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„Population density and habitat preferences
in a Tawny Owl *Strix aluco* population in floodplain forests
in Eastern Austria“

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ABSTRACT

Owls are among the most secretive birds on Earth. Hence, few data about these species are available, especially from the highly dynamic and often inaccessible floodplain forest ecosystems. In this study we assessed population density and habitat preferences of Tawny Owls *Strix aluco* in lowland floodplain forests along Danube and Morava River in Eastern Austria. Owls were surveyed using playbacks. To avoid double counting we recorded their calls, which allow individual recognition of the majority of birds. Following 50 river kilometres and covering an area of more than 10,600 ha altogether, we recorded and identified 60 individual male Tawny Owls. The high territory densities (4.9–7.7 territories/km²) indicate a high habitat quality of floodplain forests for this species. While our habitat models indicate no significant difference of the occurrence probability of Tawny Owls between hardwood and softwood floodplain forests and no avoidance of Eagle Owl *Bubo bubo* territories, old trees (>80 years), a certain amount of openland and high amounts of standing deadwood did positively affect the species' occurrence. Our study provides evidence that the heterogeneous forest landscapes with patches of old forest stands characterized by a high density of dead trees, as found in the last remaining extensive floodplain landscapes along Danube and Morava River in Eastern Austria, represent high quality habitats for Tawny Owls.

Key words Vocal individuality, habitat model, Donau-March-Auen, Donau-Auen National Park, Petronell, WWF-Nature Reserve Marchauen, standing deadwood, age of forest stands, Eagle Owl *Bubo bubo*

“Aus der Sicht der Naturschutzplanung erhielten die Eulen einen praxisorientierten Stellenwert als Zeigerarten für vielfältige Lebensräume: Über ein langlebiges Vorkommen höhlenbrütender Kleineulen kann z.B. auf ein funktionsfähiges Zusammenwirken von naturnaher Waldstruktur, Altbäumen und Totholz, Insektenreichtum und Spechtbestand geschlossen werden.“

Mebs & Scherzinger 2008

ZUSAMMENFASSUNG

Die nächtliche Lebensweise vieler Eulenarten macht diese Vogelgruppe schwer erfassbar. Besonders in dynamischen Auwäldern, die von regelmäßigen Überschwemmungen geprägt werden und dadurch oftmals unzugänglich sind, erweisen sich Erhebungen als schwierig. In dieser Studie wurden Populationsdichten und Habitatpräferenzen des Waldkauzes *Strix aluco* in Tiefland-Auwäldern entlang der Donau und March in Österreich ermittelt. Die Gesangsaktivität wurde mithilfe von Klangattrappen stimuliert. Doppelzählungen konnten durch Audio-Aufzeichnungen der Reviergesänge weitgehend vermieden werden, denn Waldkäuse sind anhand ihrer Gesänge individuell unterscheidbar. Das Untersuchungsgebiet umfasst mehr als 10.600 ha und erstreckt sich 50 Flusskilometer entlang der Donau und March. Es konnten insgesamt 60 männliche Waldkauz-Individuen aufgenommen und identifiziert werden. Hohe Populationsdichten (4.9–7.7 Territorien/km²) deuten auf den hohen Stellenwert der Auwälder als Lebensraum für Waldkäuse hin. Unsere Habitatmodelle zeigen für die Wahrscheinlichkeit des Waldkauz-Vorkommens in Hartholz- und Weichholzaue keine signifikanten Unterschiede. Territorien des Uhu *Bubo bubo* wurden nicht gemieden. Alte Baumbestände (>80 Jahre), ein gewisser Anteil an Offenland und hohe Mengen an stehendem Totholz hingegen erhöhten die Wahrscheinlichkeit des Auftretens dieser Art. Unsere Studie beweist die hohe Habitatqualität heterogener Wälder mit alten Waldbeständen und hohem Totholzanteil, wie sie in den letzten größeren, noch zusammenhängenden Auwäldern Mitteleuropas entlang der Donau und March gefunden werden können.

INTRODUCTION

Due to their nocturnal activity and secretive lifestyle, many owl species are difficult to monitor (Terry et al. 2005). Hence population estimates of various owl species are fragmentary (Berg 1992, Mebs & Scherzinger 2008, Bauer et al. 2012, Mikkola 2013, Nationalpark O.ö. Kalkalpen Ges. m. b. H. 2014). For some bird species – especially for nocturnal species - their vocalizations turned out to be an effective and high-valued investigation-tool. Structural features of bird songs as phrase length, frequency rhythm and hoot harshness are individual distinctive and consistent over time (Galeotti 1998). Vocal individuality is proven for e.g. Tawny Owls *Strix aluco* (Appleby & Redpath 1997a, Galeotti 1998), Eagle Owls *Bubo bubo* (Lengagne 2001), European Scops Owls *Otus scops* (Galeotti & Sacchi 2001, Denac & Trilar 2006, Dragonetti 2007, Muraoka et al. 2009), Great Horned Owls *Bubo virginianus* (Mikkola 2013), African Wood Owls *Strix woodfordii* (Delpont et al. 2002), Pygmy Owls *Glaucidium passerinum* (Galeotti et al. 1993), Barred Owls *Strix varia* (Freeman 2000), Christmas Island Hawk Owls *Ninox natalis* (Hill & Lill 1998), Northern Spotted Owls *Strix occidentalis caurina* (Waldo 2002), Queen Charlotte Saw-whet Owl *Aegolius acadicus brooksi* (Holschuh 2004) and Seychelles Scops Owls *Otus insularis* (Terry et al. 2005). Besides for owls, individual recognition proved to be helpful in assessing populations of other nocturnal species such as Corncrakes *Crex crex* (Peake et al. 1998) and European Nightjars *Caprimulgus europaeus* (Rebbeck et al. 2001).

The Tawny Owl, the most common owl species in Austria (Berg 1992), has good preconditions for a successful individual recognition: Tawny Owls have stable territories (site fidelity) and are highly territorial (Hirons 1985, Galeotti 1990, Redpath 1995, Avotinš 2000, Sunde & Bølstad 2004). Furthermore they behave aggressively against other owl species (Bergmann et al. 2008). Vocalisations of males are honest signals, delivering quality traits (territory quality, male quality; Kappeler 2009), serving as boundary mark, female attraction, recognition trait (Appleby & Redpath 1997a, Galeotti 1998) and informing about sex and age (Mikkola 2013). Vocal expressions are very diverse (Melde 1995). Males and females hoot. Hoots of male Tawny Owls are composed of three notes, ranging from fluting to howling, whereas the female's hoot shows four notes and it is hoarser (Galeotti & Pavan 1993). The female's characteristic contact call (also made occasionally by the male) is a short "kewitt" or "kuitt", often in duet with its partner (Glutz von Blotzheim 1987, Bergmann et al. 2008, Bauer et al. 2012). Pairs are normally lifelong monogamous and defend their territory corporately (Wendland 1972). However, some males are bigamous (Hirons 1985, Galeotti 1998, Bauer et al. 2012).

Due to its low ecological specialization the Tawny Owl is a widespread, non-spec (E) species in Austria, counting 9,000–16,000 breeding pairs (BirdLife International 2004, Wichmann et al. 2009, Bauer et al. 2012). Depending on land coverage and habitat structure, the territory size of *S. aluco*

fluctuates (Hirons 1985). At low owl densities they hunt even outside their territory (Bauer et al. 2012). In the European temperate climate zone the diet composition of Tawny Owls varies between the warm and the cold season (Romanovski & Žmihorski 2009).

Floodplain ecosystems are represented by high hydrological dynamics, creating a broad spectrum of habitats. This dynamic has significant effects on the abundance of small mammals (Wijnhoven et al. 2005). The life rhythm of animals occurring in floodplains is determined by the alternation of flooding and dryer periods, thus such species have to cope with an extreme range of conditions. Due to alternating high and low water levels, floodplains are very dynamic ecosystems. The recurring flooding events generate a mosaic of habitats and provide constant natural fertilization resulting in high regional biodiversity and high ecosystem productivity, respectively. Related to their flooding regime, floodplain forests can be separated into different vegetation zones. The softwood floodplain forest, located close to the river, is flooded several times per year (up to 190 days). The hardwood floodplain zone is situated at slightly higher elevations and remains submerged under water for a maximum of 90 days per year (Colditz 1994).

In this study the population density and habitat use of the Tawny Owl was assessed for one of the last regions with large blocks of connected lowland riparian forests in Central Europe, the Danube and Morava river floodplains in Eastern Austria. For this unique ecosystem conservation measures are essential. Changes in the hydrologic balance, intense forest management measures, forest damage, immigration of neophytes and excessive game stocks threaten the balance and existence of floodplain ecosystems and its species richness (Lazowski 1999). Additionally their protection is an important step to maintain near-natural forests and their associated high biodiversity. Primeval/near-natural forests differ from commercial forests especially in respect to deadwood volume and the presence of ancient trees (Scherzinger 1996, Nationalpark O.ö. Kalkalpen Ges. m. b. H. 2014), simultaneously increasing the availability of prey and breeding sites for owls. Tawny Owls are often documented to breed in woodpecker cavities (Glutz von Blotzheim 1987, Carlson et al. 1998, Mebs & Scherzinger 2008, Bauer et al. 2012). In floodplain forests east of Vienna eight out of ten European woodpecker species can be found (Zuna-Kratky et al. 2000, Wichmann et al. 2009, Riemer 2009). In turn, habitat choice and population densities of Tawny Owls may be negatively affected by the Eurasian Eagle Owl *Bubo bubo*, which is recorded as frequent predator (Sergio et al. 2007).

Ultimately the balance of key factors as prey availability and the disposability of roosting- and breeding places is of great importance for a successful owl population (Wendland 1972, Petty 1989, Jędrzejewski et al. 1994, Redpath 1995, Salvati et al. 2002, Mebs & Scherzinger 2008, Bauer et al. 2012). Thereby the cavity-nesting and hence forest-dependent Tawny Owl is – despite its low

ecological specialization (Hirons 1985, Mebs & Scherzinger 2008) – a good indicator for habitat quality. Moreover the Tawny Owl is classified as flagship species for hardwood floodplain forests (Flade 1994).

The aim of this study was to assess population densities of the nocturnal species *S. aluco* in large floodplain forests along Danube and Morava River and to gain a more detailed insight into the species' habitat preferences in this ecosystem. Therefore, (1) vocal individuality of the Tawny Owl was used as tool to assess (2) population density in the Danube-Morava-floodplain forests. Further, habitat models were calculated to evaluate (3) the importance of landscape and forest structure as well as (4) the occurrence of a potential predator (Eagle Owl *B. bubo*) on the species' habitat use.

MATERIAL AND METHODS

Study site

The Donau-March-Auen cover 38,500 ha and are protected by the Ramsar Convention since 1983 (Lazowski 1997, Tiefenbach 1998). In 1996 an area of more than 9,300 ha along Danube River was declared as Donau-Auen National Park and accepted by the IUCN as national park category II one year later. Even much earlier (1977) the Untere Lobau was listed as biosphere reserve by the UNESCO and was declared as nature reserve in 1978 (Manzano 2000). In the same year the WWF-Nature Reserve Marchauen was declared as biggest conservation area of Lower Austria, outstanding with its unique biodiversity and near-natural forests (Wedenig 2000). The protected areas of the Donau-Auen National Park are characterised by summer floods, generating a high diversity of habitat types (Tiefenbach et al. 1998). The main part of the Donau-Auen National Park is covered by forest (62.6%). The remaining areas are covered by water bodies (19.0 %), meadows (6.1%), agricultural land (5.1%), dry grassland ("Heißländer") (2.1%), shrub land (1.7 %) and others (3.4%) (Manzano 2000). In the WWF-Nature Reserve Marchauen the forest coverage reaches 77.2 %. With an area of 160 ha, meadows represent 14.2% and 8.2 % is covered by water bodies (Wedenig 2000). Floodplain forests along Morava River are regularly inundated during spring (Zuna-Kratky et al. 2000).

Tawny Owls were surveyed in 10,937 ha lowland floodplain forest along the Danube River and Morava River in northeastern Austria. Surveyed floodplain forests along the Danube River comprise 9,908 ha. The main part of 9,338 ha belongs to the Donau-Auen National Park. Additionally, 570 ha are located in a non-protected forest along the Danube at Petronell-Carnuntum. Furthermore, Tawny Owl surveys were conducted in the WWF-Nature Reserve Marchauen (1,129 ha, exclusively

Nanni-Au) (Fig. 1). Due to a high traffic noise level (airport Vienna-Schwechat, motorway), an area of 334 ha (Mannswörth) was excluded for further analyses. Hence the study area covers 10,602.91 ha and ranges from Vienna (N 48°11'36.5" E 16°28'16.7") to the Slovakian border (N 48°11'36.5" E 16°28'16.7"), following approximately 36 river kilometres along Danube River with an average altitude of 145 m a.s.l. and 14 km along Morava River with an average altitude of 140 m a.s.l.

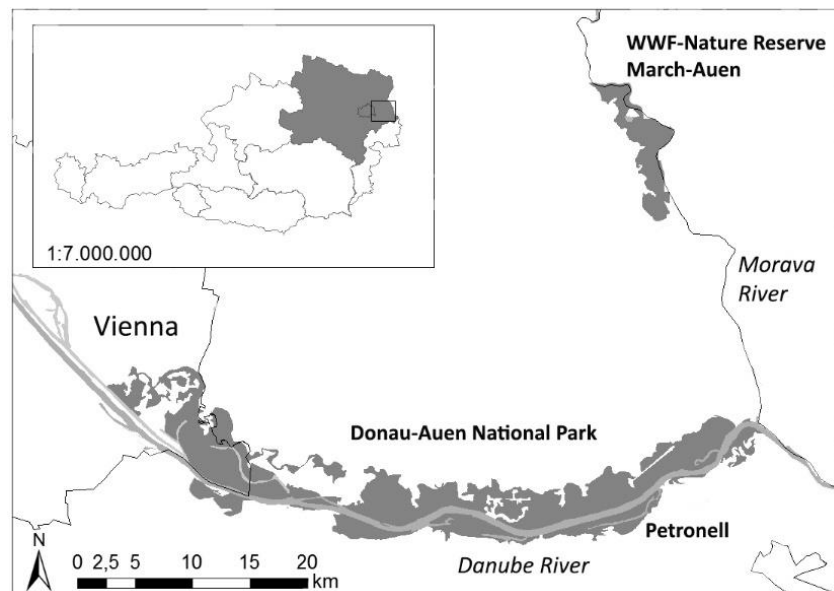


Fig. 1. Study areas along Danube and Morava River marked in dark grey. Source: Esri.

Tawny Owl survey

Tawny Owls show highest vocal activity for territory establishment and defence from March to May/June (spring mating season) and September to November/December (autumn mating season; Glutz von Blotzheim 1987, Galeotti 1998, Bauer et al. 2012). Hence, owl surveys were conducted between 1 March and 18 June 2012 covering the entire spring mating season. Owl territories were located using a playback method (Zuberogitia & Campos 1998) combined with a point-count methodology (Bibby et al. 1992, Gregory et al. 2004, Jedicke 2009). In total 203 census points were visited once (census time: 30 min, Redpath 1994). The census points were more or less equally distributed over the study area and, according to the estimated territory size and voice power of Tawny Owls, located at a minimum distance of 0.5 km between each other (Redpath 1994). Coordinates of census points and flooding regime are listed in Appendix Table I. Census points were visited during spring mating season between 18:15 pm and 3:15 am. Hootings of territorial Tawny Owls were stimulated by using a playback of a duet of an unfamiliar male and female Tawny Owl (record made by J.C. Roché; duration 1 min.; repeated 2-3 times; Altec Lansing Orbit iMT227

loudspeaker connected to MP-101 BD Schuss Home Electronic MP3-player). Additionally playbacks of two other owl species were used to assess their population status in the study area: the Eurasian Eagle Owl *Bubo bubo* and the Long-Eared Owl *Asio otus*. To avoid hushing of small owl species due to the predator-prey-relation, we used the playback sequence Tawny Owl – Long-Eared Owl – Eagle Owl.

