

Factors affecting the goldcrest/firecrest abundance ratio in their area of sympatry

Jelena Kralj^{1,*}, Jirí Flousek², Miljenko Huzak³, Davor Ćiković¹ & Zdravko Dolenc⁴

¹ Institute of Ornithology, Croatian Academy of Sciences and Arts, Gundulićeva 24, HR-10000 Zagreb, Croatia (*corresponding author's e-mail: zzo@hazu.hr)

² Krkonose National Park Administration, Dobrovského 3, CZ-54301 Vrchlabí, Czech Republic

³ Department of Mathematics, Faculty of Science, University of Zagreb, Bijenička cesta 30, HR-10000 Zagreb, Croatia

⁴ Department of Zoology, Faculty of Science, University of Zagreb, Rooseveltov trg 6, HR-10000 Zagreb, Croatia

Received 19 Nov. 2012, final version received 2 Feb. 2013, accepted 30 May 2013

Kralj, J., Flousek, J., Huzak, M., Ćiković, D. & Dolenc, Z. 2013: Factors affecting the goldcrest/firecrest abundance ratio in their area of sympatry. — *Ann. Zool. Fennici* 50: 333–346.

The goldcrest (*Regulus regulus*) and the firecrest (*Regulus ignicapilla*) are sympatric over a large part of Europe, but with different abundance ratios. We studied the effects of geographical location, vicinity of the species range boundaries, habitat and climate factors on the goldcrest/firecrest abundance ratio. At the continental scale, a weighted multiple linear regression model resulted in four significant covariates: temperature, precipitation, forest type and occurrence rate (representing the vicinity of the species' range boundaries). The firecrest dominates in warmer and more humid areas and its dominance is more pronounced in mixed forests. The projection of the model showed that in any combination of temperature, precipitation and occurrence rate, the probability to encounter the goldcrest is higher in coniferous forests. Studies in Croatia and the Czech Republic showed regional differences in habitat preferences related to forest type. A significant effect of the seasonal dynamics of precipitation was confirmed in Croatia. Climate change and changes in forestry may influence the distribution and abundance of these two *Regulus* species in Europe.

Introduction

The coexistence of species is possible only if their niches (*sensu* Hutchinson 1957) are not identical. A group of closely related or similar species must differ among themselves sufficiently to ensure that each obtains an adequate share of the resources it needs (Pielou 1974). Niche segregation may have diverse forms: spe-

cies may differ in their (micro)habitat or diet requirements or in the time when they utilize the available resources at the highest rate. Differences in food sources or foraging techniques are often reported among sympatric congeneric avian species (Dyrce & Flinks 2003, Navarro *et al.* 2009). Interspecific competition for food resources among sympatric species is known to result in the divergence of species morphol-

ogy (Reifová *et al.* 2011). Trophic segregation is most often related to adaptations in body size and bill, leg or wing morphology (James 1982, Reifová *et al.* 2011). Studies on the relative densities of sympatric congeneric avian species may help in understanding the effects of climate and habitat factors on bird populations (Järvinen & Väisänen 1979).

Two of the six species of the family Regulidae are widespread across Europe and are sympatric over a large part of the continent. The goldcrest (*Regulus regulus*) belongs to the Palearctic faunal type with an extensive but discontinuous distribution from western Europe to Japan. Its European breeding area largely overlaps with that of the Norway spruce (*Picea abies*), extending between the July isotherms of 14–23 °C and up to 2200 m a.s.l. The firecrest (*Regulus ignicapilla*) belongs to the Holarctic faunal type and is confined to southwestern and central Europe and northern Africa (Baker 1997). The breeding range of the firecrest in Europe extends between the July isotherms of 16–24 °C and is usually found below 1000 m a.s.l. (del Hoyo *et al.* 2006). The northeasterly distributed goldcrest and southwesterly distributed firecrest coexist across a large area of sympatry in central Europe. The two species often have overlapping territories, and there is no evidence of interspecific territoriality (Fouarge 1974, Leisler & Thaler 1982). However, hybridization occurs on rare occasions (Cobb 1976, Thorpe 1983, Jennings 1985).

For sympatric sibling species, coexistence in the same habitat is associated with two main ecological processes: competition and interbreeding. The goldcrest and firecrest reduce competition through differences in their feeding ecology. The diet of both species consists almost exclusively of arthropods, but the goldcrest specialises on smaller prey than the firecrest. They have also evolved different foraging behaviours: goldcrests more often cling vertically and hang, especially along undersides of dense branches, whereas firecrests also forage in less dense branches, often standing (Leisler & Thaler 1982, Thaler & Thaler 1982). Interbreeding is prevented by ethological barriers of readily distinguishable behavioural patterns. It has been shown that in these two *Regulus* species, differences in antago-

nistic and courtship behaviours serve as isolating mechanisms, while isolation through vocalisation appears to be of minor importance (Thaler 1986, del Hoyo *et al.* 2006).

Both the goldcrest and firecrest inhabit mixed and coniferous forests, but their habitats differ across the continent. Glutz and Bauer (1991) found a strong association of the goldcrest with coniferous trees, while Becker (1977) found no differences in the species' main habitat requirements. The external morphology and foraging behaviour of the goldcrest support its preference for spruce (Leisler & Thaler 1982). Goldcrest habitats are dominated by Norway spruce and silver fir (*Abies alba*), while pines, except the mountain pine (*Pinus uncinata*), are generally avoided (del Hoyo *et al.* 2006). The study of forest bird trends in Europe showed a positive correlation between winter weather (winter temperature anomaly) and the goldcrest population trend in Europe (Gregory *et al.* 2007). Habitat choice of the firecrest is broader and it accepts even a small admixture of spruce, fir or pine in deciduous forests as a suitable nesting habitat (Hagemeijer & Blair 1997). It also breeds in deciduous forests, showing a preference for oak (del Hoyo *et al.* 2006). The firecrest's preference for pines was noted in some parts of Europe (Archaux & Bakkaus 2007, Ukmar *et al.* 2007), but not in others (Wesołowski *et al.* 2002, Nikolov 2007), while Becker (1977) suggested the avoidance of pine forests by both species. Towards its southern limit, the firecrest becomes more typical in montane forests (Leisler & Thaler 1982, Hagemeijer & Blair 1997); it also occupies more humid habitats (Glutz & Bauer 1991).

In forest stands where the two *Regulus* species coexist, one often dominates, sometimes with more than ten times higher densities (Bodenstein 1985, Saniga 1995). Despite the number of studies in different forest areas of Europe, there is currently a lack of research on factors affecting the ratio of the two *Regulus* species at regional and broader scales. Moreover, ecological studies from different areas showed differences in habitat preferences of each species. By studying the abundance ratio of the two species which is not affected by local differences

in absolute abundances caused by a number of factors, such as habitat quality, patchiness, unfavourable weather conditions etc., the patterns of dominance of one species over the other can be uncovered. It also enables the use of heterogeneous published data and the analysis at a larger spatial scale. The differences in relative densities of other congeneric forest passerines (*Parus* and *Fringilla*) have been attributed to differences in habitats and, to some extent, climate factors (Järvinen & Väisänen 1979). The combination of climate change and changes in forestry, resulting in the spread of coniferous and especially pine forests, may influence the distribution and abundance of forest birds in Europe. To understand such changes, it is necessary to improve our knowledge of habitat requirements of those birds on wider scale.

