Ornis Fennica 83:27–33. 2006

Booming activity of male Bitterns *Botaurus stellaris* in relation to reproductive cycle and harem size

Marcin Polak

Dept. of Nature Conservation, Institute of Biology, Maria Curie-Skłodowska University, Akademicka 19, 20-033 Lublin, Poland. mpolak@hektor.umcs.lublin.pl

Received 13 September 2005, revised 28 November 2005, accepted 29 November 2005

The relationship between vocalization rate and nesting parameters in the polygynous Great Bittern *Botaurus stellaris* was studied in a breeding population of eastern Poland. There was a difference between individuals in mean length of boom train and males with high booming rate had longer boom trains. No correlation between the booming parameters and components of breeding success and harem size has been found. However, females settled earlier in the territories of males with early start of booming activity and high vocalization rates. The peak of the calling activity season was synchronised with the female fertility period. These results suggest that in relation to the laying date the seasonal pattern of booming indicates a mainly intersexual function of vocal activity among bitterns.

1. Introduction

The Great Bittern *Botaurus stellaris*, a vulnerable reedbed heron, is a poorly-studied, secretive species. Characteristic features of its ecology are the polygynous mating system and long-range vocalization. Most males are supposed to be territorial and have harems of one to five females (Gauckler & Kraus 1965, Cramp & Simmons 1977). However, males do not provide material benefits to females or their offspring and do not feed and rear nestlings; uniparental care and polygyny are unusual among herons (*Ardeidae*; Voisin 1991).

In the breeding season, males utter repetitive trains of signals (booms), filling the oesophagus with air, which is used as a soundbox (Voisin 1991, Puglisi *et al.* 2001). Males have a long seasonal period of booming activity which is supposed to serve as an advertising call for territorial defence and mate attraction (Cramp & Simmons 1977). Booming output is not constant within a breeding season (Puglisi *et al.* 1997, Poulin & Lefebvre 2003a), and booming season length is variable among sites, years and individuals (Gilbert *et al.* 1994, Puglisi *et al.* 2003). The function of the bittern vocal activity is not yet fully understood, although it has been the subject of recent studies (Gilbert *et al.* 1994, Puglisi *et al.* 1997, Puglisi *et al.* 2001, Poulin & Lefebvre 2003a, Poulin & Lefebvre 2003b, Puglisi & Adamo 2004).

Most of these studies are focused on the possibility to discriminate and re-identify individual males by their vocalizations. Male bitterns undergo seasonal anatomical modifications to produce their calls (Puglisi *et al.* 2001). Booms of different quality exist and they are distinguished as poor and full booms. The significance of poor booms and their mechanism of emission are unknown (Gilbert *et al.* 1994, Puglisi *et al.* 2001). The number of booms per boom train, boom duration, poor boom occurrence, time interval between booms are in some way related (Puglisi *et al.* 2001)

