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The structure and function of drumming in the Middle Spotted Woodpecker *Dendrocoptes medius*

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Abstract. The disputed occurrence of drumming in Middle Spotted Woodpecker *Dendrocoptes medius* is due to a lack of sufficient, substantive evidence. In order to obtain a more reliable resource for assessing possible use of drumming in this species, breeding pairs were observed close to potential nest holes in south west France over five years. Drumming was heard in two of the six territories identified and sound recordings were made over four breeding seasons. Analysis of the recorded files consisted of counting and measuring intervals between strikes in all instrumental signals consisting of or containing drumrolls. The results showed that a form of drumming was performed but that it was infrequently produced in a discrete roll. It was usually soft and lacked the regularity of pattern found in the territorial drumrolls of other European woodpeckers. There was also a marked lack of consistency in the amplitude of strikes. As an acoustic signal, this study suggests its principal function to be a communication between partners in relation to the location and construction of a nest site.

Key words: Middle Spotted Woodpecker, *Dendrocoptes medius*, drumming, tapping, instrumental signal, roll, burst, series

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INTRODUCTION

Drumming by woodpeckers has been defined as a rapid, repetitive series of strikes with the bill on a substrate and is distinct from the mechanical sounds produced during foraging or cavity excavation (Pynnönen 1939, Short 1974). It is a unique method of communicating information about ownership of suitable breeding territory (Winkler & Short 1978) and serves to establish and maintain the pair (Gorman 2004, Tremain et al. 2008). Territorial drumming needs to be loud, regularly repeated and consistent in pattern (Blume 1975, Blume & Tiefenbach 1997). Several studies have been undertaken into the characteristics of territorial drumming (Zabka 1980, Stark et al. 1998, Dodenhoff et al. 2001) and in Europe, the time structure within the rolls has been shown to be species-specific (Florentin et al. 2016). Zabka (1980) employed three parameters to describe the individual drumrolls of European woodpeckers: duration — the length of time between the first and last strikes (measured in milliseconds); the number of strikes and; time structure — an analysis of acceleration, deceleration, or constancy of interval lengths. In North America, a further parameter, 'cadence' (number of strikes per second) was found to provide additional accuracy in species identification (Stark et al. 1998).

Consistent descriptions of these distinctive signals have been documented for all of the European Picinae except Middle Spotted Woodpecker which appears to have replaced drumming by its 'miaowing' call (Gorman 2004). This is possibly due to the competitive effect of territorial drumming as a signal by other species sharing the same habitat (del Hoyo et al. 2002). The sporadic written accounts of drumming by Middle Spotted Woodpecker published during the first half of the Twentieth Century were not convincing to the pre-eminent authors on woodpecker behaviour (Blume 1977, Winkler & Short 1978, Glutz von Blotzheim & Bauer 1980). A review of evidence gathered later in the century commented on the contradictory data (Wallschläger 1980) and the range of observations has since been expanded (Pasinelli 2003). To date, two contrasting versions have been described. The first, indicated constant volume and strike rate (Ferry 1962, Kaiser 1990, Günther 1991, Gebauer et al 1992). A sonogram illustrating regular 57 millisecond intervals between strikes in a drumroll appeared in a

comparison of drumming in European woodpeckers (Zabka 1980) as well as in Wallschläger's (1980) review. The recording, made in Germany in 1967 by Dr. Alscher featured a sequence of thirteen rolls ranging from 18 to 30 strikes. A recording of two two-part drum rolls described as typical of the species contained 17 plus 11 and 20 plus 9 strikes with average intervals of 55 ms (Palmér & Boswall 1969). A further sonogram from a recording made in Germany in 1989 by K. Conrads showed a roll of 8 strikes with average intervals of 80 ms (Conrads & Conrads 1997). And an analysis of eight drumrolls sourced from open access archives calculated a mean of 25.5 strikes but did not calculate average intervals (Florentin et al. 2016).

The second version of drumming in Middle Spotted Woodpecker was described as weak and erratic (Feindt 1956, Heinze 1994) and a sonogram from a video-recording by U. Haufe in 1993 illustrates both irregular intervals and amplitude (Conrads & Conrads 1997). More recently, irregular strike patterns have been shown from three confirmed sources: a sound-recording made in Belgium (Boesman 2016), a description from an observation made in Germany (Münchenberg 2017) and in a video recording of a bird by its nest-hole in Germany (Fröhlich-Schmitt 2017).

Less structured forms of drumming are also used by several European species in other behavioural contexts such as antagonism and anxiety (Heinze 1994, Blume & Tiefenbach 1997) and softer forms, sometimes combined with tapping are used more intimately during the breeding season (Tremain et al. 2008, Florentin et al 2017). These signals may represent a transitional form between tapping and territorial drumming but are not intended for long-distance communication.

Authors of comparisons of European woodpecker drumming have acknowledged the limitations presented by small sample sizes for some species (Zabka 1980, Florentin et al. 2016) and this is compounded by problems of possible mis-identification (Turner 2011).

The present study sets out to address the paucity of examples of verified drumming by Middle Spotted Woodpecker by making new sound-recordings of observed birds in an attempt to establish a clear reference for this species.

