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Effects of season, plasma testosterone and body size on corncrake (*Crex crex*) call rhythm

Tomasz S. Osiejuk[1a], Bogumiła Olech[2], Katarzyna Ratyńska[1b],
Andrzej Owsiński[3] & Joanna Gromadzka-Ostrowska[4]

[1)] *Department of Animal Morphology, Institute of Environmental Biology, Adam Mickiewicz University, ul. 28 Czerwca 1956/198, PL-61-485 Poznań, Poland (e-mail: [a]osiejuk@amu.edu.pl, [b]kasiek@amu.edu.pl)*
[2)] *Kampinoski National Park, ul. Tetmajera 38, PL-05-080 Izabelin, Poland (e-mail: buki1@poczta.onet.pl)*
[3)] *Department of Ecology, Warsaw University, ul. Miecznikowa 1, PL-02-096 Warszawa, Poland*
[4)] *Department of Dietetics and Functional Food, Warsaw Agricultural University, ul. Nowoursynowska 166, PL-02-787 Warsaw, Poland*

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We tested whether the temporal parameters of corncrake (*Crex crex*) call change seasonally and/or individually. We defined a new, compound variable called RHYTHM, which quantitatively describes how corncrake call is perceived. Temporal parameters of calls, including RHYTHM, were significantly associated with both the time within the breeding season and body size. The most striking variation of call production was related to between-call intervals, which define a range of calls from monotonous (low values of RHYTHM) to intermittent (high values of RHYTHM). We found very clear, seasonally repeatable patterns of corncrake call with respect to syllable length, interval duration, and RHYTHM. Intermittent rhythm was more frequent in the beginning of the season, and to some extent before the second breeding attempt. While males sometimes changed call rhythm within a season, in general males with larger body size produced more intermittent calls. Simultaneously, intermittent rhythm was associated with less continuous and slower calling, leading to presumably lower energy expenditures. Building on previous results, we suggest that call rhythm is a conventional signal of aggressive motivation, with receiver retaliation as a possible stabilizing cost.

Introduction

The corncrake, *Crex crex,* is a globally-threatened rail species (Tucker *et al*. 1995, Hagemeijer & Blair 1997). Unlike other rails, which are typically monogamous and provide biparental care, corncrakes are sequentially polygamous. Both males and females are likely to change partners between breeding attempts, and only females incubate and care for the chicks (Green *et al*. 1997). Corncrakes are hard to observe and estimates of population parameters, such as productivity or density, are hard to assess.

To alleviate this problem, ornithologists have tried to identify acoustic characters that could be used in individual recognition of males and, consequently, in estimating the size of monitored populations (May 1994, 1998, Peake *et al.* 1998, McGregor *et al.* 2000, Kenyeres *et al.* 2000, Peake & McGregor 2001, Terry & McGregor 2002). This search has resulted in the discovery that the inner call structure, expressed as intervals between maximal amplitude peaks (called pulse-to-pulse duration or PPD), is stable over long periods and serves as an individual signature (Peake *et al.* 1998, Peake & McGregor 1999). However, pulse-to-pulse duration is not the only call characteristic that is highly variable (Cramp & Simmons 1980, Schäffer *et al.* 1997). For example, Schäffer (1995), and Tyler and Green (1996) found that overnight calling performance is related to a male's mating status: males reduce continuous calling when mated. Mason (1940) found that calls changed in quality during season, specifically that calls become weaker and shorter in mid-June.

Owsiński (2002) classified corncrake calls by ear to three rhythm classes: monotonous, intermediate and intermittent, and provided some experimental evidence that males respond to playbacks of irregular and monotonous calls as a function of their own call pattern (Owsiński 2002). Males that called with an intermittent rhythm frequently slowed down their calling rate after playback, and this change was more common when the playback was an intermittent call than when the call was monotonous. Owsiński (2002) also found that after an intermittent playback, males frequently approached the loudspeaker and circled it for a long time. Perhaps the most interesting finding, however, was that a corncrakes' response depended not only on the rhythm of calls played back, but also on call produced by the subject. These data suggest that call rhythm encodes information crucial for male–male interactions, and that intermittent patterns are related to an increased aggressive motivation.

Passerines and non-passerines substantially differ in mechanisms of both song and call production and its respective transfer between generations (Baptista 1996). It is generally accepted that the craking call of corncrake males is the functional equivalent of song for those passerines with relatively simple repertoires (Cramp & Simmons 1980, Schäffer 1995). The craking call announces territory establishment and most likely serves a double function: repelling rivals and attracting females (Cramp & Simmons 1980). In Scotland, 92% of radio-tagged single males were found calling, while only 12% of paired males called during the night (Tyler & Green 1996). Paired males reduce calling during the egg-laying period (Schäfer 1995, Schäfer *et al.* 1997) and females are known to call in captivity (Schäffer *et al.* 1997). Occasional recording from the wild, however, revealed a different structure of such a call (Ottval 1999).

The typical call of males is very specific and differs strongly from passerine vocalization in design and performance. The call is audible from up to 1500 m, which means that the amplitude level at a distance of 1 m may even exceed 100 dB SPL (Bradbury & Vehrencamp 1998). Males vocalize at a high rate, producing ca. 10 000 calls during the night hours (Green *et al.* 1997, Peake *et al.* 1998). Craking call is structurally a toneless, pulse repetition signal. Such signals consist of a series of energy bursts, often with broadband spectrum, and are more typical for anurans, marine mammals or insects than for birds (Beeman 1998). As corncrakes inhabit dense environments, in which visual communication is severely limited, we may expect that their loud call is used in long-range communication, and may carry information about quality, motivation, or location for potential mates or rivals (Green *et al.* 1997).

