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„Population density and habitat preferences of the Collared Flycatcher (*Ficedula albicollis* TEMMINCK, 1815) in floodplain forests – A case study from the Donau-Auen National Park, Lower Austria"

verfasst von / submitted by

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„I came from the city – now I return to the city and in my heart, the floodplain forest grows“
– extract from a re-print of „Aublätter“, a single-sheet newspaper released during the occupation of Hainburg, 1984.
This occupation was crucial for the subsequent foundation of the Donau-Auen National Park.
(modified after Re-Print der AUBLÄTTER, Au-Dokumentationsgruppe am Medienzentrum der TU Wien (Eds)).

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ABSTRACT

The Collared Flycatcher (*Ficedula albicollis*, Temminck 1815, Muscicapidae) is one of a few insectivorous long-distance migrants with a slightly positive population trend. In spring 2015, the habitat preferences of a population in the floodplain forests of the Donau-Auen National Park, Lower Austria, were examined. Assuming that territories in good habitats will be occupied first, the following questions were addressed: In which order are territories established? What are the most important factors for a high quality habitat for Collared Flycatchers in the Donau-Auen? Is an early territory establishment related to a close distance to water bodies and a high insect density? Singing males were counted at randomly chosen points in six survey rounds. Additionally, possible breeding competitors and/or cavity providers, woodpecker holes, standing deadwood, flying insects, vegetation parameters (canopy surface roughness, forest type, forest age) and landscape variables (distance to water bodies and open land) were assessed. A model selection approach was used to identify the factors important for territory presence. 57% of the census points contained territories resulting in a population density of 7.28 territories/10 ha and 21.4 territories/10 ha estimated for a 50 m radius and a 25 m radius around the census points, respectively. The *Distance Sampling* method estimates densities of 8.68 to 13.72 singing males/10 ha. Canopy surface roughness proved being the best predictor for Collared Flycatcher territories. Established territories were found with a higher likelihood at sites with higher canopy roughness. Further, territories with higher canopy roughness showed a tendency to earlier occupation. As forestry measures were stopped just recently (20 years ago) and canopy roughness is known to increase with stand age, the habitat quality of the remaining Danube floodplain forests east of Vienna for the Collared Flycatcher will most likely remain similar or will even further increase in the mid to long term.

Keywords: cavity breeder, forest structure, playback, territory establishment, canopy surface roughness, deadwood.

ZUSAMMENFASSUNG

Der Halsbandschnäpper (*Ficedula albicollis*, Temminck 1815, Muscicapidae) ist einer von wenigen insektivoren Langstreckenziehern mit einem positiven Bestandstrend. Im Frühjahr 2015 wurden die Habitatpräferenzen einer Population im Nationalpark Donau-Auen, Niederösterreich, untersucht. Unter der Annahme, dass zuerst Territorien in gut geeigneten Habitaten etabliert werden, lag der Fokus auf den folgenden Fragen: In welcher Reihenfolge werden Territorien etabliert? Welches sind für Halsbandschnäpper in den Donau-Auen die wichtigsten Parameter für eine hohe Habitatqualität? Besteht ein Zusammenhang zwischen früher Territorienetablierung und geringer Distanz zu Gewässern sowie einer hohen Insektendichte? Singende Männchen wurden in sechs Untersuchungsrunden an zufällig gewählten Punkten gezählt. Zusätzlich wurden potenzielle Brutkonkurrenten und/oder Bruthöhlenlieferanten, Spechthöhlen, stehendes Totholz, Fluginsekten, Vegetationsparameter (Kronenrauigkeit, Waldtyp, Waldalter) sowie Landschaftsvariablen (Distanz zu Gewässern und Offenland) berücksichtigt. Mithilfe einer Modellselektion wurden die wichtigsten Faktoren für Territorienpräsenz ermittelt. An 57% der Zählpunkte konnten Territorien festgestellt werden. Die ermittelte Populationsdichte für das Untersuchungsgebiet lag bei 7.28 Territorien / 10 ha (basierend auf einem 50 m Radius um die Zählpunkte) und bei 21.4 Territorien basierend auf einem Radius von 25 m um die Zählpunkte. Mittels *Distance Sampling* konnten Dichten von 8.68 bis 13.72 singenden Männchen/10 ha geschätzt werden. Die Kronenrauigkeit erwies sich als der beste Prädiktor für Halsbandschnäpper-Territorien. Zudem zeichneten sich früher besetzte Territorien durch eine tendenziell höhere Kronenrauigkeit aus. Da die Waldbewirtschaftung erst kürzlich (vor 20 Jahren) eingestellt wurde und die Baumkronenrauigkeit mit Zunahme des Waldalters steigt, ist zu erwarten, dass die hohe Habitatqualität der verbleibenden Donau-Auwälder östlich von Wien für den Halsbandschnäpper erhalten bleibt oder es mittel- bis langfristig sogar zu einer weiteren Verbesserung der Bedingungen für diese Art kommt.

Keywords: Höhlenbrüter, Waldstruktur, Klangattrappe, Territorienbesetzung, Kronenrauigkeit, Totholz.

CONTENT

1 INTRODUCTION

Floodplain river systems are highly dynamic systems shaped by a complex disturbance regime. The result is a mosaic of various heterogene habitats and ecotones on a small scale, what makes floodplains hotspots for biodiversity (Ward et al. 1999; Brawn et al. 2001). By definition, a floodplain forest (=riparian forest, fluviatile forest or alluvial forest) is

"[…] *a complex of plant formations which develop because of a […] number of physical factors […]: the rate of flow of floodwater, granulometric characteristics of the alluvial deposits, the rate of flow of ground water and how long the flood water remains. Like the dates when floods occur, these factors depend on the location of the site in relation to the longitudinal profile of the river, the climate and the geological characteristics of the catchment area and its recent history.*" (Yon & Tendron 1981)

On a global scale, they are highly endangered ecosystems (Dynesius & Nilsson 1994). The floodplain forests in Europe had been exposed to severe anthropogenic impacts like land use change, flood regulation, building of power stations, leisure activities, game management and fragmentation (Klimo & Hager 2001). There had been a decline of 25% of floodplain forests along the river Danube and of 50% along the Rhine since the exploitation of hydroelectric powers and large-scales stream canalisations; in Austria, the Danube riparian forests declined to 8 000 ha in 1981 vs. 33 000 ha in 1930 (Yon & Tendron 1981). According to the EU Habitats Directive Appendix 1, floodplain forests are protected throughout Europe (Council Directive 92/43/EEC). In terms of disturbance, edge-richness and productivity, floodplain forests offer diverse opportunities for birds (Brawn et al. 2001, Iwata et al. 2003) and are important habitats for woodpeckers and secondary cave-breeders (Remm et al. 2006) like the Collared Flycatcher (*Ficedula albicollis*, Temminck 1815, Muscicapidae). This small, insectivorous, long-distance migranting, facultatively polygynous passerine has a mainly Eastern European distribution with its largest populations in Ukraine, Romania, Slovakia and Russia (Bauer et al. 2012, BirdLife International, 2004). In Central Europe, the largest breeding populations are in Hungary, Slovakia, Czech Republik, Southern and Eastern Poland and Eastern Austria. It returns from its wintering grounds in tropical Africa earliest by end of March; most of the individuals arrive at their breeding areas by mid-April up to May and leave earliest by June. Cavities are occupied and defended by the earlier-arriving males and are shown to the later arriving females. The conservation status is NT on the Austrian red list of endangered species; on the EU's Birds Directive it is listed on Appendix 1, Spec E (Bauer et al. 2012, Sachslehner 1995, Lundberg & Alatalo 1992, Löhrl 1951). Natural-cavity breeding populations are regarded to be threatened on a long-term scale due to land use (e.g. Sachslehner 1995). The Collared Flycatcher is a well-researched model species for secondary cave breeders, whereas habitat studies with populations breeding in natural cavities are relatively scarce (but e.g. Martinovic 2016, Götz 2016, Kralj et al. 2009, Sachslehner 1995 & 1993, Maurizio 1987 and many detailed studies from Bialowieza, Poland, e.g. Wesolowski 2007, Walankiewicz 1991).

The Collared Flycatcher prefers broad-leafed forests, but depending on the specific habitat, different tree species are used (Hornbeam and Maple in Bialowieza, Poland, Beech and Oak in Central Croatia, European Chestnut and Cherry in Southern Switzerland, Beech in the Viennese Forests; Martinovic 2016, Kralj et al. 2009, Mitrus et al. 2007, Walankiewicz et al. 2007, Sachslehner 1993, Maurizio 1987). Foraging (gleaning and flycatching from perches) takes place in heights of above 8 m as well as near the ground (Sachslehner 1993, Alerstam et al. 1978). Many studies implicate a strong intra- and interspecific competition (with Great Tits *Parus major* and Eurasian Blue Tits *Cyanistes caeruleus*) for cavities resulting in adult mortality (e.g. Merilä & Wiggins 1995, Gustafsson 1988). However, strong effects could be observed in nest-box studies only (Walankiewicz & Mitrus 1997). There is also evidence for interspecific information (Collared Flycatchers observing Great Tits) used in the habitat selection process (e.g. Jaakkonen et al. 2015, Forsman & Thomson 2008). In near-nature forests there seems to be little intra- and interspecific competition but a surplus of cavities (Wesolowski 2003, Mitrus et al.

1996, Walankiewicz 1991, Carlson et al. 1998). Still, the importance of cavity quality over quantity should not be neglected (Lõhmus & Remm 2005). In Bialowieza, there are sufficient empty territories even for late-arriving yearling Collared Flycatcher males (Mitrus et al. 1996). However, Mitrus et al. (2007) found, that holes re-used by Collared Flycatchers often (more than 5 times) were occupied first and mostly by old males; the clutch size was bigger, but the breeding success did not differ. Most of the preferred holes were not excavated by woodpeckers and not in dead trees (predator avoidance; Walankiewicz et al. 2007, Wesolowski 2007, Maurizio 1987). Contrastingly, most of the cavities in the Viennese Forests were excavated by woodpeckers and were found in dead trees. Here the Collared Flycatcher used even strongly decayed woodpecker cavites, not used any more by other cave breeders (Sachslehner 1995). However, in Bialowieza, the majority of holes develop by decay, probably due to snow breakage (Walankiewicz 1991).

In primeval forests, the limitating factor seems to be predation, not cavitiy supply (Wesolowski 2003, Walankiewicz 2002b, Walankiewicz 1991). In his detailed study, Walankiewicz (2002b) found that predation was the reason for 91% of all breeding-loss events of Collared Flycatchers; the main predators being rodents and mustellides, whose prey-predator oscillations seemed to be connected to nest predation, and Great Spotted Woodpeckers (*Dendrocopos major*). Woodpeckers do play an important role as excavators of cavities for secondary cave breeders worldwide. However, it seems that in North America secondary cave breeders are most dependent on woodpecker holes, while in Eurasia, Australia and South America more cavities of other origin are used (Cockle et al. 2011). Unfortunately, these conclusions were based on just one study area per continent – the Eurasian one being Bialowieza. In a mature floodplain forest in Estonia, 88% of all cavities suitable for secondary cave breeders had been excavated by woodpeckers (Remm et al. 2006), emphasizing that the results reported by Cockle et al. (2011) cannot be generalized. In a Swedish deciduous forest, most of cavities were not woodpecker-excavated and also the majority of cavities used by secondary breeders were not woodpecker-excavated. Most woodpecker-excavated cavities were found in Aspen (*Populus tremula;* Carlson et al. 1998). Moreover, the Great Spotted Woodpecker, who provides cavities, is a facultative nest predator (Wesolowski 2007, Walankiewicz 2002a & 1991, Sachslehner 1993). In Austria, between 9 000 and 18 000 breeding pairs of Collared Flycatchers were estimated between 1998 and 2002 (Bauer et al. 2012), the main local populations are in the East and Southeast (pannonic and illyric climate), however there are also some interspersed populations at the foothills of the alps (Dvorak et al. 1993). The most detailed survey was done in 1988-1990 in the Viennese Forest, where a local population was using only natural cavities (Sachslehner 1993). In the Danube floodplain forest, the Collared Flycatcher is an abundant species with a population size of 600-1000 breeding pairs (Standarddatenbogen für das Europaschutzgebiet AT1204V00 – Donauauen östlich von Wien. Amt der NÖ Landesregierung, Abteilung Naturschutz, Update 2015-12). There had been some breeding bird surveys between the 1980ies and early 2000s dealing with Collared Flycatchers in the area, but just one recently focussing on the species' habitat traits (Götz 2016, Dvorak in Dvorak 2009, Kollar & Seiter 1990, Winding & Steiner 1988). In the Viennese part of the national park, Lobau, the Collared Flycatcher was found mostly in hard wooded floodplain forest (Dvorak in Dvorak 2009). In the central part of the national park, near Eckartsau, the Collared Flycatcher was observed mainly in mature forests with a high deadwood value (Kollar & Seiter 1990). In an area of 256 ha near Orth an der Donau (Donau-Auen National Park), where the Collared Flycatcher was mapped in the year 2007, forest age did not emerge as important factor for territory selection. However, there the mean stem diameter of standing deadwood was significantly higher within territories compared to reference plots. Further, territories were located significantly closer to the nearest forest edge and were found more often in stands with lower canopy closure than reference plots (Götz 2016).

The aim of this thesis was a larger-scaled survey on population density and habitat use of Collared Flycatchers, covering the floodplain forests of the river Danube east of Vienna on the northern bank

(Jones 2001, Karr, 1990). Quality traits of habitats were identified and evaluated based on the time of territory establishment by Collared Flycatchers. Differences in forest structure were considered as well as landscape factors and food availability (Iwata et al. 2003, Sachslehner 1993).