We propose that the ratio of the two *Regulus* species must be a result of different factors: geographical location and occurrence patterns across the continent (with dominance of the goldcrest in northeastern parts and that of the firecrest in the southwestern parts of the area of sympatry), altitude, habitat type and climate factors. We noticed great differences in dominance of one species over the other in apparently similar habitats in the same region, so we presume that geographical location and forest type cannot be the main underlying factors causing such differences. In this study, we tested the hypothesis that the vicinity of the species range boundaries and local climatic conditions significantly affect the abundance ratio of the two *Regulus* species. These local conditions do not fully account for pan-continental climatic gradients therefore causing the considerable difference in the two species ratio across the area of sympatry. To test this hypothesis, two approaches were used. Firstly, at the continental scale, we analyzed the available literature to explore differences of the ratio between goldcrest and firecrest densities in their zone of sympatry, and identify geographical, climate and habitat factors that correlate with the ratio of the two species. Secondly, at a regional scale, we analyzed our own field data from two study areas to identify in more detail the correlation between climate factors, structural and floristic composition of forests and the ratio of the two *Regulus* species.

Methods

Continental scale

The data used in the analysis at the continental scale included our own bird censuses and information obtained from the literature, totalling 63 samples from 26 sites. We obtained published data from the zone of sympatry, covering the area between 41°N and 53°N, and 3°W and 24°E (Table 1 and Fig. 1). We used only data based on standard methodology (point count, line transect and mapping methods) dated from the end of the 1970s onwards (i.e. obtained within the last ca. 30 years), with densities given for the two *Regulus* species. We considered only investigations in coniferous and mixed forests (including plots of deciduous forests with admixture of coniferous trees, that fulfilled other assumptions), and excluded those where the two *Regulus* species were present at very low densities (density of the dominant species smaller than 1 pair/10 ha). If data for several years were available, we calculated average values. Densities obtained by different methods cannot be directly compared, which prevented us from studying each species separately, but we presumed that each method gives the same bias for both species, so the abundance ratio between the two *Regulus* species remains unbiased. For some localities, several neighbouring study plots with different altitude, habitat type, forest age or level of tree damage were included.

The ratios of goldcrest and firecrest densities were related to geographical location, occurrence rate, climatic variables and forest structure. Latitude and longitude were expressed in decimal degrees, while altitude was given in meters. Latitude and longitude were either obtained from the literature or determined from topographic maps. For larger areas, we considered the central point of the region the reference point. Altitude was obtained from the literature. For assessing the effect of species range boundaries on species abundance ratios, we used maps presented in Hagemeyer and Blair (1997). For each studied species, occurrence was calculated as the number of occupied mapping squares in a 3 × 3 square area (corresponding to 150 × 150 km²) around the

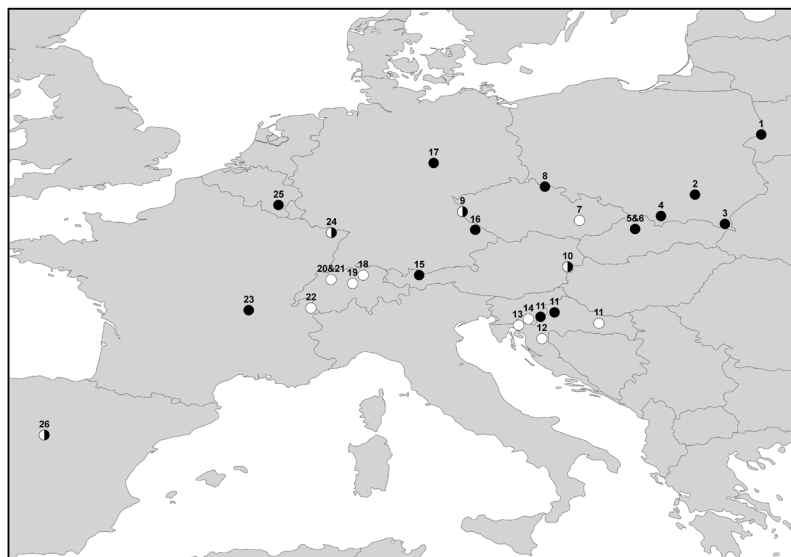


Fig. 1. Locations of the sites used in the analysis. Sites are numbered as in Table 1. Symbols: filled circles show localities where the goldcrest dominates, empty circles are localities where the firecrest dominates and half-filled circles are localities where their ratio is 1 or both species dominate (each in the one or more samples from the same site).

study localities (with the study locality situated in the central square). The logarithm of the ratio of values obtained for the two species was used in the analysis. We obtained climate data from the

literature, but when they were lacking we used Hijmans *et al.* (2005) (<http://www.worldclimate.com>). We used annual precipitation (mm) and mean annual temperature (°C), as the two most

Table 1. Sources of the data used. Site numbers, their names, applied methods and census years are given.

Study area	Sites	Method	Census years	Reference
1. Bialowieza (PL)	3	mapping	1995–1999	Wesolowski <i>et al.</i> (2002)
2. Kielce (PL)	1	transect	1995	Polak (1996)
3. Bieszczady (PL)	1	transect	1987–1988	Cichoń & Zajac (1991)
4. Gorce (PL)	2	mapping	1988	Głowaciński (1990)
5. Velka & Mala Fatra (SK)	2	transect	1989–1991	Saniga (1995)
6. Šramkova (SK)	1	mapping	1997–2001	Kornan (2004)
7. Brezina (CZ)	1	point count	1993–2005	Krist & Střiteský (2005)
8. Krkonose (CZ/PL)	8	point count	1991–1994	Flousek & Gramsz (1999)
9. Farske bažiny (CZ)	5	transect	1979–1981	Řepa (1984)
10. Sopron (HG)	1	point count	2002	Winkler (2005)
11. Northern Croatia	3	point count	2006–2007	this study and Dumbović (2007)
12. Mountain Croatia	4	transect	2005	this study
13. Risnjak (HR)	3	transect	1986	Sušić (1988)
14. Pečka & Rajhenav (SV)	4	mapping	1989	Perušek (1992)
15. Gurgltal (A)	1	transect	1977–1983	Bodenstein (1985)
16. Bavarian forest (D)	1	square grid	2001	Lang <i>et al.</i> (2003)
17. Harz Mts. (D)	2	mapping	1991–1992	George (1993)
18. Zurich (CH)	2	transect	1986–1999	Weggler & Widmer (2001)
19. Schwarzenberg (CH)	1	mapping	1995	Bernet (1997)
20. Solothurn (CH)	3	mapping	1981–1982	Christen (1983)
21. Combe Grede (CH)	1	mapping	1988	Schaffner (1990)
22. Giffre (FR)	1	point count	2000–2001	Archaux & Bakkaus (2007)
23. Haut-Beaujolais (FR)	6	point count	1983–1984	Lebreton & Pont (1987)
24. Vosges du Nord (FR)	3	point count	1979–1984	Muller (1988)
25. Ardenne (B)	2	point count	2000	du Bus de Warnaffe & Deconchat (2008)
26. Sierra de Ayllon (ES)	1	transect	1981–1982	Potti (1985)

