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# Effects of Exotic Habitat on Nesting Success, Territory Density, and Settlement Patterns in the Blackcap (*Sylvia atricapilla*)

VLADIMÍR REMEŠ

Department of Zoology, Palacký University, Tr. Svobody 26, 771 46 Olomouc, Czech Republic,  
and U.S. Geological Survey Biological Resources Division, Montana Cooperative Wildlife Research Unit,  
University of Montana, Missoula, MT 59812, U.S.A.

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**Abstract:** *Animals are expected to distribute themselves in a heterogeneous environment in such a way that they maximize their reproductive output. When the environment is profoundly changed by human pressure, however, cues used for habitat selection in the past may no longer provide reliable information about habitat quality. I monitored the nesting success of Blackcaps (*Sylvia atricapilla*) in two types of forest in southern Moravia in the Czech Republic. I assessed their breeding density and territory size using a territory mapping method and the minimum convex polygon method. I determined spring arrival through direct observations and measured vegetation characteristics and pattern of spring leafing of shrubs in both forests. I show that Blackcaps preferentially settled in a plantation of introduced black locust (*Robinia pseudoacacia*) upon their return from spring migration. In this plantation, they reached twice the density as that observed in a natural floodplain forest nearby. However, they had significantly lower nesting success (15.5%) than in the floodplain forest (59%). Returning migrant Blackcaps may be lured by early-leafing shrubs in the exotic plantation to settle earlier and at higher densities in the reproductively inferior habitat. My results show that (1) it is not possible to assess habitat quality based solely on breeding densities, (2) human-modified habitats can function as ecological traps by luring settling birds into unsuitable habitats, and (3) by replacing exotic plant species with native ones we can restore native communities and increase the breeding productivity of bird populations.*

Efectos de Hábitat Exótico sobre el Éxito de Anidación, Densidad Territorial y Patrones de Establecimiento de *Sylvia atricapilla*

**Resumen:** *Se espera que los animales se distribuyan en un medio heterogéneo de tal modo que maximicen su producción reproductiva. Sin embargo, cuando el ambiente es cambiado profundamente por la presión humana, los indicios para la selección de hábitat usados en el pasado pueden no proporcionar información confiable sobre la calidad del hábitat en la actualidad. Se hizo un monitoreo del éxito reproductivo de *Sylvia atricapilla* en dos tipos de bosque en el sur de Moravia, república Checa. Se evaluó su densidad reproductiva y el tamaño del territorio utilizando un método de mapeo de territorio y el método de mínimo polígono convexo. Se determinó la llegada en primavera por medio de observaciones directas y se midieron las características de la vegetación y el patrón de desarrollo foliar de arbustos en los dos bosques. Se muestra que *Sylvia atricapilla* preferentemente se establecieron en una plantación de *Robinia pseudoacacia* a su regreso de la migración primaveral. En esta plantación alcanzaron una densidad dos veces mayor que la observada en un bosque inundable cercano. Sin embargo, tuvieron un éxito de anidación (15.5%) significativamente menor que en el bosque inundable (59%). Las aves retornantes pueden ser atraídas por los arbustos con hojas jóvenes en la plantación exótica y por lo tanto se establecen más temprano y en mayores densidades en el hábitat reproductivamente inferior. Los resultados muestran que (1) no es posible evaluar la calidad del*

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Address correspondence to Department of Zoology, Palacký University, Tr. Svobody 26, 771 46 Olomouc, Czech Republic,  
email remes@prfnu.upol.cz

*hábitat basado en las densidades reproductivas únicamente, (2) los hábitats modificados por humanos pueden funcionar como trampas ecológicas al atraer aves hacia hábitats inadecuados y (3) reemplazando las especies de plantas exóticas con nativas podemos reestablecer comunidades nativas e incrementar la productividad reproductiva de poblaciones de aves.*