MATERIALS AND METHODS

Fieldwork

Evidence of breeding pairs of Middle Spotted Woodpecker, in the form of the distinctive advertising call (song), had been observed within the Parc Naturel Régional des Causses du Quercy in the Occitanie Region of France (formerly Midi-Pyrenées). The area is a rolling limestone plateau rising to 465 metres with mostly subterranean water courses but also intersected by river valleys and gorges. The principal habitats are the patchwork of dry grassland still used for sheep rearing and, where this has been discontinued, the naturally regenerating woodland. The predominant tree species are Downy Oak *Quercus pubescens* and Montpellier Maple *Acer monspessulanum* together with Hornbeam *Carpinus betulus*, mostly in the valleys.

A total of 74¼ hours was spent sound recording over three years (2014–2016) in two locations 15 kilometres apart during the period of nest site selection and excavation in March and April (the peak of drumming activity by other woodpeckers). Each location contained one territory. The first location was near the source of a small river bordered by partially decaying Black Poplar *Populus nigra* and surrounded by steep slopes of Oak, Hornbeam and Maple. The second location was a wooded ridge between two small, wooded valleys. More sound recordings were obtained in the first location in early June 2018 from one bird of a pair possibly engaged in a late nesting attempt. Fieldwork was concentrated between 07:00 and 10:00 (06:00 and 09:00 in June) when the birds were most actively communicating. Sound recordings were made of all instrumental (non-vocal) signals, at distances from 20 to 100 m from the birds. No use was made of playback.

Recording equipment used was a Sound Devices 722 file recorder at 16bit/44.1kHz and 24bit/48kHz, with a pair of DPA 4053 compact omnidirectional microphones in an Atherstone 50 x 13 cms parabolic reflector mounted on a tripod. All files were extracted at 44.1kHz, with counts and measurements (to the nearest millisecond) carried out using the spectral view of Cool Edit Pro 2.0 (Adobe Audition) sound editing software. Microsoft Excel (2016) was used for spreadsheet analysis. Spectrograms were created on Raven Lite version 2 (Cornell Lab. of Ornithology) sound analysis software and Avisoft SASlab Lite was used to produce pulse train analyses (measuring signal amplitude in millivolts). Four drumroll parameters were measured: roll duration (ms), number of strikes, mean of strike intervals (ms) and cadence (number of strikes/second).

Analysis

Terms used: 'roll' refers to the rapid, uninterrupted sequence of strikes with the bill which forms the structure of an individual drum; 'burst' refers to a slower sequence of 'ritualised' tapping used as a signal (Lawrence 1967). The majority of candidate drumrolls recorded were combined with tapping in a 'series', so for the purposes of this study it became necessary to delineate a clear boundary between the two forms.

Separation of drumming from tapping. Ritualised, or 'demonstrative' tapping is a relatively slow signal used between breeding partners (Tremain et al. 2008). Unlike the more random tapping used for foraging and excavating it is a clear, emphatic communication used for 'nest showing' (during the construction of a nest-hole), or 'nest relief' (at the pair's changeover during incubation and brooding). The distinguishing structural parameter between drumming and demonstrative tapping is the length of the time interval between strikes (Zabka 1980) (Fig. 1).

Both forms show very evenly spaced strikes but the average interval in the tapping burst is more than twice the length of that in the drumroll. For Middle Spotted Woodpecker, average intervals for drumming in the published examples ranged from 57ms (Zabka 1980) to 80ms (Conrads & Conrads 1997). For demonstrative tapping, average intervals were 200 ms (data from 85 bursts, author's collection).

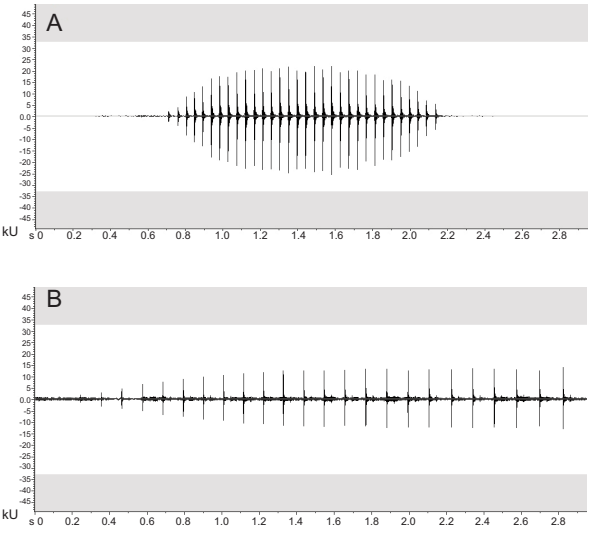

Fig. 1. Waveforms of Lesser Spotted Woodpecker drumming and tapping. A — drumroll (mean interval 46milliseconds) – 5th April 2009, France; B — demonstrative tapping burst (mean interval 112ms) – 13th March 2016, France.

In this study, the upper limit for strike intervals in a roll was set at 90ms, the maximum found in European woodpeckers (Florentin et al. 2016). Two other criteria were defined at the outset: the minimum number of strikes in a roll was set at 4 (occasionally heard from other woodpeckers) and a minimum gap of 300ms was set for separating series containing rolls.

Most of the examples recorded during the fieldwork for this study were not loud enough to have been processed using the sophisticated analytical tools recently designed for autonomous programmes (Florentin et al. 2016). Instrumental signals were consequently first identified by ear and then counted manually to the nearest millisecond from spectrographs on sound editing software. Insufficiently clear examples were rejected.

