

# THE BREEDING PERFORMANCE OF BLACKCAP *SYLVIA* *ATRICAPILLA* IN TWO TYPES OF FOREST HABITAT

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The breeding density of Blackcap was about four times higher in deciduous (D) riparian linear vegetation than in mixed (M) coniferous woodlots in the farmland of Eastern Bohemia, Czech Republic, over two years. Laying started and peaked about two days later in M habitat, possibly because of delayed leafening of preferred nesting shrubs in forest undergrowth and consequently delayed availability of concealed nesting sites. No significant differences in egg size, clutch size, brood size, nest success (31%,  $n = 320$  nests, Mayfield method) and mortality factors (predation  $\geq 68\%$ ,  $n = 193$  failed nests) were found between habitats or years. In all data pooled across years, the mean clutch size was marginally larger in D habitat. The minimum productivity was 1.4-2.2 fledglings territory<sup>-1</sup> and did not differ consistently between habitats or years. The absence of a clear difference in reproduction despite large differences in breeding density is in line with the predictions of the ideal free distribution model.

Key words: *Sylvia atricapilla* - breeding success - habitat selection - laying date - open nesting passerines

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## INTRODUCTION

Individuals distribute themselves over habitats differing in quality through the process of habitat selection. Two basic models of habitat selection have been proposed (Fretwell & Lucas 1970; Bernstein *et al.* 1991). The ideal free distribution (IFD) assumes that individuals are free to settle in any habitat and that they maximise their fitness by selecting the best habitat currently available. According to the ideal despotic distribution (IDD) individuals are not free to settle, because early settlers exclude (by territorial behaviour) later settlers from the best habitat. The two models generate different predictions concerning the average fitness of settled individuals at equilibrium: the IFD predicts equal fitness across habitats while the IDD predicts higher fitness in the habitat with higher densities.

Several recent studies of passerines support

the predictions of IDD (Holmes *et al.* 1996; Petit & Petit 1996). Other studies (Hatchwell *et al.* 1996a; Huhta *et al.* 1998) suggest that individuals may distribute themselves among habitats in an ideal-free manner, while the IDD is likely to explain distribution at a finer spatial scale. Differences in net reproductive success and/or survival rates among habitats form the basis of the concept of source-sink population dynamics (Dias 1996). Hence, knowledge of the distribution of individuals among habitats and their breeding performance are essential for understanding population processes on a landscape scale (Holmes *et al.* 1996).

A process of habitat selection involves behavioural responses to stimuli provided by different habitats (Fretwell & Lucas 1970). Under both the IFD and IDD birds are assumed to be ideal, i.e. make optimal choices. An alternative hypothesis is that habitat selection is suboptimal. Gates &

Gysel (1978) proposed that some of the man-made habitats such as abrupt forest-field edges with dense vegetation might attract birds by structural cues indicating availability of nesting sites and/or food. Birds that were misled to settle and breed at high densities in these apparently suitable habitats ('ecological traps') may then experience low breeding success due to density-dependent nest predation (Chamberlain *et al.* 1995). The typical agricultural landscape in Central Europe undergoes continual changes, characterised by loss and/or fragmentation of nesting habitat of many bird species, with potential harmful effects (increased nest predation: Møller 1988; Hoover *et al.* 1995; Donovan *et al.* 1997; but see Tewksbury *et al.* 1998; lower pairing success: Gale *et al.* 1997; Huhta *et al.* 1998; stochastic environmental and/or demographic effects: Saether *et al.* 1998) on populations of some species.

The Blackcap *Sylvia atricapilla* is widespread in Central Europe where it breeds in all habitats characterised by dense tree and shrub vegetation (Glutz von Blotzheim & Bauer 1991), being one of the most abundant bird species in the lowland floodplain or humid deciduous forests (Hubálek 1997; Storch 1998). In this study I compare breeding performance of Blackcaps between linear deciduous vegetation and mixed coniferous forest, which are characterised by markedly different breeding densities. My objectives were to test the following predictions of the proposed habitat selection models: (i) breeding success is equal in both habitats (IFD); (ii) breeding success differs between habitats (IDD); (iii) nest predation is higher in the linear deciduous habitat (ecological trap hypothesis).