2 MATERIAL AND METHODS

2.1 STUDY AREA

The Donau-Auen National Park is located in the southeast of Vienna and extends eastwards to the Slovakian border. The national park had been established in 1996 and protects one of Europe's last free flooding lowland river ecosystems (Manzano 2000). Inspite of various human impacts (including river regulation, forestry, flood control, agriculture) it contains a high diversity of species and habitats (Hager & Schume 2001). A total of 109 breeding birds, over 161 species of birds in total and more than 700 species of higher plants are recoreded from the national park (Manzano 2000, Winding & Steiner 1988), which is also part of the IBA (Important Bird Area) "Danube Floodplains East of Vienna" and Natura 2000 area "Donauauen östlich von Wien" (Teufelbauer & Frank 2009). In the eastern part of the national park near Stopfenreuth, up to 23 species of cave-breeding species were recorded in 1982-83 (Stock Dove *Columba oenans*, Tawny Owl *Strix aluco*, Hoopoee *Upupa epops*, Green Woodpecker *Picus viridis*, Grey-Headed Woodpecker *Picus canus*, Black woodpecker *Dryocopus martius*, Great Spotted Woodpecker *Dendrocopos major*, Middle-Spotted Woodpecker *Dendrocopos medius*, Lesser Spotted Woodpecker *Dendrocopos minor*, Wryneck *Jynx torquilla*, Collared Flycatcher, Common Redstart *Phoenicurus phoenicurus*, Marsh Tit *Poecile palustris*, Willow tit *Poecile montanus*, Blue Tit *Cyanistes caeruleus*, Great Tit *Parus major*, Coal Tit *Periparus ater*, European Nuthatch *Sitta europaea*, Eurasian Treecreeper *Certhia familiaris*, Short-toed Treecreeper *Certhia brachydactyla* as well as Eurasian Tree Sparrow *Passer montanus*, Common Starling *Sturnus vulgaris* and Jackdaw *Corvus monedula*), emphasizing the great value of the old-growth forest stands (Winding & Steiner, 1988). In the 19th century, after the regulation of the Danube river, a dike ("Hubertusdamm" or "Marchfeldschutzdamm") was constructed which separates the floodplain forests in a northern and a southern part, the southern part being dominated by softwooded floodplain forest (with *Populus alba, Populus nigra, Prunus padus, Salix sp.*), the northern part being dominated by hardwooded floodplain forest (with *Fraxinus excelsior*, *Quercus robur, Ulmus campestre, Acer campestre, Carpinus betulus and Tilia cordata;* Hager & Schume 2001) . In 1995, 31% of the trees were introduced species such as *Populus canadensis*, *Acer negundo, Ailanthus altissima and Juglans nigra*. Since the designation of the national park, deadwood is remaining in the forest and management measures support autochtonous vegetation (Riemer & Schulze, 2007). In the course of the forest management, small amounts of wood are lokally removed (Nationalpark Donau-Auen, 2009). In 2003, the "Flussbauliche Gesamtprojekt Donau östlich von Wien" had been launched. In the framework of the river restoration project several measures were implemented to maintain and improve the fairway channel of the Danube as well as to protect and restore the floodplain river system by stabilizing and increasing the hydrological dynamic of the network of waterbodies and the adjacent floodplains (Österreichische Wasser- und Abfallwirtschaft aktuell, 2008).

The survey area was about 31 km long and stretched from the Viennese-Lower Austrian border to the mouth of the Morava river at the national border to Slovakia. Due to practical reasons the southern shore of the Danube was excluded. The survey area is mainly covered by floodplain forest interspersed with meadows, water bodies and walking-paths. In the north, it is terminated by arable land and settlements, in the south by the Danube river (Fig.1).

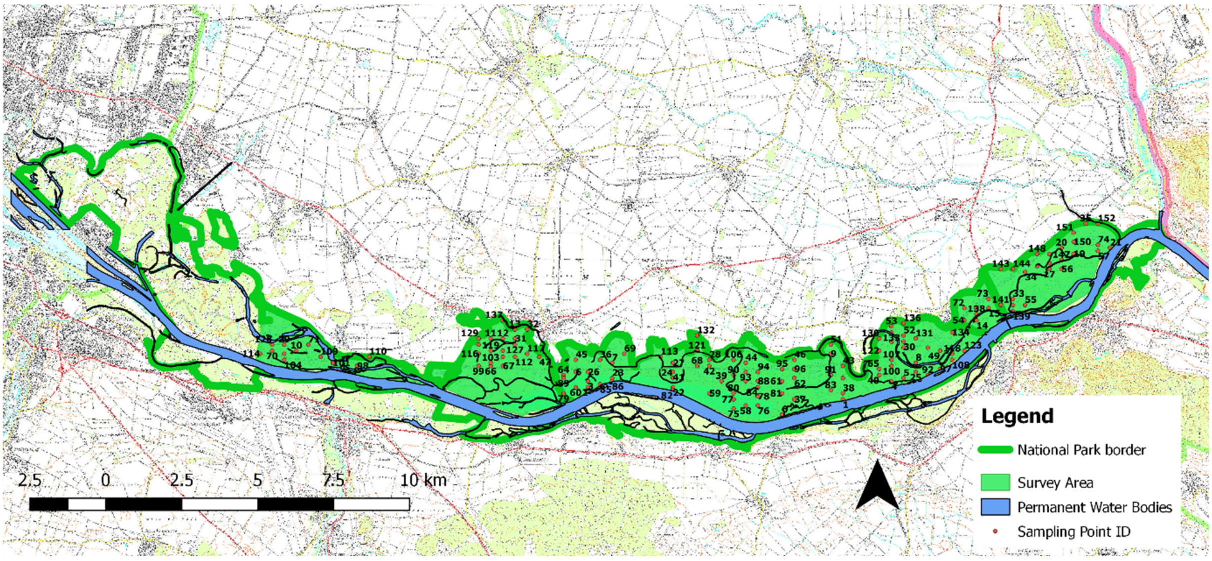


Fig. 1: Map of the study area. (background map: altered after BEV 2013 & 2015)

2.2 Point counts

The Collared Flycatchers and selected species of birds of potential importance for Collared Flycatchers (tits, woodpeckers, nuthatches) were registered in multiple point counts (e.g. Bibby 1995). This approach was chosen to be able to cover a large sampling area with an effort still possible for one counter. A total of 147 points were chosen randomly (Bibby et al. 1995; Fig. 1) from an already existing grid of points every 100m, used by the Österreichische Bundesforste AG and the Magistratsabteilung 49 (Vienna Municipal Department 49) for the forest inventory. The points had to fullfill the following criteria: (1) at least 200 m distance from each other (Bibby et al. 1995; 2 exceptions happend unintentionally), (2) maximum 100 m distance from ways for quick access, (3) 50% of the points totally forested within a radius of 50 m, (4) 50% of the points at least 50% forested within a radius of 50 m, (5) as far as possible equal groups within defined strata of distance to the next permanent water body to guarantee a sufficient sampling size for different distances to water bodies. The groups in (5) resulted in 45 points between 0-75 m, 22 between 75-150 m, 36 between 150 and 250 m and 44 between 250 and 1000 m distance from permanent surface waters. Criterion (2) only excluded a relatively small proportion of potentially available points due to the national park's unusually dense network of paths and forest roads. A total of 58 points were located north of the Marchfeldschutzdamm and 89 south of it. Photos of the majority of points are provided in Appendix 4. The field work took place from 3 April to 24 May 2015. The 147 census points were visited „as often as possible" in order to get most detailed information on the temporal pattern of territory establishment. If the weather conditions were unfavourable (precipitation), the counts were stopped in most cases as rain is known having a strong impact on point count results (e.g. Hansbauer et al. 2003). Thus, within 40 days of sampling (313:09 h working hours by the author, 27:11 h by Christian Schulze without way time to the first point and back from the last point) each census point was visited six times, once during each of the following six time periods: (1) 3-16 April, (2) 17-21 April, (3) 23-27 April (4) 28 April-4 May, (5) 5-12 May and (6) 14-24 May. Surveying of the target species is recommended until 5 hours after dawn (Collared Flycatcher), until noon (woodpeckers), unitl 3 hours after dawn (Great Tit and Marsh Tit), until 4 hours after dawn (European Nuthatch) and unitl late morning (Blue Tit; Südbeck et al. 2005). However, as the focus was on a precice temporal pattern of territory establishment and the target species, especially the Collared Flycatcher (Neubauer & Sikora 2013), do not entirely stop their singing activity, the field work was operated throughout the day. When approaching a point all target species were registered either visually (Swarovski EL 8,5x42) or acoustically in a five minute counting period. If there was no observation of Collared Flycatchers within the counting period, a playback was used. The 1'35'' playback consisted of call and song from individuals from Poland (recorded by Tomek Tumiel) and Baden-Württemberg, Germany (recorded by Frank Holzapfel). It was played with an Olympus Digital Voice Recorder (VN-8500PC) at full volume. The sound files had been downloaded from xeno-canto (http://www.xeno-canto.org/species/Ficedula-albicollis 2.4.2015) as mp3-files and cut together using Easy mp3 Ogg Wma Wav Cutter V 2.1 (Koyote Soft, 2010). After the playback, two minutes were waited for a response of Collared Flycatchers. It was also noted if other species seemed to react on the playback. For the Collared Flycatchers, distance classes of 0-25 m, 25-50 m, 50-75 m and 75-100 m distance to the point were estimated.

2.3 Standing deadwood

Standing deadwood was measured with a standard measuring tape from 3 April to 17 April at 145 of 147 points (2 were forgotten) within a radius of 20 m (determined with Nikon Laser 800 6x216 rangefinder) before the vegetation period started. All standing dead trees with a circumference at breast height of at least 10 cm (=3.2 cm diameter at breast height i.e. DBH) or more were counted and their circumference measured. The height of each tree was estimated with an accuracy of 0.5 m. Only entirely dead trees were measured, and only those having their roots still in the ground. The height of the tree meant the highest point of the tree and not the length of the stem. In case a tree was branching below breast height, all stems were measured. In case the dead tree was lower than breast height, it was measured at its highest point (this was the case in some trunks). As an approximation to solid cubic meters, a rough volume was calculated by simplifying the tree to a cylinder with $V = \pi * (DBH/2) * h$.

2.4 Woodpecker holes

The woodpecker holes were sought at 145 of 147 points with the unweaponed eye and binoculars (Swarovski EL 8.5x42). Holes were estimated being small, medium or large referring to the size of a tit, a Great Spotted Woodpecker or a Black Woodpecker. If holes were found, their height was estimated, the breast height circumference of the tree was measured and it was noted wether the tree or the part of the tree was dead or not. For further analysis, only the small and medium holes were considered as cavities with a smaller entrance are preferred (Lõhmus & Remm 2005, Sachslehner 1992).

2.5 Flying insects

We counted flying insects at all points from 28 April to 25 May by focussing with the binoculars (Swarovski EL 8,5x42 or Swarovski EL 10x42) in a right angle on the height of the uppermost branches in a light opening in the forest. All insects crossing the field of vision within one minute were counted (Flashpohler 1997). In a few cases when counting was impossible due to larger swarms (e.g. of Chironomidae or Culicidae), the number was estimated. In addition, the wind intensity was estimated and unfavourable weather conditions (precipitation) were noted. Temperature data was purchased from the Zentralanstalt für Meterologie und Geodynamik (ZAMG) and had been measured at the weather station Groß-Enzersdorf every 10 min.

2.6 Caterpillar feces

To collect data on moth larvae, plots occupied by Collared Flycatchers (more than one observation) early (4-21 April), intermediate (23-27 April), late (28 April-12 May) or not occupied by 12 May were selected. At the peak of frass, on 16 and 17 May, plastic foil was put out for 48 hours under the tree apparently most affected in the plot (radius of 20 m). The foil of 140x100cm (70x100cm black plastic waste bags cut open) was set about 20 cm high on four sticks found locally in the forest two metres away from the trunk. The tree species was noted and also woody understorey species if protuding over the foil; photographs of the tree were taken in a right angle from above the foil. After recollecting the foil on 18 and 19 May, the feces were dried. Due to heavy rain between 18 and 19 May half of the data was affected by soaking or flushing from the foil. For this sites it was tried to estimate „small“, „medium“ or „large“ amounts of feces still in situ by estimating the number of feces pills drifting in the water on the foil. However, because of the potential inaccuracy this data has not been used for further analysis (but see discussion).

2.7 Tree species composition

Data on the tree species composition was provided as forest stand data from the forest inventory (data collected in 2013) mainly by the Österreichische Bundesforste AG (ÖBF) and, for the area near Schönau owned by the town of Vienna, Magistratsabteilung 49 (Vienna Municipal Department 49). The forest stand data consisted of information on stand age and the percentage of species per vegetation layer. The layer was named either 1, 2 or 3 (ÖBF) or „Di“ (Dickung, thicket), „Sth“ (Stangenholz, pole stage forest) or „Bho“ (Baumholz, tree stage forest). In the further proceeding, layer 1 was equated with Bho, layer 2 with Sth, and layer 3 with Di. The covering of the forest stands per plot (r=20 m) were assessed in ArcMap 10.2 by intersecting the plot and the forest stands and then calculating the area via the function "field geometry". The relative contribution of individual tree species tree species composition in percent was calculated for the same radius. For modelling, only layer 1 was used, as the tree layer is most representative for the character of the forest.

2.8 Mean forest age

The mean age of the tree layer per plot (r=20 m) was used. The data was calculated from data provided by the Österreichische Bundesforste AG and Magistratsabteilung 49 (see above).

2.9 Vegetation height and woodland surface roughness

Remote sensing data as light detection and ranging (lidar) increases in importance for woodland bird-habitat studies over the last years (e.g. Clawges et al., 2007). The remote sensing data for this study was recorded in the context of the Flussbauliche Gesamtprojekt. The surveying flight took place in April 2010. As a measure for canopy roughness, the standard deviation of the mean canopy roughness was calculated for a radius of 50m around the sampling point in a resolution of 2 m (Reiter unpublished). The mean vegetation height of the plot was obtained excluding areas without vegetation (e.g. streets).

2.10 Territories

Male Collared Flycatchers do not start singing and defending their territory until they have found a sufficient breeding cavity (Löhrl 1951). Hence, territories were defined after the recommendation in Südbeck (2005): at least two observations of singing males with at least seven days difference, of which at least one should be within 20 April – 10 June (recommended survey time). Afterwards, the territories found were classified according to the time of their establishment. The day of the first observation of singing males was counted as the day of establishment, if at least one more observation with at least 7 days difference was made. For further analysis, territories were grouped after the survey round (1, 2, 3, 4, 5) in which they were established, however, establishment in survey round 1 and 2 was pooled, as survey round one was in the enhanced survey time. Moreover, all the territories established in survey round 1 stayed occupied throughout the survey time.

2.11 SPATIAL AND STATISTICAL ANALYSIS

The territory density was calculated for a radius of 25 m and a radius of 50m around the census point. The total area of all circles with the radius of 25 m and 50 m, respectively, was added and divided through the total number of territories found within each distance class. From the resulting number, a density per 10 ha was calculated.
We further used the Distance Sampling method to estimate territory densities (e.g. Lloyd et al. 1998). The software Distance 7.0 was used to calculated all possible models (detectability functions) using uniform, half-normal, hazard rate and negative exponential key function and all possible expansions (cosine, simple polynomial, hermit polynomial) and ranked them according to their AIC values. We considered density estimates of all models with an AIC difference (Δ AIC) < 6 when compared to the best model.
Most spatial analysis was performed with ArcGis 10.2 (ESRI 2011). The maps presented in this thesis were made with QGis 2.14.3 (QGis Development Team 2016) The statistical analyses were done with R (Version 3.1.3, R Core Team 2015) and R Studio (Version 0.99.489, RStudio Inc. 2009-2015), using the following packages: glmulti (Calcagno, 2013), ape (Paradis et al., 2004), sp (Pebesma & Bivand 2005), lme4, (Bates et al. 2015), ggplot2 (Wickham 2009). A Chi-square-test was used to test if the playback efficiency (proportion of Collared Flycatchers attracted without prior visual or acoustical detection at census points) changed with ongoing season and to test for differnces in the pattern of territory establishment on each side of the Marchfeldschutzdamm.
To correct out the effects of varying weather conditions on the abundance of flying insects assessed at census points, the residuals of a generalized linear mixed model (GLMM, fit by maximum likelihood (Laplace Approximation), log-link function) were used for further analysis (function "glmer", R-package lme4, Bates et al., 2015). The residuals of the third survey round were not used as the counting method was learned in that round. In the GLMM, the survey round was set as random effect and precipitation (presence/absence), temperature (°C) and wind intensity (0-4) were the predictor variables. The median of the 3 residual values of round 4, 5 and 6 per plot was used in the further analysis.
To find the most important parameters for habitat use, a generalized linear model (GLM, logit-link function) was fitted. Not all census points could be included in the model as the canopy roughness data was available for only 111 of the 147 points. In advance, a correlation matrix including all potential predictor variables was calculated to evaluate the extent of non-independence of the factors. Only variables with a correlation coefficient below 0.4 were included in the model. The only variables that were highly correlated with other variables (either with cavities or canopy surface roughness) were deadwood volume values. Here the number of large standing deadwood (>20cm DBH, >8m height) was chosen as independent measure. As response variable, the occurrence of territories (at least 2 observations of singing Collared Flycatcher males with at least 7 days in between) within a radius of 50m were used. Predictor variables included in the GLM were forest age, several variables quantifying forest structure and composition, two landscape variables, food and nest site availability as well as the abundance of potential competitors (Tab. 1).

