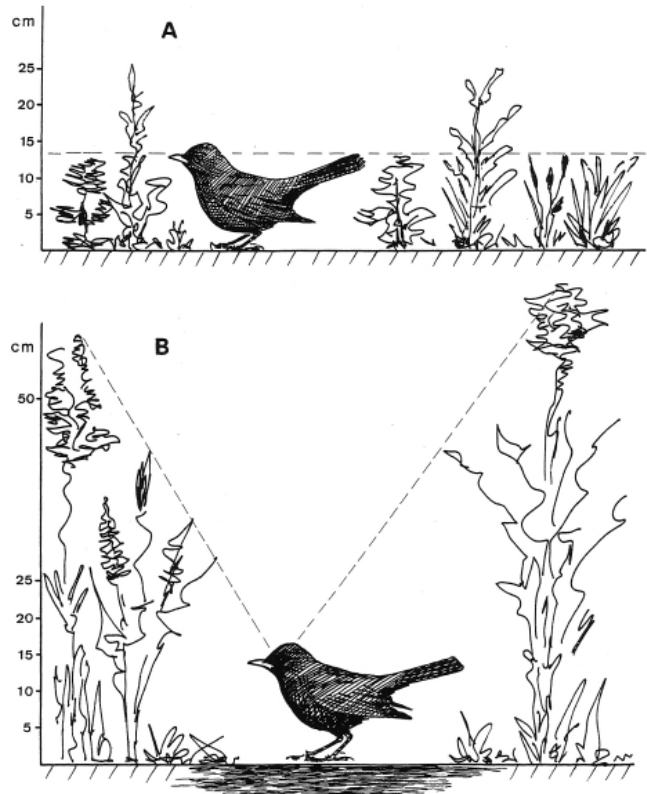


Figure 1 - Visibility radius by a foraging vigilant Blackbird in two habitats of BNP. A - wide angle while in the low herb-layer of the oak-lime-hornbeam forest, B - a limited visibility while amongst the high herb-layer of the riparian ash-alder forest.



Figure 2 - A male of Siberian Thrush by the nest. Note black-and-white mosaic of willow thickets, and a white eye brow which disrupts the bird's silhouette. Photo by O. Bourskiy.

Table 1 - Mean coverage (%) by herb and low-bush vegetation in the main old-growth forest habitats of the Bia³owieża National Park. N – sample size: number of points of measurements taken in May-June 1979 by J. Blondel (unpubl.). Habitats: Aa – Ash-alder riparian forest; Olh – Oak-lime-hornbeam; Mcd – Mixed coniferous-deciduous.

VEGETATION LAYERS	HABITAT (N)		
	Aa (300)	Olh (395)	Mcd (250)
50–100 cm	17.6	3.3	2.8
25–50 cm	49.6	16.4	2.8
0–25 cm	79.6	72.1	23.2

Dark brown coloration as a possible camouflage. The predominant dark brown coloration of all Blackbird life stages, except the adult male, apparently constitutes a derived trait separating this species from probably pale-coloured ancestral forms. The dark brown color of the “average” Blackbird, and of other dark thrushes, could work as a camouflage when such individuals are either on their nests located in semi-darkness or foraging on the dark forest floor. In close-to-pristine stands of BNP, most Blackbird nests are found indeed in structures hidden in deep shadow (Tomiaśojć, 1993). Also Blackbirds foraging during the breeding season tend to remain within dark patches on the forest floor, or in the shadow of tree stems, thus involving a special behavioral response, and avoid foraging in open, even if they regularly do so elsewhere or while on migration. Partly for this reason, Blackbird densities may be much higher in complex old-growth woodland than in structurally simple managed stands (Flade, 1994; Bursell & Dyck, unpubl.).