## METHODS

The fieldwork was conducted in cultivated agricultural landscape around the village Luže (49°54'N, 16°02'E, 280-365 m a.s.l.) in the Eastern Bohemia, Czech Republic in 1988 and 1989. Two types of forest habitats were distinguished: (1) managed mixed forests ('mixed' or 'M' here-

after) with a prevalence of coniferous trees (dominant trees: spruce *Picea excelsa*, oak *Quercus robur*, *Q. petraea*, hornbeam *Carpinus betulus*; shrub: elder *Sambucus nigra*, Red Elder *S. racemosa*, Blackthorn *Prunus spinosa*, bramble *Rubus fruticosus*); (2) remnants of secondary riparian vegetation ('deciduous' or 'D' hereafter) forming a belt along the river Novohradka (dominant trees: poplar *Populus nigra*, alder *Alnus glutinosa*, ash *Fraxinus excelsior*, elm *Ulmus* spp., willow *Salix* spp.; shrub: Bird-Cherry *Padus racemosa*, elder). Three study plots (M1-M3) were selected in the mixed habitat: two isolated woodlots surrounded by arable land ('M1': 29 ha; 'M2': 5.5 ha) and a forest belt 50 m wide ('M3': 1.5 ha). Four study plots (D1-D4) represented the deciduous habitat: one 2.8 km long section of a narrow riparian belt consisting of one line of trees and shrubs on each riverside ('D1': c 4 ha), and three sections of wide (10-50 m) riparian belt ('D2': 1.9 ha; 'D3': 3.8 ha; 'D4': 1.1 ha). All study plots were located within an area of c 16 km<sup>2</sup>, the centres of the two most intensively observed plots (M1 and D1) were 1.5 km apart, the two most remote plots were 7 km apart.

Fieldwork lasted from beginning of April to the end of June (1988) or beginning of July (1989). The late nesting attempts initiated in July were slightly underrepresented in this study (4% vs. 6-14% in the completely covered breeding seasons; K. Weidinger, in press). Breeding density was estimated on plots M1 and D1 by the mapping method combined with information on number of simultaneously active nests. Nests were located by direct searching in the shrub and herbaceous undergrowth. Most nests were checked several times until the clutch was completed, next on the expected day of hatching and on the day when nestlings were eight days old. Additional visits were made in about mid-incubation and mid-nestling period, so that each nest was checked at least once within a five-day period. The following nest site characteristics were recorded: species of nest bearing plant; height of nest above ground (m); maximum height of vegetation above the nest (m); distance of the nest from forest-field edge

(m); nest concealment category (subjective scale ranked 1-4).

Only the nests in which at least one egg was laid were considered in this study. Eggs were measured with a calliper ( $\pm 0.05$  mm) and their volume was calculated as  $0.51 \times \text{length} \times \text{width}^2$  (Hoyt 1979). An average egg volume per clutch was used in the analyses. A nest was considered successful if at least one nestling survived until the age of eight days. A nest was considered predated when nest contents disappeared with no signs of another mode of failure (broken eggs or dead nestlings, human disturbance) or successful fledging. Since predator attack could be a primary cause of nest desertion or eggs/nestlings falling out of the nest, the effect of predation on total nest losses is likely to be underestimated. Hatchability of eggs/clutches is defined as the proportion of hatched eggs/complete clutches among those that survived over the incubation period. The nest success was estimated by the Mayfield method (Hensler 1985) by extrapolating the daily survival rates over the egg (16 days) and nestling (8 days) periods.