Tab. 1: Predictor variables used in the GLM and the area around the census points in which the data was collected.

Independent variables	Considered area
Mean age of forest (i.e. mean age of the tree layer)	20m radius
Distance from the point to permanent water bodies [m]	No spatial limit
Distance from the point to open land [m]	No spatial limit

Number of standing deadwood of at least 20cm DBH and 8m height	20 m radius
percentage of *Populus alba* (indicating softwood floodplain forest)	20 m radius
Percentage of *Fraxinus excelsior* (indicating hardwooded floodplain forest)	20m radius
Median of residuals of a GLMM on the insect counts	Center of census point
Sum of individuals of Great Spotted Woodpecker observed at the point	All distances
Sum of frequency of tits and European Nuthatches (“Competition factor”)	All distances
Sum of all small and medium sized woodpecker holes	20m radius
Canopy roughness (standard deviation of mean vegetation height)	50m radius

For further confirmation, an automated model selection (level 1, criterion AIC) was done with the function “glmulti” from the R package glmulti (Calcagno 2013). To test for a relationship between time of territory establishment and the most important predictor variable, a one-way ANOVA and, subsequently, a TukeyHSD-post-hoc-test were calculated. The basic model and the best model selected by “glmulti” were tested for spatial autocorrelation with the function “Moran.I” from the package ape (Paradis et al. 2004). Based on an inverted distance matrix, this function calculates Moran`s autocorrelation coefficient on a matrix of weights for the model residuals. If the observed Moran`s autocorrelation coefficient is significantly higher or lower than the expected value, this indicates positive resp. negative autocorrelation. For visualization, the function “bubble” from the R package “sp” (Pebesma & Bivand 2005) was used.

3 RESULTS

3.1 COLLARED FLYCATCHER

In a very simplified approach by adding up the area of all 147 plots with r=50 m the territory density is 84 per 115.45 ha, this is 7.28 territories/10 ha. By adding up all 147 plots with r=25 m, the territory density is 62 per 28.86 ha, this is 21.4 territories/10 ha. Density estimates (± SE) of the six best models calculated with the *Distance Sampling* approach ranged between 8.68 (± 3.32) and 13.72 (± 2.31) singing males/10 ha (Tab. 2).

Tab. 2: The six best models calculated with Distance Sampling.

Model	AIC	Δ AIC	**Density** [singing ♂♂/10 ha]	Lower 95% CL	Upper 95% CL
Hazard rate/hermit polynomial	999.39	0.00	8.68	4.20	17.93
Hazard rate/simple ploynomial	999.39	0.00	8.68	4.20	17.93
Hazard rate/cosine	999.39	0.00	8.68	4.20	17.93
Negative exponential/simple polynomial	1001.07	1.68	13.72	9.87	19.06
Negative exponential/hermit polynomial	1005.08	5.69	10.27	7.67	13.75
Half normal/simple polynomial	1006.67	7.29	4.54	3.91	5.27
Negative exponential/cosine	1030.29	30.90	7.41	6.22	8.84
Uniform/cosine	1033.17	33.79	3.66	3.01	4.35
Uniform/simple polynomial	1079.42	80.03	2.78	2.30	3.35
Half-normal/hermit polynomial	1127.95	128.56	2.59	2.27	2.96
Half-normal/cosine	1127.95	128.56	2.59	2.27	2.96
Uniform/hermit polynomial	1433.00	433.61	0.82	0.74	0.92

Collared Flycatchers were recorded at least once within any distance class at the vast majority (87.8%) of all 147 census points. At 70.1% of all census points, Collared Flycatchers were recorded at least during two survey rounds. Still at 50.0% of all census points, Collared Flycatchers were observed during three survey rounds (Fig. 2)

Female Collared Flycatchers were just seen twice at census points, once directly at a cavity copulating with a male and once together with three males.

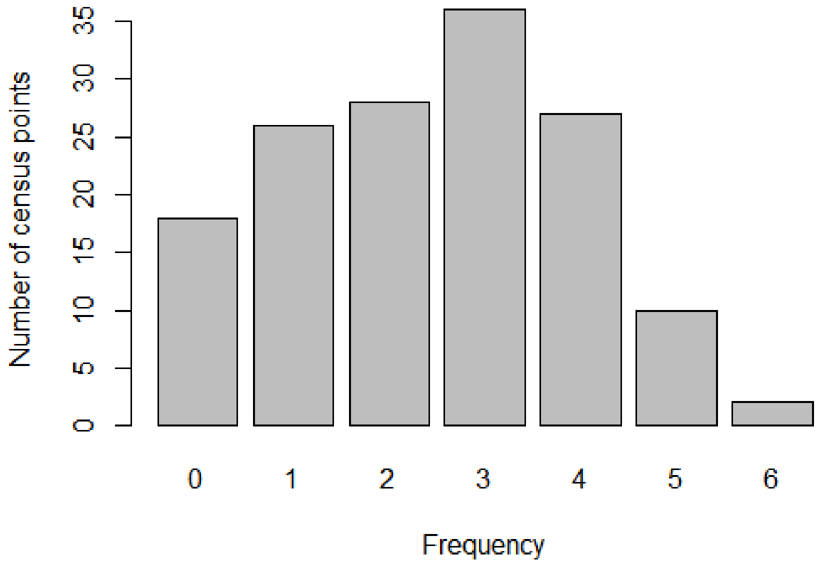
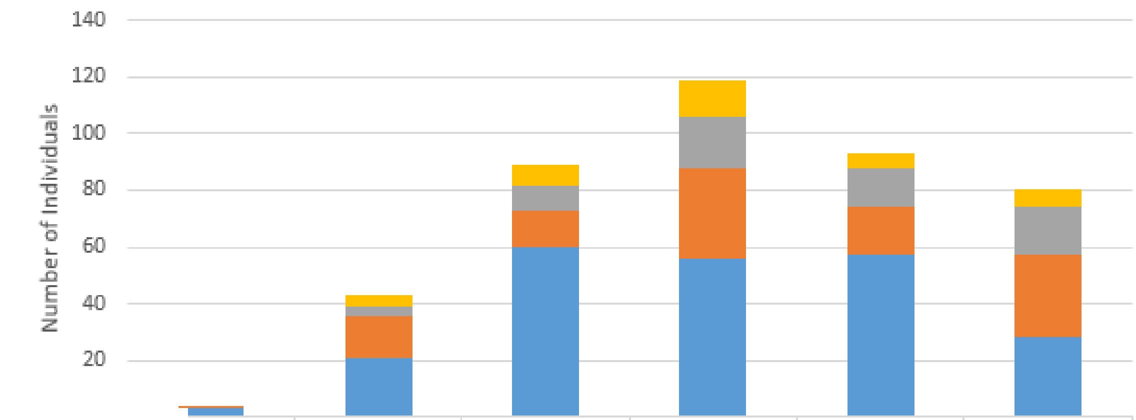


Fig. 2: Frequency of observations of Collared Flycatchers at census points.

The first individual was observed responding to the playback by 6 April, while the main arrival started by mid-April. The number of individuals increased until a peak of 119 birds was counted at all census points during the 4th survey round at the End of April/ beginning of May. Subsequently numbers slightly decreased again. Most of the birds were counted in a distance of 0-25m around the census point (Fig. 3).



Survey round		1	2	3	4	5	6
Distance (m)	75+	0	4	7	13	5	6
	50-75	0	3	9	18	14	17
	25-50	1	15	13	32	17	29
	0-25	3	21	60	56	57	28

Fig. 3: Individuals counted per survey round in different distance classes around the census points.

In total, 85.83% (309) of all Collared Flycatcher incidences were recorded without playback and 14.17% (51) with the help of playback: In survey round 1, 75% of all incidences were detected by playback. In survey round 2, 27.5%, in survey round 3, 13.33%, in survey round 4, 13.04%, in survey round 5, 7.69% and in survey round 6, 12.78% could be detected by playback (Fig. 4). Differences between the ratio of incidences detected by playback changed in the course of the survey rounds (Chi-square test: $\chi^2 = 12.25$, df = 5, $p = 0.03146$).

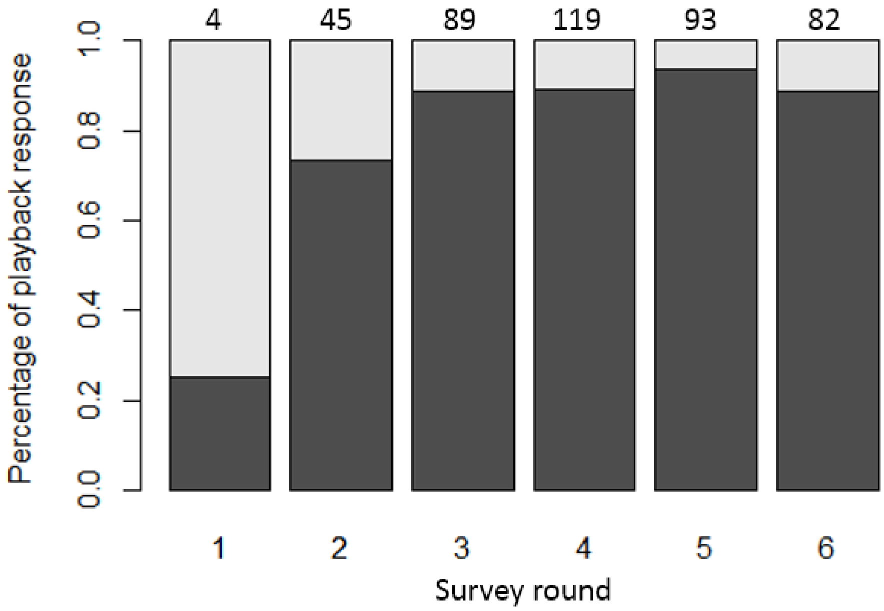


Fig. 4: Playback efficiency. The lighter parts represent the amount of birds detected by playback use. The number of individuals is given within each survey round.

Collared Flycatchers were detected throughout the day. The detection ratio (detections: total number of visits) was biggest at 05:24-07:00, 10:01-11:00, and 18:01-19:22 and smallest at 16:01-17:00 and

17:01-18:00 and 08:01-09:00 The biggest differences of the detection ratio between incidences with and without playback (>0.5) were between 07:01 and 10:00 am (Fig. 5).

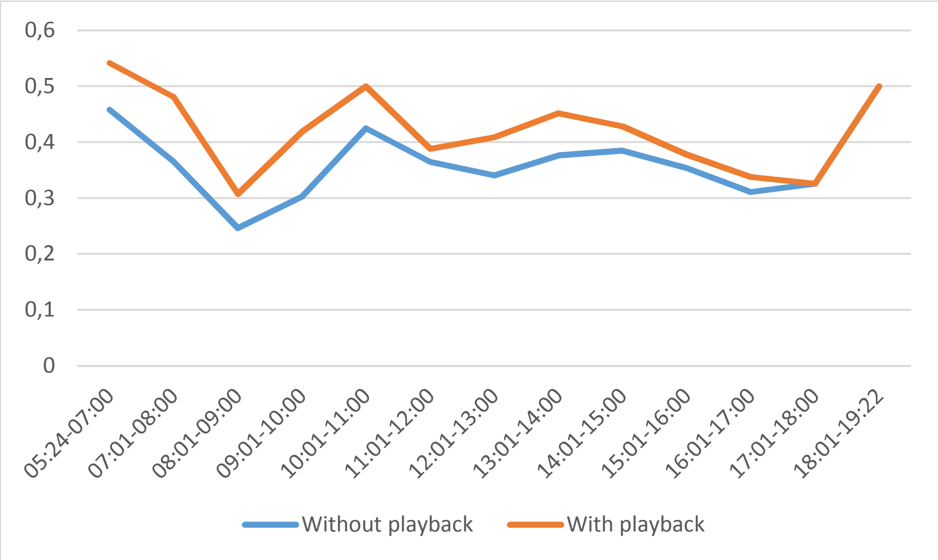


Fig. 5: Diurnal distribution of the detection ratio (detections per visits) with and without playback.

3.2 Territories

Within the 50m radius around census points, a total of 84 territories were found. A total of 34.5% (29 territories) were already established within survey rounds 1 and 2, 45.2% (38 territories) within survey round 3. Only further 16.7% (14 territories) and 3.6% (3 territories) were established within survey round 4 and 5, respectively, indicating that the vast majority (96.4%) of territories was occupied by the end of survey round 4 (until 12 May; Fig. 6 & 7). At 38 plots there were records within the 50m radius but no established territories. No Collared Flycatchers could be recorded within the 50m radius at 25 plots. Table 3 shows an overview of territory establishment.