comprehensive and most widely used indicators of climate. The general structure of the forests was characterized by forest type and age, both given as categorical variables with two categories each. The literature often did not contain percentages of tree species or detailed age structure, which prevented us from constructing a more detailed classification. We evaluated forest type by means of a classification of woodlands according to the proportion of deciduous trees: mixed forests with proportions of deciduous trees greater than 30% and coniferous forests with lower ratios of deciduous trees (categories: 0 = mixed forests, 1 = coniferous forests). No significant difference was found in the ratio of the two *Regulus* species between pine forests and other coniferous forests (Mann-Whitney *U*-test: $Z = 0.91$, $n = 25$, $p = 0.36$), therefore we analysed all coniferous forests as a single group. As for forest age, we considered woodlands older than 80 years as mature forests (categories: 0 = young stands and 1 = mature stands). We used a weighted multiple linear regression model to describe the relationship between the ratio of the two *Regulus* species and environmental variables, and to evaluate the predictive value of the environment in determining this ratio in the area of sympatry. In addition, the level of damage to trees (undamaged vs. damaged: tree defoliation by air pollution) was noted where available. This variable was not entered into the model, but was only used to compare pairs of forest plots at the same localities.

Regional scale

For the case studies at the regional scale, we used our own data collected in southern (Croatia) and central (the Czech Republic) parts of the area of sympatry. Bird and habitat data were collected from the same study plots. In Croatia, the study was conducted from 2005 to 2007 at five locations: three sites located in isolated fir-beech forests in the mountains of NW and NE Croatia (45°30'–45°55'N, 15°28'–17°41'E), and two sites in the mountain region of the NW Dinaric Alps (44°53'–44°55'N, 15°27'–15°32'E) covered with continuous fir-beech forests. We studied each site during one breeding season. We used the point count method with a fixed radius

of 50 m (Bibby *et al.* 1992) in isolated forests and line transects of 100 m width (Järvinen & Väisänen 1977) in continuous ones. Transects or points were censused 2–3 times during the breeding season. We carried out habitat sampling by the circular plot method (Cyr & Oelke 1976, Bibby *et al.* 1992) covering 0.04 ha each. We recorded tree species and their diameter (eight classes: A = 7.5–15 cm, B = 15–23 cm, C = 23–38 cm, D = 38–53 cm, E = 53–68 cm, F = 68–84 cm, G = 84–101 cm, H > 101 cm) inside the plot, shrub density and percentages of ground cover, and canopy cover. Basal area was calculated for trees in each diameter class, according to Cyr and Oelke (1976). The average tree basal area was calculated by dividing the total basal area by the total number of trees in the plot. We sampled habitat at each counting point in isolated forests and at three circular plots per kilometre of transect. Altogether 8 km of transects and 49 points were counted, and vegetation was sampled at 73 points. The spatial distribution of the study sites allowed us to investigate differences in climate data at the regional scale. Mean monthly air temperatures and precipitation were provided by the Croatian meteorological and hydrological service.

Bird counts in the Czech Republic were conducted in the Krkonose Mountains, situated in central Europe (50°35'–50°50'N, 15°23'–15°53'E), from 1984 to 1996 by using the point count method with a fixed radius of 100 m. Average values of bird counts for 108 points were included in the analysis. We obtained habitat characteristics of the points using the method in Emlen (1967) (for coniferous and deciduous tree covers, and coverage of the shrub and herb layers), from detailed forestry maps (for altitude and forest age: 30–80 years and > 80 years) and from aerial photographs (for tree layer cover and tree damage by air pollution). For tree damage, seven grades of defoliation were used (0%, 0%–5%, 6%–30%, 31%–50%, 51%–70%, 71%–100% of damaged trees, and a dead forest) (Krkonoše National Park Administration unpubl. data). For analyses at the regional scale, we used the data described above, while for comparative analyses at the continental scale we used summarized data from 1991–1994 published in Floušek and Gramsz (1999).

Statistical analysis

In the first step, we model data obtained at one observational site. Let (N, Y) represent an observation consisting of a total number of N pairs of the two *Regulus* species observed at the site, and of Y pairs of goldcrest among them. The number of firecrest pairs is uniquely determined from (N, Y) , and is equal to $N - Y$. We assumed that N is a random variable that is equal to a state of a Poisson process at time t with intensity λ . Here t is an observational time assumed to be independent of N . Let p denote a conditional probability of the goldcrest if a pair of *Regulus* species has been observed at this site. Then it follows that Y is equal to a state of the thinned Poisson process at time t and intensity λp (Colouring Theorem, Kingman 1993). Hence N and Y have Poisson distributions with means $m = \lambda t$ and mp respectively, and Y follows a binomial distribution with parameters p and n depending on the event $N = n$. So the log-likelihood of the parameters m and p based on an observation (N, Y) is given by the following expression:

$$\ell(m, p) = Y \log p + (N - Y) \log(1 - p) - m + N \log m$$

It follows that the maximum likelihood estimators (MLEs) of the parameters are $\hat{m} = N$ and $\hat{p} = Y/N$. Notice that MLE of p is equal to the ratio of goldcrests in a population consisting of goldcrests and firecrests only. Hence the parameter p can also be interpreted as expected density of goldcrests over firecrests. In this sense, $1 - p$ is expected density of firecrests over goldcrests. Since N/m converges to 1 and Y/m converges to p almost certainly by the Strong Law of Large Numbers (Kingman 1993: chapter 4.2), $\hat{p} = Y/N$ converges to p and $\hat{m} = N$ converges to infinity almost certainly, when m goes to infinity. Notice that m is large whenever observational time t is large. Moreover, by applying the method of characteristic functions, Cramér-Wold device and the Continuity Theorem (Shorack 2000: chapter 13.3) it can be proved that the properly normalized random vector (N, Y) is normally distributed asymptotically for large m , i.e. that

$$\sqrt{m} \left(\begin{bmatrix} \frac{N}{m} \\ \frac{Y}{m} \end{bmatrix} - \begin{bmatrix} 1 \\ p \end{bmatrix} \right)$$

has a bivariate normal distribution with zero mean vector, and the covariance matrix

$$\begin{bmatrix} 1 & p \\ p & p \end{bmatrix},$$

asymptotical when m approaches infinity. By the delta method (Shorack 2000: chapter 11.6), the following random quantity

$$\sqrt{m} \left(\log \frac{Y}{m - Y} - \log \frac{p}{1 - p} \right)$$

has a normal distribution with zero mean and variance equal to $1/[p(1 - p)]$ asymptotical when m approaches infinity. Since N/m converges to 1 almost certainly, the following random variable

$$\begin{aligned} & \sqrt{N\hat{p}(1 - \hat{p})} (\text{logit } \hat{p} - \text{logit } p) \\ &= \sqrt{Y \left(1 - \frac{Y}{N} \right)} \left(\text{logit } \frac{Y}{N} - \text{logit } p \right) \end{aligned} \tag{1}$$

has a standard normal distribution asymptotical when N almost certainly infinity. Here $\text{logit } q$ denotes the expression $\log q/(1 - q)$. In other words, the random variable (see Eq. 1) has a standard normal distribution for large enough observational time.