Comparison of individual breeding parameters between habitats (fixed effect) was done by a two-way ANOVA with effect of year included as a random effect. Measurements of the distance of the nest from the forest-field edge were log-transformed prior to analysis. Categorical data were analysed by fitting log-linear models to three-way contingency tables (dependent variable  $\times$  habitat  $\times$  year) and examining significance of the interactions (*G* test). The data are insufficient to include the effect of separate plots in the analysis; hence data were pooled across plots for each of the two

habitat types. When the analyses were restricted to the one intensively observed plot from each habitat (M1 and D1), this led to the same conclusions (results not reported). The daily survival rates and the derived proportions of successful nests were compared by the standard normal *z*-test (Hensler 1985). Because the large number of two-sample comparisons would increase the chance of finding a significant difference, the significance level of 0.01 was used to make the comparisons of nest success more conservative. Numerical values are presented as mean  $\pm$  SD, except where indicated. All tests are two-tailed.

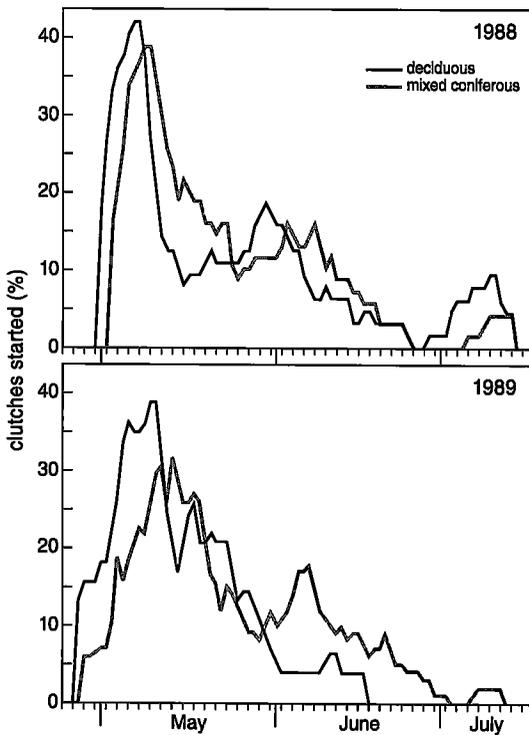
## RESULTS

### Breeding density and nest site characteristics

Breeding density of Blackcaps was about four times higher in deciduous habitat (plot D1) than in mixed habitat (plot M1) over two years (Table 1). Densities that were estimated from the number of simultaneously active nests at two other plots support this view (6.8 pairs  $\text{ha}^{-1}$  at D2 vs. 2.5 pairs  $\text{ha}^{-1}$  at M2). None of the measured nest site characteristics differed significantly (effect of habitat in two-way ANOVA, all  $P > 0.1$ ) between the mixed and deciduous habitat: height of the nest above ground,  $0.76 \pm 0.44$  m ( $n = 187$ ) vs.  $0.94 \pm 0.48$  m ( $n = 155$ ); height of vegetation above the nest,  $13.9 \pm 7.4$  m ( $n = 186$ ) vs.  $15.1 \pm 7.2$  m ( $n = 154$ ); distance from the habitat edge,  $22.3 \pm 23.1$  m (median = 15 m,  $n = 189$ ) vs.  $7.9 \pm 11.0$  m (median = 3 m,  $n = 155$ ). Nevertheless, nests were located, on average, about three times closer to

**Table 1.** The estimates of breeding density and minimum breeding productivity of Blackcap. The two study plots (M1, D1) represent the mixed and deciduous habitat, respectively.