Both sexes of the Tawny Owl have a wide range of vocal displays and pairs can imitate their partner. Songs are very diverse and variable, ranging from fluting to howling (Glutz von Blotzheim 1987). Further, the species shows a hooting dimorphism: while the male hoot is composed of three notes, the female hoot has four notes. Due to the hoarser voice of the females, the sexes can be distinguished in the field (Galeotti & Pavan 1993, Galeotti 1998). Calls of male Tawny Owls were recorded in good weather conditions (dry nights, low wind speeds) but at any lunar cycle (high and low luminosity) by using a Fostex Field Memory Recorder FR-2LE (FOSTEX CO., Musashino, Akishima-shi, Tokyo, Japan; sampling rate 48 kHz, 16 Bit dynamic range, stereo) connected to a Telinga Pro 7 parabolic microphone mounted on a flexible plastic parabolic reflector dish (diameter 57 cm).

Bioacoustical analysis

To reduce potential pseudoreplication due to double counting of individuals, high-quality records with a minimum distance of 1 m to a maximum distance of 50 m (average $\pm$ SD: 21.6 ± 14.7 m) between the recording equipment and the calling owl were selected and depicted as sonagram, using the Interactive Analysis Software RAVEN Pro 1.4 (The Cornell Lab of Ornithology, Interactive Sound Analysis Software, Ithaca). These records were used to identify individual owls using similar call parameters as described in Appleby & Redpath (1997) and Galeotti (1998). For each hoot eight temporal measures were taken: the duration of note 1 (D1), note 2 (D2), note 3 (D3), the frequency modulated part of D3 (FML), the vibrated part of D3 (Tail), the total duration of the hoot (D_{tot}), and the intervals between the notes D1 and D2 (I4) and between D2 and D3 (I5). Additionally, three frequency measures of D1 were taken: the highest (HF), the lowest (LF) and the center frequency (CF) (Fig. 2). All parameters were measured by a cursor and read off the screen (40 inches screen diagonal TV for high accuracy), whereas temporal parameters were taken from the oscillogramm and the sonagram, respectively, and frequency parameters from the sonagram. Measurements of two to nine hoots per male owl (mean: 3.2) were taken, using a sampling rate of 1203 samples/s (Hann window), 3 dB filter bandwidth (57.4 Hz), DFT size (frequency grid): 2048 samples, grid spacing (23.4 Hz), 50 percent overlap, hop size 602 samples).

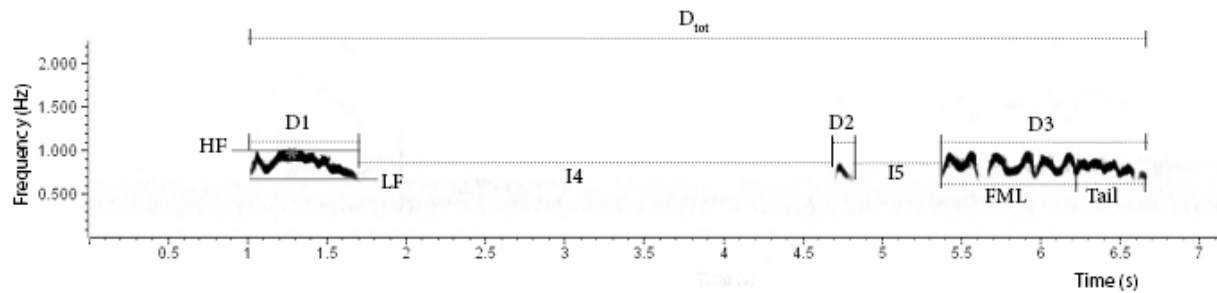


Fig. 2. Structure of the Tawny Owl hoot. Temporal and frequency measures are shown. D1, D2, D3: duration of the three notes; FML and Tail: third note splitted into modulated and vibrated part; Dtot: total duration of the hoot (Galeotti 1998); I4, I5: intervals between notes (Appleby & Redpath 1997); HF, LF: highest frequency and lowest frequency, respectively (Galeotti 1998); * = CF: center frequency of D1. Shown is a territorial hoot of a male individual (L2 “Murphy”; Lobau, 11 April 2012).

A discriminant function analysis was used to select hoot variables which prove to reliably separate between individual owls. Hence, only multiple recordings of calls, which certainly belonged to the same individuals, were considered. After data standardisation of the remaining hoot variables a principal component analysis (PCA) was calculated. Subsequently, the first two principal components (PC1 and PC2), which explained 55.44 % of the variance, were used for plotting all selected calls and to identify individuals. All analyses were performed and visualized with Statistica 7.1. (StatSoft Incorporation, Tulsa, Oklahoma, USA) and RAVEN Pro 1.4, respectively. Finally, based on these analyses, the population density of the Tawny Owl was assessed in the study area.

Habitat variables

For analyzing habitat preferences of the Tawny Owl in floodplain forests in Eastern Austria, only owl data from the part of Donau-Auen National Park located in Lower Austria were considered. Detailed forest maps covering the Donau-Auen National Park (DANP) were provided by the Austrian Federal Forests (ÖBf AG). Forest maps are based on forest stand data of 2011 and 2012. A detailed description of forest data ascertainment can be found in Posch et al. (1999).

To identify parameters important for the Tawny Owl’s territory choice, three habitat type categories (openland, softwood and hardwood floodplain forest), forest age, standing and lying deadwood classes and the occurrence of Eagle Owls were considered. Openland was defined as composed of meadows and crop fields. Hardwood and softwood floodplain forests were classified based on their dominant tree species (> 30%) (Appendix Table II). Three different categories of forest age were classified. The amount of standing and lying deadwood was quantified using four categories (Tab. 1). Furthermore, the presence of Eagle Owls was considered by measuring the

distance between the centres of each identified tawny owl territory and the nearest known Eagle Owl breeding site.

Tab. 1. Classification of deadwood amount and tree age in the Lower Austrian part of the DANP.

category	1	2	3	4
deadwood standing (THS)	no THS	single copies	groups in lines	extensive groups/ high expansion
deadwood lying (THL)	no THL	single copies	groups in lines	extensive groups/ high expansion
Tree age	1 to 40	41 to 80	>80	

We quantified the habitat composition for each assumed territory within a radius of 200 m (13 ha), determining the percentage of land coverage for the three habitat type categories, deadwood class and forest age class. Therefore we used the geographic information system ArcGIS 10.1 (Esri, New York, USA).

Statistical analyses

To identify important habitat parameters for the occurrence of Tawny Owls at census points, we calculated generalized linear models (GLMs) with binomial error distribution and logit-link function. For the evaluation of the best habitat models, finally six variables were included: HARDW, OPENL2, AGE>3, THS3-4, THL3-4 and DISTBUB (for definitions see Appendix Table III). GLMs were calculated for all variables and all possible subsets. Subsequently, models were ranked according to the Akaike's Information Criterion corrected for small sample bias (AICc), as measure for model fitness (Burnham and Anderson 2002). Best models show lowest AICc values. We considered models up to AICc differences (Δ_i) ≤ 2 as "best models".

For the model belonging to the group of best models and including the largest number of predictor variables, we plotted the relationships between predicted probability of Tawny Owl's occurrence and the respective habitat variables. All analyses were performed and illustrated in Statistica 7.1. (StatSoft Incorporation, Tulsa, Oklahoma, USA) and SPSS Statistics 20 (IBM SPSS Incorporation, New York, USA).

RESULTS

Tawny Owl hoot features

During 4 months of data sampling 203 census points were visited. In total 436 min of owl hooting records were gathered in spring time. Average distance between recording equipment and owl was 21 m.

Hoots of recorded male Tawny Owls lasted for 6.09 s (± 0.78 s; mean $\pm$ SD; $n = 127$). Note D1 lasted 0.87 s (± 0.12 s, $n = 147$), note D2 0.14 s (± 0.03 s, $n = 144$) and note D3 1.19 s (± 0.17 s, $n = 147$). The long interval I4 lasted 3.84 s (± 0.68 s, $n = 143$), the short interval I5 was terminated after 0.56 s (± 0.07 s, $n = 144$). The frequency modulated part of D3 (FML) lasted 0.53 s (± 0.13 s, $n = 130$), Tail 0.66 s (± 0.17 s, $n = 130$). Lowest (LF) and highest frequency (HF) measures were 618.21 Hz (± 67.98 Hz, $n = 145$) and 1012.52 (± 94.32 Hz, $n = 145$), respectively. CF was 883.28 Hz (± 67.98 Hz, $n = 146$).

Tawny Owls responded to the playback design on 60.0 % of the census points. About half of the recordings were of valuable quality for the calculation of a principal component analysis (PCA), on 27.5 % of census points with Tawny Owl records it was possible to acquire assignable high quality records.

Individual recognition and territory distribution

For the discrimination of different male owls, temporal and frequency measurements were taken of 149 hoots (mean = 2.9 hoots per male). To test for the reliability of hoot variables in differentiating between individual male owls, a total of 71 hoots of 22 males were used. The calculated discriminant function analysis indicated a high discriminatory power (Wilk's lambda < 0.0001, $p < 0.001$) for all selected hoot parameters, except the temporal parameters FML ($p = 0.4149$) and Tail ($p = 0.0997$). Hence, all variables except FML and Tail were considered in the subsequently calculated PCA.

The first two factors of the principal component analysis on 9 hoot variables explained 50.44 % of the total variance (Tab. 2). Factor 1 is characterized by high factor loadings of the three frequency variables LF, HF and CF. Factor 2 values are predominantly related to the temporal hoot variables I4, I5 and D_{tot} . The first two factors were used to plot individual calls and subsequently to identify individual male owls. In total 47 Tawny Owl males could be identified in the study area based on this method.

Tab. 2. Factor loadings (> 0.5) of a PCA on nine different hoot variables. Percentage variance explained by each of the first four factors is provided in brackets.

Variable	Factor 1 (30.36 %)	Factor 2 (20.08 %)	Factor 3 (16.38 %)	Factor 4 (11.67 %)
D1			0.534	
I4		0.799	-0.516	
D2			0.637	
I5		-0.550		0.597
D3				0.681
LF	-0.868			
HF	-0.726			
CF	-0.868			
D _{tot}		0.807		

Due to biotic (wind) and abiotic (plane, traffic noise, equipment noise) circumstances, distances greater than 50 m between owl and recording equipment and “fragmentary songs” (incomplete song strophes or unmeasurable parameters), 33.5 % of the records were excluded for PCA. Hence owls, which could not be distinguished by PCA, were identified by visual sonagram comparisons. Owl documentations without available sonagrams (10%) were matched to appropriate territories regarding field notes and behavioural context (Fig. 3–5).

For the DANP Lobau, eight males were separated by PCA, further five males were identified by visual sonagram comparison (Fig. 3). In the closed woodland around Orth/Donau, DANP Lower Austria, the PCA allowed a separation of nine male individuals (Fig. 4). In the WWF-Reserve March-Auen six males were separated by PCA (Fig. 5).

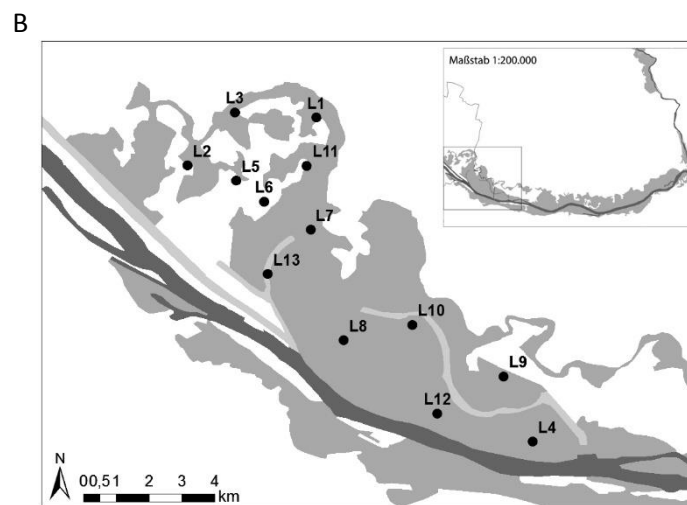
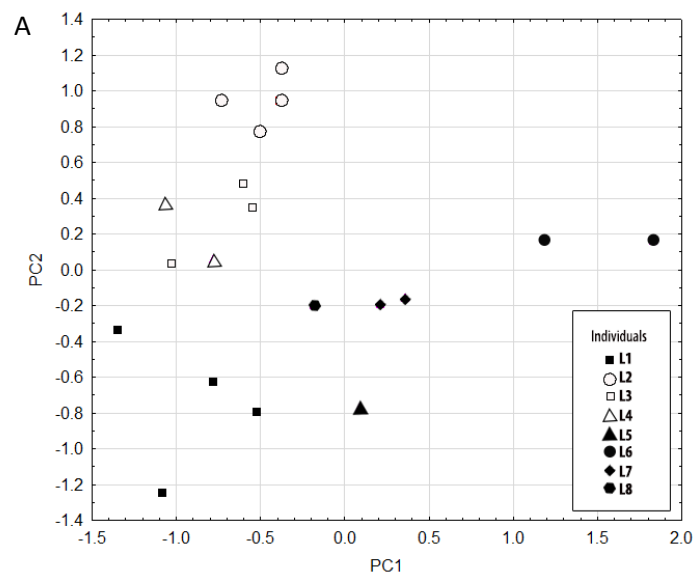


Fig. 3. (A) Principal component analysis based on two frequency and seven temporal variables of Tawny Owl hoots recorded at the Lobau, DANP. Hoots classified as belonging to the same individual are indicated by identical symbols. **(B)** Spatial distribution of the male individuals L1-L13.

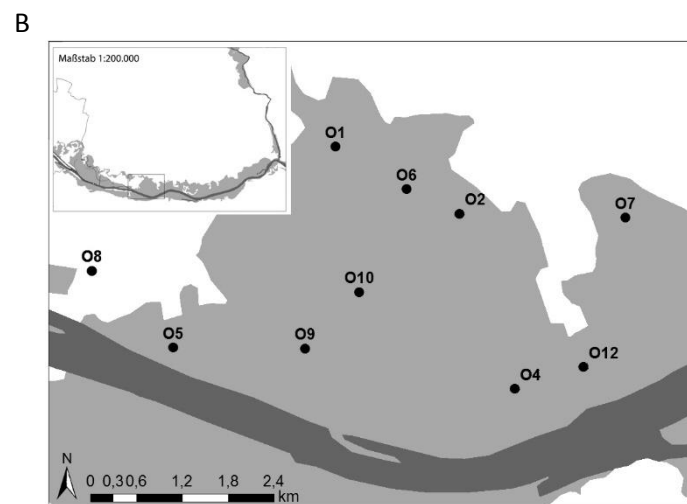
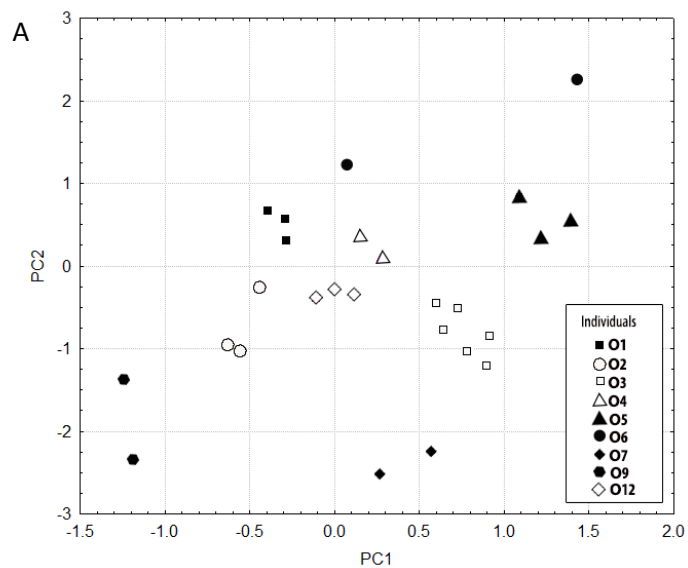


Fig. 4. (A) Principal component analysis based on two frequency and seven temporal variables of Tawny Owl hoots recorded at the Orth/Donau, DANP. Hoots classified as belonging to the same individual are indicated by identical symbols. **(B)** Spatial distribution of the male individuals O1-O12.