The observational data were summarized by a single quantity of the form

$$Z = \text{logit } \frac{Y}{N} = \text{logit } \hat{p}. \tag{2}$$

Notice that Z is equal to the natural logarithm of the ratios between the goldcrest and firecrest densities. Positive values of Z indicate dominance of the goldcrest, while negative values indicated dominance of the firecrest.

The above analysis showed that the quantity Z has weight that equals

$$W = Y \left(1 - \frac{Y}{N} \right) = Y(1 - \hat{p}) \tag{3}$$

This means that the variance of Z is equal to $1/W$ asymptotical for large enough observational time. Moreover, we assume that the (asymptotic)

mean of Z , $\text{logit } p$, linearly depends on some covariates that describe the site (i.e. environmental variables). Let us denote these covariates with x_1, x_2, \dots, x_r . Then

$$\text{logit } p = b_0 + b_1 x_1 + \dots + b_r x_r \quad (4)$$

where b_0, b_1, \dots, b_r are non-random coefficients independent of the covariates. In addition, if we assume that weight W is non-random, and observational time is large enough, it is reasonable (see Eqs. 1–4) to propose the following linear model for the data

$$Z = b_0 + b_1 x_1 + \dots + b_r x_r + \frac{1}{\sqrt{W}} \varepsilon \quad (5)$$

where the standardized error term ε has a standard normal distribution.

In the second step, we modelled a set of data that were acquired at various sites. Let $(Z_i, W_i, x_{i1}, x_{i2}, \dots, x_{ir})$, $i = 1, 2, \dots, k$, represent the full set of data: summarized observational data (Eq. 2) together with the corresponding weights (Eq. 3) and covariate values describing the sites. The main reason why we present all observational data in a summarized form (Eq. 1) is that some authors reported total numbers of individuals of both *Regulus* species, while many others reported only densities per different area units. Because of the same reason we estimate all weights W_i by replacing total numbers of the observed goldcrest pairs Y_i in Eq. 3 by the numbers of the goldcrest pairs observed per area unit at the site.

The main assumption is that the data are acquired independently. Hence the model is

$$Z_i = b_0 + b_1 x_{i1} + \dots + b_r x_{ir} + \delta \frac{1}{\sqrt{W_i}} \varepsilon_i \quad (6)$$

where $i = 1, 2, \dots, k$, $\varepsilon_1, \dots, \varepsilon_k$ is a sequence of independent and identically distributed standard normal random variables representing standardized errors. Here $1/\delta^2$ represents an average number of observational units encountered across the sites. A strictly positive parameter δ is included in the model (Eq. 6) to adjust the error term for errors encountered in the previously

described estimation of weights. The proposed model is asymptotically equivalent to a logistic regression model in a sense that the estimators obtained by the Weighted Least Square (WLS) method from the model (Eq. 6) are asymptotically equivalent to MLEs from the corresponding logistic regression model (Ferguson 1996: chapter 23). For details on logistic regression modelling, see e.g. Christensen (1997).

We considered eight environmental variables as independent variables: latitude, longitude, altitude, annual precipitation, mean annual temperature, forest type, forest age and occurrence rate. A correlation matrix was calculated between all independent variables to examine possible co-linearity. Multiple correlation coefficients between latitude and the other independent variables (with constant vector included) were equal to a high value of 90.7%. In order to avoid numerical instability of regression parameter estimation, we excluded latitude from the regression analysis as a covariate. Since the model is linear with unequal variances of the error terms, we used the WLS method for model estimation with the following criterion function:

$$\text{LS}(b_0, \dots, b_r) = \sum_{i=1}^k W_i (Z_i - b_0 - b_1 x_{i1} - \dots - b_r x_{ir})^2$$

For this purpose we used the Statistica software, ver. 9.1 (Stat Soft Inc.), particularly its ‘Multiple linear regression’ module with the ‘Weighted moments’ option. The obtained minimum adequate model was selected by means of a backwards stepwise procedure with the minimal partial correlation criterion (Christensen 2011: chapter 14.2). A covariate was included in the model if its corresponding significance was at least 5%. A normal assumption was verified by normal probability plots. The model was verified by residual plots, an F -test (Christensen 2011: theorem 3.2.1), and a chi-square test (Ferguson 1996: theorem 24). For calculating standardized residuals we used the MATLAB software, ver. 7.11 (MathWorks Inc.).

The proposed model (Eq. 6) with all seven covariates included is significant ($F = 10.9$, $p < 0.001$) although some covariates are not significant. The plot of residuals (Fig. 2a) verifies

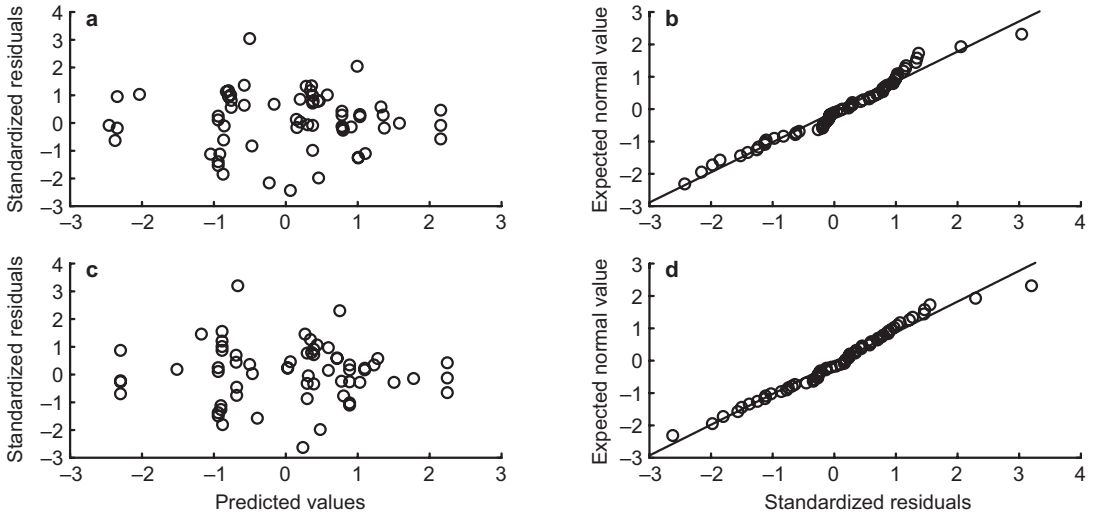


Fig. 2. Standardized plots of residuals (predicted vs. residual scores, $Z = \log\text{-ratio densities goldcrest/firecrest}$): (a) full model, and (c) minimum adequate model; and normal probability plots of standardized residuals: (b) full model, and (d) minimum adequate model.

the model. Normal probability plots (Fig. 2b) of standardized residuals show that there is no reason to reject the hypothesis that standardized errors follow the standard normal distribution. In addition, we can assume that the parameter δ has a value of 1 since the p value of the appropriate chi-square test of adequacy of the model with $\delta = 1$, is greater than 90% ($\chi^2 = 41.6$).