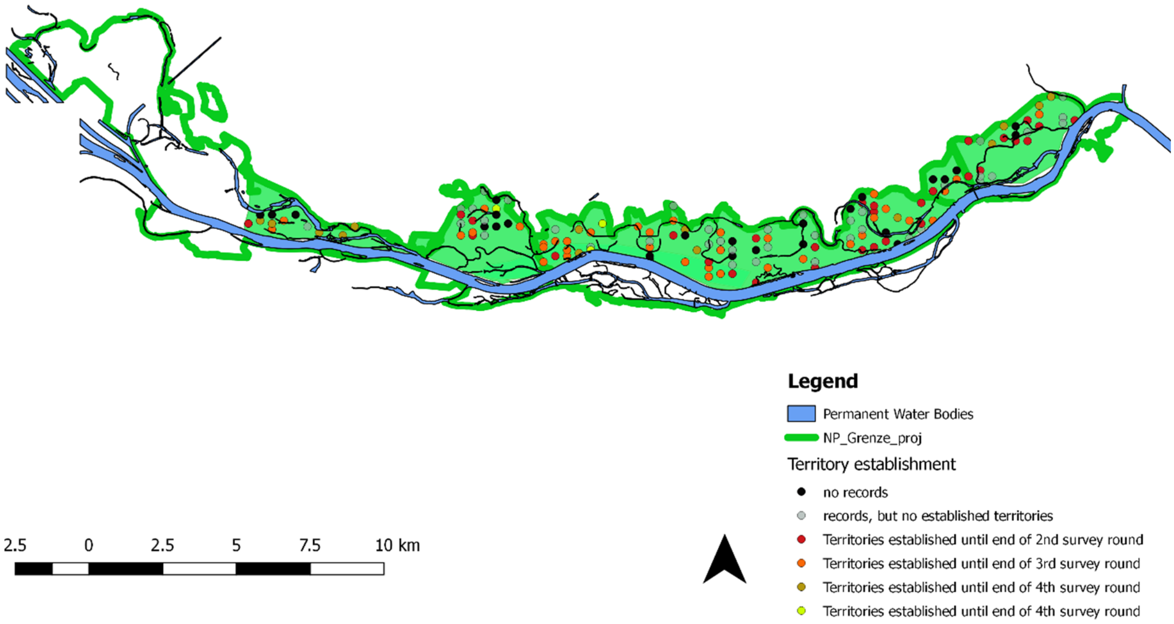


Fig. 6: Spatial distribution and time of establishment of territories at the sampling points.

Of the 58 points north of the Marchfeldschutzdamm, at 13 (22.1%) were no records of Collared Flycatchers and at 16 (27.6%), were observations but no established territories. Of the 89 points south of the Marchfeldschutzdamm, 12 (13.5%) were no records of Collared Flycatchers and at 22 (24.7%) were observations but no established territories. The proportion of points without territories, with observations only and with established territories did not differ significantly between floodplain areas at both sides of the levee (Chi-square test: $\chi2 = 2.61$, df = 2, p = 0.27066). Of the territories established within survey round 1 and 2, 8 points were north of the Marchfeldschutzdamm and 21 south of it (Fig. 6). The detailed results for each point are presented in Appendix 1.

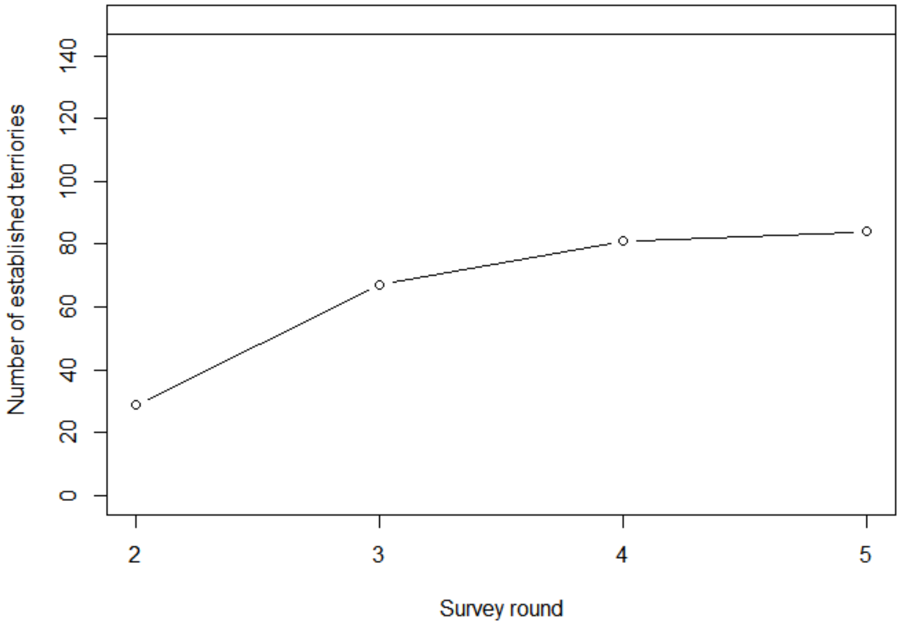


Fig. 7: Territory accumulation during survey rounds 2-5. The horizontal line at 147 indicates the total number of surveyed census point (i. e. potential territories).

3.3 HABITAT PROPERTIES

3.3.1 Standing deadwood

The total numbers of standing deadwood (including trunks) with a DBH of >3.2 cm differed strongly between the plots (Fig. 8). However, the forest stands with the highest numbers of standing dead wood consisted of rather dense, thin stems. High volume occurred rarely and did not always correspond to the numbers of trunks. For example, plot 123, with the highest volume of 49.8m³ held 10 pieces of standing deadwood, whereas plot 41 with a volume of 1.9 m³ held a number of 119 dead trees.

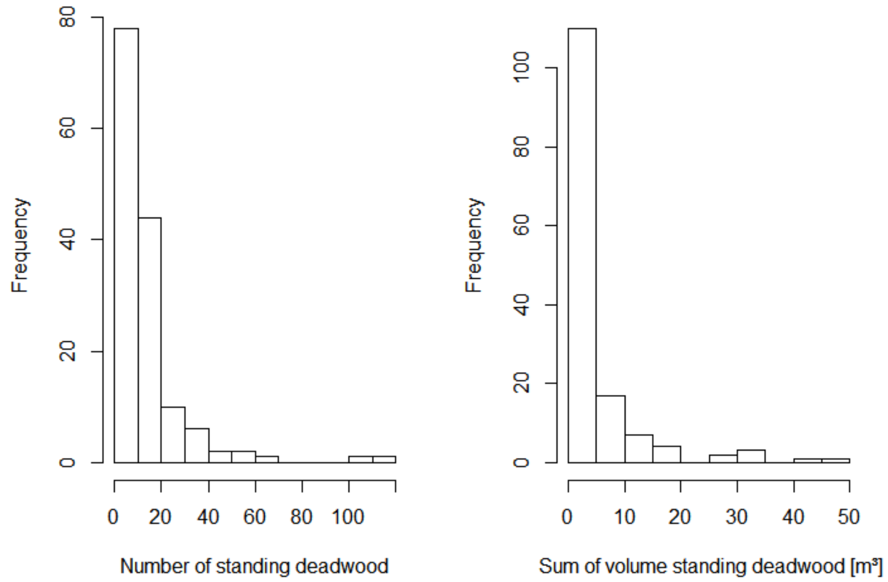


Fig. 8: (a) Frequency distribution of the number and (b) sum of volumina of standing dead wood within r=20m around census points (N=145).

3.3.2 Tree species composition

In the tree species data, a total of 23 wood taxa were recorded. The five most abundant species in the tree layer were *Populus alba* (on 72.4% (n=105) of all plots), *Fraxinus excelsior* (55.8% (82)), *Populus canadensis* (28.6% (42)), *Quercus sp.* (19.7% (29)) and *Juglans regia* (19% (28)).

3.3.3 Woodpecker holes

In total, 248 woodpecker holes were found in 58 of 145 plots (r=20 m), of which 240 were estimated in size and height and 6 more just in height due to data loss. In a very simplified approach by adding up the area of all 145 plots with r=20 m the cavitiy density is 13.61 cavities/ 1 ha. The smallest DBH of a tree with holes was 6.04 cm, the largest 127.32 cm. Of 240 woodpecker-excavated cavities, there were 19.17% (n=46) large, 50.4 % (n=121) medium and 30% (n=73) small cavities (Fig. 9). 72.6% (180) cavities were found in dead trees, and of the 27.4% (68) cavities found on living trees, 18 were on dead parts of the tree.

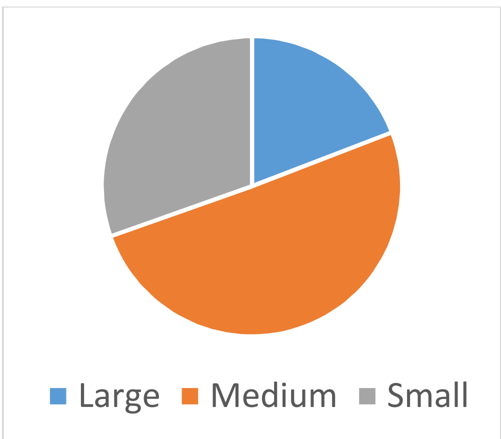


Fig. 9: Size distribution of woodpecker holes(n=240), found on 58 of 145 plots (within r=20 m around census point).

60.6 % of cavities were found in a height of ≤5 m, 18.7 % between 5 and ≤10 m, 4.9 % between 10 and ≤15 m, 8.5 % between 15 and ≤20 m, 2.4 % between 20 and ≤25 m, 3.7% between 25 and ≤30 m, 1.3% between 30 and ≤35 m. The mean height (± SD) was 7.16 (±7.45) m with a range between 0.2 and 35 m (Fig. 10).

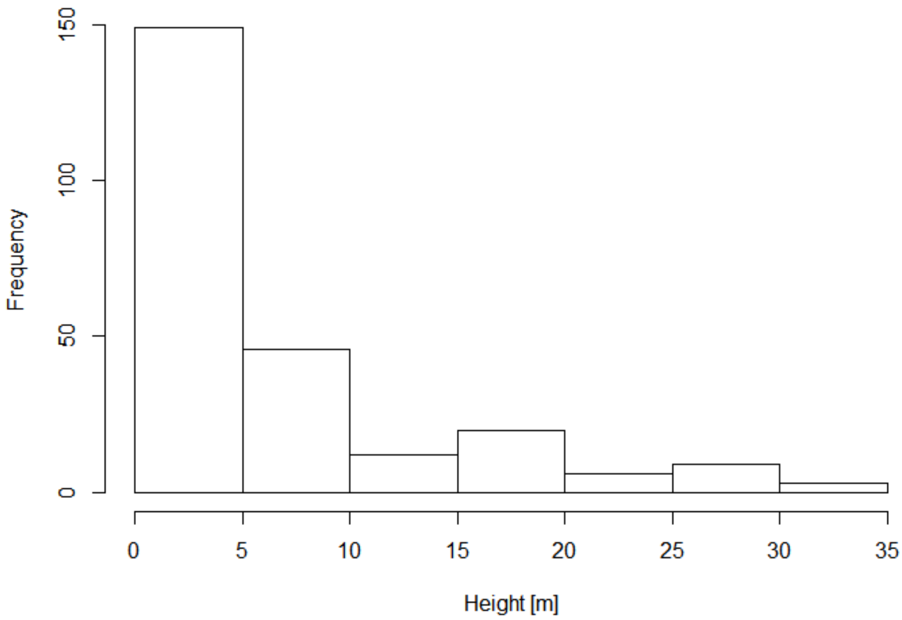


Fig. 10: Height distribution of woodpecker holes (n=246) found on 58 of 145 plots (within r=20m around census point).

3.3.4 Flying Insects

The mean number of flying insects was 26.4/min (SD=36.34, n=496) per point, the maximum being 410 individuals, the minimum 0. All climatic impacts (air temperature, wind, precipitation) on the flying insects were significant (all variables: $p < 0.00001$). The number of counted flying insects was negatively affected by increasing wind speed and precipitation and positively affected by increasing temperature. For further analysis, only the residuals of survey round 4, 5 and 6 were accounted.

3.3.5 Bird point counts

Three tit species, Great Tit (*Parus major*), Blue Tit (*Cyanistes caeruleus*) and Marsh Tit (*Poecile palustris*) were observed at our census points, a pair of Willow Tits (*Poecile montanus)* was observed only once in the floodplain forest near Stopfenreuth, but not at a census point. Recorded woodpecker species include the Green Woodpecker (*Picus viridis*), the Great Spotted Woodpecker (*Dendrocopos major*), the Middle Spotted Woodpecker (*Dendrocopos media*), the Minor Spotted Woodpecker (*Dendrocopos minor*) and the Black Woodpecker (*Dryocopus martius*). The Grey Woodpecker (*Picus canus*) was never observed. Of other Flycatcher species, there were a few observations of migrating Pied Flycatchers (*Ficedula hypoleuca*), but not on sampling points. Spotted Flycatcher (*Muscicapa striata*) was observed a few times especially later in the season. Of the tits, the Great Tit was the most abundant species, which was observed in all plots. The Blue Tit was also frequent (observed at 121 of 147 census points). The Marsh tit was only observed at 21 census points. The European Nuthatch was abundant especially during the early sampling cycles with was a weaker second peak in May after the first brood (observed at 97 census points). Of the woodpeckers, the Great Spotted Woodpecker was the most abundant species, recored at a total 126 census points. Green Woodpecker was recorded at a total of 36, Middle Spotted Woodpecker at 21, Minor Spotted Woodpecker at 20, and Black Woodpecker at 26 of 147 census points. Fig. 11 shows the frequency distributions of the counted species, i.e. during how many of 6 survey rounds the species coud be observed at individual census points.

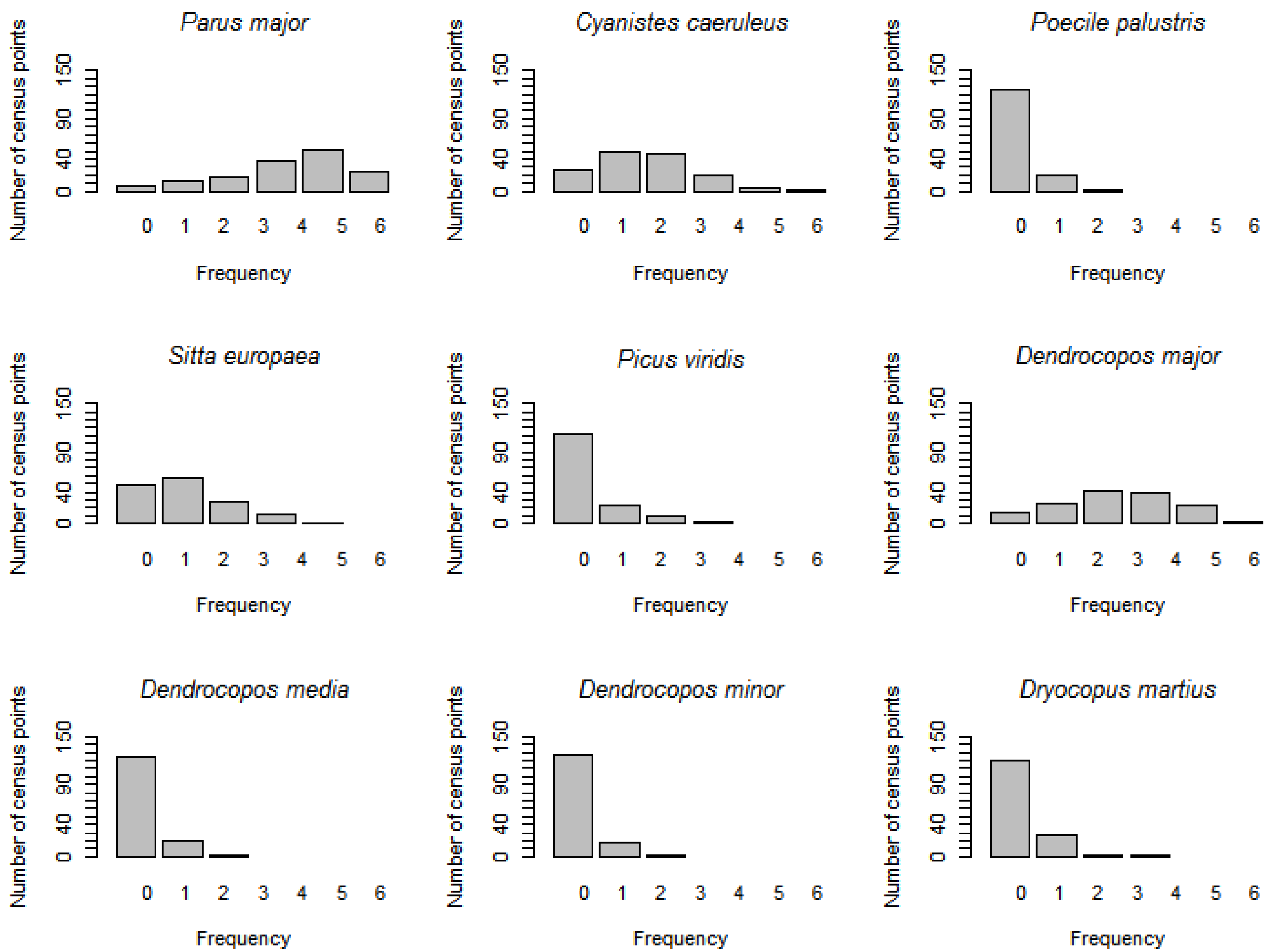


Fig. 11: Frequency distributions of the counted species (beside Collared Flycatcher) on 147 points during 6 survey rounds.