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## Introduction

Animals are expected to maximize their reproductive output in a heterogeneous environment through spatial distribution (Pulliam 1996). Under the ideal free distribution (IFD) model of habitat selection, individuals are free to settle anywhere and distribute themselves in such a way that their reproductive output in all habitats is the same (Fretwell & Lucas 1970; Bernstein et al. 1991). There is ample evidence, however, that the breeding success and reproductive output of birds can differ across habitats on multiple spatial scales (e.g., Donovan et al. 1995; Dias 1996; Hatchwell et al. 1996; Donovan et al. 1997; Huhta et al. 1998; Purcell & Verner 1998; Tewksbury et al. 1998). One possible explanation for this is provided by the ideal despotic distribution (IDD) model of habitat selection (Fretwell & Lucas 1970; Bernstein et al. 1991). Under this model, dominant individuals preempt better habitats, thus forcing subordinates to settle in poorer habitats, with reproductive parameters differing between habitats accordingly (Andrén 1990; Huhta et al. 1998).

Another explanation for habitat-specific reproductive success is based on human-induced habitat changes. Humans are exerting strong pressure on native habitats, changing them and their biotic interactions profoundly (Yahner 1988; Paton 1994; Murcia 1995; Trine 1998; Fagan et al. 1999). These changes include, among others, the introduction of exotic species, which can lead to changes in the appearance, phenology, and functioning of communities (Wilson & Belcher 1989; Penloup et al. 1997; Shigesada & Kawasaki 1997; Courchamp et al. 2000; Martin et al. 2000; Roemer et al. 2002). In a recently human-modified landscape, the cues used by animals successfully in the past for detecting highly rewarding breeding habitats and the actual current quality of those habitats can be decoupled (Rolstad 1991). This means animals no longer have complete and reliable knowledge of potential habitats as presumed by habitat selection models. This can happen if, while choosing their breeding habitat, they rely on those features of habitats that were changed by the introduction of exotic species (e.g., phenology or physiognomy) (Schmidt & Whelan 1999). Animals can be misled and can make wrong decisions about where to settle, with potentially detrimental consequences for reproduction (Pulliam 1996; Remeš 2000).

Human-modified habitats that look suitable but provide poor reproductive rewards are called ecological traps (Gates & Gysel 1978), which can be generated by habitat fragmentation (Gates & Gysel 1978; Rolstad 1991; Purcell & Verner 1998) and introduction of exotic plant species (Schmidt & Whelan 1999; Misenhelter & Rotenberry 2000). Exotic plant species have high "trap" potential because they can change habitat phenology and physiognomy profoundly. One such species is black locust (*Robinia pseudoacacia*), a tree of North American origin that was introduced into other parts of the world (including Europe) as an ornamental and timber species. Black locust accumulates soil nitrogen, facilitating dominance by nitrogen-responsive understory species, which leads to lower species diversity of shrub and herb layers (Peloquin & Hiebert 1999) and changes the phenology of the understory vegetation.

I hypothesize that habitat changes caused by black locust can have detrimental effects on breeding birds. Here, I test this hypothesis by comparing settlement patterns, territory density, and nesting success of the Blackcap (*Sylvia atricapilla*), a small, insectivorous migratory songbird, between two habitats, a black locust plantation and a native floodplain forest. If the exotic black locust plantation is inferior for breeding birds compared with the native floodplain forest, the specific predictions generated by the different habitat selection models are (1) IFD, in which both habitats are settled simultaneously with higher density in the floodplain forest and no difference in nesting success; (2) IDD, in which native-floodplain forest is settled preferentially and with resulting higher nesting success; and (3) the ecological trap hypothesis, in which the black locust plantation is settled preferentially, with higher density but lower nesting success.

## Methods

### Study Sites

This study was conducted on two 15- to 20-ha study plots, separated by 1.3 km, within the large Doubrava forest of approximately 90 km<sup>2</sup>, north of Hodonín in southern Moravia, Czech Republic (lat. 48°52'N, long. 17°05'E, 170 m above sea level). Farmland and a chain of ponds surrounded the forest. The forest cover of Dou-