The effect of defoliation was analysed with a Wilcoxon matched pairs test for seven pairs of plots (data from Flousek 1989, Perušek 1992, Weggler & Widmer 2001, Lang *et al.* 2003), with available data on bird densities in forest stands before and after defoliation, or from two neighbouring plots — one undamaged (or slightly damaged) and one heavily damaged.

In both case studies at the regional scale, the data were not normally distributed (Shapiro-Wilks' W test, $p < 0.05$), therefore we used a Mann-Whitney U -test and Spearman's correlation with a Bonferroni correction for multiple comparisons. Structural characteristics of vegetation were included in the analysis only at the regional scale and detailed climate data (mean monthly temperature and precipitation) only in Croatia, as appropriate data at the continental scale were lacking.

Results

Continental scale

The minimum adequate model (Eq. 6) has four significant covariates: mean annual temperature (temperature), annual precipitation (precipitation), occurrence rate and forest type (Table 2). It is highly significant ($F = 17.9$, $p < 0.001$), and does not significantly differ from the starting model ($F = 1.25$, $p > 0.30$ or $\chi^2 = 2.83$, $p > 0.41$, testing the hypothesis that $\delta = 1$). In this case, the hypotheses of normality of errors (the normal probability plot, Fig. 2d) and adequacy of the model with $\delta = 1$ ($\chi^2 = 44.5$, $p > 0.90$, see Fig. 2c) cannot be rejected. Both climate variables were negatively correlated with the goldcrest/firecrest ratio, revealing that the firecrest dominated in warmer and more humid areas. Absolute values of the coefficients (b_j^*) of the standardized covariate values (Table 2) indicate slightly greater (but not significant) importance of temperature over precipitation. However, in areas with annual precipitation above 1400 mm, only the firecrest dominated. Occurrence rate was positively correlated with the species abundance ratio (see Table 2), showing that near the range boundaries of one species, the other usu-

ally dominates. Forest type was correlated with the ratio of the two *Regulus* species, indicating more pronounced goldcrest domination in coniferous forests. The projection of the model showed that in any combination of temperature, precipitation and occurrence rate, the probability to encounter the goldcrest over the firecrest is higher in coniferous forests than in mixed ones. The difference between the probabilities of encountering one species over the other in these two forest types is most pronounced in warm and dry forest habitats.

The ratio of goldcrest to firecrest density increased in damaged forests (Wilcoxon matched pairs test: $Z = 2.366$, $p < 0.05$) as a consequence of the more pronounced decrease in the firecrest density.

Regional scale

At the regional scale, the correlation of the goldcrest/firecrest ratio with the geographical location for Croatian forests showed a pronounced effect of latitude (Spearman's correlation: $r_s = 0.75$, $p = 0.012$), but not of longitude ($r_s = 0.07$, $p = 0.83$). The firecrest dominated in Mountain Croatia (Dinaric Alps) and on isolated mountains of eastern Croatia, while the goldcrest was

dominant on isolated mountains of NW Croatia. The goldcrest/firecrest ratio was correlated with mean precipitation only in May ($r_s = 0.72$, $p < 0.016$). Bonferroni corrected p equalled 0.016 for both geographical and climate factors. Firecrest dominated in areas with a greater proportion of fir trees, greater average tree basal area and greater density of the largest trees (diameter at breast height > 68 cm, Table 3). The cumulative proportion of all coniferous trees in forest stands (fir, spruce, pine and larch) had no significant effect on the goldcrest/firecrest ratio ($p = 0.24$).

In the Krkonose Mts. of the Czech Republic, the goldcrest dominated in 94 of the 108 plots (87%). The goldcrest/firecrest ratio increased with the proportion of spruce trees in the study plot ($r_s = 0.33$, $p < 0.001$). There was a positive correlation between the proportion of spruce trees and altitude as well as damage, but after the Bonferroni correction the ratio of the two species was not significantly correlated with those variables.

The goldcrest/firecrest ratio was not correlated with increasing damage of trees. The mean number of birds per point for both species was negatively correlated with tree damage (Spearman's correlation: goldcrest $r_s = -0.36$, $p < 0.001$; firecrest $r_s = -0.51$, $p < 0.001$), therefore affecting the significance level of the goldcrest/firecrest ratio.

Table 2. Minimum adequate regression model. Covariates are given in their original metrics (b_j), and in standardized forms (b_j^*). t -test statistics and p values for testing the significance of each covariate included in the model are also given. The adjusted coefficient of determination is 0.52 and the δ parameter estimate is 0.88.

	b_j^*	SE (b_j^*)	b_j	SE (b_j)	t_{58}	p
Intercept			2.174089	0.654726	3.32061	0.001557
Temperature	-0.361027	0.093317	-0.266914	0.068991	-3.86881	0.000279
Precipitation	-0.258128	0.095836	-0.000600	0.000223	-2.69342	0.009232
Occurrence rate	0.333619	0.091667	2.724537	0.748612	3.63945	0.000583
Forest type	0.442996	0.089799	0.916138	0.185708	4.93322	0.000007

Table 3. Habitat characteristics showing significant differences between forests dominated by the goldcrest and firecrest in Croatia. Mean values \pm SEs are given, together with Mann-Whitney U -test p values.

Characteristic of vegetation	Goldcrest-dominated forests	Firecrest-dominated forests	p
Percentage of fir trees	22.28 \pm 3.99	43.54 \pm 5.15	< 0.001
Average tree basal area	0.11 \pm 0.02	0.19 \pm 0.02	< 0.001
Density of largest trees	46.16 \pm 7.28	60.90 \pm 4.90	< 0.001

Discussion

The resulting minimum adequate model developed by the weighted multiple linear regression showed that climate factors, occurrence rate and forest type affected the most the ratio of the two *Regulus* species. The firecrest generally dominated in warmer and more humid areas of Europe. The effects of climate on these two species were studied in the Iberian Peninsula (Telleria & Santos 1994), where firecrest densities were positively correlated with annual precipitation, while those of the goldcrest were positively correlated with precipitation and negatively with mean annual temperature. However in the Iberian Peninsula, the goldcrest is restricted to the high mountains and it is patchily distributed (Telleria & Santos 1993, Lebreton & Thévenot 2009). Therefore, these results cannot be applied as a general rule to the effects of climate on the two *Regulus* species without wider studies.