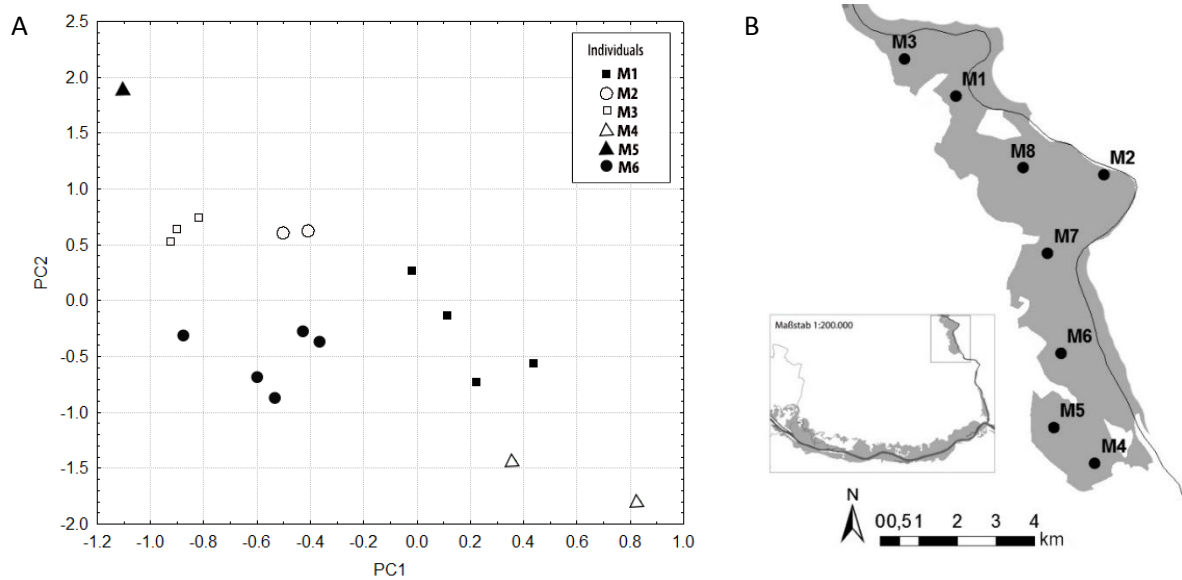


Fig. 5. (A) Principal component analysis based on two frequency and seven temporal variables of Tawny Owl hoots recorded at the WWF-Nature Reserve Marchauen. Hoots classified as belonging to the same individual are indicated by identical symbols. **(B)** Spatial distribution of the male individuals M1-M8.

Visual comparisons of hoots underline the PCA results. While in Fig. 6 comparisons of different males are shown, in Fig. 7 different sonograms of identical individuals (each recorded on two different census points) are presented. All recorded owls show distinctive hoots, which are stable over time. Especially interval I4 is adjustable, but in each individual varied constantly. Sonograms of all identified individuals can be found in Appendix Table IV.

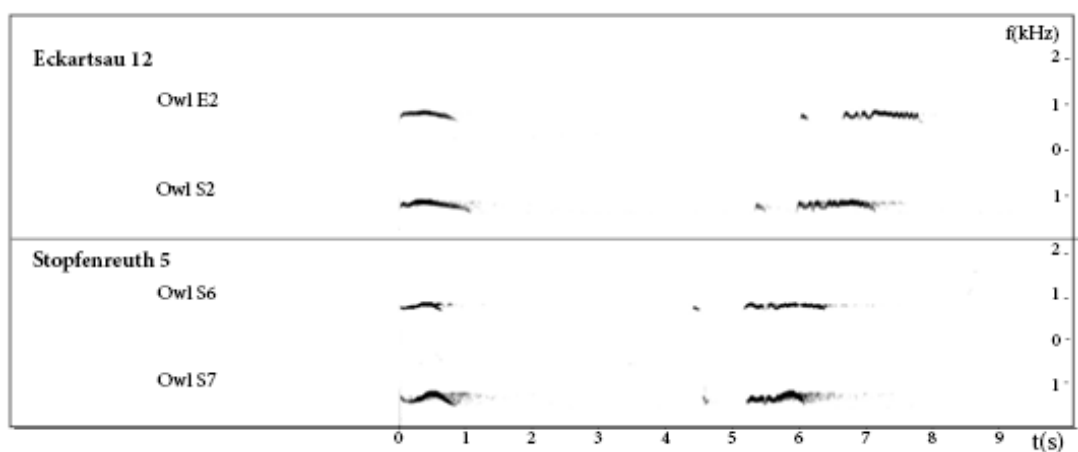


Fig. 6. Sonograms of different Tawny Owl individuals on the same census points. To highlight the patterns of the sonograms, only the base frequency is shown.

In total 12 males performed harsh hoots. Hoot harshness is particularly represented in the first note D1 (Fig. 7, e.g. Owl M6 at Marchauen 14; Owl O2 at Orth 7). Owl O2 showed harshness even in the third note D3 (Fig. 7, Orth 7).

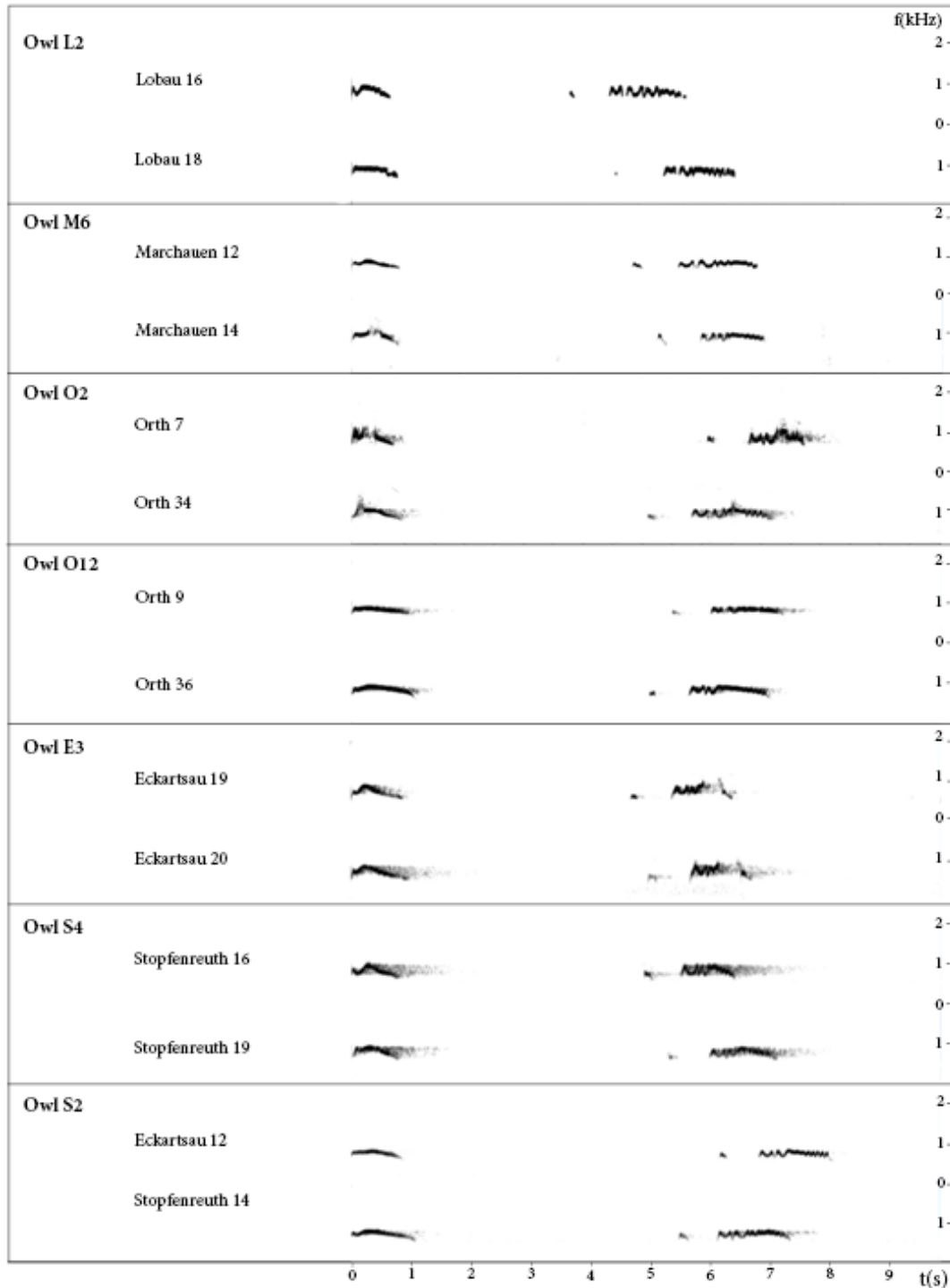


Fig. 7. Sonograms of identical Tawny Owl individuals on different census points. To highlight the sonogram patterns, only the base frequency is shown.

Population density

Based on the PCA and sonagram analyses, a total of 60 Tawny Owl territories were estimated for the entire study area, corresponding to a territory density of 0.57 territories/100 ha. Highest territory densities were found in the WWF Reserve Marchauen (0.78 territories/100 ha) and at Petronell (0.70 territories/100 ha). A slightly lower density of 0.50 territories/100 ha was recorded for the Lobau (Tab. 3).

Tab. 3. Population density (pd) of the Tawny Owl in the Donau-Auen National Park (DANP), the WWF-Nature Reserve Marchauen (excl. Nanniau) and Petronell.

location	size (ha)	Breeding pairs	pd/ 100 ha	pd/ 10 km ²
DANP*	9003.71	48	0.53	5.3
DANP Lobau*	2619.65	13	0.50	5.0
DANP Lower Austria	6384.00	35	0.55	5.5
Braunsberg		3		
Haslau		3		
Orth/Donau		10		
Eckartsau		11		
Stopfenreuth		8		
WWF Reserve Marchauen	1029.20	8	0.78	7.8
Petronell	570.00	4	0.70	7.0
Σ study area	10602.91	60	0.57	5.7

* exclusively Mannswörth

Habitat choice

All five best-ranked models include AGE>3, still three of them include THS 3-4 and two models OPENL2 (Tab. 4). The variables Eagle Owl territories (DISTBUB), percentage hardwood forest (HARDW) and lying deadwood (THL 3-4) did not occur as explanatory variables in the group of best models (Tab. 4), indicating that they had only a minor or no effect on the probability of tawny Owl occurrence.

Tab. 4. Results of GLMs evaluating effects of hardwood forest (%), openland (%; quadratic term), old (>80 years) forest (%), areas with high amount of standing and lying deadwood (%), respectively, and the distance to nearest Eagle Owl territories on the occurrence of Tawny Owl. Shown are **(A)** the best models ($\Delta_i \leq 2$) ranked according to their AICc values, included variables and **(B)** model parameters.

	1.	2.	3.	4.	5.
A model ranking					
Included variables	AGE>3	AGE>3	AGE>3	AGE>3	AGE>3
		THS 3-4	THS 3-4		THS 3-4
			OPENL2	OPENL2	
B model summary					
AICc	75.885	76.322	76.659	77.032	77.712
Δ_i	0.0000	0.4370	0.3370	0.3730	0.6800
AICc weight	0.1070	0.0860	0.0730	0.0600	0.0430
p	0.0387	0.0500	0.0482	0.0713	0.1002

The probability of Tawny Owl occurrence predicted by model 3 (compare Tab. 4) increased with forest stand age (> 80 years) (Fig. 8A), and increasing standing deadwood amount (Fig. 8B). The relationship between occurrence probability and the quadratic term of openland ratio represents an optimum model, indicating the importance of fragmented landscapes for this owl species (Fig. 8C).

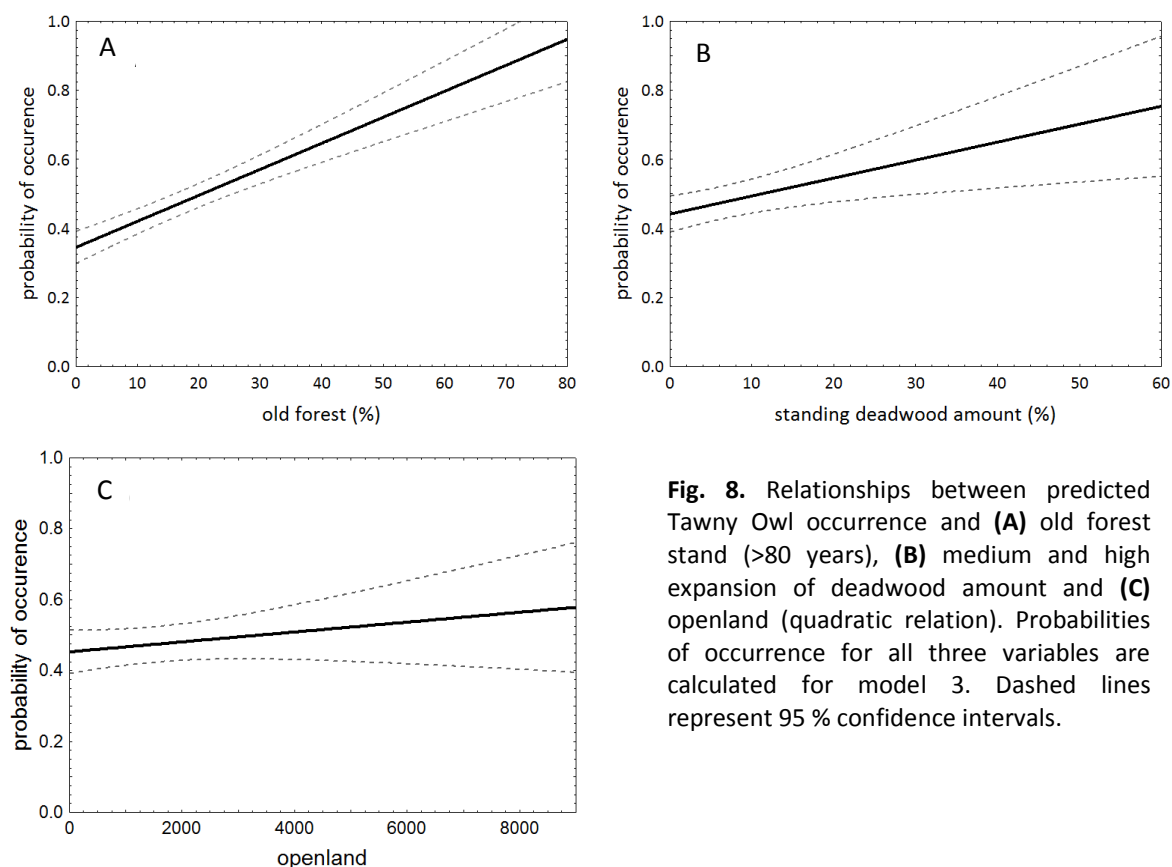


Fig. 8. Relationships between predicted Tawny Owl occurrence and **(A)** old forest stand (>80 years), **(B)** medium and high expansion of deadwood amount and **(C)** openland (quadratic relation). Probabilities of occurrence for all three variables are calculated for model 3. Dashed lines represent 95 % confidence intervals.

