The Pied and the Collared Flycatcher do not compete for microhabitats in the Białowieża Forest

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When resources are limited two species often compete, which leads to negative fitness consequences as for example with the Great Tit *Parus major* and Blue Tit *Cyanistes caeruleus* (1) or Great Tit and Pied Flycatcher (2). Our study investigates the opposite situation - what happens with two sibling species when resources are not limited but under primeval conditions? Pied Flycatcher *Ficedula hypoleuca* (PALLAS, 1764) and Collared Flycatcher *F. albicollis* (TEMMINCK, 1835) are closely related species, with similar breeding ecology regarding nest sites, food type and foraging techniques. In areas of overlapping distributions, the Collared Flycatcher (CF) is often numerous, while the Pied Flycatcher (PF) breeds in much lower densities (e.g. 3; 4; 5). Competition between these species has been described many times (e.g. 3; 6; 7). In managed forests, both species compete for nest boxes and, as a result, PFs are forced to breed mostly in poorer, coniferous stands (8). Under the primeval conditions of the Białowieża Forest (NE Poland) CF is very numerous only in deciduous stands, while PF breeds in very low densities in all habitats (9; 10; 11; 12). Thus, both species coexist in deciduous stands where no nest boxes are present, and they breed only in tree holes. It is not known, however, whether PF and CF differ in microhabitat use within primeval deciduous stands, where resources are not limited.

The goal of this work was to examine how PF and CF differ in microhabitat use in deciduous stands under primeval conditions. To achieve this goal, we compared microhabitat characteristics surrounding the nest cavities of both species in two deciduous forest types within the primeval stands of the Białowieża Forest.

The study was conducted in the Białowieża National Park (hereafter abbreviated as BNP; 52°41'N, 23°52'E). The strictly protected part (47.5 km²) has never been logged or planted. The structure of the forest there is of uneven age with multi-layers and multiple tree species. Lime-hornbeam-oak *Tilio-Carpinetum* stands are the dominant type in this forest being mainly composed of lime *Tilia cordata*, hornbeam *Carpinus betulus*, Norway spruce *Picea abies*, oak *Quercus robur*, maple *Acer platanoides*, and elms *Ulmus* spp. The dominant species in ash-alder *Circaeo-Alnetum* stands are alder *Alnus glutinosa*, ash *Fraxinus excelsior* and Norway spruce.

Data were collected in 1997 – 1999 within permanent ornithological study plots, in lime-hornbeam-oak stands (three study plots, in total 138 ha) and in an ash-alder riverine stand (one plot, 33 ha; 9). We searched for PF and CF nest cavities (methods described in WALANKIEWICZ et al. (13)). Due to the low density of PF, searches for their tree cavities were also conducted outside the study plots, in stands adjacent to the plots, and along the roads of the BNP. In July and August, we measured the habitat characteristics around

nest cavity trees and in random plots, which were chosen in the vicinity of the flycatcher sample plots. We assumed that a circle with a 20 m radius (0.126 ha) around the nest cavity tree was sufficiently large to characterize the birds' nesting habitat use. We measured within each sample plot the tree crown cover (the vertical projection of crown cover was drawn on a map, from which a total share of canopy cover was calculated as percentage), the composition of tree species, the condition of all trees (living or standing dead as snag) and the diameter of the tree trunks at breast height (DBH).

All trees with a DBH ≥ 12 cm were included in the category "trees", thinner ones into the category "saplings". For each measured tree, the basal area was calculated based on its DBH (as the round area of the tree trunk section at the breast height). Then, basal areas of all trees within each plot were added, and this sum was used for analysis as a basal area of the flycatcher/random plots. In lime-hornbeam-oak stands, 34 PF plots, 36 CF plots, and 52 random plots were measured. In ash-alder stands 10 PF, 14 CF, and 21 random plots were measured.