RESULTS

In the two territories over the four years in which recordings were made, a minimum of two individuals were recorded (since gender separation by sight was not possible with complete certainty and no information was available for mortality). Six nest sites were found, with different trees chosen each year. In the territory at the second location no nest was found in 2015 and in 2016 the nest was found after feeding of nestlings had started. No drumming was heard during the fifteen visits to this territory in these two years and overall, no drumming was heard on 21 days of the 50 days of fieldwork (Table 1). No drumming was observed in the other four territories visited.

The 89 candidate drumrolls recorded were generally rather weak and were not performed on acoustically resonant substrates. Many were

Table 1. The number hours spent, the number of days visits were made, the number of days on which candidate drumrolls were heard and the number of candidate drumrolls recorded for each territory per year.

Territory	Year	Hours	Days	Days/Rolls	Drumrolls
1	2014	13¾	7	2	3
	2015	14½	6	3	5
	2016	19¼	10	4	17
	2018	6	3	3	51
Total 1		53½	26	12	76
2	2014	15	9	3	13
	2015	7¼	6	0	0
	2016	4½	9	0	0
Total 2		26¾	24	3	13
Total 1&2		80¼	50	15	89

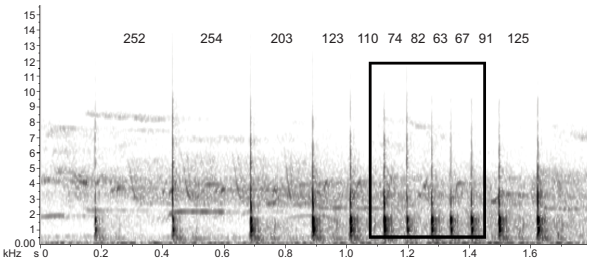

Fig. 2. Spectrogram of a series of strikes from a Middle Spotted Woodpecker combining taps with a roll (boxed) showing the intervals in milliseconds across the top — 21st March 2015 (Territory 1).

Table 2. Frequency of drumrolls and combinations with tapping by Middle Spotted Woodpeckers in the two territories. * — Ten series contained two drumrolls.

	Territory 1	Territory 2	Total*
Discrete drumrolls	5	7 (75%)	12
Taps-drum	36 (89.5%)	3	39
Taps-drum-taps	15	0	15
Taps-drum-taps-drum	4	0	4
Taps-drum-taps-drum-taps	3	0	3
Drum-taps	1	2	3
Drum-taps-drum-taps	2	0	2
Drum-taps-drum	0	1	1

barely audible without the use of the parabolic reflector. They were generally given erratically and infrequently, either next to a partially excavated nest-hole or in a tree nearby and with the mate also in the vicinity. Only 12 were given as discrete drumrolls. The majority (67.7%) were contained in a series, combined with tapping (Fig. 2).

Drumrolls were combined with tapping in both territories, but the proportion was far higher in first location, where the average number of strikes per series (18) was more than twice that found in second location (7.8). Some of the longer series contained more complex combinations and greater variation in interval length (Table 2). Despite these differences, the signals were given in the same behavioural context — near the nest site and with the mate nearby. The severe weather in March 2018 may have resulted in a failed breeding attempt. All of the examples from that year came from the same tree (high in a half dead poplar) although no nest-hole could be seen.

Drumroll strike pattern

After extracting the 77 rolls that were combined with tapping, the full set of candidate drumrolls were analysed using the parameters employed in previous studies of drumming in other woodpeckers (Table 3).

All four parameters revealed wide standard deviations and ranges and diverged markedly from the twenty-two regularly spaced examples referred to in previous studies. The mean for both roll duration and the number of strikes were half of those shown in Zabka's (1.2 secs & 23) and Florentin's (1.11 secs & 25.5) studies (Zabka 1980, Florentin et al. 2016).

Measurements of strike intervals within the extracted drumrolls revealed irregularities of tempo. Taking an average obscured these inconsistencies, which showed up clearly when measured individually and indicated that there were no regularly repeated patterns. This is illustrated by showing the position of the longest and shortest intervals (Table 4). Variation in the time pattern of strikes was too great to enable measurement by Zabka's (1980) third parameter of acceleration, deceleration or constancy. Of the 39 drum rolls that started with the longest interval, 8 contained the shortest interval by the half way point. Acceleration was erratic and not sustained. Relatively greater irregularity occurred in the larger sample from location 1. (Table 3).

In territorial drumming, the amplitude of the strikes throughout a roll is directly related to the time intervals between them. In an accelerating drumroll, the shorter the intervals become, the

Table 3. Mean (± SD) parameters for Middle Spotted Woodpecker drumming after tapping was removed. Ranges shown in brackets.

Territory	Roll duration (ms)	Strikes in roll (no.)	Strike intervals (ms)	Cadence (strikes per second)
1 (N = 76)	642 ± 390 (178–1842)	11.3 ± 6.8 (4–31)	64.5 ± 6.9 (42–90)	17.9 ± 1.8 (14.9–22.8)
2 (N = 13)	391 ± 161 (211–722)	6.6 ± 2.5 (4–12)	69.9 ± 9.4 (49–89)	17.3 ± 2.2 (14.6–21.5)
Combined	605 ± 376 (178–1842)	10.6 ± 6.5 (4–31)	65.3 ± 7.5 (42–90)	17.8 ± 1.9 (14.6–22.8)

Table 4. Positions of the longest and shortest intervals within the 89 drumrolls.