Altitude on its own could not explain the differences in the ratio between the two *Regulus* species. Both temperature and precipitation change with altitude, and they also vary across the continent, so that climatic conditions at certain altitudes also change across Europe. In our study, average annual precipitation was correlated with altitude ($r_s = 0.64$, $p < 0.001$), but not with temperature ($r_s = -0.21$, ns). In Europe, average temperature increases towards the south and southwest, while average annual precipitation depends on altitude and proximity to the Atlantic Ocean, resulting in the highest values in the Alps, the Dinaric region, and along the Atlantic coast (Huntley et al. 2007). Consequently, differences in altitudinal preferences of the two *Regulus* species occurred across the continent: the firecrest preferring montane forests in the southern parts of its range (Leisler & Thaler 1982, Hagemeyer & Blair 1997) where it is warmer, but also more humid at higher altitudes. In central Europe (the Czech Republic and Austria), the firecrest is also common in lowland areas (Dvorak et al. 1993, Šťastný et al. 2006), while the goldcrest prefers middle and higher altitudes.

The minimum adequate model and its projection confirmed dominance of the goldcrest in coniferous forests and of the firecrest in mixed

forests. Our study did not reveal differences in the ratio of the two species between pine forests and forests dominated by spruce or fir. In a study that covers France to Morocco, both species had higher abundances in fir than pine forests, which was especially evident for the goldcrest (Lebreton & Thévenot 2009). In the Pyrenees, the goldcrest was dominant in mountain pine forests, while the firecrest was more numerous in beech–fir and Scots pine (*Pinus sylvestris*) forests (Purroy 1974a, 1974b).

It is known that densities of both *Regulus* species significantly decrease with an increasing amount of damage (defoliation) to spruce trees (Flousek 1989). Firecrest populations showed a more dramatic decrease, both as a result of the damage to spruce trees (Flousek 1989) and defoliation of beech trees (Wegglar & Widmer 2001). That was also confirmed in this study, but a more detailed analysis at the continental scale was not possible, as methods for assessing damage to trees differed among surveys.

At the regional scale, in coniferous and mixed montane forests of Croatia and the Czech Republic, the ratio of the two species differed considerably among sites and habitats.

On isolated mountains in NW Croatia, the goldcrest was 3–5 times more numerous, but in Mountain Croatia its densities were more than 10 times lower than those of the firecrest. Although there were no correlations between annual temperature and precipitation and the ratio of the two species, precipitation during late spring was correlated with firecrest's dominance. In the Czech Republic, the goldcrest can be up to four times more numerous in spruce forests than the firecrest, while their densities are almost equal in forests with more deciduous trees (Šťastný et al. 2006). The goldcrest's dominance in spruce forests of the Krkonose Mts. is in line with this general pattern, but in Croatia, different results were obtained. Croatian forests are characterised by fir, not spruce. Stands with a greater proportion of fir (but not significantly greater proportion of all coniferous trees) were preferred by the firecrest, which could be identified as the characteristic breeding species of fir and fir–beech forests in Croatia. In Croatian forests, the firecrest was more abundant in older forest stands. Similar results were obtained in other regions (Lauer-

mann 1976, Muller 1988), but the opposite ratio could also be found (Řepa 1984).

The expansion of coniferous plantations at the end of the 19th century allowed the firecrest to increase its range and numbers considerably in central Europe (Gatter & Schütt 2004), resulting in a northward shift in its distribution. In France, many native fir forests were replaced by pines, which caused changes in the local ornithofauna (Lebreton & Thévenot 2009). The spatial distribution (quadrant occupancy) of the firecrest in the Czech Republic has increased by 75% in the last three decades (Šťastný *et al.* 2006). In Croatia, the firecrest also spread its range towards the north. It is abundant in continuous fir-beech forests of Mountain Croatia, but was not present as a breeding species on insular mountains of NW Croatia during the 20th century (Kroneisl 1949, Dolenc 1991). Our research is the first confirmation of breeding of the firecrest in this region of Croatia. In Europe, the firecrest is known to inhabit isolated patches of coniferous trees, but it is not the case in Croatia. In lowland Croatia, the goldcrest recently established small populations in isolated habitats with coniferous trees, including urban parks (J. Kralj pers. obs.). The occurrence rate seems to have an important effect on the abundance ratio of the two species along their range boundaries. It is known that the possibility of colonisation of new areas is related to the regional occurrence of bird species. Widely distributed and abundant species have a higher chance of colonising neighbouring forests (Villard & Taylor 1994).

The firecrest has a more southern distribution than the goldcrest, being absent from northern coniferous forests. According to Haila and Järvinen (1990), southern coniferous forests have a characteristic set of abundant species, which may originate from other types of forests. But it is more likely that the firecrest, which is a species of boreal origin (as other species of its genus), failed to spread north from refuges in Mediterranean Europe (Blondel 1990) and to recolonise the northern taiga after the last glaciation. Therefore, the recent ratio between these two species might be the result of historical changes in their ranges, as well as local climate and forest type.

The number of studies concerned with the effects of climate change on different aspects of

the bird fauna is increasing (Møller *et al.* 2004, Huntley *et al.* 2007). Since recent global climate change is likely to have caused an increase in annual temperatures in most of Europe and a decrease in annual precipitation in the western Mediterranean area (IPCC 2007) where the firecrest dominates, it would be important to monitor possible changes in the ratio of the two species — e.g. an expected spreading of the firecrest, especially northwards (as modelled by Huntley *et al.* 2007) or into higher altitudes. The case study in Croatia showed that, although annual precipitation at the regional scale had no effect on the ratio of the two species, higher average precipitation during late spring was preferred by the firecrest. Therefore, apart from annual rates of precipitation and temperature, dynamics of climate factors through the year can also be an important issue, and should be given more attention in future studies. At the continental scale, the ratio of the two *Regulus* species is influenced by climate and habitat factors (forest type), as well as by the occurrence rate. The significant role of the occurrence rate indicates that with the spreading of one species, existing ratios might change considerably. The combination of climate change and changes in forestry, resulting in the spread of coniferous and especially pine forests, may influence the distribution and abundance of these two *Regulus* species in Europe and change the local forest bird community structure.

Acknowledgements

We are grateful to Dr. Iain Taylor for improving an earlier version of the manuscript and to two anonymous reviewers for their constructive comments. This study was supported by Nature Parks Medvednica, Žumberak-Samoborsko gorje and Papuk and by National Park Plitvice Lakes and by the Ministry of Science, Education and Sports, Republic of Croatia (grants no. 101-1012682-2678, 037-0372790-2800 and 119-1012682-1221).

References

- Archaux, F. & Bakkaus, N. 2007: Relative impact of stand structure, tree composition and climate on mountain bird communities. — *Forest Ecology and Management* 247: 72–79.
- Baker, K. 1997: *Warblers of Europe, Asia and North Africa*.