However, there is paucity of detailed information about how the acoustic design of this call is related to reproduction-related tasks. If there is an analogy between passerines and corncrake vocalization, we would expect context-dependent changes in calling rate or variation in call production, both which could be used for evaluating the signal during the breeding season. In fact, corncrake males are known to call with the greatest frequency early in the breeding season, and call quality (perceived as rhythm) is known to change as the season progresses (Mason 1940, Braaksma & van der Straaten 1973, Owsiński 2002). Nevertheless, we are far from explaining quantitatively how and which parameters influence the perceived rhythm and what the biological background of this variation is.

In this paper we define quantitatively and describe the within- and between-individual pattern of call 'rhythm' variation. We assumed that 'rhythm' is a compound character which is affected by temporal call parameters (i.e. duration of syllables and intervals; Fig. 1). Accordingly, the first aim was to elucidate how basic temporal parameters affect perception of call 'rhythm'. Seasonal changes in call quality at the population level may be a result of two, not necessarily exclusive, processes. First, males may change call characteristics during a season. Second, some males may cease calling, so the population's overall pattern may reflect only the calling of a fraction of individuals, e.g. those who did not attract the female (Tyler & Green 1996). Therefore, the second purpose of this study was to test the hypothesis that corncrake males change their call rhythm during the season. Third, we tested if there was a consistent pattern of seasonal changes in call rhythm. If the rhythm, or any single temporal call parameter, is related to social context (e.g. mating status or dominance hierarchy), we may expect seasonally repeatable patterns. In addition, we may expect that call rhythm reflects not only the social context, but also attributes of the sender. Therefore, our final aim was to investigate whether the rhythm of call reflects the body size, condition, testosterone level, and hematocrit of the signaller.

Material and methods

Study area

The study was carried out in the western part of the Kampinoski National Park (central Poland, coordinates of the centre of the study area 20°23´E, 52°19´N), from May until July in 2001 and 2002. The study plot (ca. 24 km^2), called 'Farmułowskie Meadows' is an open area of swamp (a belt 2–3 km wide) between two inland dune systems. The area constitutes a mosaic of peatland as well as wet meadows, and a small proportion of formerly arable land at an early stage of succession. The area is naturally closed from the north, east and west by forest, which ensures stable breeding conditions, depending only on water level and weather (Michalska-Hejduk 2001). Corncrakes in the study area are irregularly distributed and the basic parameters of abundance and habitat selection are known from earlier studies (Juszczak & Olech 1997, Owsiński 2002; B. Olech *et al.* unpubl. data): corncrakes in the study area prefer vegetation patches dominated by larger sedge species, e.g. *Carex gracilis* or *C. acutiformis* (60% of cracking males), wet unmowed meadows (20%), reed beds composed of common reed *Phragmites australis* (5%–10%) and communities dominated by nettle *Urtica dioica* (2%–8%). Few males were noticed in other types of vegetation, such as grasslands or pastures (2%–4%).

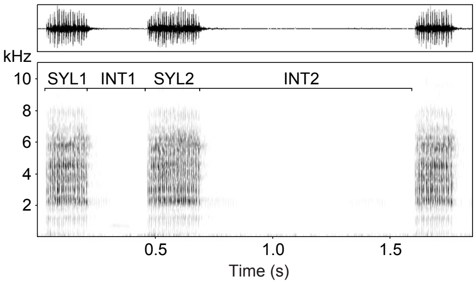

Fig. 1. Sonogram (with waveform) of a corncrake call. An illustration of basic call measurements: SYL1, SYL2, INT1 and INT2.

Recording calls and individual recognition

The study area was divided into nine parts, which were visited regularly three times a month (once in each 10-day period) at night (23:00–04:00) during the calling period (from 12 May to 21 July in 2001 and from 7 May to 13 July in 2002). These subplots were approached from the opposite direction each time to randomize the order of recording the males. The birds were recorded (for 2–3 minutes each) from a distance of about 10 m with a Tonsil Mc-382 directional microphone and a Marantz PMD222 cassette recorder. The position of all calling males was determined with the GARMIN 12 GPS receiver. We attempted to record each cracking (different spelling this time) male exactly once per 10-day period. This was accomplished by visiting the whole area during a short period (usually one subplot per night).

In 2002 we took additional recordings to test for significant within-night differences in calling pattern. We selected randomly six males, which were recorded three times during one night on 22 May 2002, when the overall activity of males was the highest. The same males were recorded on different nights, and these recordings were used for comparison of call rhythm within and between nights. In this case, males were recognised on the basis of pulse-to-pulse duration, according to the method described by Peak *et al*. (1998). We used only the first 11 PPD from each syllable, as this was the shortest number of amplitude pulses found in our population (Olech *et al*. 2002). We calibrated the method for the studied population by comparing PPD variation within and between recordings of the same and different individually marked males. Details of the method will be described elsewhere.

Birds were captured directly after the first recording or subsequent recording(s) if we failed at the first attempt. Field workers trampled 1–2 m^2 of vegetation near the place where males were calling. This area was then illuminated with an electric light and craking call was played back from the loudspeaker placed nearby. During the playback, observers remained hidden in the shadows for up to 30 minutes. During that time, males often approached the illuminated spot and were caught with a special net (diameter 80 cm) attached to a 160-cm-long pole. The behaviour of males during catching was recorded (time of reaction). Captured birds were tagged with a numbered metal ring, and biometric measurements (body weight, lengths of tarsus, wing, and head with bill) were taken. This process took ca. 15 minutes.