DISCUSSION

Hoot features and individual recognition

Floodplain forests along Danube and Morava River in Eastern Austria appear to be of great importance as breeding and hunting habitats for Tawny Owls. To assess the population density, vocal individuality proved to be a reliable tool (this study, Appleby & Redpath 1997a, Galeotti 1998). In the present study 47 males could be identified by the PCA, further thirteen males could be distinguished by behavioural traits, field notes and visual sonagram comparisons. Males and females of this nocturnal owl species show a great diversity of different song types (Glutz von Blotzheim 1987, Bergmann et al. 2008, Bauer et al. 2012). Further, the vocalisation rate and hoot features vary according to motivation (Galeotti 1998) and floater density (Sunde & Bølstad 2004). Nevertheless, hoot features of the owls were consistent over time and the inter-individual variation was higher than the individual variation of their hoots. Appleby & Redpath (1997a) reported of a correct classification of 98.6%, Galeotti & Pavan (1991) even of 99.1%.

In our study eight temporal and three frequency measures were chosen for individual discrimination. Nine of them showed a high discriminatory power, hence varying significantly

between owls but showed consistency in the hoots of each individual. For the frequency modulated part of the third note (FML) and the vibrated part of the third note (Tail) no significant differences could be found. This is a crucial difference to the findings of Galeotti (1998), where especially the modulated part (FML) was determinative. However, habitat structure influences hoot features: Tawny Owl's hoots in woodland sites differ significantly from those in farmland sites. In woodland FML did not prove to be decisive for individual separation (Appleby & Redpath 1997a). Ultimately all hoot features can be important for individual recognition (e.g. as already documented by Appleby and Redpath 1997a).

As for the majority of birds, the voice is important in communication between individual Tawny Owls – for pairs as well as for neighbours and strangers (Appleby & Redpath 1997a,b). It is decisive for territory establishment and successful defence (Sunde & Bølstad 2004). For the Tawny Owl an age of >22 years is documented for wild birds (Mikkola 2013). Due to a life-long pair bond (Mebs & Scherzinger 2008) and stable territories (Hirons 1985, Galeotti 1990, Redpath 1995, Avotinš 2000, Sunde & Bølstad 2004) it is assumed, that the female mate choice is supported by bioacoustical information, delivering honest signals (Appleby and Redpath 1997b, Galeotti 1998, Kappeler 2009). Structural features of the male's hoots reflect habitat quality and male parental ability (duration and frequency range of notes) and defence potential (hoot harshness, hooting rate and rhythm). However, males with better territory qualities are not consequently better defenders (Galeotti 1998).

The first note D1 and interval internote I4 showed a high variation within individuals, both associated with the male's motivation and determining the hoot rhythm (Galeotti 1998). Twelve males in our study area expressed harsh hoots. Hoot harshness does not directly reflect habitat quality, but probably the defence motivation: this song feature may reflect dominance and aggressiveness (Galeotti 1998).

For the present study a playback-design was chosen. Especially for large areas the playback method turned out to be very efficient for the census and monitoring of Tawny Owl populations (Zuberogoitia & Campos 1998). Tawny Owls respond with high probability (94%) within 30 min to the playback (established territories) (Redpath 1994). In our study owls responded to the playback on 60 % of census points. Despite the advantages of using the playback method, it has to be applied with caution. Attracting birds by using the calls of a potential territory intruder causes disturbance and increase their stress level. Defence against an (fictive) intruder costs energy and may increase the predation risk by exposing the approaching and vocally active bird to potential predators. However, the only relevant nocturnal predator of Tawny Owls in our study area may be the rare Eagle Owl. In addition, attracted Tawny Owls may distort territory distribution, if they follow the

fictive intruder or approach it outside their territory. But in Tawny Owls such potential negative effects may be only of minor importance, because it was shown that they are able to distinguish between neighbours and strangers (Galeotti & Pavan 1993, Sunde & Bølstad 2004). Their reaction to playbacks decreases after subsequent exposure due to recognition abilities (Galeotti & Pavan 1993).

Population density

To highlight how population density estimates can vary between surveys using vocal individuality to identify individual birds and surveys not applying this method, a comparison between the present study and population density estimates not considering information gained by analysing birds' vocal individuality (Nagl et al. 2013) are compared in Tab. 5. Without considering bioacoustic information, approximately every second male individual was double-counted. Population estimates appeared to be biased similarly for all parts of our study area (compare Tab. 5). Therefore the population density may be significantly lower than previously thought – but still high!

Tab. 5. Comparison of population densities (pd) determined by two different methods but in the same study area. In the present study double counts are reduced due to the use of bioacoustical information for identifying individual owls.

Location	Nagl et al. 2013		present study	
	Breeding pairs	pd/10 km ²	Breeding pairs	pd/10 km ²
DANP	83	11.2	48	5.3
DANP Lobau	22	10.0	13*	5.0*
DANP Lower Austria	61	9.0	35	5.5
WWF Reserve Marchauen	16	16.0	8	7.8
Petronell	9	15.0	4	7.0
study area	108	10.0	60	5.7

* exclusively Mannswörth

Depending on forest cover, average population densities of the Tawny Owl range from <0.2 to 2.75 breeding pairs/10 km² (Glutz von Blotzheim 1987), regional densities can reach 9.1 breeding

pairs/10 km² (Bauer et al. 2012). The Tawny Owl is historically documented as regular breeding bird in the region of the Donau-Auen National Park (Steiner 1961), but data about the actual population size and, hence, its population density is rare. For Petronell, Witzelsdorf and Stopfenreuth 17-64 breeding pairs were estimated in 1987 (Winding & Steiner 1988). In 1990 surveys in Eckartsau resulted in 2 breeding pairs/10 km² (Kollar & Seiter 1990). For floodplain forests along Morava River a density of up to 1 breeding pair/100 ha (=10 breeding pairs/10 km²) is documented (Zuna-Krakty et al. 2000). Comparable surveys in a suburban area in Vienna (Lainzer Tiergarten) resulted in 0.8-1.1 breeding pairs/km² (= 8-11 breeding pairs/10 km²) (Wichmann et al. 2009). For montane forests in the Kalkalpen National Park (Upper Austria) 0.3-1.4 territories/100 ha (= 3-14 breeding pairs/10 km²) were reported (Nationalpark O.ö. Kalkalpen Ges.m.b.H. 2014). In a long-term study in Germany, 10-12 breeding pairs/42 km² (= 2.4-2.9 breeding pairs/10 km²) were found (Melde 1995).

Habitat choice

Although Tawny Owl territories appeared to be more or less evenly distributed across our the study areas, the presence of forest stands older than 80 years, a high deadwood amount and a certain percentage of openland increased the likelihood of territory occurrence.

Old forest stand & standing deadwood amount

Forests of the Donau-Auen National Park are mainly between 20 and 60 years old (>74 %), only about 14 % of the trees are older than 80 years. Core areas of ancient trees are in Orth/Donau, Eckartsau and Stopfenreuth (Posch et al. 1999). Mature oaks, for example, are twofold beneficial: they are cavernous (Carlson et al. 1998) and during mast crop years they support prey productivity (Jędrzejewski et al. 1994). Furthermore forest age is a reliable basis of assessment for near-natural forests (Scherzinger 1996).

Standing deadwood amount varies between different parts of the DANP. Highest amounts of standing deadwood can be found at Stopfenreuth and Orth/Donau (Posch et al. 1999). Variations between regions may be linked to different management measures. High forests are richer in deadwood than coppices (Paletto et al. 2012). In managed forest sections these regions may be frequented more often by the Tawny Owl, which prefers densely structured forests with low understorey amount to better prey availability (Gstir 2012).

Old trees as well as standing dead wood represent valuable nesting sites for primary cavity nesters (e.g. woodpeckers) and secondary cavity nesters (Hagan & Grove 1999). Hole-breeding Tawny Owls do not build any nests. Hence, they depend on cavity-building species as woodpeckers. In

exceptional cases they breed in old raptor nests (Mebs & Scherzinger 2008). In the DANP Lower Austria five woodpecker species were investigated: Great Spotted Woodpecker *Dendrocopos major*, Lesser Spotted Woodpecker *D. minor*, Green Woodpecker *Picus viridis*, Middle Spotted Woodpecker *D. medius* and Black Woodpecker *Dryocopus martius* (Riemer et al. 2011). As Tawny Owls require large cavities (Carlson et al. 1998), *D. martius* is supposed to be most important as primary cavity nester for this owl species (Glutz von Blotzheim 1987). This woodpecker species uses hardwood and floodplain forest equally (Riemer et al. 2011).

Openland

Tawny Owls are dependent on forest cover and simultaneously the occurrence probability in our study increased with available patches of openland habitats. Redpath (1995) documented Tawny Owls in all surveyed woods >4 ha and suggested an optimum situation in intermediate-sized woods due to balanced energy costs for territory defence and food availability. A higher habitat diversity offers a broader food spectrum (Petty 1989). Hence, the combination of more than 60% wooded area, approximately 20 % water area inclusively reeds, sand banks and gravel banks, approximately 10% meadows and dry grassland and about 5% agricultural land makes the DANP to a heterogeneous and attractive habitat for the Tawny Owl.

Intraguild predation

Interspecific competition is discussed as key factor for habitat suitability. However, the occurrence of Eagle Owls in the investigated floodplain forests did not influence Tawny Owl's territory distribution, although it is recorded as predator (H. Frey, pers. comm., Tab. 6). The breeding effort of the Eagle Owl in the studied floodplain forests appears to be a recent development. While in 1961 and before the Eagle Owl was not recorded in the Donau-March-Auen (Steiner 1961), it has been recorded to breed in the DANP since 1995 (Zuna-Kratky 2000). Eleven years later already 6-7 calling males were found (Thoby 2006). In this study, five territories were recorded (apparently the same as in the previous work) along Danube River. Four of them are documented in Nagl et al. (2013), additionally one more was found at Orth/Donau (C. Nagl, pers. obs.). Currently, three Eagle Owl territories are known for the WWF Reserve March-Auen (M. Schindlauer, pers. comm.), including one pair breeding in the large heronry near Marchegg since 1999 (Zuna-Kratky 2000) until now (Nagl et al. 2013).

Tab. 6. Pellet analysis of the Eagle Owl *B. bubo* in Stopfenreuth (DANP Lower Austria) (H. Frey, pers. comm.).

prey	Amount	%
Birds		43.3
	Tawny Owl <i>Strix aluco</i>	1
	Long-eared Owl <i>Asio otus</i> (ad., juv.)	2
	Barn Owl <i>Tyto alba</i>	1
	Eagle Owl <i>Bubo bubo</i> (juv.)	1
	Common Kestrel <i>Falco tinnunculus</i>	1
	Rook <i>Corvus frugilegus</i>	1
	Ring-necked Pheasant <i>Phasianus colchicus</i>	1
	Common Quail <i>Coturnix coturnix</i>	1
	Feral Pigeon <i>Columba livia</i> f. Domestica	2
	Common Blackbird <i>Turdus merula</i>	1
	Blue Tit <i>Cyanistes caeruleus</i>	1
Mammals		36.6
Amphibians		16.6
Fish		3.3

Tawny Owls did not avoid the predator's territory in the study area. Is coexistence of intraguild prey with its predator possible? Sergio et al. (2007) illuminates this relationship. The key for the coexistence is flexibility: "As predicted, tawny owls were indifferent to predator distance in an area of low predation risk, they switched to distance-sensitive avoidance in an area of medium predator density and to habitat-mediated avoidance in an area of high predator density with few available refugia." During breeding season Eagle Owls are territorial and defend an area of 9-12 km², but during post-breeding season they hunt in a home range of a size up to 100 km² (Leditznig 1992, 1996). According to these findings, predation pressure in the study area seems to be lower than previously thought, since the likelihood of Tawny Owls occurrence was not affected by the distance to known Eagle Owl territories.

Floodplain forest type

Our habitat models did not indicate any preference of Tawny Owls for a certain floodplain forest type. The Tawny Owl is classified as flagship species for hardwood floodplain forests (Flade 1994). It can be assumed, that the prey availability is of main importance for the ubiquitary occurrence of the Tawny Owl. Pellet analyses of the region (collected in the Lobau) showed a preference for small mammals (59.94%) and amphibians (24.22%). Birds (8.07%), insects (5.90%) and fish (1.86%) were of minor importance (Steiner 1961). In deciduous forests the abundance of crop feeding mice is influenced by the tree mast (Kühn et al. 2011) and follows the synchronised masting rhythm of oaks, hornbeams and maples (Jędrzejewski et al. 1994). In 2012, the year when surveys were conducted, prey availability was presumably good due to mast crop in 2011. Moreover reed beds support rodent richness and densities (Scott et al. 2008). Surveys on White-footed Mice in Illinois (USA) showed similarities of the population structure (e.g. breeding season, adult survival and age structure) in floodplain forests and upland forests (Batzli 1977). In turn, periodical inundations influence the abundance of small mammals. Recolonization patterns are species-dependent and affected by frequency, duration and timing of floods (Wijnhoven et al. 2005). The present study supports, that there is no evidence that the flooding regime has negative effects on habitat suitability for the studied owl species. Further, in case of low mammal densities the generalist Tawny Owl is able to switch to another prey class. Gstir (2012) documents in the Biosphere Reserve Wiener Wald (Austria) for example birds as main prey (60%), followed by mammals (26.7%). It can be assumed, that also in European floodplain forests Tawny Owls breeding in softwood forest areas are capable of exploiting alternative prey after and during inundation events.

CONCLUSION

Riparian lowland forests represent a unique ecosystem. The high population densities of Tawny Owls recorded in this study suggest, that the floodplain forests along Danube and Morava River represent high quality habitats for the generalist Tawny Owl, as there are valuable amounts of old trees and standing deadwood volume. Furthermore the edge habitats appear to have a positive effect on the Tawny Owl's occurrence. Hence this generalist owl species shows preferences for characteristics of near-natural forests (Scherzinger 1996), interspersed with patches of openland.

Hardwood floodplain forests are rich in bird species and individuals. For Central European floodplain forests 15 flagship species are listed, including the Tawny Owl (Flade 1994). The Tawny Owl showed an ubiquitary distribution in the study area and our habitat models resulted in similar occurrence probabilities of Tawny Owls in hardwood and softwood floodplain forests. Hence we

recommend classifying the Tawny Owl as flagship species for the entire range of floodplain forests in Eastern Austria.

Decreasing forest management measures in protected floodplain forest areas, as implemented in the Donau-Auen National Park and the WWF-Nature Reserve Marchauen, are supposed to have long-term effects on cavity richness, deadwood amount, tree age and prey availability. Hence, these conservation aims most likely will further optimize Tawny Owl habitats.

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Appendix

Table I. Coordinates and flooding regime of the census points. F = flooded, NF = non-flooded, D = flood protection dam.