Why is the Blackbird’s coloration adjusted to a less common habitat? Today, most forest Blackbirds inhabit, even if at lower densities, the pale-litter tree-stands on a dry substrate (Glutz v. Blotzheim & Bauer, 1988; Tomiaśojć, 1993; Flade, 1994). Judging from old literature (Gloger, 1833; Taczanowski, 1882; Naumann, 1905), this apparently secondary situation had to last, in spite of preference to humid sites, for at least two hundred years (= 200 generations) or longer. So, why has its plumage become adjusted to a dark substrate which in the temperate forest was always less frequent, even if originally (before land reclamation and forest clearing) the riverine forests were in Europe five times more widespread than nowadays (Imboden, 1987). A hypothetical scenario can be offered: the Blackbird coloration has been adjusted to the background of its pristine habitat – the riparian forest. Yet, paradoxically, this seems to be a less safe habitat for nesting (the breeding success 30.3 % versus 35.7% in the oak-lime-hornbeam of BNP, $p < 0.05$, and for foraging on the ground (higher herb vegetation), even if it may be safer for a bird when pursued by an avian-specialist, the *Accipiter* hawk (Tomiaśojć, 1994; in prep.). Conversely, the lack of plumage matching in the pale-litter forest seems neutral, as this disadvantage may be compensated by the bird’s more effective vigilance amongst the low herb vegetation of such sites, as well as by the presence in pristine dry ground stands of several (even if fewer than in riparian ones) dark sites.

The field data are consistent with this scenario. The height of herb vegetation in BNP is very different: high in riparian, much

sparser and lower in pale-litter habitats (Tab. 1). Diversification of this type gives a foraging Blackbird a wider field of view in the latter habitat (Fig. 1). Consequently, in dry-ground habitats the crypsis might not be a critical requirement, while in riparian forest the foraging bird being surrounded by high vegetation may easily be closely approached by a predator. Better camouflage against a black soil patch may be crucial for survival. A parallel reasoning is applicable to the Song Thrush. Unlike Blackbirds, most Song Thrushes inhabit pale-litter sites in deciduous and mixed coniferous-deciduous forests (Siivonen, 1939; Tomiaśojć et al., 1984 and in prep.). In BNP a small proportion of them breeds in swampy stands, even if at comparable or higher density. This species has, as it seems, retained the ancient buff coloration of the back as it matches the litter colour in the most widespread of forest types. Its poorer matching of the riparian substrate is compensated behaviorally, but in a reversed way: when watched from the hide, the Song Thrushes were seen to forage within the pale-colour dry-ground “islands” (only a couple of records, because of poor visibility in rough terrain), instead of in muddy patches exploited by Blackbirds.

The crypticity of Blackbird plumage is made additionally effective by the behavior of forest populations. In early spring, before the leaves open up in deciduous trees, the forest Blackbirds of both sexes avoid being exposed in the numerous sunny spots; they stop or land in the shade of tree trunks. An alternative possibility, that such sites abound with food, is unlikely for BNP since in that high forest (35-50 m) the patches of light on forest floor move quickly during the daytime. In the cool micro-climate (morning frost up to the end of first brood in the 1970s and 1980s), patches of ground briefly warmed up by the sun cannot get dried up, in contrast to what happens on open suburban lawns. Warmed up sites could even be preferable to invertebrates.

At the forest edge of BNP the Blackbirds have never been noticed foraging in the daytime in high grass (hindered visibility and movements). In the morning, with dew on the ground and long shadows, they make use of mown meadows in the immediate neighbourhood of thickets or woodland edge. Under comparable conditions, Song Thrushes more often forage in the open, chiefly on the ploughed fields. The habit of the synanthropic Blackbirds and Song Thrushes of foraging regularly in the open may well have been strengthened by the fact that for two-three centuries the anthropogenic environment in large parts of Europe was deprived (Bijleveld, 1974; Yalden, 1999) of main predators (*Accipiter*, *Buteo*, *Falco*, *Bubo*, *Martes* and *Mustela*)

as a threat to adult thrushes. The absence of these predators turned plumage coloration into a more neutral feature.