Plot-year	Mapped territories	Nests found	Territories $\text{ha}^{-1}$	Nests territory <sup>-1</sup>	Nest success (%)	Fledglings successful nest <sup>-1</sup>	Fledglings territory <sup>-1</sup>
M1-1988	40	59	1.38	1.48	34.1	4.04	2.03
M1-1989	50	81	1.72	1.62	24.4	3.61	1.43
D1-1988	25	37	6.25	1.48	31.3	3.89	1.80
D1-1989	25	39	6.25	1.56	34.8	4.04	2.19



**Fig. 1.** Distribution of laying dates of Blackcap in deciduous and mixed coniferous habitat over two years. Shown are the nine-day running histograms. For sample size and summary statistics see Table 2.

the habitat edge in the deciduous habitat because of its predominantly linear nature. The frequency of nest concealment categories was similar in both habitats ( $G_3 = 1.43$ ;  $P = 0.699$ ). The frequency of the nest bearing plants differed between habitats: mixed (elder 28.0%, dead wood 13.6%, Gooseberry *Ribes grossularia* 10.7%, spruce 9.8%, bramble 9.8%,  $n = 214$ ); deciduous (elder 21.2%, Bird-Cherry 19.6%, Gooseberry 19.6%, Hop-plant *Humulus lupulus* 11.1%, hawthorn *Crataegus* spp. 4.8%,  $n = 189$ ).

### Laying date and clutch size

In both years laying started and peaked about two days earlier in the deciduous habitat (Fig. 1). The mean laying dates were similar in both habitats in 1988 ( $F_{1,131} = 0.09$ ,  $P = 0.768$ ), but dif-

fered by nine days in 1989 ( $F_{1,175} = 16.35$ ,  $P < 0.001$ ; Table 2). The spread of laying (measured as the inter-quartile range) was similar in both habitats in 1988 (27 days) while in 1989 laying was more synchronised in deciduous habitat (14 vs. 25 days; Fig. 1). No significant effect of habitat on mean egg volume, clutch size and brood size was detected, although clutches and broods were slightly smaller in the mixed habitat in both breeding seasons (Table 2).

### Nesting success and breeding productivity

The daily survival rates of nests (Table 3) did not differ between the egg and the nestling period in any year or in the pooled data ( $z = 0.31$ ,  $P = 0.763$ ). Out of all nesting attempts over two years, about 46% survived until hatching and 31% produced at least one fledgling (Table 4). Similar values were obtained also by two other methods: proportion of successful nests among those found before/during the start of laying, 32% ( $n = 105$ ); modification of the intercept method (Johnson 1979), 31%. No significant differences in proportion of successful nests were found between habitats in any year or in data pooled across years (egg period:  $z = 0.74$ ,  $P = 0.457$ ; nestling period:  $z = 1.08$ ,  $P = 0.278$ ; entire nesting cycle:  $z = 0.05$ ,  $P = 0.958$ ). Hatchability of clutches did not differ between habitats ( $G_1 = 2.30$ ,  $P = 0.129$ ), hatchability of eggs was marginally lower in deciduous habitat ( $G_1 = 5.91$ ,  $P = 0.015$ ).

Most of the complete nest losses during the egg period ( $n = 142$ ) were attributable to predation (64%) and clutch desertion (28%, see Methods for definition). Most nest losses during the nestling period ( $n = 51$ ) were due to predation (78%) and death of nestlings (12%). No significant interactions among the type of nest loss and habitat and/or year were found. Predation alone accounted for a minimum of 68% of all nest losses, which proportion did not differ significantly between habitats (mixed, 67%; deciduous, 73%;  $G_1 = 0.81$ ,  $P = 0.368$ ). An estimated minimum breeding productivity ranged from 1.4 to 2.2 fledglings/territory at M1 and D1 study plots over two years (Table 1).