brava is disrupted by openings, clearcuts, and roads but is still relatively continuous. Forest management activities include selective logging of trees and systematic cutting of shrub understory. The first plot was located within a black locust plantation. The shrub layer consisted solely of common elder (*Sambucus nigra*), and the herb layer was dominated by catch-weed bedstraw (*Galium aparine*) and nettle (*Urtica dioica*). The second plot was located within a natural floodplain forest that was floristically much richer. It had at least nine tree species (mostly oaks [*Quercus* spp], limes [*Tilia* spp], poplars [*Populus* spp], European ash [*Fraxinus excelsior*], and black alder [*Alnus glutinosa*]) and 14 shrub species (mainly saplings of limes; hawthorns [*Crataegus* spp], red dogwood [*Cornus sanguinea*], raspberry [*Rubus idaeus*], common buckthorn [*Rhamnus cathartica*], bird-cherry [*Padus racemosa*], blackthorn [*Prunus spinosa*], wayfaring tree [*Viburnum lantana*] and rose [*Rosa* sp]).

### Vegetation Structure and Leafing

I characterized the vegetation by measuring shrub cover and height and tree cover, height, and density on both study plots. I counted the trees (tree density) in 50 randomly distributed circles (5-m radius) on both plots. I divided each circle into four quarters, and in each quarter I measured the height of shrubs and estimated shrub and canopy cover. I averaged the values from each quarter to obtain shrub height and shrub and tree cover for the circle. I chose seven trees at random on each plot and measured their height with a clinometer. In 2000–2001 I measured the leafing of understory vegetation, which is defined as growth of new leaves from buds after a winter period of vegetative inactivity. On both study plots, I chose 20 shrubs at random. I chose one branch of each of these shrubs randomly and measured all its new leaves with a caliper. The average length of these leaves provided one data point for subsequent analyses. Thus, for both study plots I collected 20 measurements of leaf lengths (averages of individual shrubs) approximately every third day (for exact dates see Fig. 1).

### Nesting Success, Territory Density, and Settlement Patterns

In 1998–1999 I monitored the nesting success of Blackcaps. I searched for nests by systematically inspecting all shrub and herbaceous vegetation on the study plots and subsequently checked them every 1–7 days (median, 3 days). Nest searches and nest checks were performed from late April to early July. For each nest, I recorded height, supporting plant species, clutch (or brood) size, and egg size (1999 only). With a caliper, I took egg length and two measurements of egg width in two perpendicular directions. I used these measurements to calculate egg volume according to the formula given by

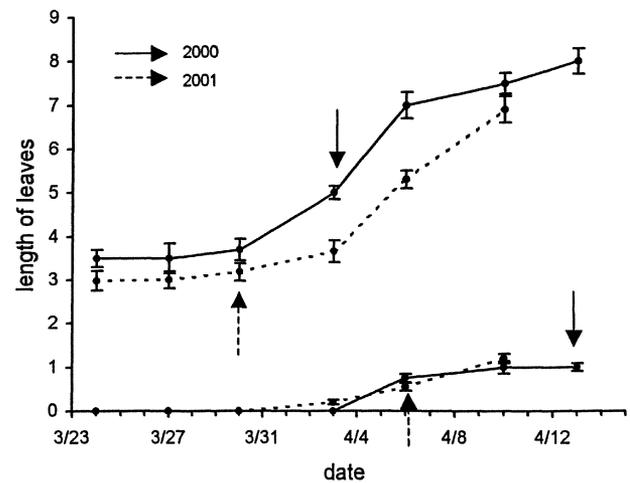


Figure 1. A schematic depiction of leafing of understory shrubs in the black locust plantation (two upper curves) and the floodplain forest (two lower curves) in 2000 and 2001 (cm, mean  $\pm$  SE,  $n = 20$  in all cases). Arrows show the date of the first detection of a singing male on each plot. Trees were completely without leaves at that time in both habitats.

Hoyt (1979). For computation of nesting success, I used the Mayfield method (Mayfield 1975). Nests that fledged at least one young were considered successful. Disappearance of nest contents was taken as evidence of predation. Number of fledglings was defined as number of young deemed to have fledged from the nest.