Interval position	Territory 1 (N = 76)		Territory 2 (N = 13)		Combined (N = 89)	
	longest	shortest	longest	shortest	longest	shortest
First	35	4	4	3	39	7
Within the first half	8	33	3	3	11	36
Middle	2	5	1	2	3	7
Within the second half	11	22	2	3	13	25
Last	20	12	3	2	23	14

softer the strikes (Kaiser 1990). In spectrograms loudness is shown by tonal intensity, with the Y axis measuring pitch frequency (Herz) — which is useful for vocal analysis. For the mechanical hammering of woodpecker tapping and drumming, where pitch is a function of size and or acoustic quality of a substrate, a clearer visual representation of the physical energy used is provided by pulse train analysis. This measures amplitude in millivolts on the Y axis, providing a focus on the relative strength of the strikes throughout each series and drumroll. The results of this study, in accordance with Kaiser's findings, showed that tapping elements were generally louder. Within the drumrolls however this principal did not seem to apply (Fig. 3).

DISCUSSION

Many of the sporadic written accounts of possible drumming in Middle Spotted Woodpecker confirm the lack of any regular pattern (Heinze 1994). Heinze's own account of four 'rather stuttering drums sounding more like quick tapping', heard on 24th June 1994, were the only examples encountered in approximately 500 hours of observation during a ten-year study of 35 broods. His description accords with the findings of the present study, and adds to the probability that many pairs may not adopt this behaviour at all. This would explain why the foremost authority on the species has never heard it (Gilberto Pasinelli, pers. com.).

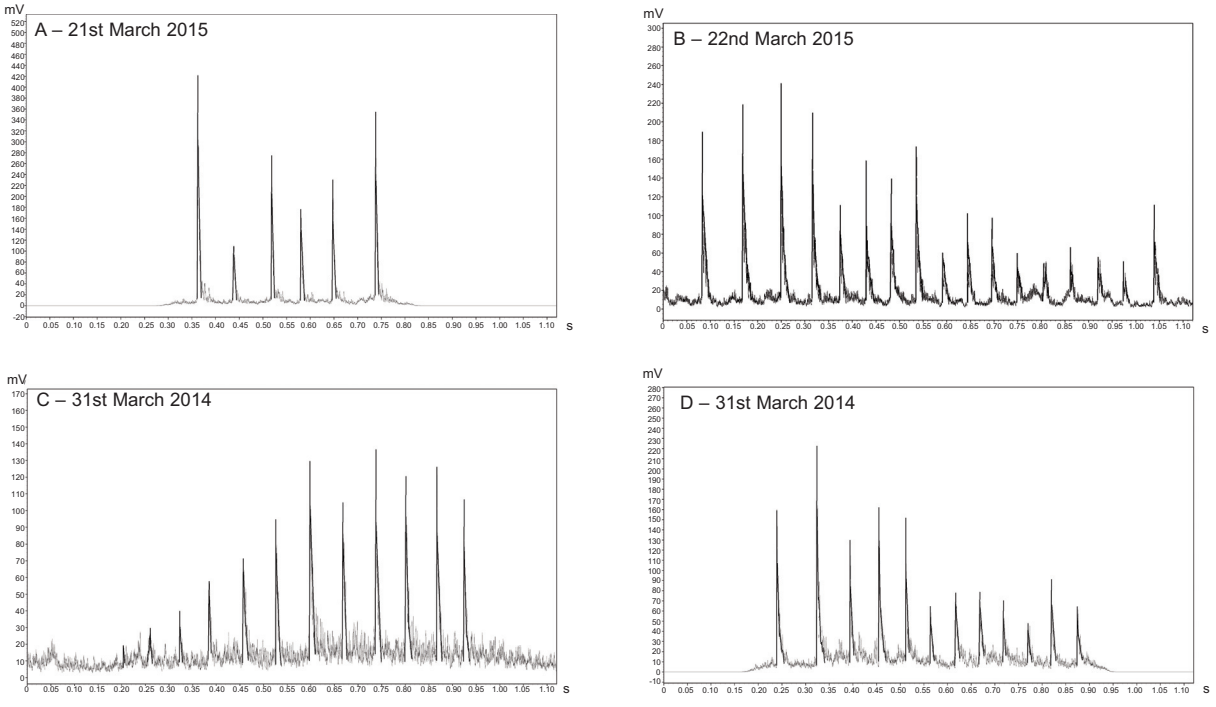

Fig. 3. Variable amplitude patterns within drumrolls. Largely opposite trends are shown in A and B (territory 1) and C and D (territory 2). A partial resemblance is indicated between B and D, representing different individuals. Differences in the scales on the Y axis relate to the proximity of the subject to the microphones.

Looking at the function of the various avian acoustic signals (Hauser 1996, Kroodsma & Miller 1996): 1 — territorial advertisement and defence, 2 — formation and maintenance of a pair bond, 3 — coordination of reproductive cycles within pairs and populations, 4 — individual recognition, and 5 — advertisement of motivation; the weakness and lack of consistency in the drumming of Middle Spotted Woodpecker appear to rule out the first and fourth categories while behaviourally they match aspects of the second and more particularly the third and fifth.