**Table 2.** Breeding parameters of Blackcap in mixed and deciduous habitat.

Habitat-year	Laying date (1 = 1 May) <sup>a</sup>		Egg volume (mm <sup>3</sup> ) <sup>b</sup>		Clutch size <sup>c</sup>		Brood size <sup>d</sup>	
	Mean ± SD (n)	Med	Mean ± SD (n)	Med	Mean ± SD (n)	Med	Mean ± SD (n)	Med
mixed habitat								
1988	22.4 ± 17.6 (69)	18.0	2160 ± 163 (58)		4.61 ± 0.67 (49)		3.98 ± 0.87 (33)	
1989	23.3 ± 17.0 (100)	17.0	2175 ± 203 (86)		4.47 ± 0.74 (77)		3.65 ± 1.07 (43)	
total	22.9 ± 17.2 (169)	17.0	2169 ± 188 (144)		4.52 ± 0.71 (126)		3.80 ± 0.99 (76)	
deciduous habitat								
1988	23.4 ± 21.4 (64)	17.5	2150 ± 158 (59)		4.71 ± 0.74 (49)		4.03 ± 1.06 (39)	
1989	14.0 ± 12.2 (77)	10.0	2114 ± 159 (76)		4.74 ± 0.75 (61)		3.79 ± 0.94 (33)	
total	18.3 ± 17.6 (141)	13.0	2130 ± 159 (135)		4.73 ± 0.74 (110)		3.92 ± 1.00 (72)	

Results of two-way ANOVAs testing for effect of habitat (fixed) and year (random):

<sup>a</sup>  $F_{\text{habitat}} = 0.65, P = 0.568; F_{\text{year}} = 4.56, P = 0.034; F_{\text{interaction}} = 6.76; P = 0.010$

<sup>b</sup>  $F_{\text{habitat}} = 1.97, P = 0.394; F_{\text{year}} = 0.26, P = 0.609; F_{\text{interaction}} = 1.44; P = 0.232$

<sup>c</sup>  $F_{\text{habitat}} = 4.90, P = 0.270; F_{\text{year}} = 0.40, P = 0.529; F_{\text{interaction}} = 0.76; P = 0.384$

<sup>d</sup>  $F_{\text{habitat}} = 3.42, P = 0.315; F_{\text{year}} = 3.01, P = 0.085; F_{\text{interaction}} = 0.08; P = 0.771$

**Table 3.** Daily survival rates (DSR) of Blackcap nests in mixed and deciduous habitat. DSR and their standard errors (SE) were estimated by the Mayfield method (Hensler 1985).

Habitat-year	Egg period			Nestling period		
	Nests	Nest-days	DSR ± SE	Nests	Nest-days	DSR ± SE
mixed habitat						
1988	59	467	0.9593 ± 0.0091	51	280	0.9428 ± 0.0139
1989	97	747	0.9485 ± 0.0081	64	379	0.9472 ± 0.0115
total	156	1214	0.9527 ± 0.0061	115	659	0.9453 ± 0.0089
deciduous habitat						
1988	60	533	0.9596 ± 0.0085	45	265	0.9679 ± 0.0108
1989	81	707	0.9484 ± 0.0083	45	259	0.9517 ± 0.0133
total	141	1240	0.9532 ± 0.0060	90	524	0.9599 ± 0.0086

## DISCUSSION

### Evaluation of breeding parameters

Of the breeding parameters estimated in this study, the median laying date and the mean clutch and brood size correspond well to data from Central Europe, while the breeding densities are among the highest values reported from elsewhere (Glutz von Blotzheim & Bauer 1991; Hubá-

lek 1997; Storch 1998). The estimated nest success of 31% is the lowest among the published values known to me (Bairlein *et al.* 1980; Glutz von Blotzheim & Bauer 1991), which is, however, a consequence of the method used (Mayfield vs. conventional method; Johnson 1979; Hensler 1985). Application of the conventional method to my data resulted in an overestimated nest success of 43% ( $n = 335$ ). The minimum breeding produc-

**Table 4.** Hatchability (%) and nest success (%) of Blackcap in mixed and deciduous habitat. Nest success was calculated from the daily survival rates (Table 3) according to Hensler (1985).