In 1997–1998 I quantified breeding density of the Blackcap using the territory mapping method, which provides absolute densities of breeding pairs (Bibby et al. 1992). I surveyed plots weekly, in either the morning or evening. Each census lasted over 3 hours. Morning censuses started before sunrise, and evening censuses continued until sunset. I began mapping territories in late April and continued until early July. During a slow walk through the study plot, I recorded all Blackcaps noted both visually and aurally and recorded their location on a map of the study plot. Typically, registrations from subsequent censuses form clusters on the map, and each cluster depicts a territory of a single male (minimum number of registrations forming a territory was set at three). To determine the size of singing territories, I connected outermost registrations in each cluster by a straight line and computed the extent of the area using the minimum convex polygon method (White & Garrott 1990). To compare spacing of territories in the two habitats, I calculated the mean distance between neighboring territories on both plots. These distances were taken between visually estimated centers of the territories.

In 2000–2001 I monitored the spring arrival of Blackcaps on breeding grounds by careful visual and audi-

**Table 1.** Vegetation structure characteristics of the two study plots (mean  $\pm$  SE).

Variable	Plantation (n)	Floodplain forest (n)
Shrub cover (%)	32.8 $\pm$ 0.60 (50)	31.6 $\pm$ 0.58 (50)
Shrub height (m)*	2.9 $\pm$ 0.03 (50)	3.7 $\pm$ 0.03 (50)
Tree cover (%)	93.8 $\pm$ 1.73 (50)	92.5 $\pm$ 1.70 (50)
Tree height (m)	27.8 $\pm$ 1.32 (7)	24.5 $\pm$ 1.22 (7)
Tree density (no. in 10-m-diameter circle)	2.1 $\pm$ 0.03 (50)	2.0 $\pm$ 0.03 (50)

\*Significantly different at  $p < 0.01$ . All other variables not significant (Mann-Whitney  $U$  tests).

tory inspection of the study plots and their broader surroundings approximately each third day (for exact dates see Fig. 1). On both study plots I established six observation points 100 m apart. From each observation point I recorded all birds for 30 minutes. I also recorded all birds I observed while moving between the observation points.

### Potential Predators

To assess potential nest predators, I used snap-traps to catch small mammals on both study sites from late April to mid-July in 1997 (25 traps  $\times$  2 transects  $\times$  1 night exposure  $\times$  5 times per season = 250 trap-nights per study site). During censuses of Blackcaps and nest searches, I also recorded observations of potential avian predators. Of the species known to prey on Blackcap nests (Sell 1998; Weidinger 2002), I trapped bank vole (*Clethrionomys glareolus*) and wood/yellow-necked mouse (*Apodemus sylvaticus/A. flavicollis*) and recorded Jay (*Garulus glandarius*) and Great-spotted Woodpecker (*Dendrocopos major*) on both study sites. The presence of Eurasian badger (*Meles meles*), Pine martin (*Martes martes*), and stoat (*Mustela erminea*) was probable but not directly proved.

### Statistical Analyses

Breeding parameters of Blackcaps were similar in all years (all  $p > 0.1$ ); thus, I pooled data across years, except for egg volume, which was measured in 1999 only. Vegetation height, density, and cover data were not normally distributed, and no transformation improved their distribution, so I tested the difference between the two plots by Mann-Whitney  $U$  tests. I analyzed the pattern of leaf growth with repeated-measures analysis of variance and the difference in arrival date of the first male by Wilcoxon signed-ranks test for paired data. All statistical tests were two-tailed, and the differences were considered significant at  $p < 0.05$ . All statistical analyses were performed with SPSS (SPSS 1996).

## Results

### Vegetation Structure and Leafing

Despite floristic differences, the two plots had similar vegetation structure and differed only in the height of the shrub layer (Table 1). However, the difference in timing of leafing between the two plots was highly significant ( $F_{1,76} = 961.16$ ,  $p < 0.001$ , Fig. 1). There was also significant difference between years ( $F_{1,76} = 8.70$ ,  $p = 0.004$ ) due to an overall earlier growth of leaves in 2000 than in 2001 in the black locust plantation. Finally, there was a significant interaction between leaf growth and plot ( $F_{3,74} = 3755.31$ ,  $p < 0.001$ ) and between leaf growth and year ( $F_{3,74} = 6007.64$ ,  $p < 0.001$ ; Fig. 1).