Calls analysis and bioacoustics terminology

All recordings were transferred from the tape recorder to a PC workstation with SoundBlaster Live! 5.1 (full version) by using 22.05 kHz/16 bit sampling. Recordings were analysed with Avisoft SASLab Pro 4.1 software within the following set of parameters: 512 FFT-length, Frame (%) = 25, Window = Hamming, Temporal Overlap = 87.5%, and both spectrograms and waveforms shown. This gave a 224 Hz bandwidth with 42 Hz frequency and 2.9-ms time resolution (Specht 2002).

Territorial vocalization of corncrake males consists of two loud syllables (SYL1 and SYL2) repeated in a long series. The syllables are short (0.18–0.22 s) and the first is usually significantly shorter than the second (Kenyeres *et al*. 2000, Olech *et al*. 2002). Visual inspection of sonograms show that the characteristic rhythm of calling depends on ratios between duration of syllables and intervals (Figs. 1 and 2). Therefore, we defined a compound variable named RHYTHM, which quantitatively describes the auditory perception of call rhythm (*see* Table 1 for details and Fig. 2 for illustrations). Note that in this paper when we use the word ‘rhythm’, we mean a whole spectrum of variables affecting the temporal perception of corncrake call, (e.g. syllables duration, intervals duration etc.),

Table. 1. Definitions of variables describing simple and compound temporal parameters of corncrake calls.

Variable	Definition
SYL1	Duration of the first syllable unit (ms)
SYL2	Duration of the second syllable unit (ms)
INT1	Within-call interval, i.e. length of the interval between SYL1 and SYL2 (ms)
INT2	Between-call interval, i.e. length of the interval between the end of SYL2 of the preceding call and the begining of SYL1 of following call (s)
SYL_R	SYL2/SYL1; describes the extent that the second syllable unit is longer then the first one
INT_R	INT2/INT1; describes the extent that the between-call intervals are longer than the within-call intervals
CALL	SYL1+INT1+SYL2 (ms); duration of both syllables and within-call interval
RHYTHM	INT2/CALL; describes quantitatively the human impression of calling “rhythm”

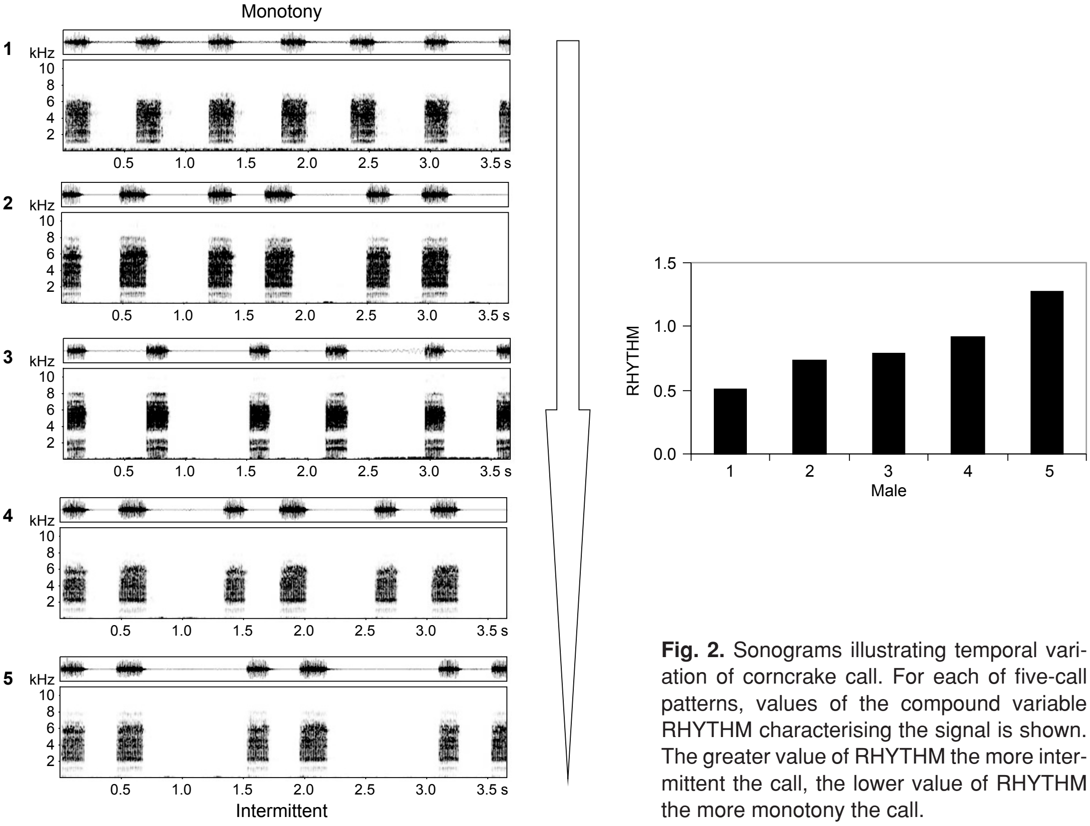

Fig. 2. Sonograms illustrating temporal variation of corncrake call. For each of five-call patterns, values of the compound variable RHYTHM characterising the signal is shown. The greater value of RHYTHM the more intermittent the call, the lower value of RHYTHM the more monotony the call.

while 'RHYTHM' is a strictly defined variable corresponding to how rhythm is perceived on the monotony–intermittent axis (Table 1).