Generalized linear mixed models (GLMM), computed with the freely accessible statistical software R (R 2.10.0), were used to analyze microhabitat selection. With this multiple logistic regression we quantified the relationship between several predictor variables (habitat properties) and a response variable (presence and absence data). This is a standard approach in habitat selection analysis (14). We computed three types of GLMMs: the first was composed of plots with PF and plots with CF, the second was composed of plots with PF and random non-occupied plots, while the third was composed of plots with CF and random non-occupied plots. The habitat selection analyses with full GLMM models involved seven variables: 1) crown cover, 2) basal area of living trees, 3) basal area of snags, 4) number of living trees, 5) number of snags, 6) number of saplings and 7) number of spruces. The habitat type (lime-hornbeam-oak stand (L-H) or ash-alder stand (A-A)) was included as a random factor.

We identified the best model by stepwise omission of non-significant terms. The inflection point of the fitted logistic regression function, where the estimated probability of species presence equals 0.5, was used to classify habitat according to suitability for each species. The classification performance was tested with a chi-square test of independence (adjusted with Yates' correction for continuity). This was computed on the "confusion matrix" composed of frequencies of correctly and wrongly assigned presences or absences. The percentage data were transformed using arcsine square root transformation prior to analysis into data that were close to a normal distribution (15). For comparison of tree stand composition between sample plots, we used a G-test.

In the full model comparing the habitat used by the two flycatcher species, none of the terms were statistically significant predictors. In the reduced model that contained a single predictor, basal area of living trees, the predictor was almost significant ($z=-1.95$, $p=0.051$) and the intercept was significant ($z=2.04$, $p=0.041$). The model indicates that basal area of living trees is slightly larger in PF sample plots than in CF sample plots (Table 1). The full model correctly classified 34.1% of plots used by PF and 78.0% of CF plots ($\chi^2=16.43$, df=1, $p<0.001$). The reduced model correctly classified 45.5% of plots used by PF and 72.0% of plots used by CF ($\chi^2=2.38$, df=1, $p=0.123$).

In the second model, we compared random unoccupied sample plots with those used by each flycatcher species. In the full model estimating the presence probability of PF, crown cover ($z=-2.43$, $p=0.015$), number of saplings ($z=2.04$, $p=0.041$) and number of spruces ($z=-2.12$, $p=0.034$) were statistically significant predictors. The full model correctly classified 31.8% of plots used by PF and 83.3% of unoccupied plots ($\chi^2=4.47$, df=1, $p=0.034$). In the reduced model, PF sample plots differed from random ones in all four covariates: crown cover ($z=-2.54$, $p=0.011$), basal area of living trees ($z=2.23$, $p=0.026$), number of saplings ($z=2.14$, $p=0.032$), and number of spruces ($z=-2.11$, $p=0.035$), and the

TABLE 1

The average values of sample plot parameters (per plot 0.126 ha, with ± standard deviation, and sample size in parentheses) for two flycatcher species and random plots in the Białowieża National Park. L-H – lime-hornbeam-oak stand, A-A – ash-alder stand.