3.4 Quality traits of Collared Flycatcher Territories

3.4.1 Basic GLM

Canopy surface roughness turned out as the most important predictor for territory presence. The number of standing dead trees with a DBH of ≥ 20cm and a height of ≥ 8m emerged as a significant negative factor (Tab. 3). Close to the significance treshold were the number of woodpecker cavities as a positive factor and the sum of individuals of Great Spotted Woodpecker as a negative factor. The insect availability, the tree species and the "competition factor" of tits and Nuthatches had no significant effects. The correlation matrix of the predictors is provided in Appendix 2.

Tab 3: GLM evaluating effects of different habitat variables on the occurrence of Collared Flycatcher (N= 111 census points). Red variables have negative effects; green variables have positive effects.

Variable	p value	Signif.code	z value
Mean age of tree layer	0.186215		1.322
Distance to water	0.443576		0.766
Distance to open land	0.452116		0.752
Number of standing dead wood >20cm DBH, higher than 8m	0.023410	*	-2.267
Percent of *Populus alba*	0.143850		-1.462
Percent of *Fraxinus excelsior*	0.822944		-0.224
Median Residuals of Insect GLMM	0.288311		-1.062
Sum of individuals of *Dendrocopos major*	0.070258	.	-1.810
Sum of frequency of all tits and European nuthatches	0.513012		-0.654
Number of small and medium woodpecker cavities	0.075810	.	1.776
Surface roughness	0.000184	***	3.740

3.4.2 Best GLMs

According to the model selection, the best ranked 21 models within an AIC range of 2 are listed in Appendix 3. Fig. 12 shows the model-averaged relative importance of terms, i.e. the proportion of the 100 best of 2100 calculated models the predictor variables were included. Here, surface roughness and standing dead wood were included in all models, woodpecker cavities in 90% of the models.

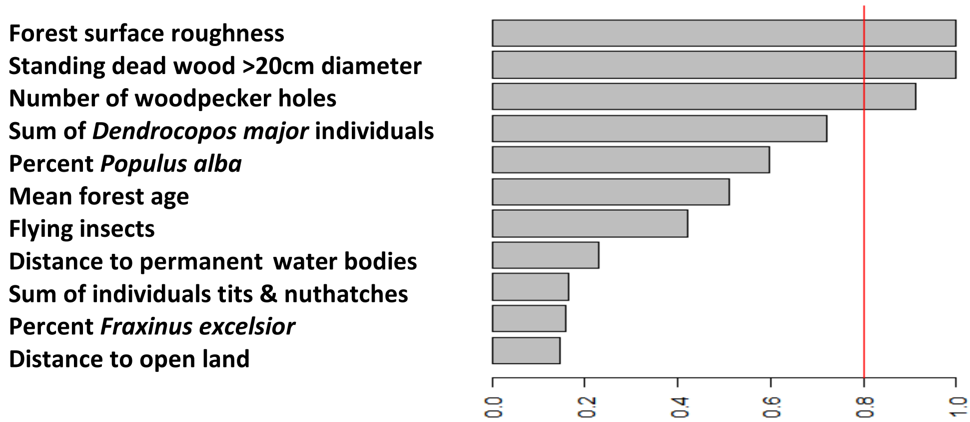


Fig. 12: Model-averaged importance of terms; red line at 80%.

3.4.3 Spatial Autocorrelation

If the observed Moran's autocorrelation coefficient is significantly higher or lower than the expected value, this indicates positive resp. negative autocorrelation. The differences between the observed and the negative expected value were significant for the basic GLM indicating a positive autocorrelation (Tab. 4, Fig.13). However, in the best model obtained by the model selection, the differences between observed and expected value were not significant (Tab. 5, Fig. 14)

Tab. 4: Results of Moran.I for the basic glm

Observed	0.0378
Expected	-0.0091
Standard deviation	0.0224
p value	0.0365

The positive and negative residuals were distributed more or less evenly for the two tested models apart from a cluster of positive residuals just west of the center of our study area; however, the spatial autocorrelation was considered neglectable for further analysis (Fig. 13 and 14).

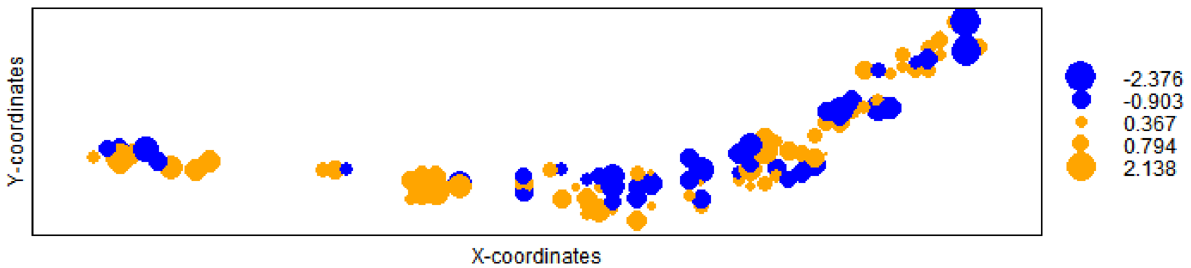


Fig. 13: Spatial distribution of positive and negative model residuals for the basic model.

Tab. 5: Results of Moran.I for the best model of the glmulti-selection.

Observed	0.0279
Expected	-0.0091
Standard deviation	0.0224
p value	0.0995

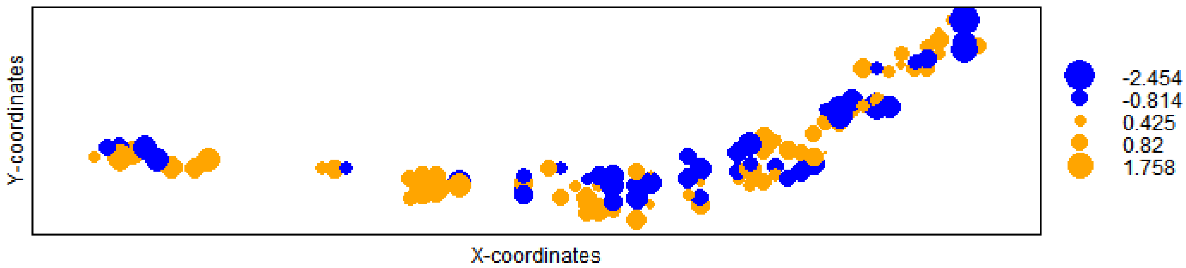


Fig. 14: Spatial distribution of positive and negative model residuals of the best model.

3.5 Time of establishment and habitat quality

As shown above, the GLMs indicate that surface roughness is the most important of the variables considered. In order to test the hypothesis that the best territories are the first to be established, both surface roughness and establishment time were connected. As the surface roughness values were not available for the entire area, only 67 of 84 territories could be included in this analysis. Half of the 67 territories is clustered in a smaller range of higher canopy roughness. The middle third is clustered in a rather small range of intermediate standard deviations, whereas the first third is distributed over a wide range from ~346 cm to ~699 cm, which also covers the majority (nearly two thirds) of points with no established territories (Fig 15)

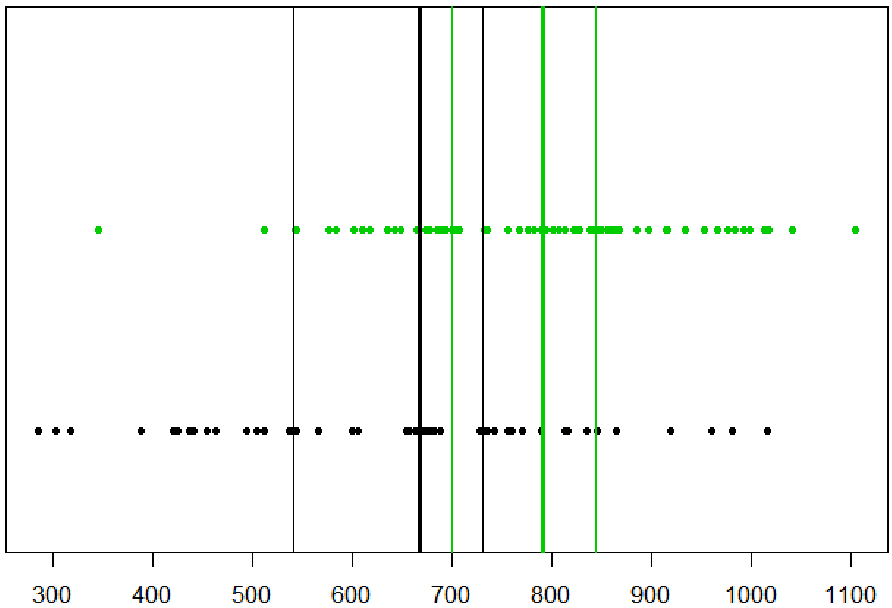


Fig. 15: Distribution of established territories (green, n=67) and plots without established territories (black, n=44) on a gradient of surface roughnes via standard deviation of vegetation height from 286cm to 1105cm. The green bold line separates the first 33 from the other 34 territories, the thin green lines separates the thirds (1-22 [n=22], 23-44 [n=22], 45-67 [n=23]). The black bold line separates the first 22 from the other 22 points, where no territories were established (n=44), the thin black lines separate the thirds (1-15 [n=15], 16-29 [n=14], 30-44 [n=14]).

We further ranked all census points with established territories according to their canopy roughness and seperated them into two groups of equal size. To avoid unequal groups, the territory ranked at place 34 had been removed. It turned out, that the territories at plots with higher canopy roughness have been occupied faster (Fig. 16).

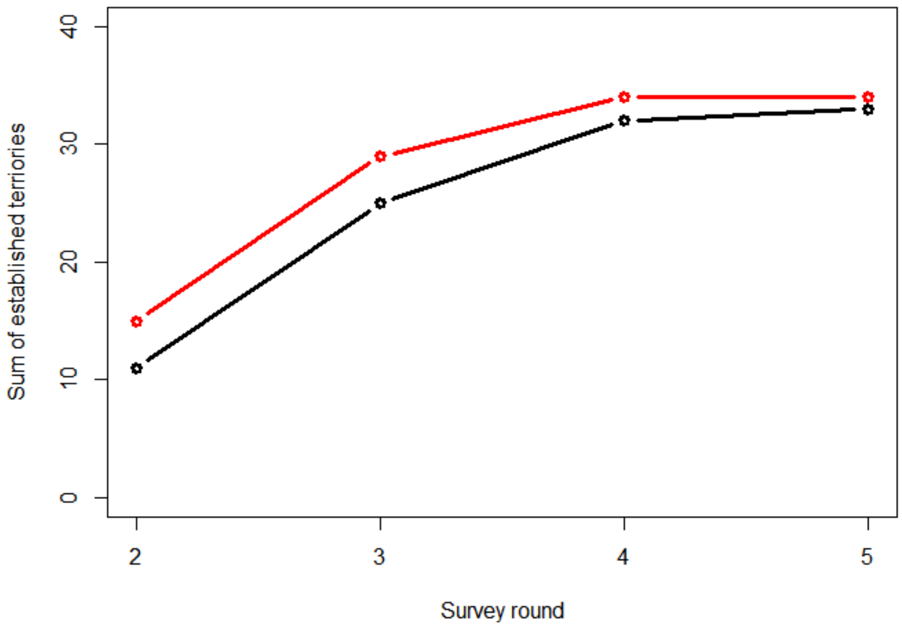


Fig. 16: Temporal pattern of territory occupation with progressing survey rounds, separately analyzed for census points with lower (black line) and higher (red line) canopy surface roughness (N = 33 cenus points for each group).

The mean canopy roughness within the territory establishment classes (0-5) differed significantly [One-way ANOVA: F (5, 105) = 6.585, p = <0.0001)]. However, TukeysHSD post-hoc-test indicates significant differences in canopy roughness only between points with no established territories and points with territories established until survey round 2 and 3 (i.e between class 0 - 2 and 0 - 3); no significant differences could be detected between census points where territories were established at different times (Tab. 6), although mean surface roughness decreased from census points with territories occupied earlier in the season towards points where territories were established later. The mean canopy surface roughness of territories established in survey round 2 and 3 was above the overall mean canopy roughness while the mean canopy roughness of points without records was below the overall mean canopy roughness (Fig 17).