Plasma testosterone and haematocrit

In 2002 we took blood samples from caught birds to determine the level of plasma testosterone and haematocrit. Samples (50–60 μl per male) were collected via syringe by puncturing the brachial vein. We did not observe adverse effect of this method on any bird's condition or survival for the 30 individuals recaptured during the season. In addition, male behaviour was not noticeably affected because recaptured males were found calling in their former territories.

Plasma was removed after centrifugation within 1–4 h of sampling. It was stored at –20 °C until the hormone was assayed, on average 6 months after sampling. We used the Orion Diagnostica SPECTRIA testosterone RIA test (Carlström *et al.* 1988). This is a coated tube radioimmunoassay designed for direct quantitative measurement of the concentration of testosterone in blood plasma. Using the standard curve, testosterone values were read directly by computer for each sample. The sensitivity of the method — defined as the detectable concentration equivalent to twice the standard deviation of the zero-binding value — is approximately 0.1 nmol l^{-1}. The intra-assay precision coefficient of variation was 3.8% and the inter-assay precision was 4.8%. The percentage cross-reactivity of testosterone-related steroids is as follows: 100% for testosterone, 4.5% for 5-α-dihydrotestosterone, and 0.03% for androstandione. Recoveries amounted to 98.9% ± 8.4%. Haematocrit was expressed as percentage of blood volume contributed by red blood cells.

Statistical analysis

Data are presented as means ± SE unless otherwise indicated. All tested variables, except testo-

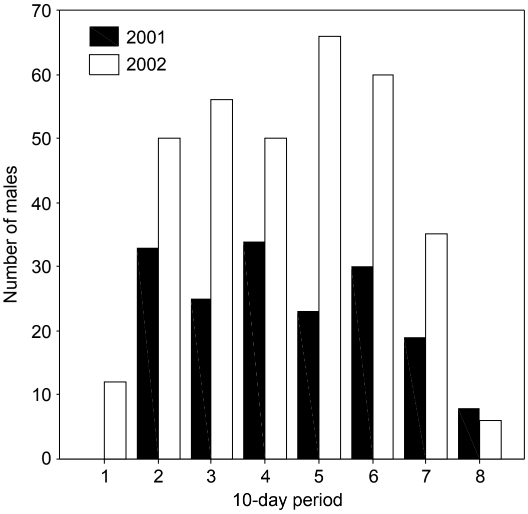

Fig. 3. Numbers of males recorded in successive 10-day periods of breeding season in 2001 and 2002 (1 = 1–10 May, 2 = 11–20 May, and so on).

sterone level, conformed to a normal distribution. Testosterone level was normally distributed after log transformation; $T = \log$ (testosterone + 1). We used general linear models (GLM) to estimate the effect of time within season and (between) year on temporal call parameters. We used regression models to identify significant predictors of RHYTHM among variables characterising corncrake males. To reduce the number of variables for body size, we used the first principal component based on three size parameters and refer to this value as 'body size'. 'Body size' explained 52.0% of variation in all body size measures and correlated positively with lengths of tarsus ($r = 0.64$), head with bill ($r = 0.81$) and wing ($r = 0.70$). Body weight can vary due to differences in nutritional stores, but also due to differences in structural body size. We, therefore, calculated residual weight, which in this study is the residual of regression of weight on body size ($R^2 = 0.15$, $N = 78$, $F_{1,77} = 13.51$, $P < 0.001$; weight = 169.5 + 3.94 × body size). Statistics were performed with SPSS for Windows (Norusis 1993).

Sound material and notes on individual recognition

This study is based mainly on 507 recordings (172 in 2001 and 335 in 2002), containing on average 107 ± 1.81 calls each (54 005 total calls). The number of recordings in both seasons were related to the abundance of corncrakes in the study area, not to recording effort. Estimation of actual corncrake abundance is difficult (Peake & McGregor 2001). Stowe and Hudson found that males called only on 75%–80% of nights, and that males may move between calling sites, sometimes more than 250 m (1988, 1991). In a dense population, like the one studied here, even the shorter movements may be a source of serious bias in census estimates because some males could be counted twice or more times at different sites and treated as different individuals (*see* Peak & McGregor 2001). Unfortunately, we also found that the method described by Peak *et al.* (1998) is unsuitable for individual recognition of larger, and *a priori* unknown, number of individuals.

The limitation is not with the method of analysing between-male variation of pulse-to-pulse duration (e.g. discriminant analysis, neural network), but with the nature of this variation. First, only the first dozen PPDs are individually stable. Second, following PPDs are not independent, but usually alternately have higher and lower values. Therefore, some part of PPDs variation results from autocorrelation between pulse duration not inter-individual divergence. Third, range of PPD variation is rather small, rarely exceeding 6 ms (Peak *et al.* 1998; T. S. Osiejuk *et al.* unpubl. data). Therefore, the more males we record, the greater the chance that we will find two or more males with indistinguishable PPD characteristics (T. S. Osiejuk *et al.* unpubl. data). In addition, we could not use capture-recapture methods, as males were captured using playback of calls to stimulate approach, which may not capture a random sample of the population (Peake & McGregor 2001). As such, we can only roughly estimate a minimum number of males on the basis of the number of calling males per census, and the number of caught males in 2002. Numbers of birds recorded in particular 10-day periods are shown in Fig. 3. The highest number of males we recorded during any 10-day census was 34 in 2001 and 66 in 2002. Birds were captured in one season only (2002), and we captured altogether 98 different males. Therefore, we can estimate minimal abundance of males as 100 in 2002 and, consequently, 50 in 2001.