Comparison with drumming by other European woodpeckers

Taking the overall statistics for the four parameters (Table 3) and comparing them with the averages for other European Woodpeckers (compiled from an analysis of the author's own recordings and employing the same methods and materials used in this paper) shows Middle Spotted closest to Great Spotted Woodpecker (Table 5). But these figures disguise the fundamental differences between Middle Spotted and all of the others.

The structure of Middle Spotted Woodpecker drumrolls, showed no regularity, especially in strike intervals and amplitude, such that they did not constitute a repeatable signal that could identify it as a species to other territory holders. This was further complicated by being combined, in the majority of cases, with tapping. The function of these erratic drumrolls appears to find a closer match with the two green woodpeckers which use drumming as a motivational signal between the pair near a potential nest site, where it is usually very soft. For a comparison of typical drum rolls selected from those analysed in Table 5, see Appendix 1.

Other forms of drumming

In Middle Spotted Woodpecker the weakness of the signal clearly illustrates that it is not a territorial advertisement. Its irregularity also precludes species identification. In structure it is more closely related to the tap/drum combinations given occasionally by other woodpeckers which are also not territorial (see Appendix 2).

The precise evolutionary explanation for the lack of territorial drumming in Middle Spotted Woodpecker is not known. Whether its use of less distinctive instrumental signals is a stage in the development towards full drumming or whether it represents a retreat from what has become a redundant signal remains a topic of speculation. As yet, there has been no detailed study of the head and neck anatomy in comparison to its regularly drumming relatives that might offer a physiological explanation.

CONCLUSION

In this study, analysed sound recordings of drumming by Middle Spotted Woodpecker were found to be mostly weak and lacking in rhythm and regularity. The contrast in structure when compared to the familiar drumrolls of other European woodpeckers seems to be explained by their very different function. The predominant combination with tapping indicates a distinct signal type. They were given as a communication between breeding pairs at potential nest sites apparently to encourage nest hole excavation and are therefore more closely related to demonstrative tapping and to the rarely heard tap/drum combinations given by other woodpeckers. They appeared to signal place rather than identity. They did not fulfil the functional definitions of drumming as a territorial signal or for mate attraction, they were not repeated in regular sequences, nor were they performed using acoustically enhancing substrates. With no evidence of drumming in four out of the six territories visited and possibly one bird responsible for 57% of drumrolls, the number of individuals

Table 5. Mean parameters of drumrolls for all European woodpeckers. Abbreviatons: B — Black Woodpecker *Dryocopos martius*, WB — White-backed Woodpecker *Dendrocopos leucotos*, S — Syrian Woodpecker *Dendrocopos syriacus*, GS — Great Spotted Woodpecker *Dendrocopos major*, TT — Three-toed Woodpecker *Picoides tridactylus*, LS — Lesser Spotted Woodpecker *Dryobates minor*, GH — Grey-headed Woodpecker *Picus canus*, IG — Iberian Green Woodpecker *Picus sharpei*, G — Green Woodpecker *Picus viridis* MS — Middle Spotted Woodpecker.

	B	WB	S	GS	TT	LS	GH	IG	G	MS
Duration (ms)	1800	1694	852	654	1224	1090	1465	1135	1111	605
Strikes (no.)	33	32	21	15	20	23	29	20	24	10.6
Intervals (ms)	58	54	46	48	71	47	51	60	51	65
Cadence (no.)	18.5	19.2	22.4	22	15	21.8	19.7	17.9	21.8	17.8
Drumrolls	284	277	193	223	97	188	130	21	76	89

recorded represents a small sample. But the findings of this study agree with other isolated observations recently made elsewhere in Europe. Confusion resulting from the comparison of structure alone could be avoided by a better understanding of the precise function of these acoustic signals.

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STRESZCZENIE

[Struktura i funkcja bębnienia u dzięcioła średniego]

Występowanie typowego dla dzięciołów bębnienia jest dla dzięcioła średniego często kwestionowane. Jednocześnie istniejące rzadkie nagrania tego zachowania nie wskazują na jednolity wzorzec bębnienia u tego gatunku. Celem pracy było zweryfikowanie struktury bębnienia u dzięcioła średniego.

Badania były prowadzone w sześciu terytoriach dzięcioła średniego we Francji, w latach 2014–2018, łącznie dokonano ponad 80 h nagrań (Tab. 1). Zostały one dokonane w okresie wyboru miejsc na gniazdo oraz wykuwania dziupli (marzec –kwiecień), kiedy przypada szczyt częstości

bębnienia także u pozostałych gatunków dzięciołów. Do celu analizy nagrań autor wyróżnił dwa rodzaje dźwięków: typowe bębnienie oraz demonstracyjne stukanie, różniące się okresem czasu pomiędzy poszczególnymi uderzeniami (Fig. 1). Analiza zarejestrowanych dźwięków składała się z określania czterech parametrów: długości trwania bębnienia, liczby uderzeń, średniego czasu pomiędzy uderzeniami oraz częstotliwości (liczba uderzeń/sekundę).