Tab. 6: Tukey multiple comparisons of canopy-roughness-means beween the different establishment cl asses, 95% family-wise confidence level (Establishment classes: 0 – no records, 1 – records but no estab lished territories, 2 – territories established until end of survey round 2, 3- territories established until e nd of surves round 3, 4 – territories established until end of survey round 4, 5 – territories established u ntil end of survey round 5). Abbreviations: diff = difference between the compared pairs; lwr = lower co nfidence limit; upr = upper confidence limit; p adj = p-value *after adjustment for the multiple compariso ns.*

Pairwise comparisons	diff	lwr	upr	*p* adj
1-0	136.45455	-4.431005	277.34010	0.0633976
2-0	231.81014	89.881663	373.73862	0.0000964
3-0	245.79729	106.801415	384.79317	0.0000192
4-0	162.74176	-13.336068	338.81959	0.0872887
5-0	24.54644	-443.682500	492.77538	0.9999883
2-1	95.35560	-29.674865	220.38606	0.2401976
3-1	109.34275	-12.348571	231.03406	0.1042722
4-1	26.28721	-136.477415	189.05184	0.9971050
5-1	-111.90811	-575.294838	351.47862	0.9814354
3-2	13.98715	-108.910092	136.88439	0.9994639

4-2	-69.06838	-232.736583	94.59982	0.8236513
5-2	-207.26370	-670.968586	256.44118	0.7857513
4-3	-83.05553	-244.187278	78.07621	0.6673337
5-3	-221.25085	-684.066559	241.56485	0.7342290
5-4	-138.19532	-613.465692	337.07505	0.9584292

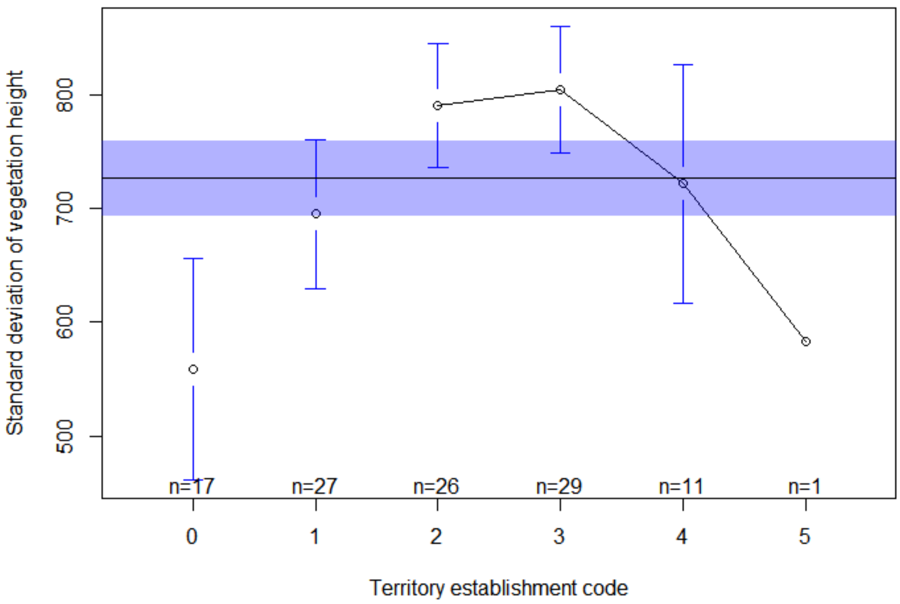


Fig. 17: Mean overall canopy surface roughness (black horizontal line) and 95% CI (marked by blue area around mean), (n=111), and mean canopy surface roughness (± 95% CI) at census points with no records (0), records but no established territories (1) and territories occupied during different times (survey round 2, 3, 4 or 5). Means of territories occupied in the course of the spring (from code 2-5) are connected by a black line.

A GLM with establishment code as response variable (establishment code 0 and 1 excluded) and surface roughness as predictor did not show significant effects (p = 0.155). Also a GLM considering data of all plots (establishment code 0 and 1 excluded) with the number of standing dead trees (any size) on temporal differences in territory occupation did not achieve a significant level (p = 0.874)

4 Discussion

4.1 Territory density

The Collared Flycatcher reaches high densities in the Donau-Auen floodplain forests east of Vienna. The mean territory density at 147 plots within a radius of 25 m around the census points was 21.4 territories/10 ha, the mean territory density in a radius of 50 m around the census points was 7.28 territories/10 ha. The *Distance Sampling* method estimates a density (± SD) between 8.68 (± 3.32) and 13.72 (± 2.31) singing males/10 ha. The detection probability is highest within 25 m around the point, what actually stresses the territory density based on observations in a radius of 25 m as the most likely. However, the value of 7.28 territories/10 ha is corresponding better to the density (± SD) of 8.68 (± 3.32) and 13.72 (± 2.31) singing males obtained by distance sampling. The very high calculated density of 21.4 territories/10 ha could be biased by the use of playback: Collared Flycatchers attracted by the playback could have lead to an increased number of singing individuals within the radius of 25 m around the

census points. Meanwhile, birds in a distance of >50 m were less attracted to enter the radius of 50 m around the census point due to the decreasing audibility of the playback in a distance of >50 m.
Densites reported formerly from the Donau-Auen floodplain forests are persistantly lower: In 1983, Winding & Steiner (1988), found densities of 2.0, 3.0 and 2.7 territories/10 ha in different survey areas near Stopfenreuth south of the Marchfeldschutzdamm, 2.9, 1.6 and 1.6 territories/10 ha in 3 survey areas near Witzelsdorf, 1.8 territories/10 ha in one survey area near Petronell and 7.3 territories/10 ha in a survey area north of the Marchfeldschutzdamm in the area around Witzelsdorf and Stopfenreuth ("Abgedammte Au"). In a survey from 1982-1990 in a 106 ha area near Eckartsau, Kollar & Seiter (1990) found a density of 3.4 breeding pairs/10 ha within their survey area and up to 5.8 breeding pairs/10 ha outside of the survey area. For the Viennese part of the national park (Lobau), in 2001 a population density of 0.9-2.1 territories/10 ha (mean density 1.4 territories/10 ha) was observed (Dvorak in Dvorak 2009). In 2007, Götz (2016) calculated a density of 1.25 breeding pairs/ 10 ha in an area of 256 ha near Orth an der Donau.
In other floodplain forests of the catchment area, the Collared Flycatcher locally reaches densities almost as high as our results: In floodplain forests along Morava and Thaya/Dyje up to 4-5 territories/10 ha are reported in old-growth floodplain forests with a high proportion of oaks. However, over large areas lower densities of 0.5-1 territories/10 ha are the rule. A very high density of 20 breeding pairs/10 ha was counted in a floodplain forest area with nestboxes at the confluence of Morava and Thaya/Dyje (Czech Republic, Zuna-Kratky et al. 2000). In floodplain forests near Tulln, 17-64 breeding pairs were estimated on an area of 410 ha near Korneuburg (Straka et al. 1990) and 40 – 67 territories on 370 ha near Stockerau (Straka 2009). In Danube floodplain forests in the Machland at the border of Lower to Upper Austria, the Collared Flycatchers is a common breeding bird, but no detailed densities are reported (Kaindl et al. in Kaindl et al. 2009). Also in other riverine forests of Pannonian and Illyric climate, as in Styria and Burgenland (Lazowski 1997), the Collared Flycatcher is a common breeding bird. Densities from 2.4-12.6 territories/10 ha (mean density 6.8/10 ha, 2003) were reported from the Natura 2000-area "Steirische Grenzmur mit Gamlitzbach und Gnasbach" in the floodplain forests of the river Mur resulting in a total of 500-600 territories in an area of 12.2 km², emphasizing this local population as one of the biggest in Austria (Ilzer 2009, Brunner & Huemer 2004). From riverine forests along the river Lafnitz, Styra, 17 territories were reported for an area of 1534.68 ha (2013) in the Natura 2000-area "Lafnitztal und Neudauer Teiche" (Thurner et al. 2014). In riverine forests at the river Leitha at the border of Lower Austria to Burgenland, Collared Flycatchers are breeding, but no densities are reported, however from the Natura 2000-area "Neusiedler See - nordöstliches Leithagebirge" in the northeastern Leitha mountains, which includes small parts of floodplains south of the river Leitha, 510-920 breeding pairs occur, however the main habitat are deciduous forests on the Leitha mountains (Standarddatenbogen für das Europaschutzgebiet AT1110137 Neusiedler See - Nordöstliches Leithagebirge Amt d. Burgenländischen Landesregierung, Abt. 5/III Natur- und Umweltschutz, Update 2015-08; Standarddatenbogen für das Europaschutzgebiet AT1220V00 Feuchte Ebene - Leithaauen. Amt der NÖ Landesregierung, Abteilung Naturschutz, Update 2015-12, Dvorak 2009b, Dvorak et al. 1993). In other deciduous forest types with populations breeding only in natural cavities, high densities range up to 9.6 pairs/10 ha were found in the Viennese Forests and up to 10 pairs /10 ha in Bialowieza (Sachslehner 1995, Weslolowski & Tomialjoc 1992, Walankiewicz 1991). According to Birdlife International (2016), the Collared Flycatcher has a positive population trend. Since the 1980ies the population seems to be at least stable in the Lower Austrian Donau-Auen. For the total area of the Lower Austrian part of the national park on the northern shore of the river Danube (47.764 km²) a total mean densitiy of a threefold of the estimated population for Austria (Bauer et al. 2012) could be grossed up based on the estimates by Distance Sampling! However, an overestimation is on hand as not the entire area is covered with forest. Moreover, Collared Flycatcher populations can strongly fluctuate between years (Walankiewicz 2002b) and higher singing activity of non-breeders (Neubauer & Sikora 2013) could

bias the estimate. Further, we have no information on the proportion of females in the population of Collared Flycatchers in the Danube floodplains east of Vienna. Yet our results indicate that the population size of 600-1000 pairs estimated for the area (Standarddatenbogen für das Europaschutzgebiet AT1204V00 – Donauauen östlich von Wien. Amt der NÖ Landesregierung, Abteilung Naturschutz, Update 2015-12) is strongly underestimated. The high densities reported by our study may mirror structural improvements of the floodplain forests due to management measures undertaken in the national park since it was founded in 1996 and emphasize the national importance of this area for Collared Flycatchers.

4.2 TIME OF ARRIVAL

Usually, Collared Flycatchers arrive at their Central European breeding areas in mid April (Glutz von Blotzheim & Bauer 1993). Hence, the observation of the first individual on 6 April was rather early compared to known arrival dates. Sachslehner (1993) recorded the first males in the Viennese Forests on 7 April in 1989. Earliest records from the Moravia floodplain forests are from 9 April (1985) and 11 April (1971; Zuna-Kratky et al. 2000). Südbeck et al. (2005) recommended surveys from 10 April-10 June while observations from 01-20 April are reckoned as extended survey time. In a study from Eastern Styria, Austria, for the years 1967–1979, the median date of arriving birds was 13 April (Samwald & Samwald 2005). In 2016, Collared Flycatchers were already observed on 3 April in the Donau-Auen east of Vienna (Wyhlidal, J., pers. comm.). This is consistent with the results of Zdeněk et al. (2009) in riverine forests in Czech Republic, reporting a shift of first laying date of Collared Flycatchers between 8.5 and 9.3 days over the last 47 years.

4.3 QUALITY TRAITS OF TERRITORIES

The most important parameters for territory establishment in our study were surface roughness, standing dead wood and cavity availability. The importance of forest structure for Collared Flycatchers was also shown in a comparable approach in regions with only natural cavities by Kralj et al. (2009) in central Croatia. In their results, a high density of trees was negatively correlated with good territories (points with more than one singing male in their study). Both canopy surface roughness as well as the number of standing dead trees can be related to that structural parameter. Canopy roughness will most likely be lower in young forest stands compared to old growth forests, which are typically characterized by lower tree densities (e.g. Parker & Russ 2004) and a higher volumen of dead trees (Hansen et al. 1991) as well as a higher horizontal structural complexity (Franklin & Pelt 2004).

4.3.1 Canopy surface roughness

Canopy surface roughness emerged as crucial factor for the presence of Collared Flycatcher territories and there was even a trend for earlier establishment of territories, stressing the relevance of light for Collared Flycatchers, who seem to prefer **forests with a high density of canopy gaps, e.g. due to tree fall gaps** (see next chapter; personal observations, Götz 2016, Sachslehner 1993). In the context of temperate forests, canopy surface roughness might be an indicator for structural diversity typical for near-natural forests (e.g. more light openings in old growth stands, Franklin & Pelt 2004) as well as disturbance in terms of floodplain dynamics.

4.3.2 Standing deadwood

In the model-averaged importance of terms, the number of standing deadwood with a diameter over 20 cm was as important as canopy surface roughness, but in the best models, it has – surprisingly - a negative effect. In contrast, a study in different beech forests in Italy identified the diversity and the volume of deadwood as important factor both positively influencing the abundance of cave-breeding birds (Redolfi De Zan et al. 2016). In the Austrian Woodland Bird Index (Teufelbauer et al. 2014), the

Collared Flycatcher is listed as deadwood bird. In their large-scale study based on forest inventory data, Teufelbauer et al. (2014) found a highly significant positive relationship between lying dead wood and Collared Flycatcher incidences. Walankiewicz et al. (2007) showed that in Bialowieza, Poland, the preferred holes of the Collared Flycatcher were in living trees, while in the Viennese Forests, 56.3% of the breeding trees were dead, 75% of breeding cavities were in dead wood and 25% were in diseased wood (Sachslehner 1993). For Collared Flycatchers in the Viennese forest, a positive correlation between deadwood near the nest box and the number of fledged young was found, possibly caused by a higher amount of deadwood in open, sunny habitats or better foraging conditions at habitats with higher amount of deadwood (e. g. more nutritious larvae available; Hoffmann 2011). Sachslehner (1993) provided strong evidence that Collared Flycatchers prefer deadwood perches over perches on living trees. In the Donau-Auen, observations of singing males on high, rather free-standing dead trees are frequent. As those trees are standing alone, the number of standing dead trees certainly not reliably represented this habitat feature. In contrast, the amount of standing deadwood was negatively related to the occurrency of Collared Flycatcher territories, most likely indicating that forest sites with a higher density of dead trees may have been too dense. Also Götz (2016) observed that the canopy closure categories "roomy" (räumig), "light" (licht) and "loose" (locker) predominated over "closed" (geschlossen) and "dense" (gedrängt) within Collared Flycatcher territories, as well as Sachslehner (1993) observed Collared Flycatchers were attracted to clearings when they had chicks in the nestling phase. Hence, a value for strong lying deadwood would possibly have been a better measurement, including forest openness (as a high amount of lying deadwood causes light openings) as well as deadwood richness (Berg, H-M., pers. comm.) There was a strong negative correlation between the total number of standing deadwood and canopy roughness as well as between the number of standing deadwood ($F_{1,109}$ =43.87, p<0.0001, multiple r^2 = 0.287) and the mean age of the tree layer ($F_{1,109}$ =6.36, p<0.0131, multiple r^2 = 0.055; Fig. 18). Hence, the apparently negative effect of deadwood on the Collared Flycatcher in the Donau-Auen rather may indicate a negative effect of former forestry measures (high density of smaller dead trees as result of high density of originally planted trees? – tree mortality caused by competition can lead to forest homogenity, Franklin & Pelt 2004) than a minor importance of deadwood for insectivorous floodplain forest birds.