Data from the six males recorded repeatedly during single nights were not used to explore the seasonal pattern of call variation. Bird measurements, including testosterone and haematocrit assays, were taken in 2002. We had these data for 80 males and twelve of these males were caught and tested (body weight, testosterone, etc.) twice during the season. Unfortunately, due to background noise, we have no recordings for some captured birds. To investigate the relationships between male properties and call output we used only recordings collected just before the male was captured. Therefore, the sample sizes (*N*) may differ between analyses.

Results

Relationships between temporal parameters of single calls and call series

Despite the apparently simple design of corncrake territorial vocalization, their elementary components, i.e. syllables and intervals, are quite variable (Table 2). Furthermore, variation of particular elements seems to be mutually dependent, regardless of the type of analysis (i.e. within- or between-performance variation of the same and different males). An analysis of a large sample of sound material revealed that there are problems with the defined call parameters. All problems, however, seem to be related to exceptions from relatively simple rules of call production. These rules could be presented as two inequalities: SYL1 < SYL2 and INT1 < INT2. Rarely, but in almost each longer recording, SYL1 may equal SYL2 and/or INT1 may equal INT2. Just as with other vocalizing animals, corncrakes sometimes produce atypical calls during longer performances (Podos 1996, 1997). The exceptions are easy to detect by measuring sonograms, but have no influence on perception of the signal as they appeared with a frequency below once per 100 calls. A typical example of such a mistake is omitting the second syllable of the call from time to time, or — less frequently — the first syllable. Exceptionally, INT1 could be longer than INT2, but when this happened the temporal relationship between syllables remained typical (i.e. SYL1 < SYL2), and in the next call the relationships between intervals returned to normal (i.e. INT1 < INT2). The second class of atypical vocalizations were calls with extremely shortened or elongated syllables (first or second, never both). We considered all such observations as typical but rare events (< 1% of calls) and did not remove them from analysis. These instances had no substantial influence on average values of parameters measured even for the shorter recordings.

Another problem concerns variable INT2. Namely, corncrake males sometimes make longer pauses between call series. In this paper we focused on relationships within a continuous series of calls, therefore we had to decide for which value of INT2 we assume that the series had finished. We arbitrarily choose value INT2 = 2.33 s, which was calculated as mean INT2 + 2SD, and covered 99.4% of measured calls. Accordingly, all calls with INT2 exceeding 2.33 s were assigned as terminal for the series and removed from the analysis.

Call rhythm changes within and between nights

Comparison of repeated recordings of the same males revealed that temporal parameters of

Table 3. Results of MANOVA model testing for the influence of 10-day period and year on four basic call parameters. (*N* = 507).

Call variable	10-day period		Year		Interaction	
	F	*P*	*F*	*P*	*F*	*P*
SYL1	4.314	< 0.001	0.186	0.667	0.265	0.953
SYL2	2.663	0.011	1.573	0.210	0.296	0.939
INT1	1.109	0.356	0.922	0.337	1.114	0.353
INT2	8.242	< 0.001	0.149	0.700	0.763	0.599

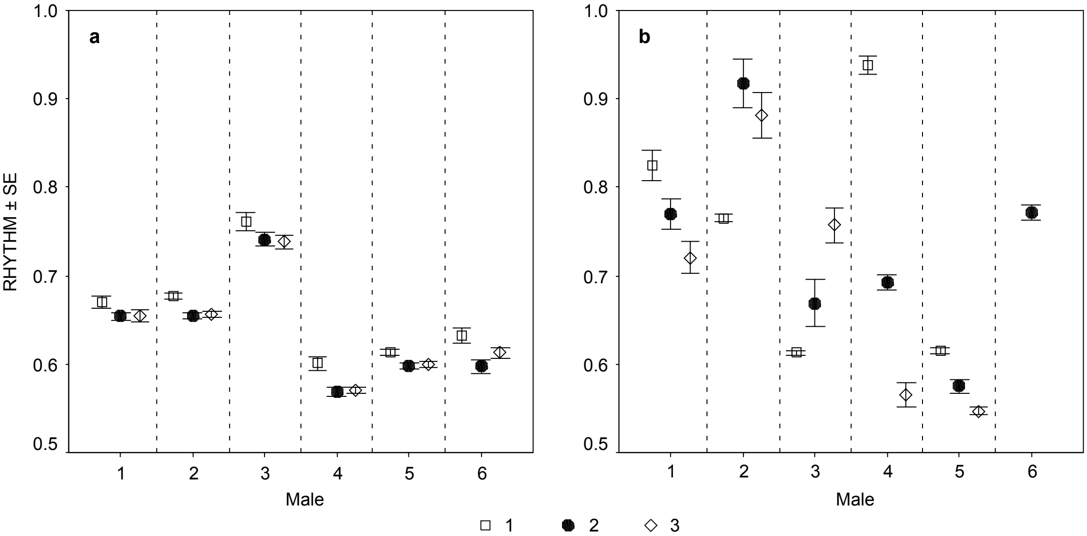

Fig. 4. — **a**: Mean (± SE) call RHYTHM of six males recorded three times during a single night (22 May 2002). Recording time: male 1 (23:00, 00:30, 03:00), male 2 (23:15, 00:45, 03:15), male 3 (23:30, 01:00, 03:30), male 4 (23:45, 01:15, 03:45), male 5 (00:00, 01:30, 04:00) and male 6 (00:15, 01:45, 04:15). — **b**: Mean (± SE) call RHYTHM of the same six males recorded three times (except male 6) with at least a 10-day interval between recordings during a single breeding season (2002). Sample sizes for each recording range between 64 and 150 calls.