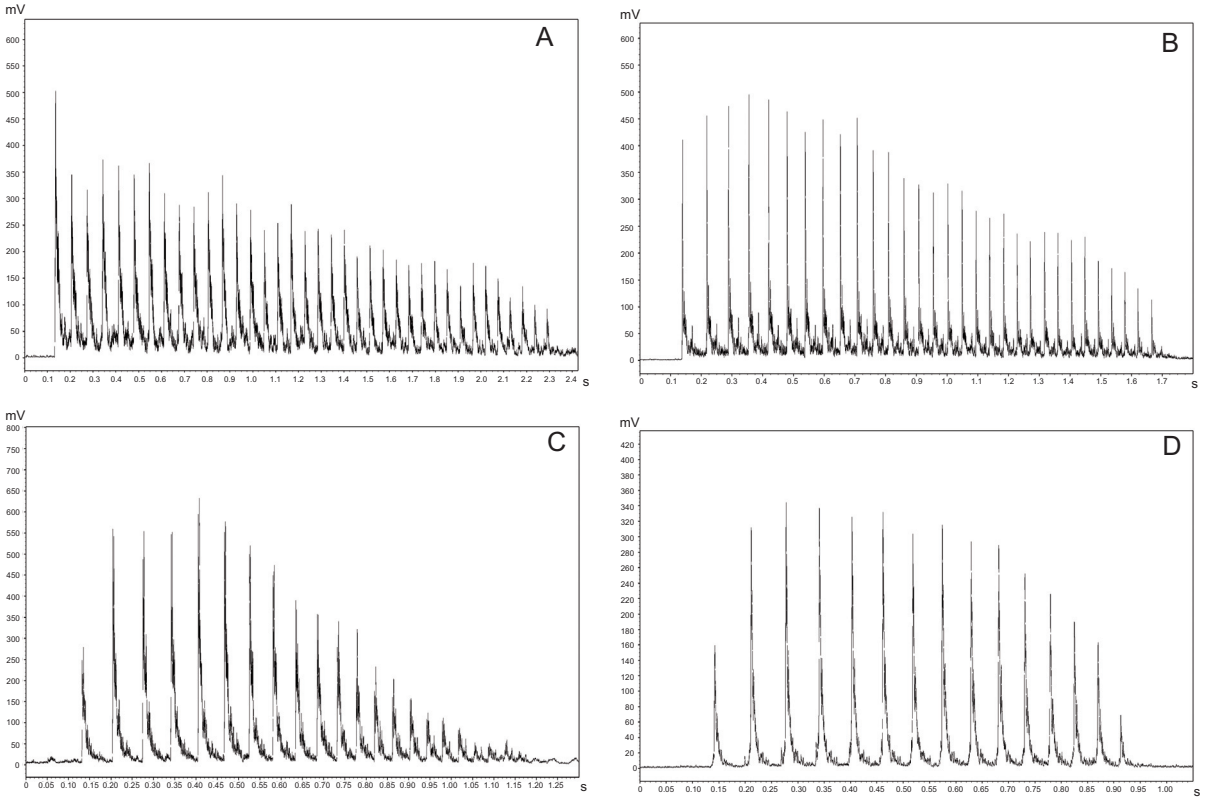
Obserwacje bębnienia były bardzo rzadkie. Zarejestrowano je tylko w dwóch terytoriach, podczas mniej niż połowy dni spędzonych na pracach terenowych (Tab. 1). Zarejestrowano 89 nagrań zawierających potencjalne bębnienie. Większość nagrań zawierało zarówno bębnienie, jak i stukanie (Fig. 2). Tylko w 12 przypadkach zarejestrowano wyłącznie bębnienie, w pozostałych było ono połączone ze stukaniem (Tab. 2). Opisane parametry bębnienia charakteryzowały się dużą zmiennością (Tab. 3) i różniły się od opisywanych dotychczas. Wyraźna była także zmienność tempa czy amplituda dźwięków (Tab. 4, Fig. 3). Stwierdzono, że bębnienie u dzięcioła średniego jest pozbawione regularności występującej w bębnieniu terytorialnym innych europejskich dzięciołów, a jego parametry różnią się dość znacznie od tych opisywanych dla innych gatunków (Tab. 5, Apendyks 1).

Autor sugeruje, że główna funkcja bębnienia u dzięcioła średniego nie jest związana z terytorializmem (podobne wzorce stukania i bębnienia obserwowane są u innych gatunków dzięciołów w kontekstach nieterytorialnych — Apendyks 2), a raczej z komunikacją między partnerami w odniesieniu do miejsca lęgowego.

Appendix 1

Structural comparison of European woodpecker drumrolls

For European woodpeckers other than Middle Spotted, despite apparent similarities in the structure of drumrolls between species that accelerate and between those that maintain a steady rhythm or slightly decelerate, it is relatively simple to distinguish them both by ear and by graphic representation. Interestingly, the drumrolls of the two green woodpeckers, which are not used territorially, while still recognisable, have a looser structure, particularly in the amplitude of the strikes (Fig. S. 1).