Region	census point	N(°)	E(°)	flooding regime
Orth/Donau	Orth1	48.1442	16.6808	NF
Orth/Donau	Orth2	48.1397	16.6719	NF
Orth/Donau	Orth3	48.1349	16.6649	D
Orth/Donau	Orth4	48.1339	16.6919	D
Orth/Donau	Orth5	48.1369	16.6839	F
Orth/Donau	Orth6	48.1408	16.6892	F
Orth/Donau	Orth7	48.1363	16.7057	NF
Orth/Donau	Orth8	48.1312	16.7074	F
Orth/Donau	Orth9	48.1285	16.7085	F
Orth/Donau	Orth10	48.1242	16.7094	F
Orth/Donau	Orth11	48.1473	16.6950	NF
Orth/Donau	Orth12	48.1411	16.6972	NF
Orth/Donau	Orth13	48.1339	16.6906	D
Orth/Donau	Orth14	48.1261	16.6969	F
Orth/Donau	Orth15	48.1283	16.6772	F
Orth/Donau	Orth16	48.1247	16.6710	F
Orth/Donau	Orth17	48.1284	16.6617	F
Orth/Donau	Orth18	48.1338	16.7309	D
Orth/Donau	Orth19	48.1334	16.7451	D
Orth/Donau	Orth20	48.1362	16.7343	NF
Orth/Donau	Orth21	48.1386	16.7149	NF
Orth/Donau	Orth22	48.1432	16.6998	NF

Orth/Donau	Orth23	48.1339	16.6953	D
Orth/Donau	Orth24	48.1387	16.7338	NF
Orth/Donau	Schönau1	48.1352	16.6522	D
Orth/Donau	Orth 25	48.1428	16.6748	NF
Orth/Donau	Orth 26	48.1396	16.6691	NF
Orth/Donau	Orth 27	48.1346	16.6711	D
Orth/Donau	Orth 28	48.1339	16.7037	D
Orth/Donau	Orth 29	48.1420	16.6901	NF
Orth/Donau	Orth 30	48.1365	16.6828	NF
Orth/Donau	Orth 31	48.1313	16.6805	F
Orth/Donau	Orth 32	48.1300	16.6738	F
Orth/Donau	Orth 33	48.1342	16.6875	D
Orth/Donau	Orth 34	48.1386	16.6951	NF
Orth/Donau	Orth 35	48.1403	16.7025	NF
Orth/Donau	Orth 36	48.1261	16.7107	F
Orth/Donau	Orth 37	48.1277	16.6648	F
Orth/Donau	Orth 39	48.1436	16.6915	NF
Orth/Donau	Orth 57	48.1443	16.6946	NF
Eckartsau	Eckartsau1	48.1339	16.7557	D
Eckartsau	Eckartsau2	48.1385	16.7571	NF
Eckartsau	Eckartsau3	48.1338	16.7824	D
Eckartsau	Eckartsau4	48.1338	16.7642	D
Eckartsau	Eckartsau5	48.1337	16.7943	D
Eckartsau	Eckartsau6	48.1339	16.7999	D
Eckartsau	Eckartsau7	48.1339	16.8114	D
Eckartsau	Eckartsau8	48.1344	16.8236	D
Eckartsau	Eckartsau9	48.1349	16.8308	D

Eckartsau	Eckartsau10	48.1400	16.8309	NF
Eckartsau	Eckartsau11	48.1408	16.8405	NF
Eckartsau	Eckartsau12	48.1368	16.8504	D
Eckartsau	Eckartsau13	48.1377	16.8574	D
Eckartsau	Eckartsau14	48.1396	16.7913	NF
Eckartsau	Eckartsau15	48.1400	16.7972	NF
Eckartsau	Eckartsau16	48.1435	16.7733	NF
Eckartsau	Eckartsau17	48.1373	16.7638	NF
Eckartsau	Eckartsau18	48.1258	16.7769	F
Eckartsau	Eckartsau19	48.1269	16.7953	F
Eckartsau	Eckartsau20	48.1287	16.8013	F
Eckartsau	Eckartsau21	48.1238	16.8203	F
Stopfenreuth	Stopfenreuth1	48.1356	16.8843	F
Stopfenreuth	Stopfenreuth2	48.1396	16.8799	F
Stopfenreuth	Stopfenreuth3	48.1458	16.8829	D
Stopfenreuth	Stopfenreuth4	48.1400	16.8613	NF
Stopfenreuth	Stopfenreuth5	48.1423	16.8743	D
Stopfenreuth	Stopfenreuth6	48.1440	16.8951	F
Stopfenreuth	Stopfenreuth7	48.1511	16.8930	F
Stopfenreuth	Stopfenreuth8	48.1502	16.9058	F
Stopfenreuth	Stopfenreuth9	48.1613	16.9104	D
Stopfenreuth	Stopfenreuth10	48.1677	16.9225	D
Stopfenreuth	Stopfenreuth11	48.1774	16.9400	D
Stopfenreuth	Stopfenreuth12	48.1695	16.9299	F
Stopfenreuth	Stopfenreuth13	48.1734	16.9450	F
Stopfenreuth	Stopfenreuth14	48.1508	16.8982	F
Stopfenreuth	Stopfenreuth15	48.1768	16.9450	F

Stopfenreuth	Stopfenreuth16	48.1615	16.9256	F
Stopfenreuth	Stopfenreuth17	48.1544	16.9269	F
Stopfenreuth	Stopfenreuth18	48.1626	16.9150	F
Stopfenreuth	Stopfenreuth19	48.1643	16.9213	F
Maria Ellend	MariaEllend1	48.1166	16.6871	F
Maria Ellend	MariaEllend2	48.1182	16.7059	F
Maria Ellend	MariaEllend3	48.1166	16.6731	F
Haslau	Haslau1	48.1166	16.7790	F
Haslau	Haslau2	48.1192	16.7706	F
Haslau	Haslau3	48.1233	16.7595	F
Haslau	Haslau4	48.1225	16.7445	F
Haslau	Haslau5	48.1220	16.7185	F
Haslau	Haslau6	48.1180	16.7384	F
Haslau	Haslau7	48.1181	16.7385	F
Haslau	Haslau8	48.1161	16.7403	F
Haslau	Haslau9	48.1185	16.7410	F
Haslau	Haslau10	48.1182	16.7311	F
Haslau	Haslau11	48.1269	16.7358	F
Haslau	Haslau12	48.1213	16.7669	F
Wildungsmauer	Wildungsmauer1	48.1218	16.8411	F
Wildungsmauer	Wildungsmauer2	48.1206	16.8346	F
Wildungsmauer	Wildungsmauer3	48.1164	16.8118	F
Petronell	Petronell1	48.1184	16.8453	F
Petronell	Petronell2	48.1156	16.8323	F
Petronell	Petronell3	48.1210	16.8646	F
Petronell	Petronell4	48.1190	16.8750	F
Petronell	Petronell5	48.1245	16.8757	F

Petronell	Petronell6	48.1370	16.8969	F
Petronell	Petronell7	48.1351	16.8918	F
Petronell	Petronell8	48.1284	16.8834	F
Petronell	Petronell9	48.1281	16.8740	F
Petronell	Petronell10	48.1259	16.8683	F
Petronell	Petronell11	48.1247	16.8779	F
Petronell	Petronell12	48.1221	16.8453	F
Petronell	Petronell13	48.1211	16.8828	F
Braunsberg	Braunsberg1	48.1611	16.9544	NF
Braunsberg	Braunsberg2	48.1628	16.9555	F
Braunsberg	Braunsberg3	48.1612	16.9556	NF
Braunsberg	Braunsberg4	48.1623	16.9593	F
Braunsberg	Braunsberg5	48.1567	16.9493	F
Braunsberg	Braunsberg6	48.1628	16.9555	F
Braunsberg	Braunsberg7	48.1653	16.9618	F
Braunsberg	Braunsberg8	48.1698	16.9627	F
Braunsberg	Braunsberg9	48.1708	16.9673	F
Braunsberg	Braunsberg10	48.1573	16.9522	NF
Hainburg	Hainburg1	48.1452	16.9183	NF
Hainburg	Hainburg2	48.1454	16.9215	NF
Hainburg	Hainburg3	48.1454	16.9325	NF
Lobau	Lobau1	48.1359	16.6308	D
Lobau	Lobau2	48.1364	16.6115	D
Lobau	Lobau3	48.1368	16.5993	D
Lobau	Lobau4	48.1374	16.5894	D
Lobau	Lobau5	48.1389	16.5789	D
Lobau	Lobau6	48.1426	16.5636	D

Lobau	Lobau7	48.1450	16.5770	F
Lobau	Lobau8	48.1529	16.5749	F
Lobau	Lobau9	48.1509	16.5859	D
Lobau	Lobau10	48.1472	16.5976	D
Lobau	Lobau11	48.1908	16.4753	NF
Lobau	Lobau12	48.1922	16.4844	NF
Lobau	Lobau13	48.1902	16.4867	NF
Lobau	Lobau14	48.1830	16.4882	NF
Lobau	Lobau15	48.1986	16.4910	NF
Lobau	Lobau16	48.1915	16.5022	NF
Lobau	Lobau17	48.1874	16.5021	NF
Lobau	Lobau18	48.1837	16.4978	NF
Lobau	Lobau19	48.1976	16.5132	NF
Lobau	Lobau20	48.2001	16.5306	NF
Lobau	Lobau21	48.1868	16.5157	NF
Lobau	Lobau22	48.1891	16.5192	NF
Lobau	Lobau23	48.1895	16.5331	NF
Lobau	Lobau24	48.1954	16.5388	NF
Lobau	Lobau25	48.1808	16.5082	NF
Lobau	Lobau26	48.1813	16.5212	NF
Lobau	Lobau27	48.1772	16.5316	NF
Lobau	Lobau28	48.1848	16.5353	NF
Lobau	Lobau29	48.1463	16.5509	D
Lobau	Lobau30	48.1506	16.5409	D
Lobau	Lobau31	48.1556	16.5309	D
Lobau	Lobau32	48.1619	16.5250	D
Lobau	Lobau33	48.1682	16.5170	D

Lobau	Lobau34	48.1407	16.5711	D
Lobau	Lobau35	48.1474	16.5771	F
Lobau	Lobau36	48.1565	16.5727	F
Lobau	Lobau37	48.1626	16.5620	F
Lobau	Lobau38	48.1728	16.5380	F
Lobau	Lobau39	48.1615	16.5454	F
Lobau	Lobau40	48.1573	16.5586	F
Lobau	Lobau41	48.1500	16.5656	F
Mannswörth	Mannswörth1	48.1388	16.5463	NF
Mannswörth	Mannswörth2	48.1408	16.5378	NF
Mannswörth	Mannswörth3	48.1352	16.5463	NF
Mannswörth	Mannswörth4	48.1366	16.5581	NF
Mannswörth	Mannswörth5	48.1325	16.5767	NF
Mannswörth	Mannswörth6	48.1309	16.5643	NF
Marchauen	Marchauen1	48.3279	16.8998	F
Marchauen	Marchauen2	48.3307	16.8887	F
Marchauen	Marchauen3	48.3351	16.8718	F
Marchauen	Marchauen4	48.3449	16.8561	F
Marchauen	Marchauen5	48.3410	16.8606	F
Marchauen	Marchauen6	48.3429	16.8689	F
Marchauen	Marchauen7	48.3280	16.8839	F
Marchauen	Marchauen8	48.3185	16.8857	F
Marchauen	Marchauen9	48.3257	16.9067	F
Marchauen	Marchauen10	48.3212	16.8953	F
Marchauen	Marchauen11	48.3135	16.8906	F
Marchauen	Marchauen12	48.3061	16.8876	F
Marchauen	Marchauen13	48.3026	16.8968	F

Marchauen	Marchauen14	48.2961	16.8962	F
Marchauen	Marchauen15	48.2883	16.8951	F
Marchauen	Marchauen16	48.2831	16.9044	F
Marchauen	Marchauen17	48.2793	16.8976	F
Marchauen	Marchauen18	48.2861	16.8862	F

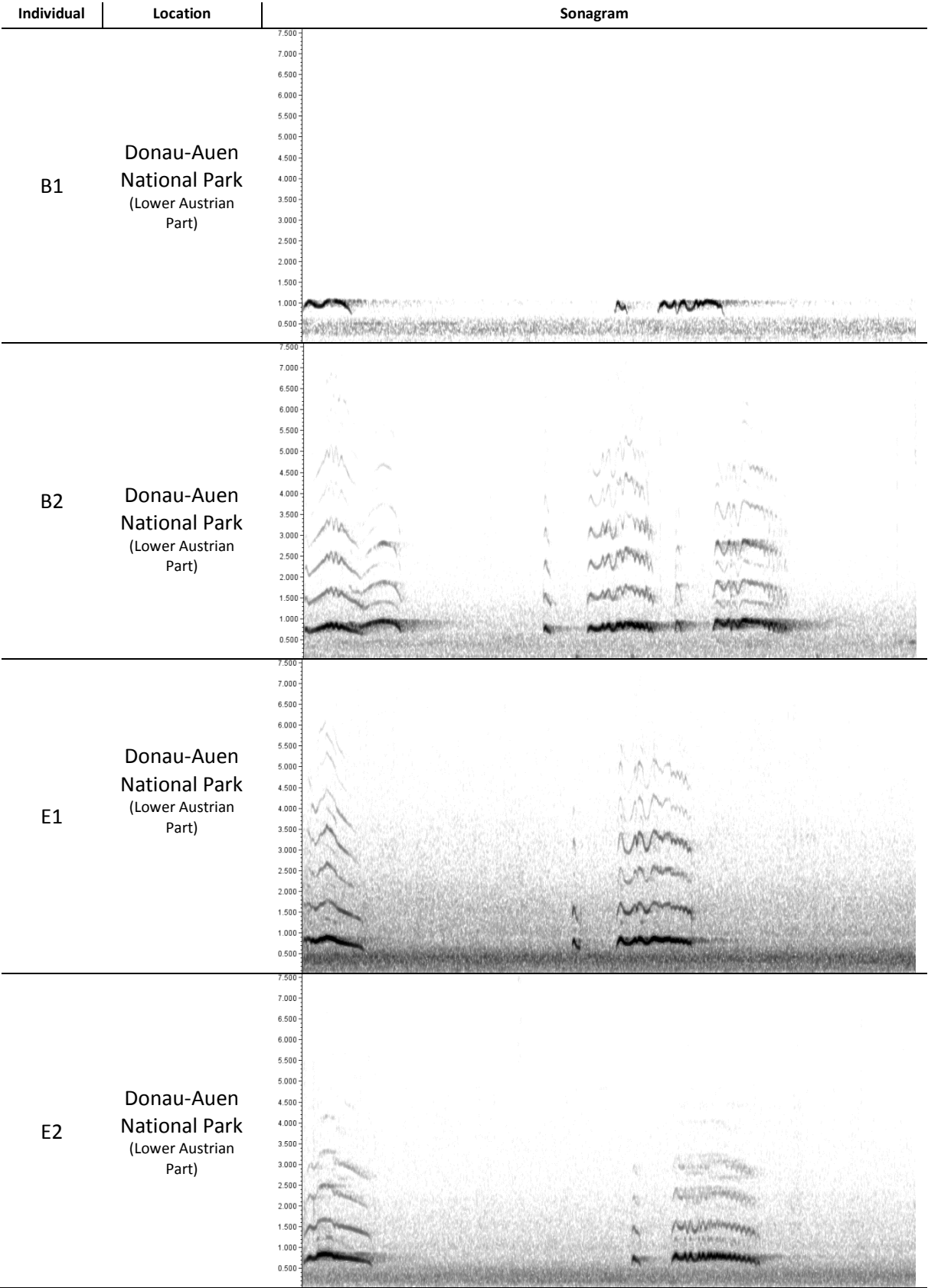
Table II. Classification of hardwood and softwood floodplain forest in the DANP Lower Austria based on dominant tree species.