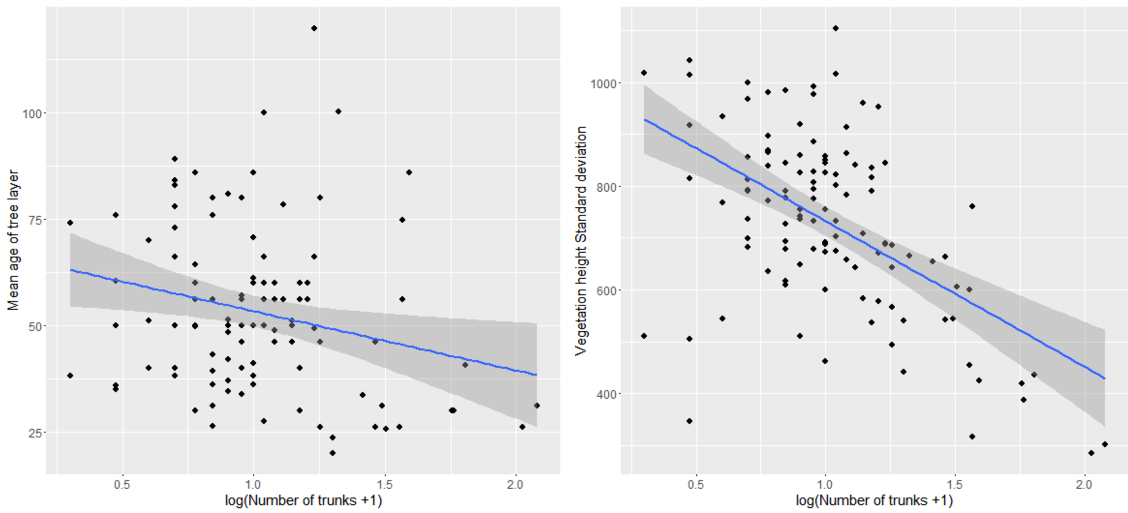


Fig. 18: Relationships between mean age of tree layer and number of standing deadwood (left graph) and canopy roughness and number of standing deadwood. Shaded area: 95 % confidence intervals.

4.3.3 Tree species composition

Tree species in the composition of the upper canopy layer had little effects. Martinovic (2016) concluded in his point count-approach that forest structure seemed to be more important for Collared Flycatchers than individual tree species. Also Walankiewicz et al. (2007) emphasized that other traits of the cavity proved being more important for cavity choice of tree-hole breeding birds than tree species identity. In a boreal riverine forest in Mongolia, the majoritiy of cavities were found in *Populus* sp., which was strongly preferred by woodpeckers; consistingly, also in natural forests in Sweden most of cavities were found in *Populus ssp*. (Bai et al. 2003, Sandström 1992). As the majority of the 111 points used in the model is located south of the Marchfeldschutzdamm and thus in softwooded (*Populus ssp*.-dominated) floodplain forest, the negligible effects of *P. alba* and *F. excelsior* should be interpreted with caution. Regarding all 147 points, the majority of territories (72.4%) established until the end of survey round 2 are located south of the Marchfeldschutzdamm. 13.8% of all points north of the Marchfeldschutzdamm and 23.6% of all points south of the Marchfeldschutzdamm were established until the end of survey round 2. The proportion of "unfavoured" sites (i.e. points without records and without established territories) is remarkably higher (50%) among points north of the Marchfeldschutzdamm than among points south of the Marchfeldschutzdamm (38.2%). This could be interpreted as a trend to preference of softwooded floodplain forest - in contrast to the preference of hardwooded floodplain forest in the Lobau (Dvorak in Dvorak 2009, Zuna-Kratky et al. 2000).

4.3.4 Forest age

We could not detect any effect of mean forest age on the occurrence of territories, though forest age is known to have a positive impact on diversity and abundance of birds, especially cave-breeders (e.g. Moning & Müller 2008, Poulsen 2002).

4.3.5 Woodpecker cavities

The cavity density of 13.61/ 1ha in our studied floodplain forest is relatively low compared to other near-natural forest areas, such as the Viennese Forest (beech-dominated) with local densities of 78-92 cavities / 1 ha and the global mean cavity density of 16/ 1 haresult from 103 studies worldwide; Remm & Lõhmus 2011, Remm et al 2005, Sachslehner 1995). In deciduous and deciduous mixed woodland, densities of 6.2–30 cavities / 1 ha are reported from the Netherlands (Van Balen 1982), 39.3 ± 18.8/ 1 ha floodplain forests in Mongolia (Bai et al. 2003), 41/ 1 ha from Sweden (Sandström 1992) but only 0.5-0.6/ ha^{-1} from mixed woodland in Estonia (Lõhmus et al. 2005). Possibly a higher survey effort would have been necessary for our study as cavities are not easy to detect, e.g. with a minimum searching time and more than one search per plot during different light conditions (e.g. Lõhmus et al. 2005, Weggler & Aschwanden, 1999). Further, most of the cavities found in this study were in a height range below 10 m and in dead trees. This could also be caused by a sampling bias, as cavities in dead trees with decayed bark are better visible than cavities on trees with intact bark. In the Viennese Forest, Collared Flycatchers used cavities from 1-17 m above ground, (Sachslehner 1995); in Bialowieza, heights from 0.5-23 m above ground are reported as well as entrance diameters from 1.5 to 17.5 cm (measured at the smallest diameter, Walankiewicz 2007). However, lower cavities are stronger predated (Sachslehner 1995, Nilsson 1984). Thus, the majority of cavities found could be potential breeding holes for Collared Flycatchers although they strongly differ in quality (Lõhmus & Remm 2005, Sachslehner 1992).

The positive effect of woodpecker cavitiy availability on the occurrence of Collared Flycatcher territories most likely mirrors breeding opportunities. However, in Bialowieza, Poland the majority of available cavities for secondary cave-breeders were not excavated by woodpeckers and the Collared Flycatchers preferred non-excavated cavities (Walankiewicz et al. 2007, Walankiewicz 1991). Although in floodplain forests in Estonia the majority of available cavities was made by woodpeckers, passerine secondary cavity breeders still preferred natural holes in living trees (Remm et al. 2006). Similarly, in Switzerland 18 of 26 breeding cavities used by Collared Flycatchers in a submontanous forest of European Chestnut (*Castanea sativa*) were not excavated by woodpeckers (Maurizio 1987). In the Viennese Forests up to 70% of the breeding cavities used by Collared Flycatchers had been excavated by the Great Spotted

Woodpecker or Middle Spotted Woodpecker; still 6% had been excavated by Minor Spotted Woodpecker, 4% by Green or Grey-Headed Woodpecker, in 3% the entrance had been minimized by Nuthatch and 16% were not-excavated (Sachslehner 1995). The Collared Flycatcher in the Donau-Auen seemed to rely predominantly on woodpecker-excavated cavities (Götz 2016: just one breeding cavitiy of 14 was not a woodpecker hole). Also during the field work for this study, I scarcely saw any suitable cavities that had not been excavated. As woodpeckers play the most important role in cavity provision in the earlier succession stages of a forest (Remm & Lõhmus 2011), this situation will possibly shift in the future as soon as the favoured process-orientated conservation approach of the national park is implementated and the forests move to the next succession stages.

In contrast to the number of woodpecker-excavated cavities, the abundance of the Great Spotted Woodpecker had a negative effect on the presence of territories. This woodpecker species is an important nest predator and Collared Flycatchers commonly avoid its breeding trees (e.g. Sachslehner 1993 & 1992).

4.3.6 Breeding competition

Potential breeding competition with tits and European Nuthatches (*Sitta europaea*) had little effect, at least at the large scale of our study. However, as known from long term-studies from Poland, competition plays a minor role in near-natural systems (Wesolowski 2003, Mitrus et al. 1996, Walankiewicz 1991). Maurizio (1987) observed non-mortal fights with Blue Tits (*Cyanistes caeruleus*) and Common Redstart (*Phoenicurus phoenicurus*; a species not common in the Donau-Auen floodplain forests), but also observed Great Tit (*Parus major*), Marsh Tit (*Poecile palustris*), European Nuthatch, Starling (*Sturnus vulgaris*) and Green Woodpecker (*Picus viridis*) breeding on the same tree as the Collared Flycatchers. To find competition effects on the small scale – the cavity – a different survey approach would have been necessary.

4.3.7 Food availability

Flying insect density did not appear playing a substantial role for predicting the occurrence of Collared Flycatcher territories. In fact, Collared Flycatcher are capable of using opportunistically a wide variety of insect groups (e.g. Glutz von Blotzheim & Bauer 1993). However, caterpillars, especially the larvae of winter moths (*Operophtera spp.),* which occur in large amounts in riverine forests, can represent a main food source for nestlings and the date of laying is synchronised with the hatching of the caterpillars (e.g. Zdeněk et al. 2009). Unfortunately, we failed to assess the availability of caterpillars (see Methods part). If this trait would be considered in habitat choice, the male Collared Flycatchers would have to pre-estimate or remember caterpillar abundance in their chosen territory, possibly via the tree-species most prone to frass. As the Collared Flycatcher has a high fidelity to breeding places (Pacher & Pacher 1986) this is not utterly impossible. In our study, of 41 trees identified as the most affected in the plot, *Acer campestre* was the most important caterpillar feeding plant with 11 affected trees followed by *Fraxinus excelsior* with 7 trees. Of *Ulmus* sp*.* and *Populus* sp. four trees with heavily damaged leaves were counted. Although no conclusions for habitat choice can be based on those results, the interplay between territory choice and nestling food could be an interesting topic of further research.

4.3.8 Landscape variables

Both the distance to open land and permanent water bodies did not affect the occurrence of Collared Flycatcher territories in the Donau-Auen National Park. Particularly the distance to water bodies proved to affect the density of insectivorous birds, including flycatchers, in floodplain forest in other studies (Iwata et al. 2003). This could not be confirmed for the Collared Flycatcher in our study area.

4.4 QUALITY CHANGES BY TIME OF ESTABLISHMENT

There were no significant differences between the different times of establishment but between sampling points with and without territories. In a more detailed study in a near-to-primeval plot in Bialowieza forest, Poland, Mitrus et al. (1996) found no qualitative differences between the cavities occupied (1) earlier and (2) by younger males and concluded that competition effects have little impact under primeval conditions. This could also be the case in Donau-Auen, as indicated by the high density of Collared Flycatcher territories. However, a trend of declining canopy surface roughness could be observed in territories established after survey round 3, perhaps indicating that habitats with a higher canopy heterogeneity are occupied preferentially before other still suitable territories are filled.

4.5 PREDATION

Nest predation by other species than woodpeckers was not considered in our study. Potential predators observed during the fieldwork in the Donau-Auen riverine forests are Red Squirrel (*Sciurus vulgaris*), European Pine Marten (*Martes martes*), and Weasel (*Mustela nivali*s; Walankiewcz 2002a) were observed. Of predators of adult birds, Edible Dormouse (*Glis glis*) could not be observed in the area, Sparrowhawk (*Accipiter nisus*) was observed regularly (Glutz von Blotzheim & Bauer 1993). Tawny Owl (*Strix aluco*) whose main prey items are rodents, has a certain proportion of cave breeders among its bird prey (Bauer et al. 2012). Morsinotto et al. (2009) showed in their study that Pied Flycatchers (*Ficedula hypoleuca*) distinguish between different predators and avoided to select territories near Pygmy Owls (*Glaucidium passerinum*). The predator landscape of Collared Flycatchers as a factor for habitat selection should not be neglected and could be topic of further research: Nagl (2015) found an increased probability for Tawny Owls in old growth stands and areas with higher and dense amounts of standing deadwood (based on forest inventory data) in the Donau-Auen riverine forests. It is thinkable that the negative effect of the (probably too dense) standing deadwood on Collared Flycatchers was enhanced by avoidance of Tawny Owl territories, however, Maurizio (1987) found one pair of Collared Flycatchers breeding on the same tree as a Tawny Owl.

5 SYNOPSIS

Independently of the used assessment method, all our territory density estimates indicate that the population size of the Collared Flycatcher in the floodplain forests of the Donau-Auen National Park had been formerly substantially underestimated. The most important factors for habitat use by Collared Flycatchers in the Donau-Auen National Park appeared to be canopy roughness, standing dead wood and woodpecker-excavated cavity availability. In the Donau-Auen riverine forests, which are protected since 1996 and move towards a process-orientated conservation approach, the population of Collared Flycatchers could even increase in the following years as more suitable habitats are to develop. As canopy roughness - a factor most likely related to forest age and floodplain dynamics - turned out as the most important factor for the presence of Collared Flycatcher territories, the Collared Flycatcher could be a reliable indicator species for near-natural floodplain forest systems.

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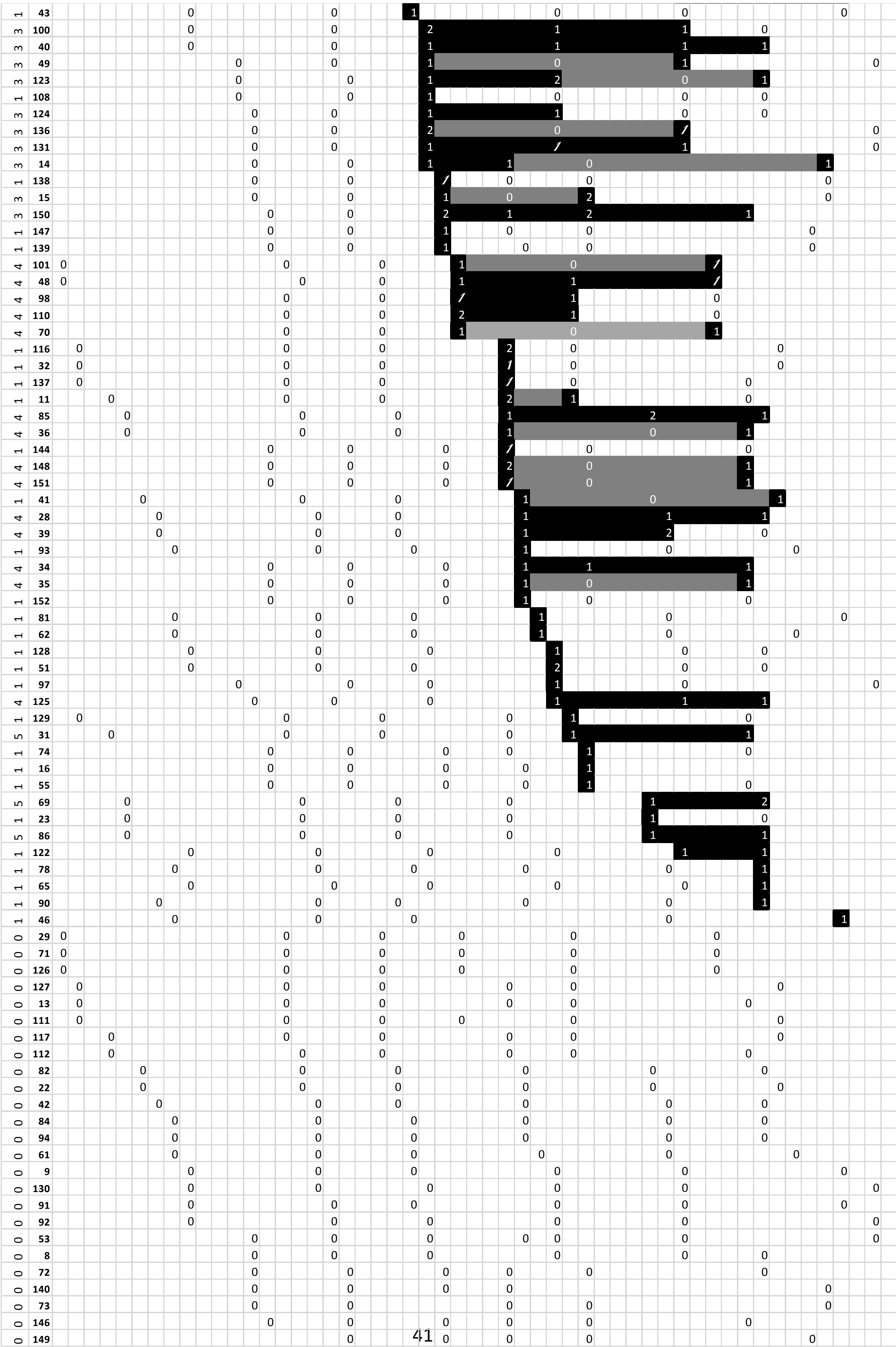
APPENDIX 1

Overview over the territories established within a 50m radius around census points, ordered by date of first observation of a Collared Flycatcher at that census point. The different colours above represent the six survey rounds. Slashed days were no field days. The numbers in a date-column show how many individuals were recorded at that date. Italic numbers stand for records obtained via playback. Black background shows continuous records, grey background shows gaps in records. On the left, column „Terr. Class." shows how the territories were classified: 0: no records. 1: records, but no established territories. 2: Territories established until end of 2nd survey round. 3: Territories established until end of the 3rd survey round. 4: Territories established until end of 4th survey round. 5: Territories established until end of 5th survey round. The column „Plot" shows the individual number of the plot.