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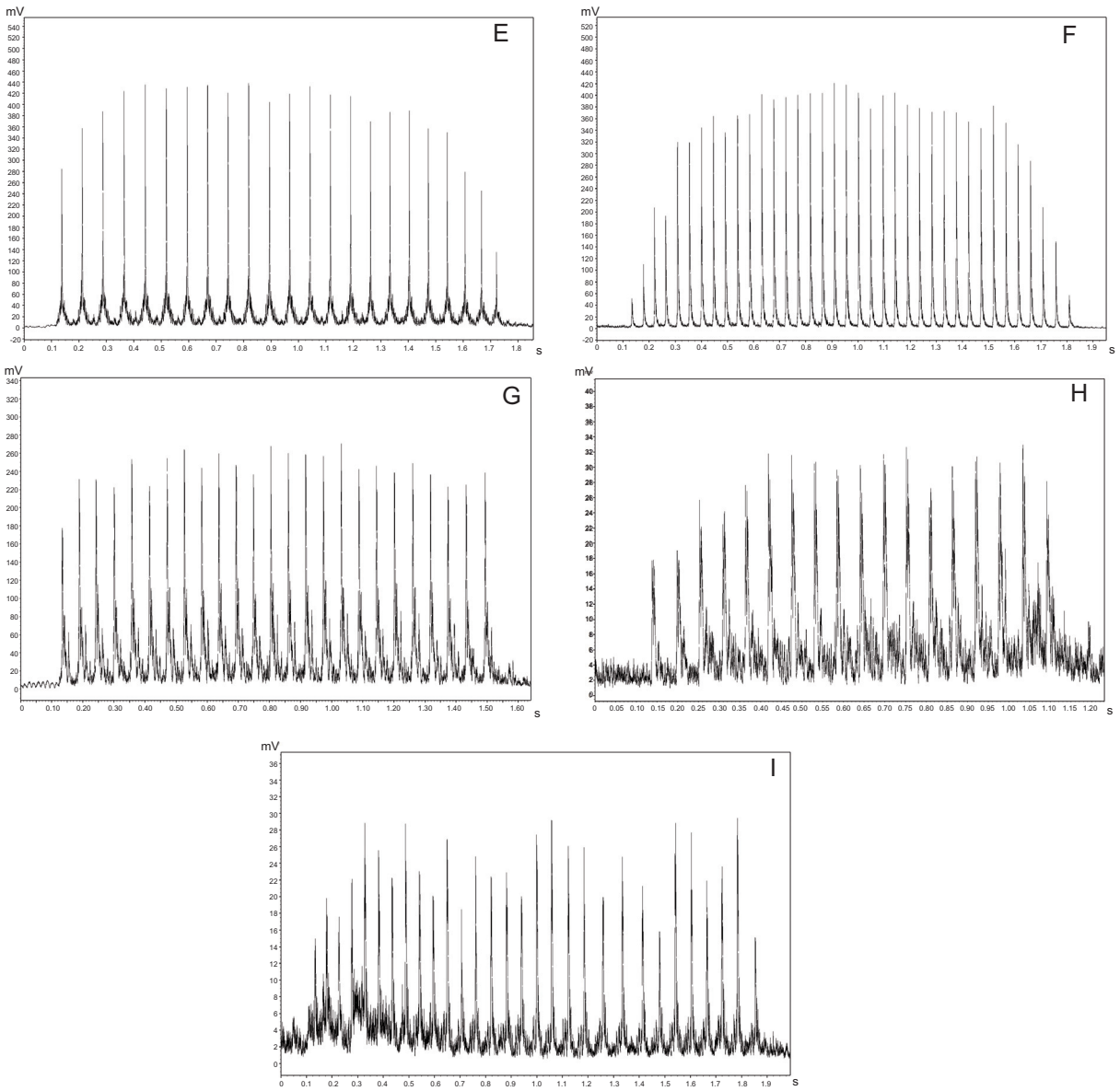

Fig. S. 1. Comparison of European woodpecker drumrolls (pulse train analysis). X axis — strike intervals. Please note that the scales are not directly comparable, e.g. the duration of the roll in (A) at 2.2 seconds is almost three times the length of (D) at 0.78 sec. Y axis — amplitude of strikes, showing the relative strength through each roll. Species size, choice of drumming post and distance from the microphones all have an influence on the appearance of the rolls, but it is the pattern within each roll that is significant to this study. A–G: typical territorial drumrolls showing a high degree of consistency in both axes. In accelerating rolls (A–D) strikes become softer, whereas in evenly spaced or slightly decelerating rolls (E–G) the amplitude of strikes is steadier. In H and I the non-territorial drumrolls of these species show some irregularity in both axes. A — Black Woodpecker (territorial): 37 strikes with gradual acceleration (first interval 74ms, last 54ms) and a fairly smooth reduction in amplitude from the first, loud strike (9th April 2010, Slovakia); B — White-backed Woodpecker (territorial): 31 strikes, smoothly accelerating (first interval 80ms, last 45ms), with a gradual reduction in amplitude after the start (25th April 2006, Hungary). C — Syrian Woodpecker (territorial): 22 strikes accelerating (first interval 71ms, last 34ms), with a long and gradual reduction in amplitude after the start (22nd April 2007, Hungary). D — Great Spotted Woodpecker (territorial): a short, accelerating roll of 15 strikes (first interval 69ms, last 43ms) with a smooth reduction in amplitude after a weak first strike (17th March 2002, France); E — Three-toed Woodpecker (territorial): 23 strikes, evenly spaced until an acceleration at the end (first interval 74ms, last 54ms), with regular amplitude except at start and end (21st April 2006, Slovakia); F — Lesser Spotted Woodpecker (territorial): 37 strikes, evenly spaced until the slight deceleration at the end (first interval 44ms, last 51ms) and a smooth increase and decrease in amplitude at start and finish (5th April 2009, France); G — Grey-headed Woodpecker (territorial): 25 strikes, evenly spaced until the slight deceleration at the end (first interval 54ms, last 60ms), with a fairly constant amplitude after the first, weaker strike (2nd April 2010, Hungary), H — Iberian Green Woodpecker (non-territorial): 31 strikes loosely accelerating (first interval 70ms, last 60ms), with an irregular increase in amplitude (14th April 2012, France); I — Green Woodpecker (non-territorial): 30 strikes with a slightly irregular deceleration (first interval 44ms, last 70ms) and fluctuating amplitude (16th March 2002, France).