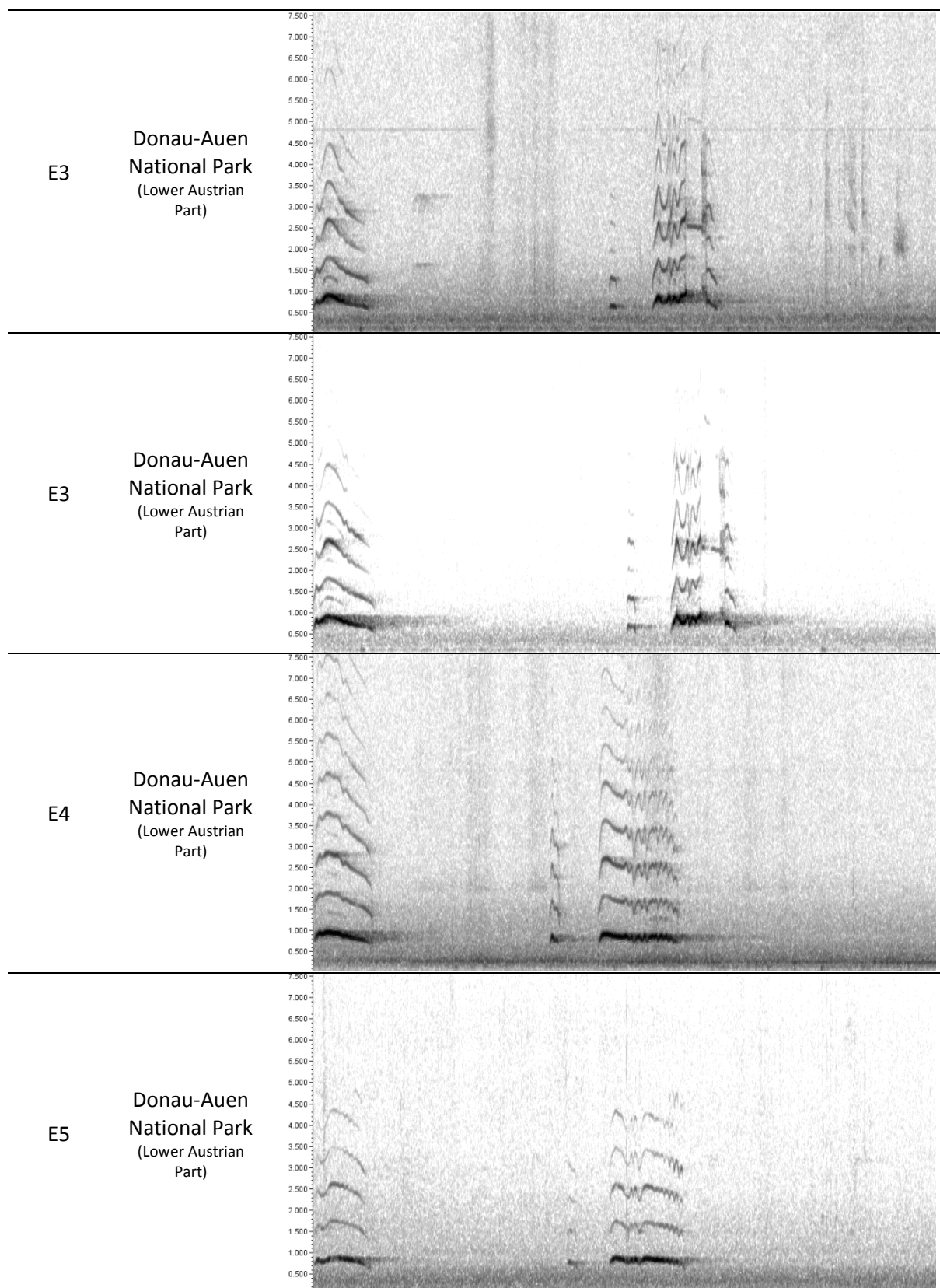
Trivial name (English)	Species name (latin)	Floodplain forest type
Hybrid Poplar	<i>Populus canadensis</i>	softwood floodplain forest
White Poplar	<i>Populus alba</i>	softwood floodplain forest
Willow	<i>Salix</i> sp.	softwood floodplain forest
Grey Alder	<i>Alnus incana</i>	softwood floodplain forest
Acer	<i>Acer</i> sp.	hardwood floodplain forest
European Hornbeam	<i>Carpinus betulus</i>	hardwood floodplain forest
Ash	<i>Fraxinus</i> sp.	hardwood floodplain forest
Black Walnut	<i>Juglans nigra</i>	hardwood floodplain forest
Walnut	<i>Juglans regia</i>	hardwood floodplain forest
European Black Pine	<i>Pinus nigra</i>	hardwood floodplain forest
Oak	<i>Quercus</i> sp.	hardwood floodplain forest
Shrub		hardwood floodplain forest

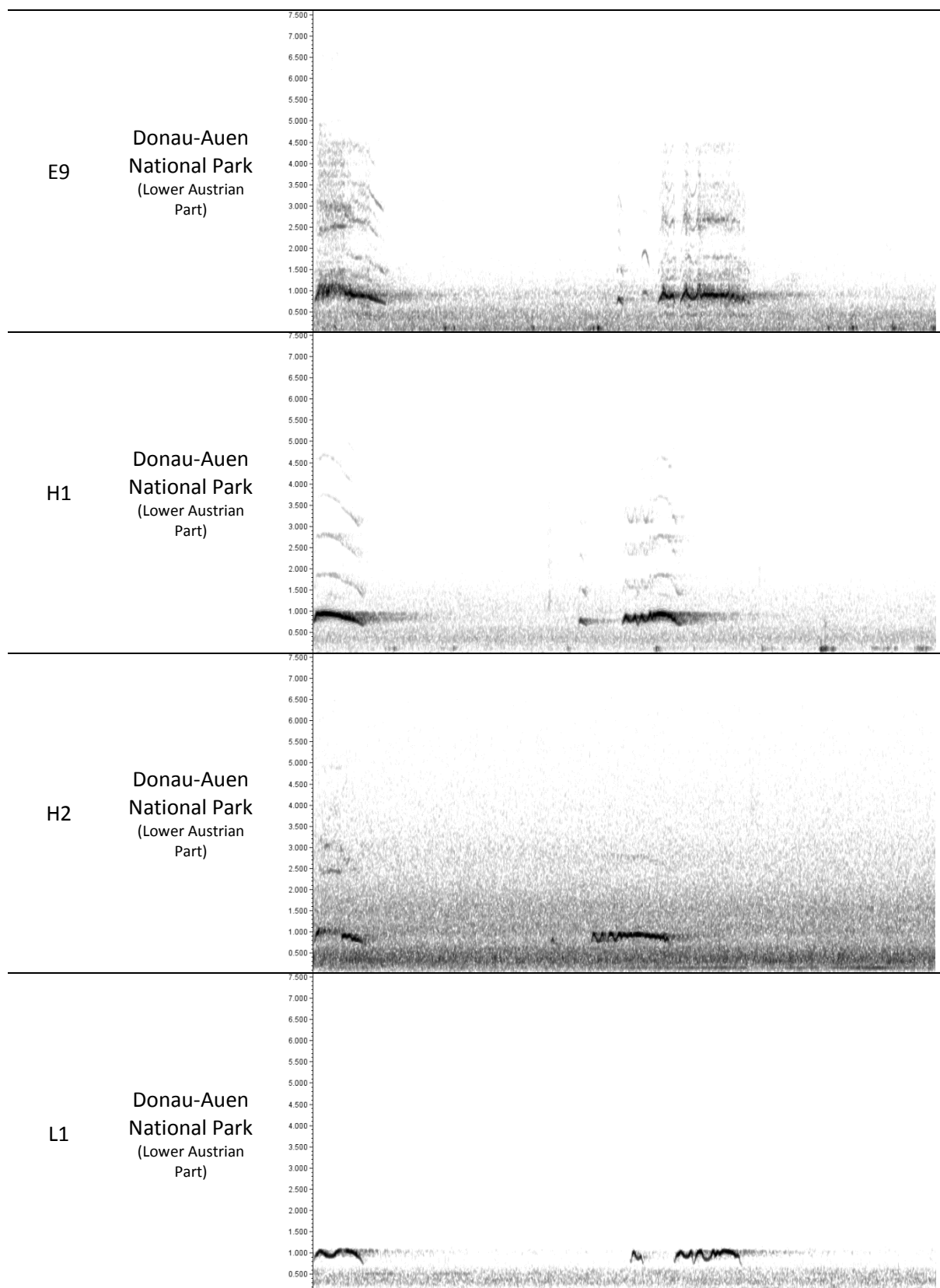
Table III. Habitat variables used for evaluating habitat use of Tawny Owls in floodplain forests in Eastern Austria. Variables included in the best GLMs are printed in bold.

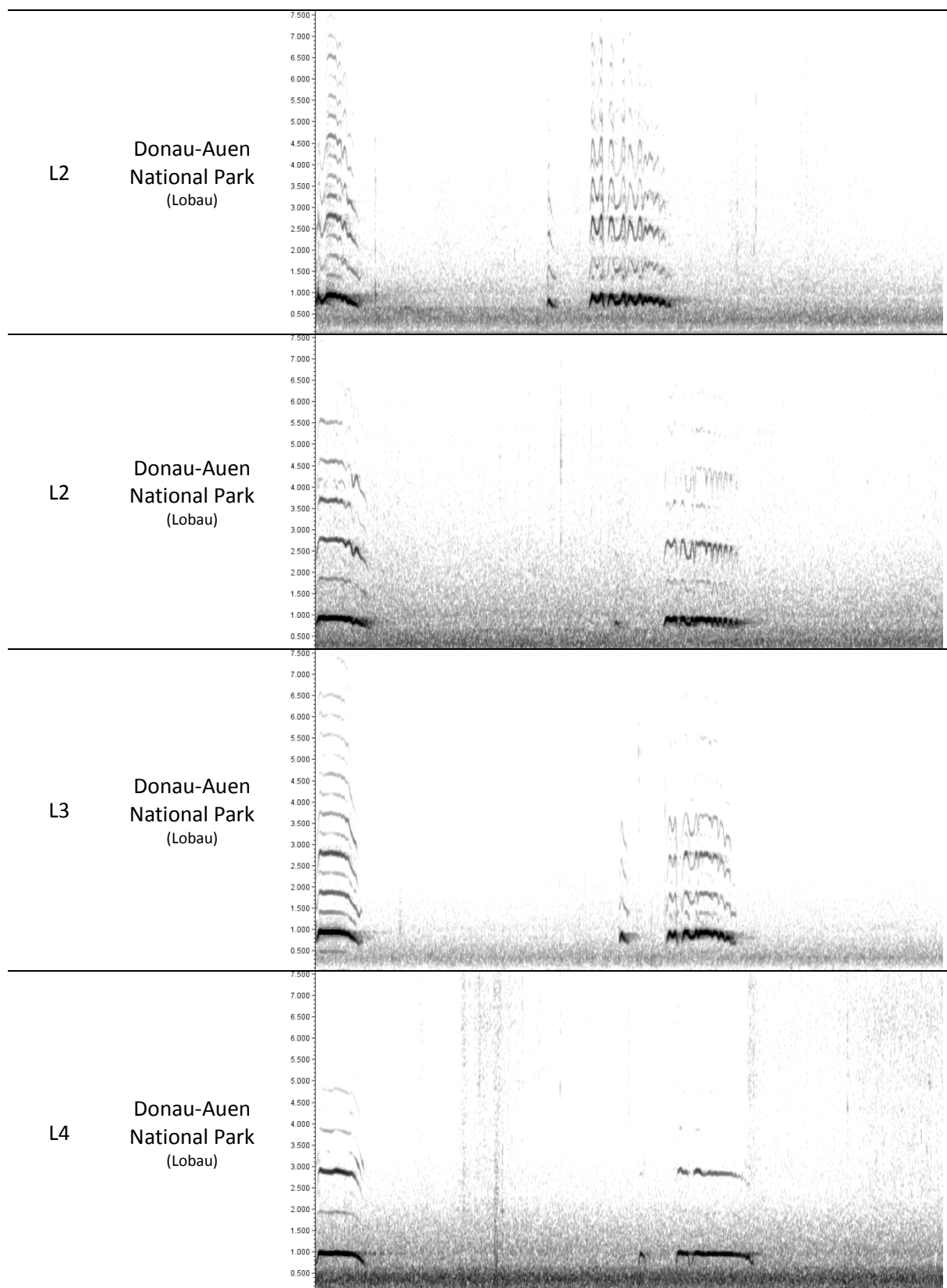
Variable	Shortcut	Definition	Source
Hardwood floodplain forest	HARDW	% hardwood floodplain forest	GIS ÖBf
Openland ²	OPENL2	Area of meadows & crop fields (excl. water bodies), quadratic term	GIS ÖBf
Forest age >3	AGE>3	Tree age > 80	GIS ÖBf
THL_3-4	THL 3-4	Medium to high lying deadwood amount (groups in lines to high expansion)	GIS ÖBf
THS_3-4	THS 3-4	Medium to high standing deadwood amount (groups in lines to high expansion)	GIS ÖBf
Distance_Bubo bubo	DISTBUB	Distance of census point or Tawny Owl territory center to next Eagle Owl territory, square rooted term	Calculated in ArcGIS

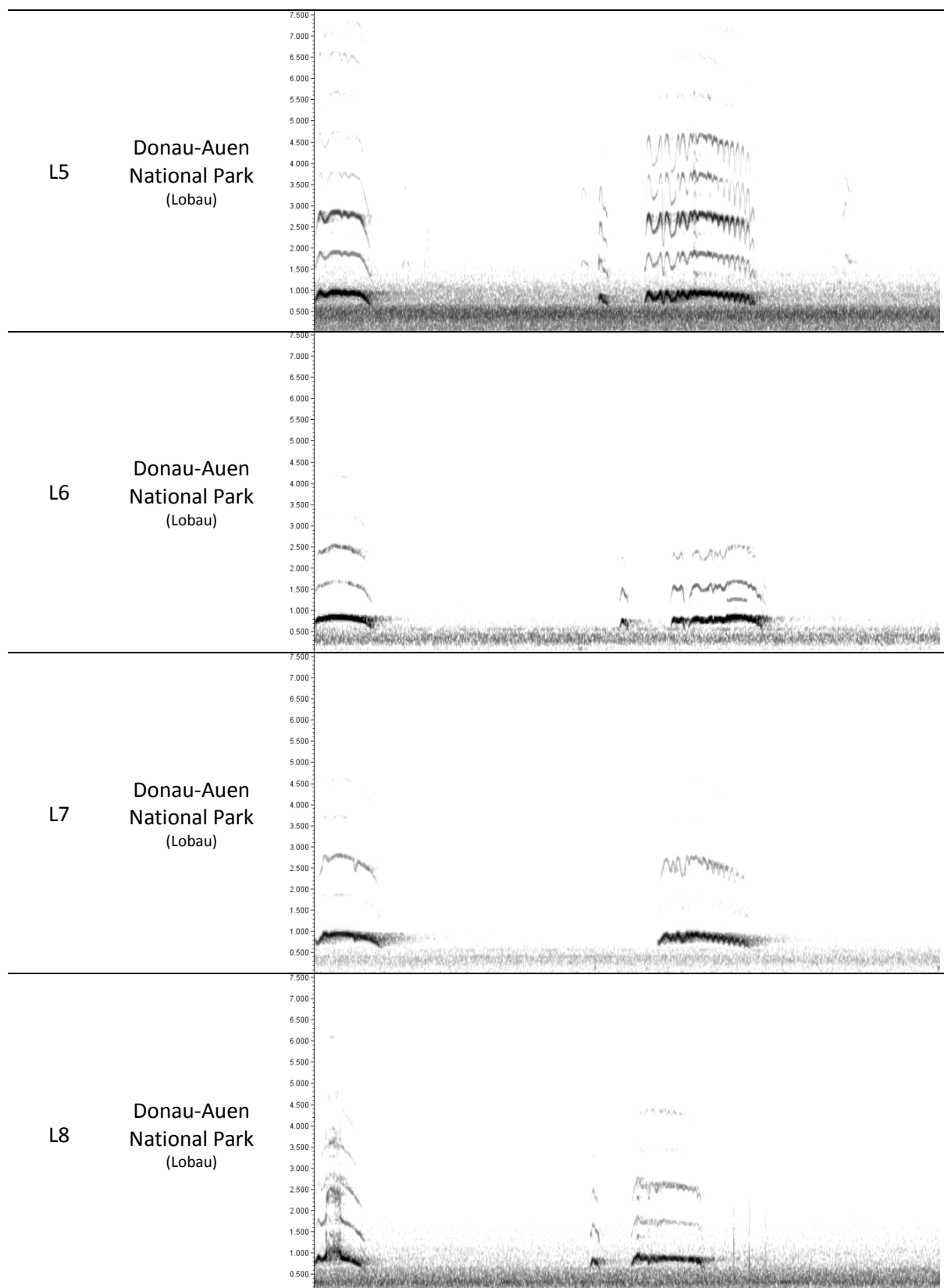
Table IV. Sonograms of all individuals used for PCA. Individuals are listed in alphabetic order.
Horizontal axis: time (10 s), vertical axis: frequency (Hz).