Crypsis while on the nest. The back coloration of Blackbirds and Song Thrushes matches the background well while they are on or at the nest (Tomiałoć, 1993, unpubl. data for Song Thrush). The paler plumage of the Song Thrush is highly protective during incubation or nestling feeding, as in BNP its nests are situated higher ($x_{672} = 6.5$ m, SD 4.2, span 0.4–26 m) and among thinner and more insulated branches than Blackbird nests ($x_{350} = 5.3$ m, SD 4.7, span 0.3–24 m); moreover, 73% of Song Thrush nests were located in the sun-exposed southern half of tree crowns, whereas most Blackbird nests (55%) were on the northern side of tree-stems or tree crowns (Tomiałoć, 1993; unpubl. data). The Blackbird's choice of nest-site is even more specific, as in BNP ca 90% nests were in deep shadow, i.e. in tree hollows, various niches or thick-stem bifurcations. An incubating female remains invisible against the dark background, and even when it is sporadically light by sun rays, she appears pale grey, very similar to the coloration of sun-lit tree trunks or of dry soil on the root-discs of fallen trees.

Black coloration of the Blackbird male

Why did not Blackbird males, and the males of other dark-coloured thrushes, retain the dark brown coloration that was apparently ancestral for these species? A couple of theories on the advantages of black plumage have been put forward (Walsberg, 1982; Endler, 1993), but only one explains why this feature has developed in adult males: the male's black (brighter) plumage has been developed under the requirements of sexual selection, being positively correlated with dominance status (Andersson, 1994). This might apply to the European Blackbird (T. Dabelsteen, pers. com.). Although Baker & Parker (1979) suggested alternatively that birds adept at evading predators could evolve a conspicuous plumage as a signal of "unprofitable prey", this has not been confirmed empirically (Huhta et al., 1998) and is by no means plausible for Blackbirds, since they turn inconspicuous while in original habitat.

Yet, there can be an additional factor strengthening the black coloration of the Blackbird male: under conditions of a complex habitat it may be still cryptic, which means it remains uninhibited by other selective pressures. Prevailing view assumes that the evolution of bright coloration through sexual selection may be limited by a trade off with other forms of natural selection (predator avoidance) acting against too costly features (Selander, 1972, but see test by Huhta et al., 1998). A traditional interpretation of bright plumage in male passerines as conspicuous and the female plumage as cryptic is not always true under patchy environment (Götmark & Hohlfält, 1995). Thus, intra-specific signal colors for sexual selection purposes may still retain their camouflaging functions. This is the case in the Blackbird, where the male delivers the main part of food to the nestlings (Tomiałoć 1994). His black plumage in the black-and-white patchiness of the leafless (during whole first-brood) temperate forest might still lessen the chance that predators will find the nest by following the male. Camouflage and sexual selection for black plumage in this species are not working against each other.

In some species, conspicuous male plumage could have an advertising function: in spring, it may inform the passing females about the presence of an unmated male, often singing from the top of a tree. This possibility is valid in the case of the Blackbird, while not working in the case of the Song Thrush males, behaving identically but not developing any coloration for advertising. Largely black plumage is also a feature of the male of Siberian Thrush. This species is found in riverine willow thickets – e.g. along the Yenisey River – in a habitat where the soil tends to be dark or black. Those thickets when lit by the sun produce a sharp mosaic effect of black-and-white patches (O. Bourskiy, see Fig. 2). Under such conditions a male Siberian Thrush not only is camouflaged by its black plumage but also it may display a disruptive coloration effect, with its white belly and white eye stripe forming a contrast. The function of white patches in the otherwise blackish Ring Ouzel may be similar. Thus, the "black" coloration of males of all three species seems to retain cryptic properties.

Conclusions

1) Under the conditions of pristine forest, structurally complex and rich in diverse predators, the dark brown or black colour of the Blackbird's plumage appears to be cryptic. We suppose that the black plumage of the Blackbird male retains a camouflaging function, even if this feature has been shaped by sexual selection.

2) The Blackbird has adapted to the black background colour of riparian forest floor, because foraging amongst the higher herb vegetation seems to be more risky than in pale-litter habitats where safety depends more on the bird's wary behaviour.

Acknowledgements

We would like to thank Jan Dyck, Dr D. Snow, Dr Tomasz Wesoiowski and three anonymous referees for helpful comments and linguistic improvements to our text, as well as to Dr Jacques Blondel for his data on the BNP forest structure and to Grażyna Zdunek for drawing the figure.

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