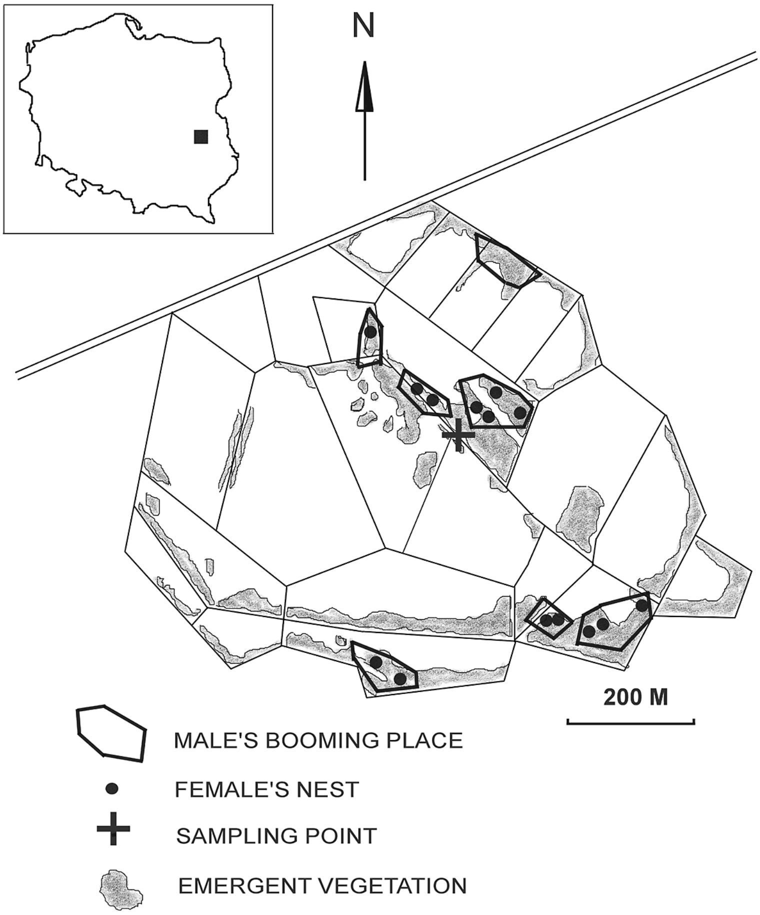

Fig. 1. Map of the study area (southern part of Samoklęski fishpond complex) and its location in Poland (box).

and are variable according to booming male density (Poulin & Lefebvre 2003a, Poulin & Lefebvre 2003b).

Due to the species decline in Western Europe (Tyler *et al.* 1998) and the difficulties involved in searching for nests, the previous investigations were limited by the lack of knowledge of breeding success. The principal aims of this study are twofold. (1), I determine the main function of booming by comparing the seasonal pattern of vocal output in relation to the nesting cycle. The changes in vocal output over the breeding period can be used to assess which of the functions prevail in a species. If vocal activity continues throughout incubation and the parental care period, then it is used mainly in territorial defence (intra-sexual functions). However, if the peak of vocalizations occurs in the pre-laying stage and then drops markedly it has inter-sexual functions (see review in Catchpole & Slater 1995). (2), I aim to determine the role of booming in mate choice by comparing booming attributes with attractiveness to females and breeding success. If females may select males according to their vocalizations (honest advertisement hypothesis, see Puglisi *et al.* 2001), we may expect that bitterns with the highest booming effort and long boom trains will be preferred by females because the intensive and energetically costly calling activity is a reliable indication of male quality. If females choose their mate based on the quality of their territories, the best of which are probably occupied first, we may expect that the early boomers are preferred by females. This explanation may be fulfilled simultaneously with the honest advertisement hypothesis. It is possible that high-quality territories are defended more vigorously and males in these territories may call more intensively.

2. Material and methods

2.1. Study area

The study of booming activity was carried in the breeding season of 2004 at the Common Carp *Cyprinus carpio* fishponds complex at Samokłęski (Lublin region, eastern Poland, N 51°27’ E 22°26’). The study area was 185.5 ha, however breeding bitterns were concentrated in the southern part of the complex (Fig. 1). Males of this species occupied small, isolated patches around ponds ranging in surface area from 2.1 to 9 ha. The ponds were partially covered (range 6–44%) by beds dominated by common reed *Phragmites australis*, reedmace *Typha angustifolia* and sedges *Carex sp.*

2.2. Sampling of vocalizations

Male bitterns repeated booms in series of one to ten (boom train). A boom consists of two elements: a first and a main element (McGregor & Byle 1992, Gilbert *et al.* 1994). The main element of the first boom is preceded by bill-clapping and a series of pumps. However, the first element and pumps seem to be linked to air intake (Voisin 1991). They are probably “functional” sounds and only the main element is assumed to play a major role in the vocalizations of bitterns (Puglisi *et al.* 2001). Some booms have less structured main elements: these are referred to as “poor booms” (Gilbert *et al.* 1994, Puglisi *et al.* 2001). The sampling methods were similar to the general procedure in studies of temporal patterns of booming in bitterns in France (see Material and methods in Poulin & Lefebvre 2003a). Between late March and mid-June, 12 (six dawn and six dusk) three h listening sessions were carried out with 2 weeks interval. The dates of the sessions were as follows: 29 March, 13–14 April, 29–30 April, 11–12 May, 28–29 May, 11–12 June. Booming activity was sampled in blocks of 180 minutes, from 2 h before to 1 h after sunrise and sunset. During each listening session, the following data were collected for all males within the study area: (1) time of the start of each boom train with accuracy to 1 minute (2) number of booms per boom train (3) number and position of poor booms. Sampling was made from a single central point on fishponds and the booming activity of each individual was recorded and noticed on paper from a distance of 10–500 m. The males were recognised on the basis of their location as well as of the characteristics of their booms. Observations were conducted in stable weather without strong winds or rainfall. Following Puglisi *et al.* (1997), I define “booming rate” as the number of boom trains uttered per unit of time and “booming effort” as the number of booms uttered per unit of time.