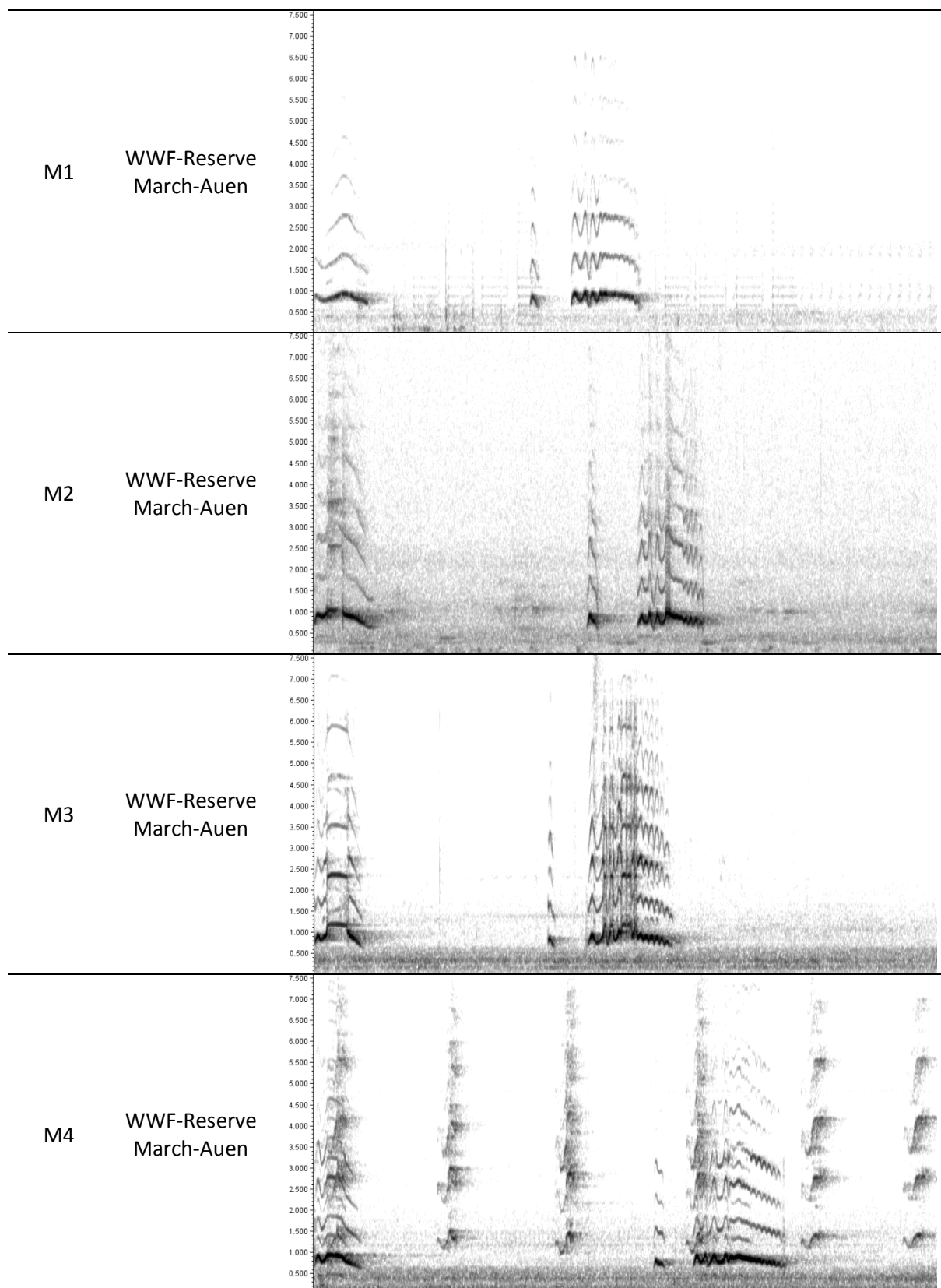


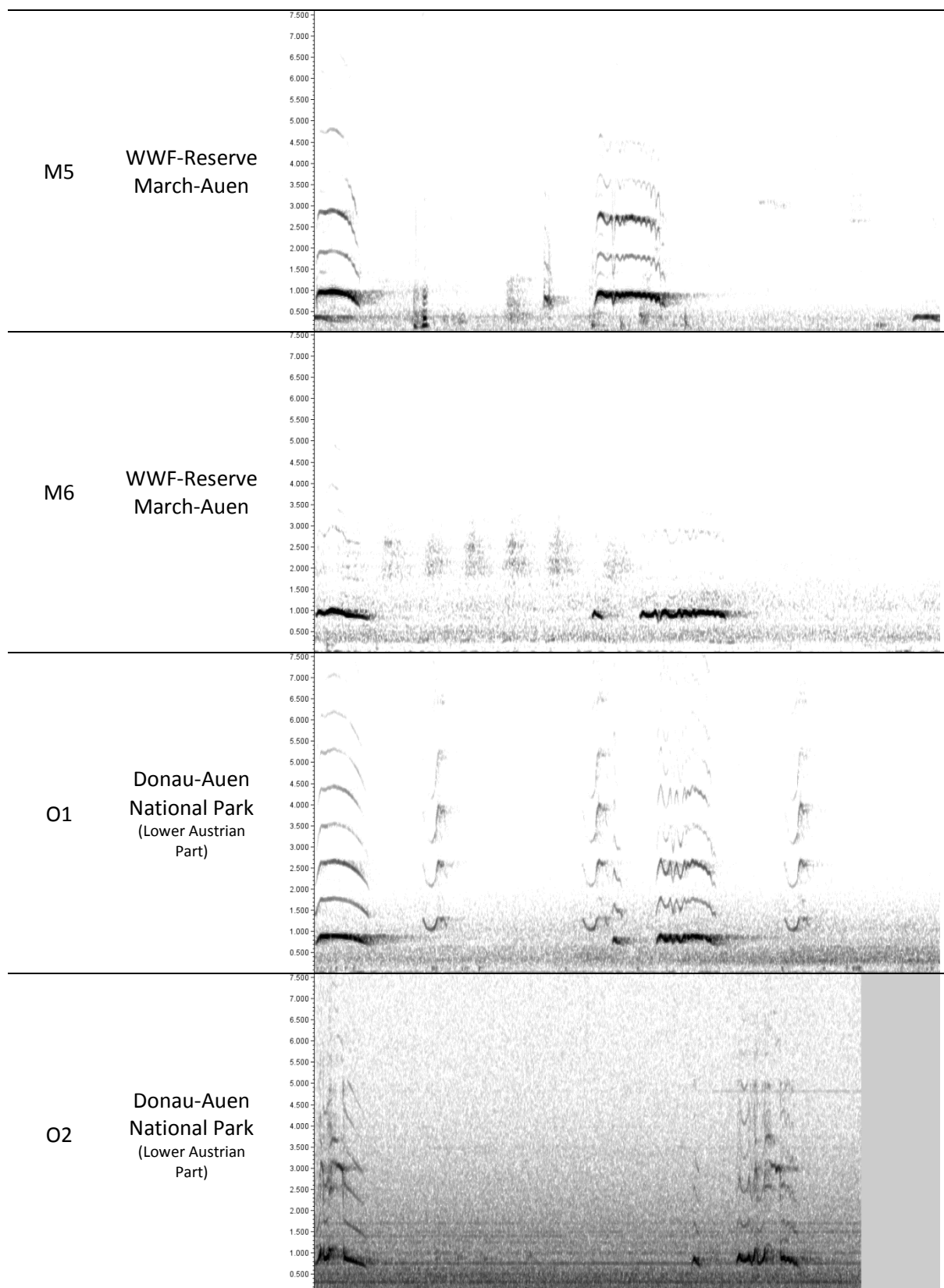


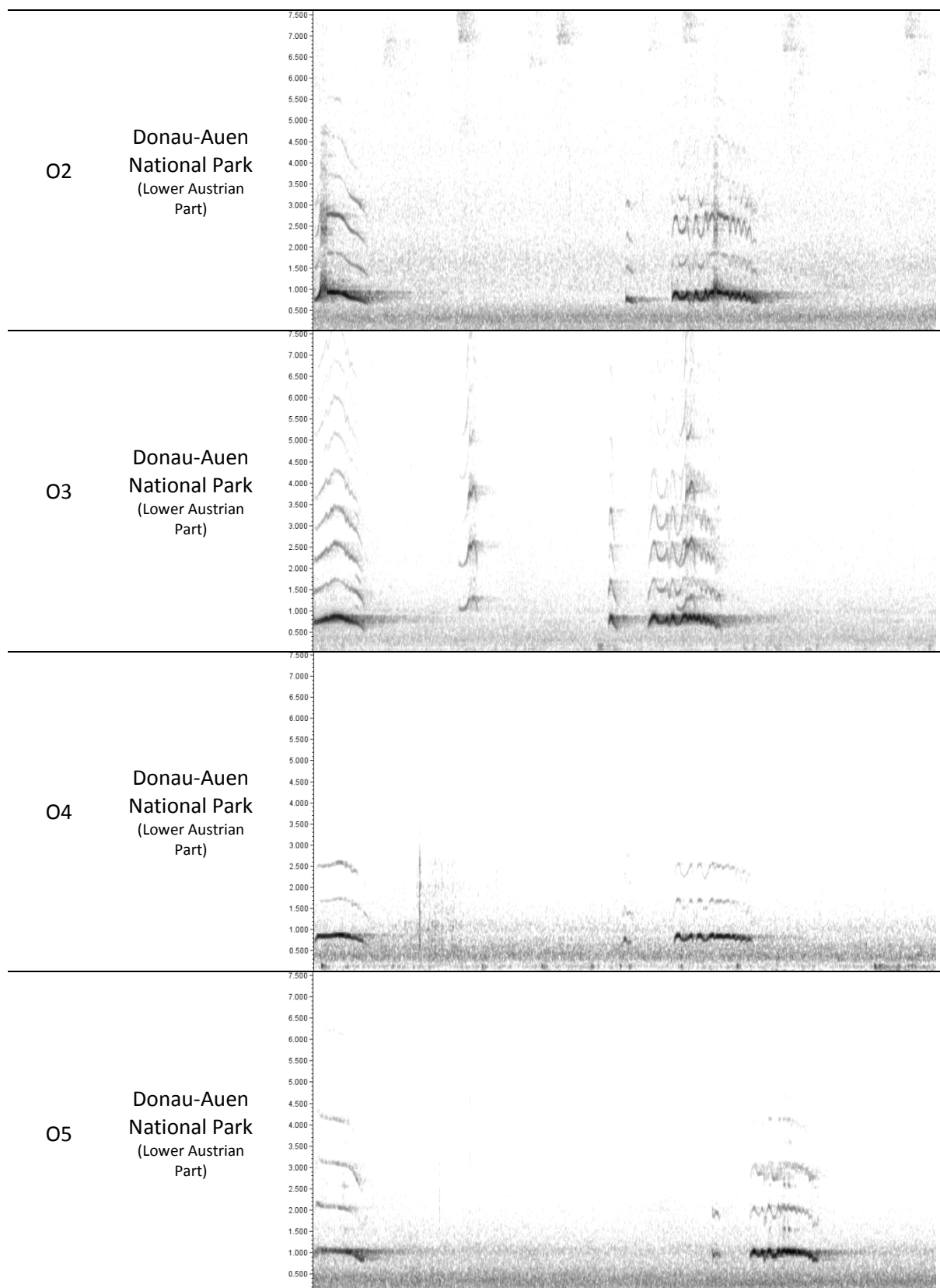


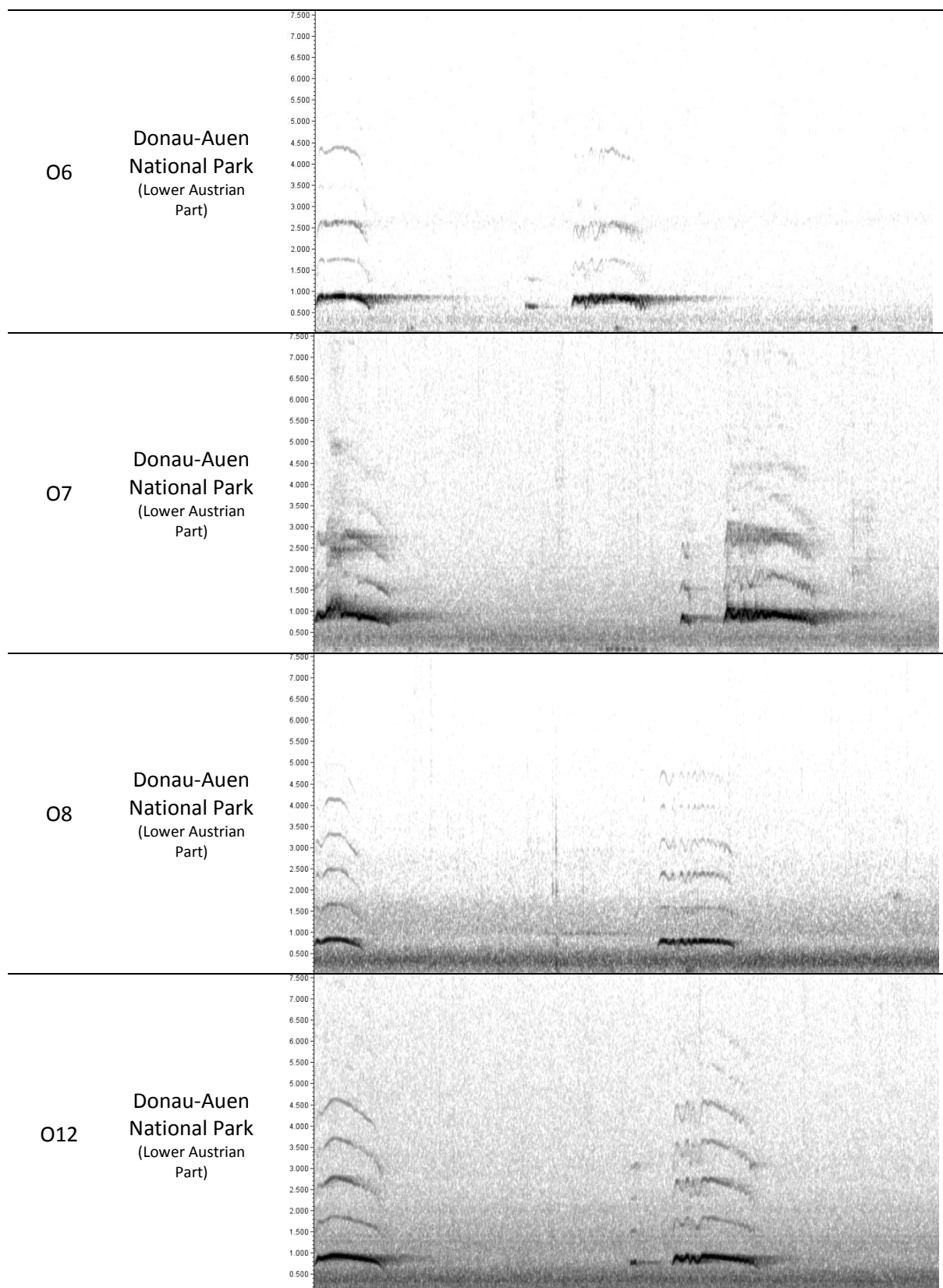


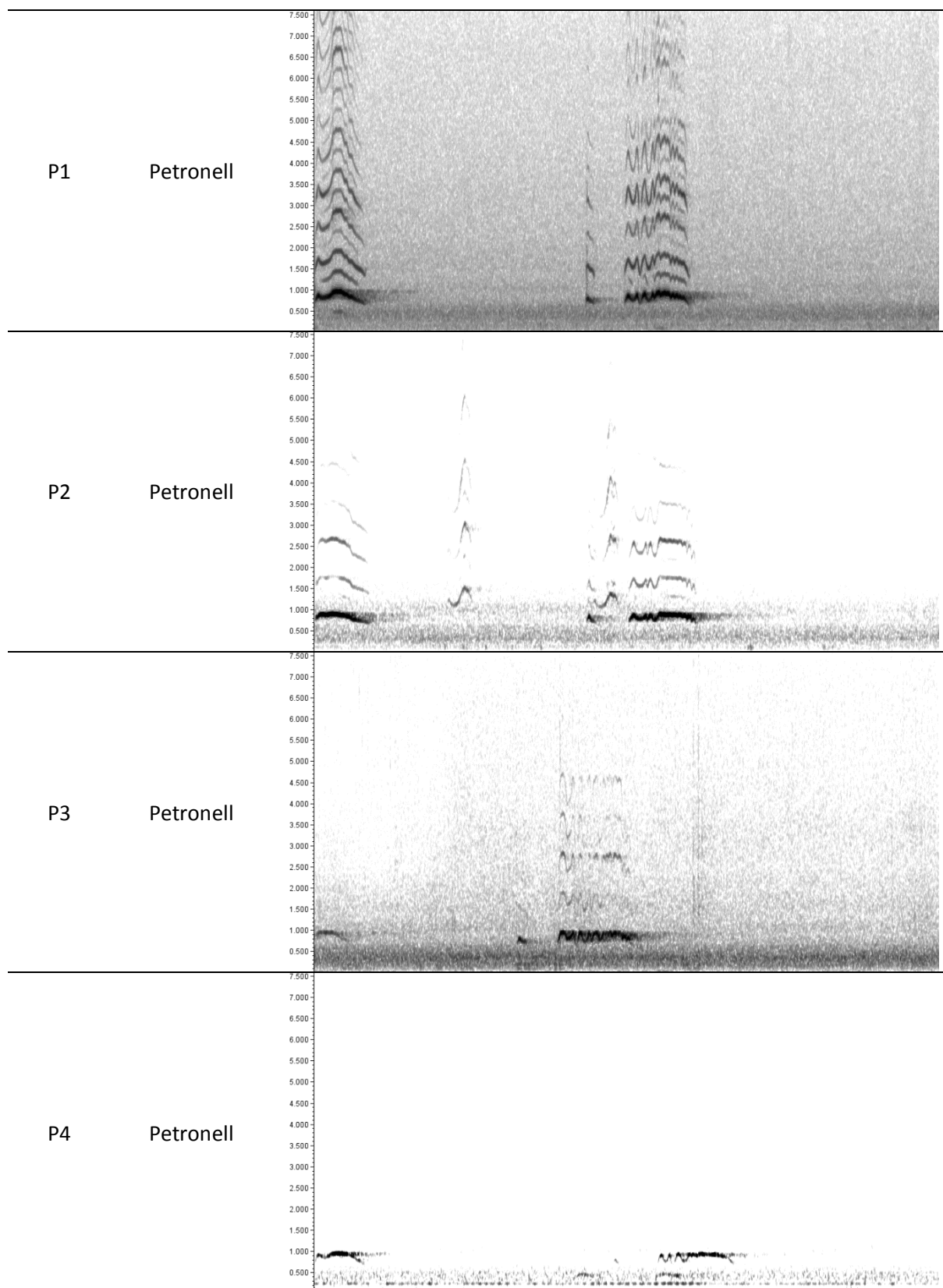


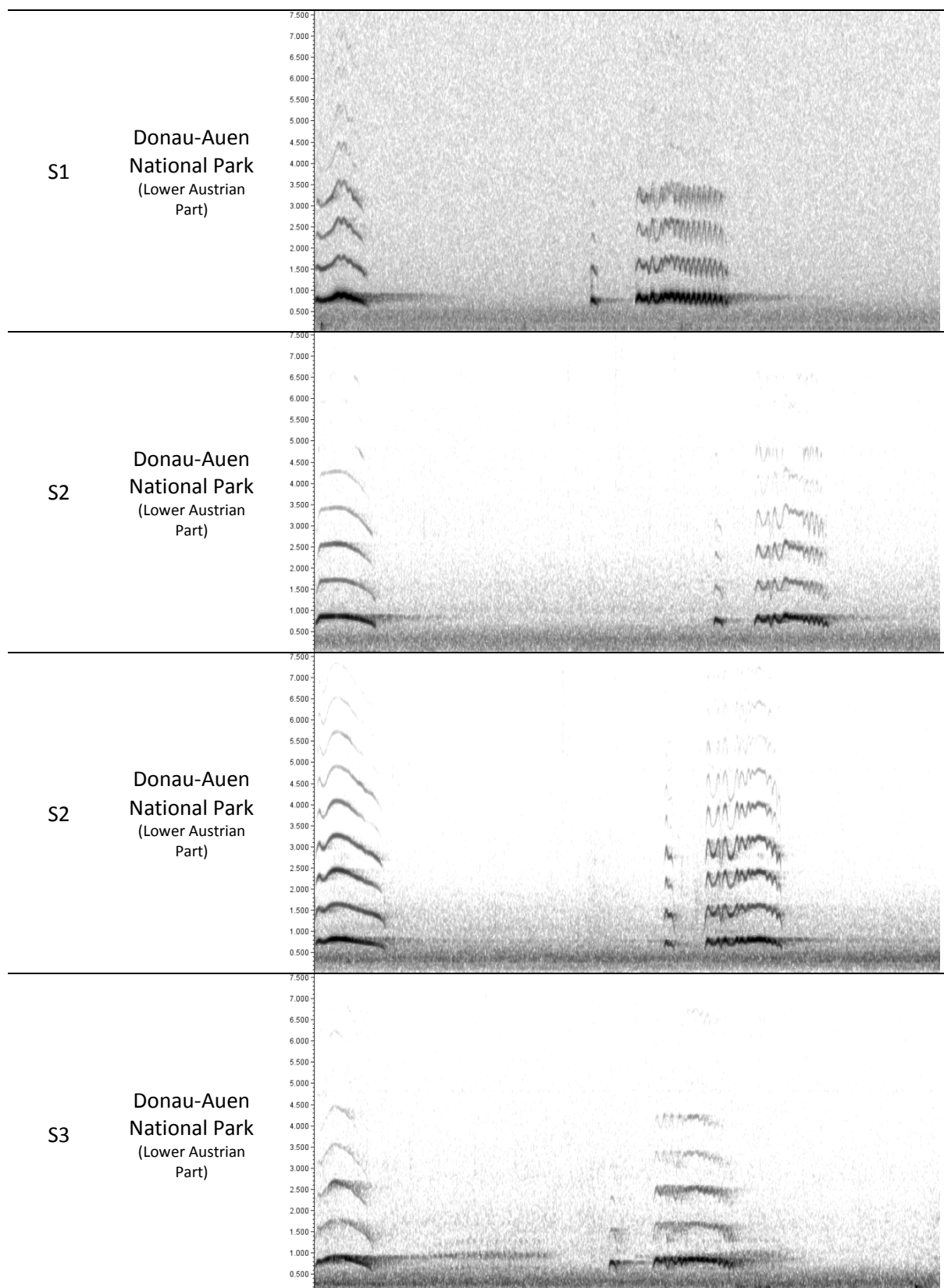


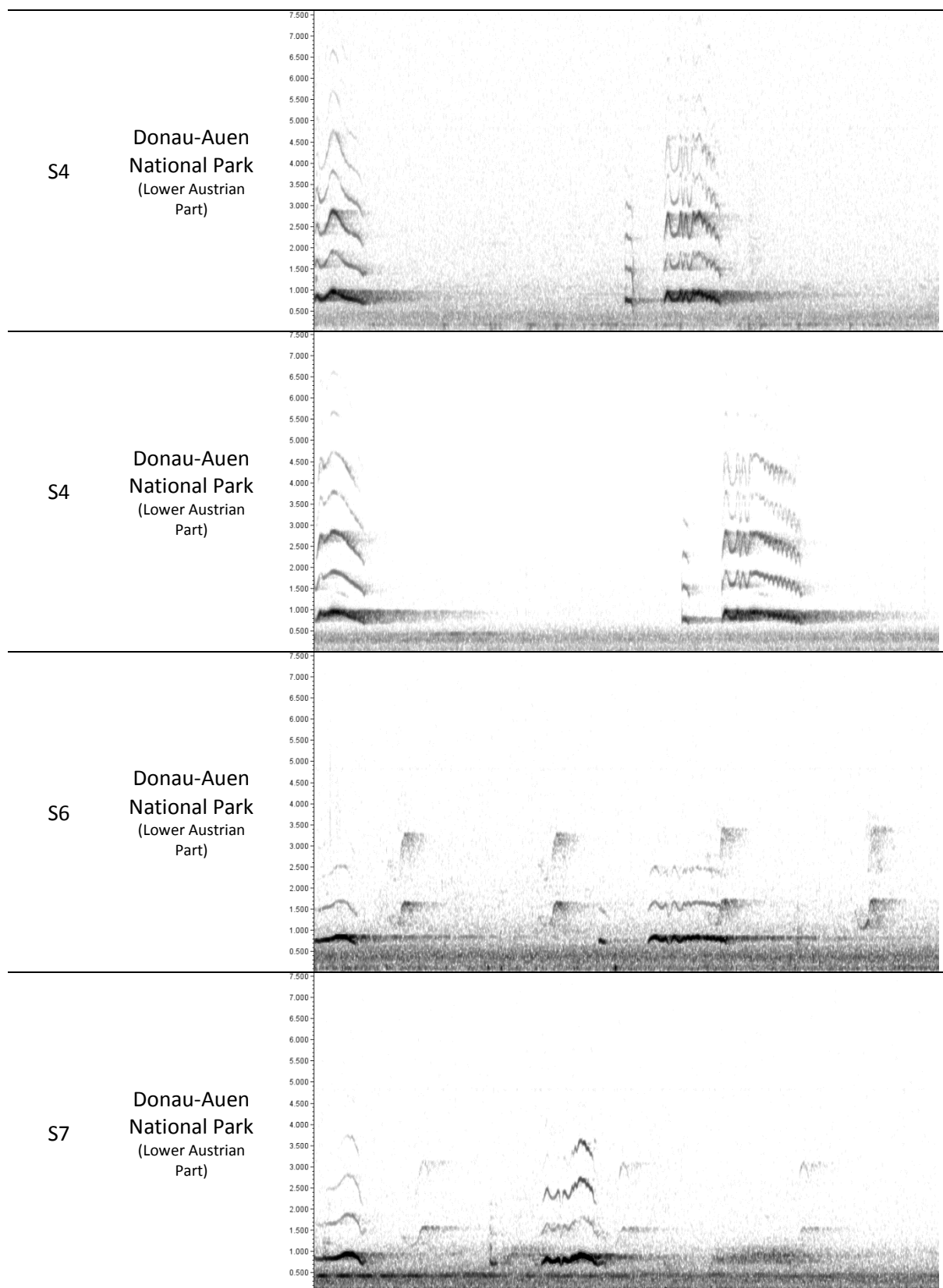












CURRICULUM VITAE

PERSÖNLICHE DATEN

Christina Nagl

Geburtsdatum	30.07.1989
Geburtsort	Tulln/Donau
Staatsbürgerschaft	Österreich

HOCHSCHUL-AUSBILDUNG

Oktober 2010 – April 2015	Masterstudium Zoologie an der Universität Wien Schwerpunkt Biodiversität der Tiere
Oktober 2007 – Oktober 2010	Bachelorstudium Zoologie an der Universität Wien Schwerpunkt Verhaltensbiologie der Tiere
September 1999 – Juli 2007	Besuch des Bundesgymnasiums Tulln/Donau Abschluss der Reifeprüfung am 1.Juni 2007

AUSBILDUNG

April 2013 – April 2014	Ausbildung zur Exkursions-Betreuerin zum Thema Trockenlebensräume der Marchregion RAMSAR ECO NATOUR Projekt zur grenzüberschreitenden Zusammenarbeit SK-AT 2007 – 2013
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BIOLOGISCHE PRAKTIKA

Juli/August 2011 September 2011 Oktober 2012 August 2013	Mitarbeit an der Biologischen Station Hohenau – Ringelsdorf (Verein AURING, Hohenau/March, Österreich)
September 2012 August 2013 August 2014	Mitarbeit an der Beringungsstation Col de Bretolet (Schweizerische Vogelwarte Sempach, Schweiz)