APRIL
MAY
Terr. Class.
Plot



APPENDIX 2

Table showing the correlation coefficients of different variables considered for the basic model evaluating habitat use of Collared Flycatchers. Critical values are marked red. Bold variables were included in the basic model. Abbreviations: Dist.WB = Distance to water bodies, Dist.OL = Distance to open land, Vol.SDW = Volumen of standing deadwood; Vol.SDW208 = Volumen of standing deadwood >20 cm DBH and 8 m height, log Vol.SDW = log-transformed volumen of standing deadwood, No.of SDW208 = Number of standing deadwood >20 cm DBH and 8 m height, log No. SDW = log transfomed number of standing deadwood, No. SDW= number of standing deadwood, %F. excelsior = Percentage of Fraxinus excelsior, %P. alba = Percentage of Populus alba, Mean age = Mean age of tree layer, Fly. insect. Res. = Flying insect residual value, D. major = Sum of individuals of Dendrocopos major, Cavities = Number of cavities, Compet. factor = Competition factor, i.e. the sum of frequencies of tits and European Nuthatches, CSR = Canopy surface roughness.

	Dist. WB	**Dist.OL**	Vol.SDW	Vol. SDW208	log Vol. SDW	**No. of SDW208**	log No. SDW	No. SDW	***% F. excelsic***	***% P. alba***	**Mean age**	**Fly. insect res.**	***D. major***	**Cavities**	**Compet.factor**	**CSR**
Dist. WB	1															
Dist.OL	-0.32687614	1														
Vol.SDW	-0.13130233	0.247547	1													
Vol. SDW208	-0.1562529	0.263748	0.86022944	1												
log Vol. SDW	-0.03501018	0.0762919	0.70948429	0.592675997	1											
No. of SDW208	-0.06428727	0.0517858	0.62984967	0.609402957	0.740306988	1										
log No. SDW	0.088685151	-0.062489	-0.0201674	-0.0290001	0.237120435	-0.003388157	1									
No. SDW	0.023640768	-0.07266	-0.0721773	-0.09344517	0.100515549	-0.1230374	0.843652557	1								
% F. excelsior	0.217372689	-0.105066	-0.0195669	-0.03157943	0.049819445	0.088279219	-0.087889702	-0.152756	1							
% P. alba	0.032513	-0.057239	-0.1509489	-0.11483769	-0.001589573	0.061603337	-0.05643049	-0.156741	-0.347475	1						
Mean age	0.201927258	-0.084979	-0.0262498	-0.01609001	-0.089552576	-0.051228904	-0.234874352	-0.260439	0.3492256	-0.137591	1					
Fly. insect res.	-0.09341704	0.0673261	-0.0031322	0.12164732	-0.05297722	-0.048476814	0.049235606	0.0350306	0.2183727	-0.124857	0.0842954	1				
D. major	0.07148999	-0.046322	-0.0545777	-0.08908025	0.005645544	-0.009897665	-0.132451367	-0.16331	0.1008615	0.0978404	0.2012677	0.005525328	1			
Cavities	0.050790475	0.045613	0.56352508	0.42886926	0.370280359	0.321135937	-0.03357119	-0.073637	0.0070078	-0.024367	-0.029015	-7.78262E-05	-0.06256	1		
Compet.factor	0.142883466	0.0803631	0.0760916	0.037708417	-0.008484734	0.14702958	-0.230006386	-0.184937	0.1846806	-0.004565	0.1590854	-0.018190054	0.060615	-0.0116	1	
CSR	0.030944599	0.1392713	0.14351912	0.171594568	0.03658539	0.175082397	-0.535716522	-0.579954	0.2623415	0.2514408	0.2949784	0.019195199	0.132366	0.13358	0.192668136	1

APPENDIX 3

The best 21 models selected automatically by “glmulti” ranked after the AIC criterion within a range of 2 degrees AIC.

Ranking	Model	AIC	weights
1	Terr50 ~ 1 + Mean tree layer age +Number of standing dead wood (> DBH 20, h 8) + Sum of individuals D. major + Number of woodpecker cavities + surface roughness	137.0593	0.034139
2	Terr50 ~ 1 +Number of standing dead wood (> DBH 20, h 8) + Percent P. alba + Sum of individuals D. major + Number of woodpecker cavities + surface roughness	137.3551	0.029446
3	Terr50 ~ 1 + Mean tree layer age +Number of standing dead wood (> DBH 20, h 8) + Percent P. alba + Insect GLMM residuals + Sum of individuals D. major + Number of woodpecker cavities + surface roughness	137.4208	0.028494
4	Terr50 ~ 1 + Mean tree layer age +Number of standing dead wood (> DBH 20, h 8) + Percent P. alba + Sum of individuals D. major + Number of woodpecker cavities + surface roughness	137.4528	0.028041
5	Terr50 ~ 1 + Mean tree layer age +Number of standing dead wood (> DBH 20, h 8) + Insect GLMM residuals + Sum of individuals D. major + Number of woodpecker cavities + surface roughness	137.4847	0.027597
6	Terr50 ~ 1 +Number of standing dead wood (> DBH 20, h 8) + Percent P. alba + Insect GLMM residuals + Sum of individuals D. major + Number of woodpecker cavities + surface roughness	137.545	0.026779
7	Terr50 ~ 1 +Number of standing dead wood (> DBH 20, h 8) + Percent P. alba + Number of woodpecker cavities + surface roughness	137.9764	0.021583
8	Terr50 ~ 1 +Number of standing dead wood (> DBH 20, h 8) + Sum of individuals D. major + Number of woodpecker cavities + surface roughness	138.0461	0.020843
9	Terr50 ~ 1 +Number of standing dead wood (> DBH 20, h 8) + Percent P. alba + Insect GLMM residuals + Number of woodpecker cavities + surface roughness	138.1621	0.019669
10	Terr50 ~ 1 + Distance to water +Number of standing dead wood (> DBH 20, h 8) + Percent P. alba + Sum of individuals D. major + Number of woodpecker cavities + surface roughness	138.492	0.016678
11	Terr50 ~ 1 + Mean tree layer age + Distance to water +Number of standing dead wood (> DBH 20, h 8) + Sum of individuals D. major + Number of woodpecker cavities + surface roughness	138.7444	0.014701
12	Terr50 ~ 1 +Number of standing dead wood (> DBH 20, h 8) + Insect GLMM residuals + Sum of individuals D. major + Number of woodpecker cavities + surface roughness	138.8403	0.014012
13	Terr50 ~ 1 + Distance to water +Number of standing dead wood (> DBH 20, h 8) + Percent P. alba + Insect GLMM residuals + Sum of individuals D. major + Number of woodpecker cavities + surface roughness	138.8911	0.013661
14	Terr50 ~ 1 + Mean tree layer age +Number of standing dead wood (> DBH 20, h 8) + Sum of individuals D. major + Frequenzsumme.Meisen..Kleiber. + Number of woodpecker cavities + surface roughness	138.8969	0.013621
15	Terr50 ~ 1 + Mean tree layer age +Number of standing dead wood (> DBH 20, h 8) + Percent P. alba + Number of woodpecker cavities + surface roughness	138.9029	0.013581
16	Terr50 ~ 1 + Mean tree layer age +Number of standing dead wood (> DBH 20, h 8) + Percent P. alba + Insect GLMM residuals + Number of woodpecker cavities + surface roughness	138.9246	0.013434
17	Terr50 ~ 1 +Number of standing dead wood (> DBH 20, h 8) + Number of woodpecker cavities + surface roughness	138.9502	0.013263
18	Terr50 ~ 1 + Mean tree layer age +Number of standing dead wood (> DBH 20, h 8) + Number of woodpecker cavities + surface roughness	139.0028	0.012919
19	Terr50 ~ 1 + Mean tree layer age + Distance to water +Number of standing dead wood (> DBH 20, h 8) + Percent P. alba + Sum of individuals D. major + Number of woodpecker cavities + surface roughness	139.0073	0.01289
20	Terr50 ~ 1 + Mean tree layer age +Number of standing dead wood (> DBH 20, h 8) + as.numeric(as.character(ES.S1)) + Sum of individuals D. major + Number of woodpecker cavities + surface roughness	139.0214	0.012799
21	Terr50 ~ 1 + Mean tree layer age + Distance to open land +Number of standing dead wood (> DBH 20, h 8) + Sum of individuals D. major + Number of woodpecker cavities + surface roughness	139.0572	0.012572

APPENDIX 4: PHOTOS OF CENSUS POINTS

Photos were taken of 125 of 147 points. The photos were not standardized, however the red pole (=the point) or the red “T”-marking made by the forest holding on three trees around the red pole can be seen on the majority of pictures. In addition to the point ID, the territory establishment status is given.

Point_0 – Territories established until end of survey round 2

Point_1 - Territories established until end of survey round 2

Point_2 - Territories established until end of survey round 3

Point_3 - Territories established until end of survey round 3

Point_4 - Territories established until end of survey round 2

Point_5 - Territories established until end of survey round 2

Point_6 - Territories established until end of survey round 3

Point_7 - Territories established until end of survey round 3

Point_8 – no records

Point_9 – no records

Point_10 - Territories established until end of survey round 3

Point_11 – Records but no established territories

Point_12 - Territories established until end of survey round 3

Point_13 – no records

Point_14 - Territories established until end of survey round 3

Point_15 - Territories established until end of survey round 3

Point_22 –no records

Point_23 - records but no established territories

Point_24 - Territories established until end of survey round 3

Point_25 - Territories established until end of survey round 2

Point_26 - Territories established until end of survey round 3

Point_27 - Territories established until end of survey round 3

Point_28 - Territories established until end of survey round 4

Point_30 - Territories established until end of survey round 2

Point_31 - Territories established until end of survey round 5

Point_32 - Territories established until end of survey round 1

Point_34 - Territories established until end of survey round 4

Point_36 - Territories established until end of survey round 4

Point_37 - Territories established until end of survey round 3

Point_38 - Records but no established territories

Point_39 - Territories established until end of survey round 4

Point_40 - Territories established until end of survey round 3

Point_41- Records but no established territories

Point_42 - No records

Point_43 – Records but no established territories

Point_44 - Territories established until end of survey round 3

Point_45 – Records but no established territories

Point_46 – Records but no established territories

Point_47 - Territories established until end of survey round 3

Point_48 - Territories established until end of survey round 4

Point_49 - Territories established until end of survey round 3

Point_50 - Territories established until end of survey round 2

Point_51 – Records but no established territories

Point_52 - Territories established until end of survey round 2

Point_53 – No records

Point_54 - Territories established until end of survey round 2

Point_58 - Territories established until end of survey round 3

Point_59 - Territories established until end of survey round 3

Point_60 - Territories established until end of survey round 2

Point_61 – No records.

Point_62 – Records but no established territories

Point_63 - Territories established until end of survey round 2

Point_64 - Territories established until end of survey round 3

Point_65 – No records

Point_66 - Territories established until end of survey round 2

Point_67 – Records but no established territories

Point_68 - Territories established until end of survey round 2

Point_69 - Territories established until end of survey round 5

Point_71 – No records

Point_72 – No records.

Point_73 – No records

Point_75 - Territories established until end of survey round 3

Point_76 - Territories established until end of survey round 3

Point_77 - Territories established until end of survey round 3

Point_78 – Records but no established territories.

Point_79 - Territories established until end of survey round 3

Point_80 - Territories established until end of survey round 2

Point_81 – Records but no established territories

Point_82 – No records

Point_83 - Territories established until end of survey round 3

Point_84 – No records

Point_85 - Territories established until end of survey round 4

Point_87 - Territories established until end of survey round 3

Point_88 – Records but no established territories

Point_89 - Territories established until end of survey round 3

Point_90 – Records but no established territories

Point_91 – No records

. Point_92 – No recordS

Point_93 – Records but no established territories

Point_94 – No records

Point_95 - Territories established until end of survey round 2

Point_96 - Territories established until end of survey round 3

Point_97 – Records but no established territories

Point_98 - Territories established until end of survey round 4

Point_99 - Territories established until end of survey round 3

Point_100 - Territories established until end of survey round 3

Point_101 - Territories established until end of survey round 4

Point_103 - Territories established until end of survey round 3

Point_104 - Territories established until end of survey round 3

Point_106 – Records but no established territories

Point_107 – Records but no established territories

Point_108 – Records but no established territories

Point_109 – Records but no established territories

Point_110 - Territories established until end of survey round 4

Point_111 – No records

Point_112 – No records

Point_113 - Territories established until end of survey round 3

Point_114 - Territories established until end of survey round 2

Point_116 – Records but no established territories

Point_117 – No records

Point_119 - Territories established until end of survey round 2

Point_120 – Records but no established territories

Point_121 - Territories established until end of survey round 3

Point_122 – Records but no established territories

Point_123 - Territories established until end of survey round 3

Point_124 - Territories established until end of survey round 3

Point_125 - Territories established until end of survey round 4

Point_127 – No records

Point_128 – Records but no established territories

Point_129 – Records but no established territories

Point_130 – No records

Point_131 - Territories established until end of survey round 3

Point_132 – Records but no established territories

Point_133 - Territories established until end of survey round 2

Point_134 - Territories established until end of survey round 2

Point_136 - Territories established until end of survey round 3

Point_137 – Records but no established territories

Point_138 – Records but no established territories

Point_140 – No records

Point_141 - Territories established until end of survey round 2

Point_143 - Territories established until end of survey round 2

Point_144 – Records but no established territories

Point_145 - Territories established until end of survey round 2

Point_146 – No records

Point_147 – Records but no established territories