	Habitat	*F. hypoleuca* (PALLAS, 1764)	*F. albicollis* (TEMMINCK, 1835)	Random plots
Crown cover (%)	L-H	88.0 ± 6.8 (34)	87.8 ± 9.3 (36)	92.1 ± 5.9 (52)
	A-A	87.5 ± 6.8 (10)	86.5 ± 5.8 (14)	83.9 ± 9.8 (21)
No. of live trees	L-H	35.1 ± 7.3 (34)	31.1 ± 5.8 (36)	35.1 ± 8.1 (52)
	A-A	36.0 ± 9.3 (10)	38.3 ± 14.4 (14)	33.6 ± 8.6 (21)
Live trees basal area (m²)	L-H	4.2 ± 0.9 (34)	3.7 ± 1.0 (36)	3.9 ± 1.0 (52)
	A-A	4.9 ± 1.4 (10)	4.5 ± 1.1 (14)	4.2 ± 1.4 (21)
No. of snags	L-H	2.3 ± 1.8 (34)	2.3 ± 1.9 (36)	2.1 ± 2.2 (52)
	A-A	2.1 ± 0.6 (10)	1.9 ± 1.2 (14)	2.6 ± 2.0 (21)
Snags basal area (m²)	L-H	0.3 ± 0.4 (34)	0.4 ± 0.4 (36)	0.3 ± 0.4 (52)
	A-A	0.5 ± 0.3 (10)	0.2 ± 0.2 (14)	0.3 ± 0.4 (21)
No. of saplings	L-H	33.1 ± 21.6 (34)	33.2 ± 19.2 (36)	32.0 ± 17.0 (52)
	A-A	0.5 ± 0.3 (10)	0.2 ± 0.2 (14)	0.3 ± 0.4 (21)
No. of spruces	L-H	4.7 ± 3.8 (34)	5.6 ± 3.6 (36)	5.0 ± 3.7 (52)
	A-A	5.3 ± 3.8 (10)	3.1 ± 2.2 (14)	7.6 ± 6.2 (21)

intercept was not significant (z=1.46, p=0.144). The reduced model correctly classified 34.1% of plots used by PF and 87.0% of unoccupied plots (χ^2=6.70, df=1, p=0.080).

None of the predictor variables in the full model for presence of CF reached statistical significance, although crown cover was close to it (z=-1.95, p=0.051). The full model correctly classified 28.0% of plots used by CF and 87.7% of unoccupied plots (χ^2=42.21, df=1, p<0.001). The reduced model contained a single predictor variable, crown cover, which explained differences between sample plots with and without CF's nests with high significance (z=3.99, p<0.001, intercept: z=1.47, p<0.001). The model correctly classified 90.0% of plots used by CF, but only 15.1% of unoccupied plots (χ^2=0.30, df=1, p=0.300). Tree species composition within PF and CF sample plots was similar (G=4.53, df=6, p=0.61 in lime-hornbeam-oak, and G=4.17, df=7, p=0.76 in ash-alder tree stands).

It has been experimentally shown that PF and CF prefer different microhabitats in sympatric populations (16, 17). However, most of the publications on *Ficedula* flycatchers come from studies in managed forests that have been deeply transformed, and where there is a shortage of nest sites. We found that PF and CF microhabitats were similar under the primeval Białowieża conditions. Models predicting the presence of each species showed that both PF and CF are selective in their choice of breeding habitats, because these differed from random unoccupied plots. The Collared Flycatcher's habitats could be reliably classified solely by their low crown cover, while PF habitats seem to be additionally characterized by high basal area, high number of saplings and low number of spruce trees. However, the role of these predictors was minute in comparison to the importance of low crown cover. This additionally demonstrates the similarity of the habitat preferred by both species. Correct classifications of plots used by flycatchers were on a low level, random plots were classified

as flycatcher plots or else the results of the model were not statistically significant. In other words, PF could freely choose its breeding microhabitat (at least at the level we have studied), possibly because the most important resources for breeding *Ficedula* flycatchers, namely tree cavities, are very abundant in primeval stands of the Białowieża Forest (18). Furthermore, there is other circumstantial evidence supporting our above findings, i.e. long-term studies conducted in BNP showed both *Ficedula* species fluctuated in breeding numbers in parallel (e.g. 5, 9, 10, 11). Therefore, the lower abundance of PF cannot be explained by competitive pressure from CF.

We conclude that the Collared Flycatcher did not force the Pied Flycatcher to use different microhabitats under primeval conditions but both species chose nesting spots freely. It is furthermore worth emphasising that both species showed similar microhabitat preferences under primeval conditions. Finally, we suggest that competition between PF and CF as described (e.g. 3; 8; 19) is most likely a result of forest management and nest box supply.

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