### Nesting Success, Territory Density, and Settlement Patterns

Of all the breeding parameters I measured, only nesting success differed between the two populations: nesting success in the black locust plantation was much lower than in the natural floodplain forest (Table 2).

**Table 2.** Parameters of Blackcap breeding populations on the plantation and floodplain forest study plots.

Variable <sup>a</sup>	Year	Plantation	Floodplain forest
Density (pairs/10 ha)	1997-1998	20	12
Singing territory size [ha, mean $\pm$ SE (n)]	1997-1998	0.23 $\pm$ 0.034 (40)	0.26 $\pm$ 0.049 (24)
Distance to the nearest neighboring territory [m, mean $\pm$ SE (n)] <sup>b</sup>	1997-1998	44.96 $\pm$ 1.708 (40)	63.94 $\pm$ 4.704 (24)
Daily nest survival rate [mean $\pm$ SE (n)] <sup>c</sup>	1998-1999	0.9253 $\pm$ 0.018 (48)	0.9783 $\pm$ 0.011 (25)
Nesting success [%, mean (95% CI), per 24 days]	1998-1999	15.5 (8.2 - 28.9)	59.0 (40.7 - 85.5)
Clutch size [mean $\pm$ SE (n)]	1998-1999	4.69 $\pm$ 0.155 (28)	4.81 $\pm$ 0.090 (20)
No. of fledglings [mean $\pm$ SE (n)]	1998-1999	3.71 $\pm$ 0.194 (14)	3.67 $\pm$ 0.291 (18)
Egg volume [cm <sup>3</sup> , mean $\pm$ SE (n)]	1999	2.17 $\pm$ 0.046 (22)	2.17 $\pm$ 0.045 (15)
Nest height [m, mean $\pm$ SE (n)]	1998-1999	0.56 $\pm$ 0.065 (45)	0.54 $\pm$ 0.100 (25)

<sup>a</sup> Except for "distance to nearest neighboring territory" and "daily nest survival rate," variables are not significant ( $t$  tests).

<sup>b</sup> Test:  $t$  test,  $t = -4.41$ ,  $p < 0.001$ .

<sup>c</sup> Tested according to Johnson (1979):  $z = 3.71$ ,  $p < 0.001$ . All other variables not significant ( $t$  tests).

Blackcaps reached much higher density in the plantation than in the floodplain forest, but territory size did not differ between the two plots (Table 2). Given the almost two times higher density of the black locust population and the identical territory sizes, there must have been much more interstitial, unoccupied space in the floodplain forest. This can be seen when comparing mean distance to the nearest neighboring territory: it was almost 1.5 times greater in the floodplain forest than in the black locust plantation (Table 2). The higher density of Blackcaps in the plantation was not due to differences in the availability of nest sites because the two plots did not differ in the cover of shrubs (Table 1), which is the nesting substrate for Blackcaps. Instead, the higher density of Blackcaps in the black locust plantation appears to reflect a preference for the exotic habitat.

This was supported by the 2000–2001 arrival data. Males settled and began to sing about 1 week earlier in the black locust plantation than in the floodplain forest (Fig. 1). Although the difference in the arrival date between the plots was not statistically significant (Wilcoxon signed ranks test:  $Z = -1.34$ ,  $p = 0.18$ ), this was caused by the extremely small power of the test (only 2 years of data were available). Although statistically non-significant, the average difference of 8.5 days in arrival time is biologically highly significant. Moreover, at the time of detection of the first singing male in the floodplain forest, it was possible to see or hear four to five males simultaneously in the black locust plantation from one observation point. Thus, it seems that not only the arrival date of the first male but also the overall settling pattern differed between the two plots, the black locust plantation being at least partially filled before any male even appeared in the floodplain forest. The settling pattern could not be explained by any geographical effect because the study plots were 1.3 km apart, a trivial distance for a long-distance migrant.

## Discussion

Arriving Blackcaps settled earlier in the black locust plantation at higher densities but suffered from lower nesting success. These findings are in accordance with predictions derived from the ecological trap hypothesis applied to this study system.