2.3. Nesting success

During each visit to the study area all male call locations were plotted onto a 1:5,000 map. Special attention was paid to record the position of simultaneously active birds on a cumulative map and borders of booming places of individual males were delimited by use of the Minimum Convex Polygon method (Kenward 1987). All male booming areas were checked at least once a week from mid-April to the end of June to obtain data on nest location, egg-laying dates, clutch size, hatching date and productivity. The number of females that have built a nest and laid at least one egg in the areas occupied by a booming male corresponds to the size of its harem. The date of laying the first egg was calculated mainly from the hatching date of the first nestling, assuming an incubation period of 26 days (Cramp & Simmons 1977, Mallord *et al.* 2000). In one case it was impossible to determine the date of laying the first egg. In 2004 on Samokłęski fishponds egg-laying occurred from 19 April to 10 May (N = 13 nests) and the first youngs hatched between 18 May and 2 June (N = 8 nests). The vocalizations parameters were compared between the pre-laying (six listening sessions from 29 March to 10 May) and post-laying (six listening sessions from 11 May to 11 June) seasons. Early productivity was estimated in the first week after hatching, because young bitterns after this time can disperse from the nest into the dense vegetation during nest checking.

3. Results

3.1. General pattern of booming activity

The duration of the booming period was 86 days (from 19 March to 12 June 2004) in the Samokłęski area. Bitterns produced more vocalizations in the morning than in the evening (Fig. 2). I analysed 1988 boom trains, containing 9961 booms. Booming effort and booming rate were highest during the pre-laying phase in the second half of April and then dropped markedly after egg laying. Characteristics of the vocalizations of all males in the pre- and post-laying season are shown in Table 1. The six males produced more booms before the laying period. However, comparing the booming effort before and after start of incubation, call activity dropped significantly for two of seven males (Table 2). Four bitterns (A, B, D, E) were active during the whole study period, male "C" was booming for 2.5 months, male "F" for 2 months and male "G" had the shortest booming activity period – 1 month. The average length of the boom train differed significantly (Kruskal Wallis test $H_{6,\ 1988}$ = 231.1; $P < 0.001$). There was a positive relationship between booming rate and average number of booms per boom train (Spearman's rank correlation $r_S = 0.85$, $n = 7$, $P < 0.05$).

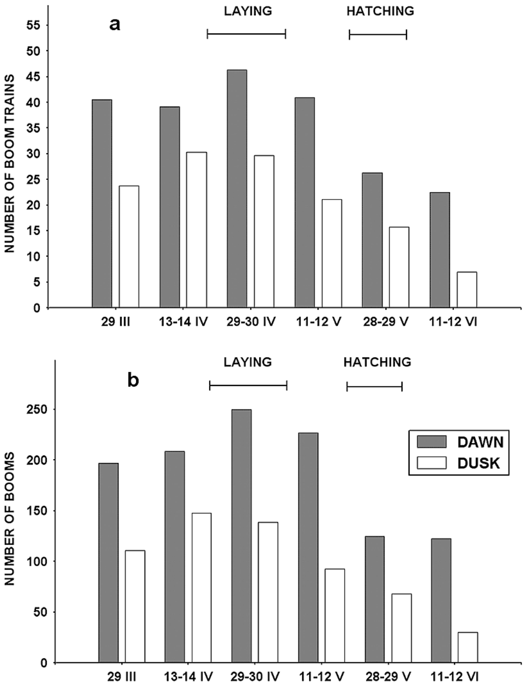

Fig. 2. The seasonal pattern of booming rate (a) and booming effort (b) of the seven male bitterns in relation to the laying- and hatching-period in 2004. The booming rate is presented as the mean number of boom trains per listening session and the booming effort is presented as the mean number of booms per listening session.