calls (SYL1, SYL2, INT1, INT and RHYTHM) differed significantly both between males and between recordings within single night (repeated measures model; all $P < 0.001$). The recording of same males between nights also differed significantly (repeated measures model; all $P < 0.001$). However, the differences between nights are significantly larger (Fig. 4). Comparison of mean within-night (0.01–0.03) and between-night (0.18–0.57) differences of RHYTHM for five males indicates significant between-night changes in RHYTHM (Wilcoxon Signed Ranks Test, $Z = -2.023$, $N = 5$, $P = 0.043$).

Seasonal variation in call rhythm

All measured call parameters changed in the course of the season, and these changes were similar in both seasons of the study. In both seasons, average lengths of SYL1 and SYL2 decreased slightly but significantly (simple linear regression for SYL1 in 2001: $\beta = -0.266$, $F_{1,171} = 12.93$, $P < 0.001$; SYL2 in 2001: $\beta = -0.238$, $F_{1,171} = 10.23$, $P = 0.002$; for SYL1 in 2002: $\beta = -0.220$, $F_{1,334} = 16.93$, $P < 0.001$; and for SYL2 in 2002: $\beta = -0.156$, $F_{1,334} = 8.28$, $P = 0.004$; Fig. 5). Different patterns of change across seasons were observed for INT1 and INT2 (Fig. 5). Within-call interval exhibits a U-shaped curve with minimal values in mid-June. Similarly, INT2 decreased in length until mid-June and showed a slight increase after that. The main difference between the observed changes is that in the case of SYL1, SYL2 and INT1, the mean differences between extreme values were small, ca. 15–16 ms. In the case of INT2, the maximum mean differences between 10-day periods were an order of magnitude greater and amounted to 155 ms.

We used a MANOVA model to test the influence of time within a season (10-day periods) on all four variables describing the call simultaneously. To test the potential difference between both seasons of the study we put year into the model as a factor. The length of both syllables and between-call interval were significantly affected by the 10-day periods (Table 3). We found no statistically significant effect, and no significant interaction, between year and 10-day periods (Table 3). Consequently, we observed significant seasonal differences in all compound