Appendix 2
Other forms of drumming

In Middle Spotted Woodpecker the weakness of the signal clearly illustrates that it does not satisfy Winkler and Short's description of a territorial advertisement (Winkler & Short 1978). Its irregularity also precludes species identification. In structure it is more closely related to the tap/drum combinations given occasionally by other woodpeckers (Fig. S. 2).

Such erratic strike patterns have been described as accompanying antagonistic reactions between potential breeding partners (Blume 1958). They are used as a form of appeasement, enabling the transition from independence to cooperation in the run up to breeding (Tembrock 1977). In the present study, no obvious antagonism was observed and the tap/drums appeared to be more closely related to demonstrative tapping in behavioural significance. This conclusion is supported by a report of tapping accelerating into a drumroll at the time of nest hole excavation (Feindt 1956). In a unique video from Germany, the same pattern appears to be used to indicate the site of the hole during its excavation (Fröhlich-Schmitt 2017). Whereas demonstrative tapping is strong and evenly spaced, the rather weak, erratic drumrolls and tap/drums suggest a more spontaneous and unprogrammed origin.

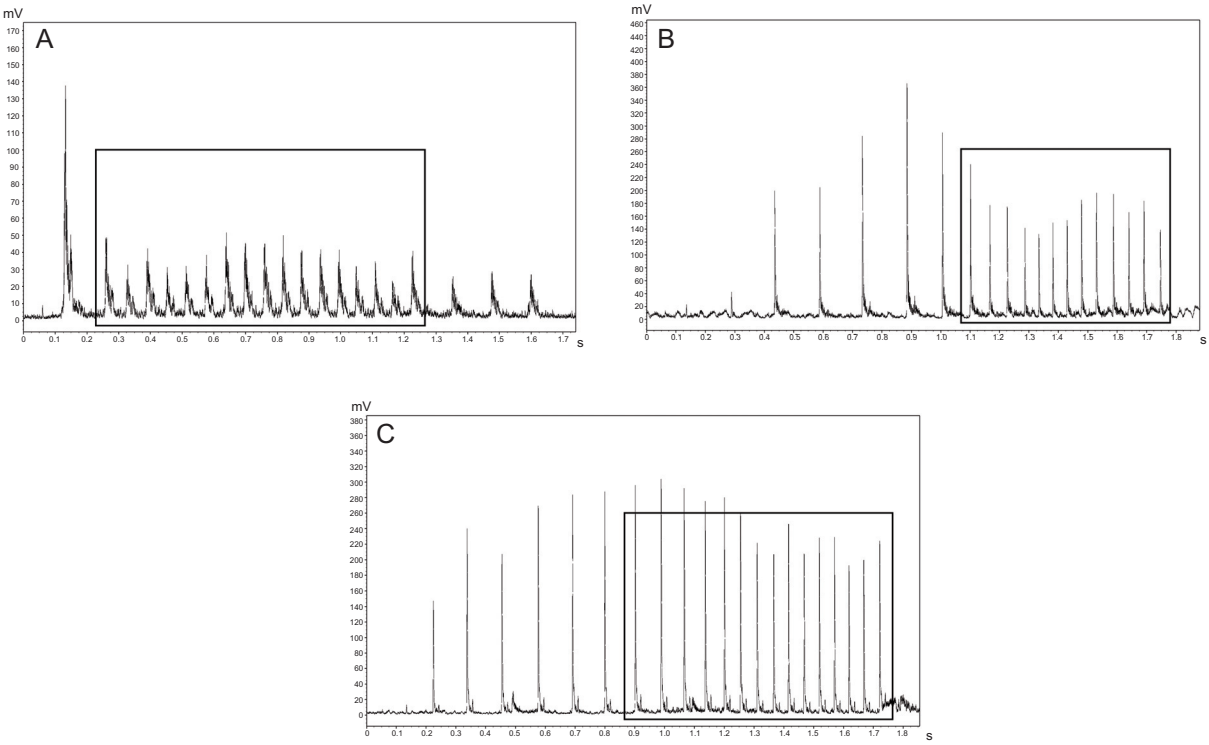

Fig. S. 2. Three examples of tap/drum combinations from other woodpeckers: A — Black Woodpecker (24th March 2012, France) — starts with one tap and ends with three, strikes in the drumroll are evenly spaced; B — Syrian Woodpecker (22nd April 2007, Hungary); C — Lesser Spotted Woodpecker (3rdMarch 2002, France) — both start with increasingly louder taps followed by a drumroll that accelerates before evening out. Strike amplitude fluctuates in all three, including within the drumrolls.

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