August 2013	Praktikum im Nationalpark Donau-Auen GmbH (Orth/Donau, Österreich)

BERUFSERFAHRUNG

August 2009 – März 2015	Geringfügige Beschäftigung bei Franz Müller Textil GmbH (Beratung, Kundenservice, Verkauf)
September 2012	Mitarbeit beim Artenschutzprojekt Sumpfschildkröte im Nationalpark Donau-Auen, Dotation Lobau.
seit März 2013	Mitarbeit bei Vogelschutz-Projekten in den March-Thaya-Auen (Großvögel, Fischfresser, Wachtelkönig)
April 2013/2014	Mitarbeit beim Monitoring des Wiedehopfes (<i>Upupa epops</i>) im Nationalpark Neusiedlersee
seit März 2014	Mitarbeit bei Vogelschutz-Projekten im östlichen Weinviertel (Windkraftzonierung, Vogelaktivität)
seit April 2014	Nistkastenkontrollen im Rahmen des Habichtskauzprojekts

PUBLIKATIONEN

Conference paper	Nagl, C., Reiter, K. & C. H. Schulze 2013. Owls in floodplain forests in Eastern Austria - Habitat use and population density. Conference Volume of the 5th Symposium for Research in Protected Areas: 531-536. Salzburger Nationalparkfonds, Mittersill, Austria.
Peer-reviewed	Landler, L., Philippi, D., Nagl, C. & G. Gollmann (accepted): Magnetic orientation in the common toad, <i>Bufo bufo</i> : a synopsis of arena experiments. Mertensiella.
POSTER	Nagl, C., Reiter, K., Zsak, K. & C. H. Schulze 2013. Owls in floodplain forests in Eastern Austria - Habitat use and population density. 5 th Symposium for Research in Protected Areas, Mittersill, Austria.