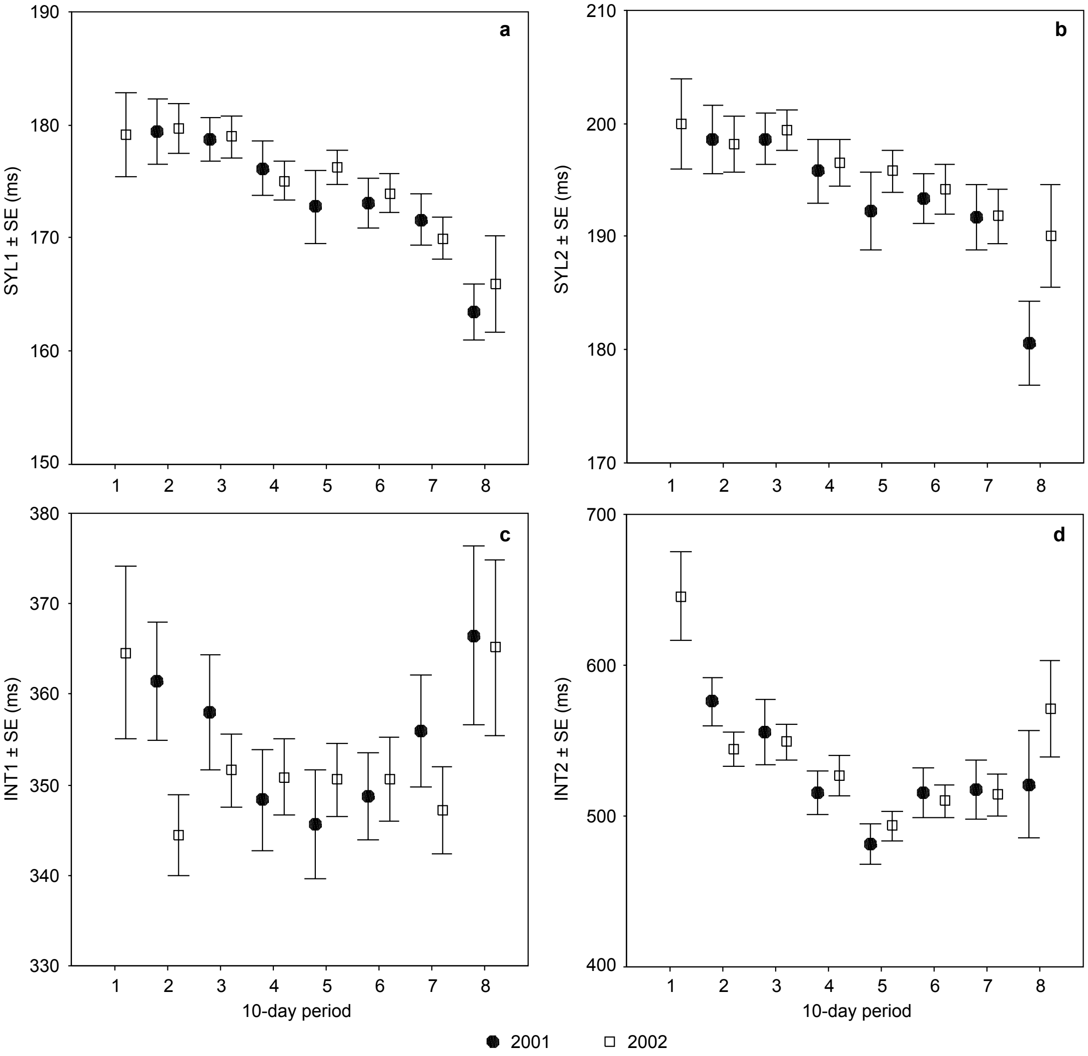

Fig. 5. Seasonal changes in length of (**a**) first call syllable (SYL1), (**b**) second call syllable (SYL2), (**c**) within-call interval (INT1), and (**d**) between-call interval (INT2) in 2001 and 2002. (1 = 1–10 May, 2 = 11–20 May and so on). For sample sizes *see* Fig. 3.

variables (Fig. 6; ANOVA, all $P < 0.01$ for 10-day period, all $P > 0.5$ for year, and $P > 0.3$ for interactions).

Call rhythm and individual variation

Comparisons of temporal call measurements between 10-day periods revealed changes in mean values of call parameters. This is presumably a combined effect of many contributors, which presumably differ with regard to condition, territorial status, mating status, etc. Therefore, we regressed call rhythm against body size, residual body weight, testosterone and hematocrit. The only significant predictor of RHYTHM was body size ($\beta = 0.319$, $t = 2.477$, $P = 0.016$). No significant correlations between body size, residual body weight, testosterone level and hematocrit were identified ($P > 0.05$ in all comparisons; Bonferroni adjustement applied). Plasma testosterone level differed significantly between successive 10-day periods (ANOVA: $F_{6,71} = 5.77$, $P < 0.001$). The highest mean level was observed in late May. We used an ANCOVA model with 10-day period

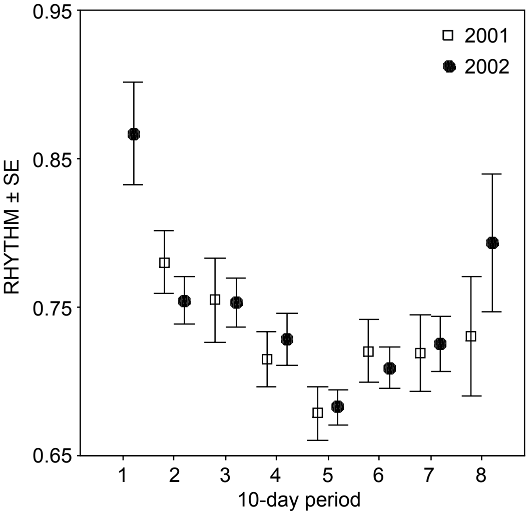

Fig. 6. Seasonal changes in mean (± SE) RHYTHM in 2001 and 2002.

as a factor and testosterone level, body size and residual body weight as covariates to test how these variables affect call RHYTHM. The only significant factor affecting call RHYTHM was body size ($F_{1,58} = 6.03$, $P = 0.018$).

Discussion

One of the most interesting findings of this study was that the relatively simple call demonstrated a seasonally repeatable pattern of variation with respect to temporal interdependencies between syllable and interval lengths. Our study shows that the temporal calling pattern represents a different level of variation, which may operate independently (in terms of possible functions and constraints) of overnight call output. This result corroborates some earlier findings of Mason (1940) and Owsiński (2002), which suffered from lack of sonogram analysis. In fact, we found two patterns of seasonal changes. First, both syllables within a call decreased in length during the course of the season. Second, both intervals and RHYTHM had U-shaped curves with the lowest values in mid-June. The majority of the variation depended on changes in INT2. Interestingly, human auditory perception can distinguish only between calls that differ markedly in the ratio of INT2 to CALL duration, but this must not be the case for birds that have a higher temporal resolution (Bradbury & Vehrencamp 1998).

The seasonal pattern of rhythm changes was found to be remarkably similar in both years (Figs. 5 and 6), although the abundance of males was markedly lower in 2001, and the beginning of territorial activity in 2001 was late due to a dry spring and delayed plant growth (Fig. 3). Variations in birds' acoustic signals are usually functional (Catchpole & Slater 1995). Early in the season, males were calling with an intermittent pattern (higher values of RHYTHM). Later in the season, most males switched to a regular, more monotonous pattern of calling (lower values of RHYTHM). The highest monotony (or lowest RHYTHM values) in both seasons were in mid-June, which coincided with breaking of pair-bonds after the first brood (Green *et al.* 1997, Owsiński 2002; B. Olech unpubl. data.). After that, call RHYTHM again became more intermittent, but not to the same degree as in the beginning of the season. The fact that RHYTHM reached the highest values or started to increase anew during crucial moments of the season (i.e. territory establishment and second breeding attempt) indicates that this parameter — intuitively chosen and defined on the basis of human auditory perception — is an adequate measure of the signal's information value for birds. The observed seasonal changes suggest that corncrake males encode some information by simply reduc-

Table 2. Variation in temporal parameters of corncrake calls (min, max, mean ± SD) calculated for averages of all recordings ($N = 507$). Additionally, extreme values of simple variables (SYL1, SYL2, INT1, INT2 and CALL) are given (these are not averages but values taken from raw measurements). In case of INT2 the longer values should be considered as stop of calls series, therefore maximal INT2 could be chosen only arbitrarily (indicated by ∞).