- Princeton University Press, Princeton.
- Becker, P. H. 1977: Verhalten auf Lautäußerungen der Zwilingsart, interspezifische Territorialität und Habitatansprüche von Winter- und Sommergoldhähnchen (*Regulus regulus*, *R. ignicapillus*). — *Journal of Ornithology* 118: 233–260.
- Bernet, D. 1997: Brutvogelkartierung eines voralpinen Wirtschaftswaldes. Ökologische Studie als Beitrag zum Entschcheid über die künftige Bewirtschaftung standörtlich schwieriger Bestände. — *Der Ornithologische Beobachter* 94: 233–256.
- Bibby, C. J., Burgess, N. D. & Hill, D. A. 1992: *Bird census techniques*. — Academic Press, London.
- Blondel, J. 1990: Synthesis: The history of forest bird avifaunas of the world. — In: Keast, A. (ed.), *Biogeography and ecology of forest bird communities*: 371–377. SPB Academic Publishing, The Hague.
- Bodenstein, G. 1985: Über die Vogelwelt des Gurgltales, Nordtirol. Versuch einer qualitativen Bestandsaufnahme. *Monticola* 5, Sonderheft 1985: 3–144.
- Christen, W. 1983: Brutvogelbestände in Wäldern unterschiedlicher Baumarten- und Alterklassenzusammensetzung. — *Der Ornithologische Beobachter* 80: 281–291.
- Christensen, R. 1997: *Log-linear models and logistic regression*, 2nd ed. — Springer, New York.
- Christensen, R. 2011: *Plane answers to complex question: the theory of linear models*, 4th ed. — Springer, New York.
- Cichoń, M. & Zając, T. 1991: Avifauna of Bieszczady National Park (SE Poland) in 1987 and 1988 — quantitative and qualitative data. — *Acta Zoologica Cracoviensia* 34: 497–517.
- Cobb, F. K. 1976: Apparent hybridisation of firecrest and goldcrest. — *British Birds* 69: 447–451.
- Cyr, A. & Oelke, H. 1976: Vorschläge zur Standardisierung von Biotopbeschreibungen bei Vogelbestandsaufnahmen im Waldland. — *Die Vogelwelt* 97: 161–175.
- del Hoyo, J., Elliott, A. & Christie, D. A. (eds.) 2006: *Handbook of the birds of the world*, vol. 11. — Lynx Edicions, Barcelona.
- Dolenc, Z. 1991: *Struktura zajednica ptica Medvednice, Ivanščice i Cesargradske gore s pregledom ornitofaune Hrvatskog zagorja* [The structure of bird communities on the mountains of Medvedica, Ivanščica and Cesargradska gora with the survey of ornithofauna of Hrvatsko zagorje region]. — Ph.D. thesis, University of Zagreb. [In Croatian with English summary].
- du Bus de Warnaffe, G. & Deconchat, M. 2008: Impact of four silvicultural systems on birds in the Belgian Ardenne: implications for biodiversity in plantation forests. — *Biodiversity Conservation* 17: 1041–1055.
- Dumbović, V. 2007: *Struktura zajednica ptica gnjezdarića šuma u Parku prirode Papuk* [Breeding bird community in the forests of Papuk Nature Park]. — M.Sc. thesis, University of Zagreb. [In Croatian with English summary].
- Dvorak, M., Ranner, A. & Berg, H. M. 1993: *Atlas der Brutvögel Österreichs. Ergebnisse der Brutvogelkartierung 1981–1985 der Österreichischen Gesellschaft für Vogelkunde*. — Bundesministerium für Umwelt, Jugend und Familie, Vienna.
- Dyrce, A. & Flinks, H. 2003: Nestling food of the congeneric and sympatric rusty-margined and social flycatchers. — *Journal of Field Ornithology* 74: 157–165.
- Emlen, J. T. 1967: A rapid method for measuring arboreal canopy cover. — *Ecology* 48: 158–160.
- Ferguson, T. S. 1996: *A course in large sample theory*. — Chapman & Hall, London.
- Fouarge, I. G. 1974: Etude de la densité de Roitelets huppés (*Regulus regulus*) et triple-bandeau (*Regulus ignicapillus*) dans une pessière âgée : premiers résultats. — *Aves* 11: 151–156.
- Flousek, J. 1989: Impact of industrial emissions on bird populations breeding in mountain spruce forests in central Europe. — *Annales Zoologici Fennici* 26: 255–263.
- Flousek, J. & Gramsz, B. 1999: *Atlas hnízdního rozšíření ptáků Krkonoše* [Atlas of breeding birds in the Krkonoše Mts. (Czech Republic/Poland) in 1991–1994]. — Krkonoše National Park Administration, Vrchlabí [In Czech with English summary].
- Gatter, W. & Schütt, R. 2004: Biomass, population density and species number in avian communities of upland and submontane broad-leaved and coniferous forests in Southwest-Germany. — *Die Vogelwelt* 125: 251–258.
- Głowaciński, Z. 1990: The breeding bird communities of the Kamienica watershed in Gorce National Park (the Carpatians, southern Poland). — *Acta Zoologica Cracoviensia* 33: 273–301.
- George, K. 1993: Untersuchung eines Landschaftsausschnitts im nordöstlichen Harz (Sachsen-Anhalt) als Lebensraum für Vögel. — *Ornithologische Jahresberichte des Museum Heineanum* 11: 31–46.
- Glutz, U. N. & Bauer, K. M. (eds.) 1991: *Handbuch der Vögel Mitteleuropas 12/III. Passeriformes 3*. — Aula Verlag Wiesbaden.
- Gregory, R. D., Vorisek, P., van Strien, A., Gmelig Meyling, A. W., Jiguet, F., Fornasari, L., Reif, J., Chylarecki, P. & Burfield, I. J. 2007: Population trends of widespread woodland birds in Europe. — *Ibis* 149 (Suppl. 2): 78–97.
- Hagemeyer, W. J. M. & Blair, M. J. 1997: *The EBCC atlas of European breeding birds: their distribution and abundance*. — T & AD Poyser, London.
- Haila, Y. & Järvinen, O. 1990: Northern conifer forests and their bird species assemblages. — In: Keast, A. (ed.), *Biogeography and ecology of forest bird communities*: 61–85. SPB Academic Publishing, The Hague.
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. 2005: Very high resolution interpolated climate surfaces for global land areas. — *International Journal of Climatology* 25: 1965–1978.
- Huntley, B., Green, R. E., Collingham, Y. C. & Willis, S. G. 2007: *A climatic atlas of European breeding birds*. — Durham University, The RSPB & Lynx Edicions, Barcelona.
- Hutchinson, G. E. 1957: Concluding remarks — *Cold Spring Harbor Symposia on Quantitative Biology* 22: 415–427.
- IPCC 2007: *Climate change (2007) Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. — IPCC, Geneva, Switzerland.