Habitat-year	Hatchability ( <i>n</i> )		Nest success ( $\pm$ SE)		
	Clutches	Eggs	Egg period	Nestling period	Entire cycle
<b>mixed habitat</b>					
1988	86.3 (51)	96.0 (176)	51.5 $\pm$ 7.8	62.4 $\pm$ 7.4	32.1 $\pm$ 6.2
1989	84.8 (59)	97.1 (239)	42.9 $\pm$ 5.9	64.8 $\pm$ 6.3	27.8 $\pm$ 4.7
total	85.5 (110)	96.6 (415)	46.0 $\pm$ 4.7	63.8 $\pm$ 4.8	29.3 $\pm$ 3.7
<b>deciduous habitat</b>					
1988	79.6 (44)	95.3 (172)	51.7 $\pm$ 7.4	77.0 $\pm$ 6.9	39.9 $\pm$ 6.7
1989	74.4 (43)	90.4 (187)	42.8 $\pm$ 6.0	67.3 $\pm$ 7.5	28.8 $\pm$ 5.2
total	77.0 (87)	92.8 (359)	46.5 $\pm$ 4.7	72.1 $\pm$ 5.2	33.5 $\pm$ 4.1

tivity found in this study is considerably lower than that expected in a self-sustaining population and that observed in a population of individually marked birds (2.9 and 4.0 fledglings per female in two years; Bairlein 1978). Obviously, the number of nesting attempts per pair was underestimated in this study, because not all active nests were found. Since it is unlikely that any methodological bias was habitat specific, inter-habitat comparisons of the estimated breeding parameters are not violated.

### Comparison of habitats

Any inter-habitat differences found in this study represent the combined effect of differences in vegetation composition (deciduous vs. mixed) and shape of the plots (linear vs. woodlot). These two effects can not be separated, however, as only two of the four possible combinations of habitat characteristics occur in the study area. Hence, Blackcaps have to select between linear deciduous vegetation and mixed woodlots, apart from urban habitats. About four times higher breeding density of Blackcaps in the deciduous riparian vegetation can not be accounted for by the linear nature of this habitat, because similar high densities (6 pairs ha<sup>-1</sup>) were found in a non-linear deciduous vegetation in a nearby area (Storch 1998; K. Weidinger, unpubl. data).

I suggest that availability of concealed nesting sites could be a proximate factor responsible for the earlier onset of laying in the deciduous habitat. Development of foliage cover on the preferred nesting shrubs is slightly delayed in the mixed coniferous forests with closed canopy, compared to linear riparian vegetation. The early Blackcap nests are under high predation pressure (K. Weidinger, unpubl. data), while density of vegetation cover around the nest and/or nest concealment was shown to decrease the risk of predation (e.g. Hoi-Leitner *et al.* 1995; Hatchwell *et al.* 1996b; but see Howlett & Stutchbury 1996 and Burhans & Thompson 1998). An earlier laying by Blackcaps in coniferous habitats in South Germany (Bairlein *et al.* 1980) contrasts with findings of this study, perhaps because of different kind of data (nest cards) collected over a broad geographical area.

Although predation was the major cause of nesting failure, no significant differences in nest success were found between habitats. Hence, the prediction of the ecological trap hypothesis (Gates & Gysel 1978) was not supported in this study. The nest success was in fact marginally higher (difference 1% and 8%), though not significantly, in the linear riparian habitat characterized by high density of open-cup nests concentrated into a distinct vegetation stratum. This finding

thus contributes to the existing controversy about generality of the edge and density effects on the risk of nest predation (e.g. Donovan *et al.* 1997; Hartley & Hunter 1998; Söderström *et al.* 1998).

No significant effects of habitat on egg size, clutch size or brood size were found, although the mean clutch and brood sizes were slightly larger in the deciduous habitat. If the random effect of year was not included in the analysis, the difference in mean clutch size between habitats was marginally significant ( $F_{1,250} = 4.62$ ,  $P = 0.033$ ). In absolute terms, the inter-habitat difference in mean ( $\pm$  SE) clutch size ( $0.20 \pm 0.09$  eggs) was of similar magnitude and of the same direction as reported from South Germany (0.13 eggs; Bairlein *et al.* 1980). Considering the limited accuracy of the estimates, no consistent differences in breeding productivity could be found between habitats.