Variable	Averages min–max	Mean ± SD	Extremes of raw data
SYL1	139–215	176 ± 13.5	52–636
SYL2	158–242	196 ± 15.2	75–661
INT1	253–488	351 ± 31.6	154–818
INT2	340–919	528 ± 90.4	163–∞
SYL_R	1.01–1.29	1.12 ± 0.044	
INT_R	1.02–2.42	1.51 ± 0.236	
CALL	619–827	723 ± 0.037	530–1360
RHYTHM	0.49–1.27	0.73 ± 0.117	

ing or lengthening inter-call intervals, and consequently changing the RHYTHM of call output.

A continuous decrease in length of both syllables should, in our opinion, be related to a decrease in aggressive motivation during the season. On average, males 'lost' 15–20 ms of SYL1 and SYL2, which means that they cut off the last 2–3 amplitude pulses. It is known that the pattern of PPD is individually distinct, but only for the initial 11–13 pulses, and that the later pulses are more variable (Peake *et al.* 1998; T. S. Osiejuk *et. al.* unpubl. data). Therefore, reducing the number of syllables probably does not affect individual recognition of males. The pattern identified suggests that the later in the season, the less carefully males uttered their calls. Correspondingly, the RHYTHM was found to decrease slightly during the night, which also suggests that some potentially important 'fatiguing' processes occur on a shorter time scale (Fig. 4a). It is hard to discuss if and how this statistically significant decrease in syllable length is a biologically relevant signal. Comparison of repeated recordings of individually recognized males indicate that RHYTHM only slightly decreases during the night, but that greater changes of RHYTHM occur over time within a season. Our results indicate that the observed pattern of seasonal RHYTHM changes should not be linked exclusively with the stopping of calling by some fraction of males.

Although we found craking call to change seasonally with a very regular pattern, our data does not indicate that all males follow this general pattern. During all examined 10-day periods of breeding seasons, we identified males calling irregularly or monotonously. Naturally, the proportion of such males varied markedly. We expected that this variation would be related to some properties of males, such as body size, body condition or hormonal status. Indeed, our results show that body size affected RHYTHM significantly. This result was surprising, however, because repeated recordings indicated that males sometimes change RHYTHM in the course of season. As such, we expected that RHYTHM changes would follow those properties also likely to change during the season (e.g. testosterone level). Its seems then, that larger males tended to call more intermittent than smaller ones regardless of testosterone level and other factors.

As was shown experimentally by Owsiński (2002), intermittent calling caused an aggressive reaction in males, especially from those that also produced intermittent calls. Males producing monotonous calls were significantly less likely to aggressively approach the loudspeaker. We think that here is the point of craking-call function, especially if we focus on cost of signalling. Larger males more often behave aggressively, but this does not mean that it always pays to be aggressive when you are bigger than rivals. Present conclusions about energetic costs of bird vocalization are inconsistent (Lambrechts & Dhont 1988, Vehrencamp *et al.* 1989, Eberhardt 1994, McCarthy 1996, Oberweger & Goller 2001). However, in the case of craking call of corncrakes, it is very likely that the call is energetically expensive. First, it is very loud, audible from up to 1500 m, which means that the amplitude level at a distance of 1 m may exceed 100 dB SPL (Bradbury & Vehrencamp 1998). Second, males vocalize at a high rate and may produce 10 000 calls during the night (Green *et al.* 1997, Peake *et al.* 1998).

Our question, however, is how the energetic costs of signalling are related to changes in RHYTHM. Intermittent calling is associated with longer INT2, which means that the rate of calling decreases with higher values of RHYTHM. A decreased calling rate should indicate lower energy expenditures (Vehrencamp 2000). Therefore, the pattern of energy expenditures was opposite to predictions from sexual selection theory, or at least those predictions related to honest advertising (e.g. Clutton-Brock & Albon 1979, however compare also Maynard Smith 1994). It is possible that the amplitude of the signal is more important for overall energy expenditure than is the temporal pattern of the call. However, to our knowledge, monotonously and intermittently calling corncrake males do not differ in signal amplitude (B. Olech unpubl. data) and we should rather expect a positive correlation between different variables related to signalling cost.

Energy expenditure, of course, is not the only cost of vocalizing (Gaunt *et al.* 1996). There are many indirect costs of calling, such as increased predation, time loss, vulnerability to a receiver's attack or retaliation (Vehrencamp 2000). If the differences in signal production costs between intermittent and monotonous calling are small, we should consider whether call rhythm is a vulnerability handicap or conventional signal (Guilford & Dawkins 1995, Vehrencamp 2000). The pattern of variation identified here suggests that call rhythm might be a conventional signal. In such signals, the context differences are a result of arbitrary convention, 'an agreement' between sender and receiver about the optimal receiver response. Conventional signals usually concern intrasexual agonistic contexts and are stabilized by receiver retaliation or punishment rule (Vehrencamp 2000). In corncrake, calling with an intermittent RHYTHM might be a signal that is more expensive because of the receiver's retaliation. Experiments conducted by Owsiński (2002) support this hypothesis, as he found a relationship between the call rhythm and the response of the subject of a trial. These data fit conventional signal game models (Enquist & Leimar 1983). Corncrakes inhabit dense environment, in which visual evaluation of male size even from a relatively short distance is unlikely. In such a system, honest signalising of size may be stabilised by the risk of retaliation when calling with intermittent RHYTHM, as was shown by Owsiński (2002). The advantage of such a system may be that large males can call monotony when not aggressively motivated.

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