One potential mechanism leading to earlier settling and higher density at the black locust plantation is the earlier leafing of shrubs in the plantation (Fig. 1). Moreover, because of monospecific (elder) species composition, all shrubs leafed simultaneously. Male Blackcaps arrive earlier in the spring than females and strive to defend territories with the biggest potential for dense vegetation later in the breeding season (Hoi-Leitner et al. 1995), perhaps because territories with dense foliage around a nest have better prospects for nesting success

(Martin 1992; Hoi-Leitner et al. 1995; Weidinger 2002). Thus, I suggest that early and simultaneously leafing elders lured arriving males into the black locust plantation. Although alternative explanations for the observed pattern could be invoked (e.g., that arriving Blackcaps cue on food instead on foliage), concealment serves to deter nest predation in Blackcaps (Hoi-Leitner et al. 1995; Weidinger 2002) and predation is the main cause of nest failure in this species (Sell 1998; Weidinger 2000, 2002; this study). Furthermore, Weidinger (2000) showed that Blackcaps breed earlier at the sites with earlier leafing of shrubs, and there is no evidence of food limitation in this species (V. R., personal observation).

Because my study lacks true spatial replicates, different nesting success at the two study plots could be explained in several ways. One, there could simply be different densities of nest predators on the two study sites. Two, the high density of birds in the black locust plantation (Table 2) could lead to low nesting success caused by density-dependent nest predation. With the exception of one nestling found dead on the nest, all nest losses on both plots were attributable to predation. Moreover, Blackcap nests in the plantation were almost all (91.9% in 1998, 95.7% in 1999) placed in elder, whereas nests in the floodplain forest were more evenly distributed among various support plants (maximum proportions of 22.2% in *Prunus spinosa*, *Tilia*, and *Crataegus* in 1998 and 56.3% in *Tilia* in 1999). A high-density concentration of nests in one shrub species could facilitate nest searching by predators (Martin 1988, 1996; Schmidt & Whelan 1998). However, more studies are needed to ascertain the actual cause of the differences in rates of nest predation.

Several researchers, based on ecological trap reasoning, suggest that birds exhibit maladaptive selection of breeding habitat (Gates & Gysel 1978; Purcell & Verner 1998) and nest sites (Misenhelter & Rotenberry 2000). However, all these researchers based their conclusions on indirect, correlative evidence. For example, higher density in a certain habitat was taken as evidence of its higher attractiveness for breeding birds and for their active selection of it. Here, I show directly that birds arriving on the breeding grounds preferentially selected reproductively inferior breeding habitat. Furthermore, I suggest that cueing on dense understory vegetation may have been a rewarding strategy in natural habitats but that human alteration of the landscape has decoupled this cue from actual habitat suitability (Gates & Gysel 1978; Remeš 2000). This finding shows that one of the most important assumptions of the habitat selection theory, namely that dispersing individuals should first select the most rewarding habitat (Fretwell & Lucas 1970; Bernstein et al. 1991), does not always hold true. Moreover, for all Blackcap life-history parameters, the black locust population falls under the self-sustaining threshold (V. R., unpublished data). This implies that human

alteration can create demographically inferior habitats that are nevertheless attractive to breeding animals (Remeš 2000).

It is known that introduced, non-native vegetation can alter the community composition and nesting success of birds (Wilson & Belcher 1989; Schmidt & Whelan 1999). Introduced black locust replaces native habitats and destroys native communities (Hruska 1991). Because this study was conducted in a single location, however, with one plot within each habitat type (native and exotic), larger-scale and multispecies studies should be conducted to confirm that black locust plantations have detrimental consequences for regional breeding bird populations. Nevertheless, three conclusions are worth stressing: (1) it is not possible to assess habitat quality based solely on breeding densities (see also Van Horne 1983; Vickery et al. 1992); (2) human-modified habitats can function as ecological traps by luring settling birds into unsuitable habitats (Gates & Gysel 1978; Rolstad 1991), possibly leading to demographically non-self-sustaining populations (Remeš 2000); and (3) by replacing exotic plant species with native ones, we might gain multiple benefits—not only the restoration of native communities but also an increase in the breeding productivity of bird populations (Schmidt & Whelan 1999).

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