The observed earlier onset of laying in habitat of higher breeding density is in favour of the IDD. However, the timing of laying may not be directly related to the time of settling and territory occupation (Bairlein 1978). I have not accurate data on the time of settling, but the first individuals of both sexes were recorded in all habitats in the study area on the same day within each season. Although the Blackcap population was increasing in the Czech Republic during the period of this study (K. Štátný & V. Bejček, pers. comm.), I observed a between-year increase in density only in the mixed habitat. This could indicate that some birds were prevented to settle in the preferred deciduous habitat, which would support the IDD model. The available evidence is weak, however, because of short duration of this study, lack of spatial replication and the confounding effect of stochastic annual variation of breeding density in small habitat patches. On the other hand, similar mean reproductive output across habitats that support markedly different breeding densities is in line with the critical prediction of the IFD. I suggest the IFD model as the most plausible explanation for the distribution of Blackcaps between two adjacent habitats in this study. Nevertheless, the relationship between intensity of male defensive

behaviour and territory quality measured by density of vegetation cover (Hoi-Leitner *et al.* 1995) indicates that the distribution of Blackcaps within habitats may conform to the IDD. Similar patterns on a comparable spatial scale (among and within habitats) were reported in Blackbirds *Turdus merula* (Hatchwell *et al.* 1996a) and Pied Flycatchers *Ficedula hypoleuca* (Huhta *et al.* 1998). In this study I considered the nesting productivity, which is just one correlate of fitness. Results would be more conclusive if possible habitat-specific differences in recruitment rate and cost of reproduction to parents had been taken into account. To explain unambiguously the observed habitat distribution of Blackcaps, additional data are needed on dynamics of habitat occupation, dispersal among habitats and phenotypic quality of breeding individuals.

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## SAMENVATTING

De auteur onderzocht Zwartkoppen *Sylvia atricapilla* in Oost-Bohemen in de Tsjechische Republiek in 1988 en 1989. Er konden twee duidelijk verschillende broedbiotopen worden onderscheiden. Enerzijds gemengde bossen (M) met een strak menselijk beheer, bestaande uit naaldbomen, eiken en vlier; anderzijds restanten van rivierbossen (D) met uitsluitend loofbomen als populier, els en wilg. De broeddichtheid was in beide jaren het hoogst in de rivierbossen, maar er waren geen duidelijke verschillen in broedsucces. In 1989 kwamen de Zwartkoppen iets eerder tot broeden in de rivierbossen, maar er bestonden geen biotoopspecifieke verschillen in eivolume, legselgrootte of broedselgrootte tussen de bostypen. Veel nesten verdwenen door predatie, maar

de overlevingskansen van eieren en jongen verschilden niet tussen de beide biotopen. Dit is te zien aan de dagelijkse overlevingskansen en aan de omrekening van deze overlevingskansen naar de kans van respectievelijk een ei of een nestjong om te overleven. De resultaten kloppen met de voorspelling van de 'ideale vrije verdeling', waarbij het broedsucces afneemt naarmate de dichtheid aan broedende vogels toeneemt en waarbij de vogels proberen een maximaal broedsucces te halen en vrij zijn om hun territorium te kiezen. In dat geval zullen de dieren zich zo verspreiden dat het succes overal hetzelfde is. Onder de 'despotische verdeling' zijn de vogels niet vrij, maar worden individuen die zich nog niet gevestigd hebben, verdreven door de al

gevestigde dieren. In dat geval wordt voorspeld dat het broedsucces hoger is in biotopen waar de broeddichtheid hoog is. Het is moeilijk voorstelbaar dat de Zwartkoppen echt volkomen vrij zijn, want ze vertonen wel territoriaal gedrag. Een mogelijke verklaring is dat de verdeling binnen de biotopen despotisch is, maar vrij lijkt als biotopen vergeleken worden. Verder is de bewijsvoering voorlopig incompleet, omdat nog niet gekeken is naar mogelijke verschillen in overleving van de uitgevlogen jongen en overleving van de oudervogels. (BJE)

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