- James, F. C. 1982: The ecological morphology of birds: a review. — *Annales Zoologici Fennici* 19: 265–275.
- Järvinen, O. & Väisänen, R. A. 1977: Line transect method: a standard for field-work. — *Polish Ecological Studies* 3: 11–15.
- Järvinen, O. & Väisänen, R. A. 1979: Climatic changes, habitat changes, and competition: dynamics of geographical overlap in two pairs of congeneric bird species in Finland. — *Oikos* 33: 261–271.
- Jennings, P. P. 1985: Observations on an instance of hybridisation between male firecrest and female goldcrest. — *Ardea* 73: 191–192.
- Kingman, J. F. C. 1993: *Poisson processes*. — Clarendon Press, Oxford.
- Kornan, M. 2004: Structure of the breeding bird assemblage of a primaeval beech-fir forest in the Šrámková National Nature Reserve, the Mala Fatra Mts. — *Biologia* 59: 219–231.
- Krist, M. & Střiteský, J. 2005: Ptactvo Vojenského újezdu Březina: populační trendy v letech 1993–2005 [Birds of the army territory Březina: population trends in 1993–2005]. — *Zprávy Vlastivědného muzea v Olomouci* 283: 72–79. [In Czech with an English summary].
- Kroneisl, R. 1949: Contributions to the ornithofauna of the upland region between the Sava and Drava in Croatia. Birds of the Mountain Medvednica. — *Larus* 3: 305–352.
- Lang, C., Scherzinger, W. & Konold, W. 2003: Sukzession der Avifauna auf Störungsflächen im Nationalpark Bayerischer Wald. — *Ornithologischer Anzeiger* 42: 1–15.
- Lauermann, H. 1976: Die Vögel des Forstes Trübenbach im nordöstlichen Waldviertel (Niederösterreich). — *Egretta* 19: 23–60.
- Lebreton, P. & Pont, B. 1987: Avifaune et altérations forestières. — *Acta Oecologica* 8: 227–235.
- Lebreton, P. & Thévenot, M. 2009: Comparaison de l'avifaune sapinères et de pinèdes médio-européennes et méditerranéennes. — *Revue D'Écologie (La Terre et La Vie)* 64: 171–188.
- Leisler, B. & Thaler, E. 1982: Differences in morphology and foraging behaviour in the goldcrest *Regulus regulus* and firecrest *R. ignicapillus*. — *Annales Zoologici Fennici* 19: 277–284.
- Møller, A. P., Fiedler, W. & Berthold, P. 2004: *Birds and climate change*. — Advances in Ecological Research, vol. 35, Elsevier Academic Press, Amsterdam.
- Muller, Y. 1988: Recherches sur l'écologie des oiseaux forestiers des Vosges du Nord. IV. Étude de l'avifaune nicheuse de la succession du Pin sylvestre. — *L'Oiseau et la Revue Française d'Ornithologie* 58: 89–112.
- Navarro, J., Forero, M. G., González-Solís, J., Igual, J. M., Bécarea, J. & Hobson, K. A. 2009: Foraging segregation between two closely related shearwaters breeding in sympatry. — *Biology Letters* 5: 545–548.
- Nikolov, S. C. 2007: Study on the habitat selection by birds in mature and over-mature Macedonian pine *Pinus peuce* forest in Pirin National park (SW Bulgaria). — *Acrocephalus* 28: 95–104.
- Perušek, M. 1992: Ptice pragozdnih ostankov Rajhenavski Rog in Pečka ter njihova odvisnost od stanja sestojev. [The birds of Rajhenavski Rog and Pečka virgin forest rests and its dependence upon the condition of forest stands]. — *Gozdarski vestnik* 7–8: 322–330. [In Slovenian with an English summary].
- Pielou, E. C. 1974: *Population and community ecology*. — Gordon and Breach Science Publishers, New York.
- Polak, M. 1996: Zgrupowanie ptaków lęgowych Góry Wierzejskiej koło Kielc. — *Kulon* 1: 21–24.
- Purroy, F. J. 1974a: Breeding communities in the beech and fir forests of the Pyrenees. — *Acta Ornithologica* 14: 151–157.
- Purroy, F. J. 1974b: Contribucion al conocimiento ornitológico de los pinares Pirenaicos. — *Ardeola* 20: 245–261.
- Potti, J. 1985: La sucesión de las comunidades de aves en los pinares repoblados de *Pinus sylvestris* del Macizo de Ayllon (Sistema Central). — *Ardeola* 32: 253–277.
- Reifová, R., Reif, J., Antczak, M. & Nachman, M. W. 2011: Ecological character displacement in the face gene flow: evidence from two species of nightingales. — *BMC Evolutionary Biology* 11: 138.
- Řepa, P. 1984: The qualitative and quantitative composition of bird communities of the forest upland moor in the State Nature Reserve Farské bažiny near Tachov (south-western Bohemia). — *Folia Musei Rerum Naturalium Bohemiae Occidentalis, Plzeň — Zoologica* 19: 1–24.
- Saniga, M. 1995: Breeding bird communities of the fir-beech to the dwarfed-pines vegetation tiers in the Velká Fatra and Malá Fatra mountains. — *Biologia Bratislava* 50: 185–193.
- Schaffner, U. 1990: Die Avifauna des Naturwaldreservates Combe-Grede (Berner Jura). — *Der Ornithologische Beobachter* 87: 107–129.
- Shorack, G. R. 2000: *Probability for statisticians*. — Springer, New York.
- Sušić, G. 1988: *Struktura zajednica ptica duž visinskog gradijenta Risnjaka i Papuka*. — Ph.D. thesis, University of Zagreb.
- Šťastný, K., Bejček, V. & Hudec, K. 2006: *Atlas hnízdního rozšíření ptáků v České republice [Atlas of breeding birds in the Czech Republic 2001–2003]*. — Aventinum, Prague. [In Czech with English summary].
- Telleria, J. L. & Santos, T. 1993: Distributional patterns of insectivorous passerines in the Iberian forests: Does abundance decrease near the border? — *Journal of Biogeography* 20: 235–240.
- Telleria, J. L. & Santos, T. 1994: Factors involved in the distribution of forest birds in the Iberian Peninsula. — *Bird Study* 41: 161–169.
- Thaler, E. 1986: Zum Verhalten von Winter- und Sommergoldhähnchen (*Regulus regulus*, *Regulus ignicapillus*) – etho-ökologische Differenzierung und Anpassung an den Lebensraum. — *Der Ornithologische Beobachter* 84: 281–289.
- Thaler, E. & Thaler, K. 1982: Nahrung und ernährungsbiologische Unterschiede von Winter- und Sommergoldhähnchen (*Regulus regulus*, *R. ignicapillus*). — *Ökologie der Vögel* 4: 191–204.
- Thorpe, R. I. 1983: Apparent hybridisation between goldcrest and firecrest. — *British Birds* 76: 233–234.
- Ukmar, E., Battisti, C., Luiselli, L. & Bologna, M. A. 2007: The effects of fire on communities, guilds and species of

- breeding birds in burnt and control pinewoods in central Italy. — *Biodiversity and Conservation* 16: 3287–3300.
- Villard, M.-A. & Taylor, P. D. 1994: Tolerance to habitat fragmentation influences the colonization of new habitat by forest birds. — *Oecologia* 98: 393–401.
- Weggler, M. & Widmer, W. 2001: Comparison of population sizes of breeding birds in the Canton Zurich in 1986–1988 and in 1999. Changes in near-natural woodland habitats. — *Der Ornithologische Beobachter* 98: 12–22.
- Wesołowski, T., Tomiałojć, L., Mitrus, C., Rowiński, P. & Czeszczewik, D. 2002: The breeding bird community of a primaeval temperate forest (Białowieża National Park, Poland) at the end of the 20th century. — *Acta Ornithologica* 37: 27–45.
- Winkler, D. 2005: Ecological succession of breeding bird communities in deciduous and coniferous forests in the Sopron Mountains, Hungary. — *Acta Silvatica et Lignaria Hungarica* 1: 49–58.