3.2. Booming activity vs breeding parameters

Males attracted 14 females and the number of nests per individual male booming area was 2.0 ± 1.3 (range 0–4). The breeding parameters for females nesting within booming areas of different males are shown in Table 3. The booming effort in the pre-laying phase was not correlated with the

Table 1. The booming activity parameters of male bitterns in the pre- and post-laying period (see details in Material and methods).

Code of male	Number of all booms		Number of all boom trains		Boom train length		Percentage of poor booms to all booms (%)	
	Pre-laying	Post-laying	Pre-laying	Post-laying	Pre-laying	Post-laying	Pre-laying	Post-laying
A	1558	1175	289	221	5.4	5.3	6.3	28.2
B	1389	517	258	111	5.4	4.7	5.0	3.5
C	952	450	192	93	5.0	4.8	18.2	2.9
D	681	236	147	52	4.6	4.5	7.2	3.0
E	743	288	162	66	4.6	4.4	3.8	0.7
F	672	874	132	165	5.1	5.3	10.4	8.4
G	274	152	63	37	4.3	4.1	75.2	80.9

Table 2. Comparison of the booming effort of males bittern in the pre- and post-laying period by use Wilcoxon matched pairs test.

Code of male	Booming effort (mean number of booms/30 minutes)			
	Pre-laying period (SD)	Post-laying period (SD)	Z value	Significance
A	43.3 (31.3)	32.6 (36.7)	4.06	P < 0.001
B	39.7 (33.9)	24.6 (18.2)	1.22	P = 0.223
C	28.8 (19.0)	25.0 (25.9)	0.23	P = 0.816
D	22.0 (17.6)	16.9 (13.6)	1.64	P = 0.101
E	24.8 (19.6)	19.2 (16.4)	2.80	P < 0.01
F	32.0 (25.0)	41.6 (49.0)	0.54	P = 0.590
G	24.9 (12.5)	25.3 (23.8)	0.52	P = 0.600

harem size ($r_S = 0.11$, n = 7, P = 0.812), nor to the number of nestlings per nest ($r_S = 0.44$, n = 7, P = 0.381). The harem size did not correlate with boom train length (mean number of booms per boom train) before egg laying ($r_S = 0.09$, n = 7, P = 0.841). However, females tended to nest earlier in the areas occupied by males with an early start of booming activity (Fig. 3a; $r_S = 0.59$, n = 13, P < 0.05) and high vocal output (Fig. 3b; $r_S = -0.65$, n = 13, P < 0.05).

3.3. Production of poor booms vs breeding parameters

All bitterns uttered poor booms with frequencies ranging from 2.9% to 77.2% (mean = 12.8%). The proportion of poor booms over the breeding season was low (4.8%–14.8%) with the exception of the first half of June (95.2%) when the four males still active output only boom trains with poor booms. There was a negative relationship between the female's preferences for males and the proportion of poor booms in the pre-laying season, however this was not statistically significant (Fig. 4; $r_S = -0.63$, n = 7, P = 0.13).

4. Discussion

Booming behaviour is thought to have an intersexual function as well as that of territorial defence (Cramp & Simmons 1977, Voisin 1991). In a previous study conducted in the Mediterranean area (Puglisi *et al.* 1997), a second peak in booming activity was found just before the end of the booming season and it was suggested that booming could contribute to the defence of a feeding territory during the nestling period. In contrast, the seasonal pattern of booming described in this

Table 3. The harem size and the breeding parameters of females in territories of male bitterns.

Code of male	Harem size	Mean date of laying the first egg (1=1 January)	Number of eggs/nest	Number of nestlings/ nest	Number of nestlings/ successful nest	Number of nestlings of all females
A	4	114.5	4.7	3.25	4.3	13
B	2	122	3.5	3.0	3.0	6
C	0	–	–	–	–	–
D	2	123	5.0	1.5	3.0	3
E	3	122	4.5	3.0	4.5	9
F	1	120	5.0	0	0	0
G	2	128.5	5.0	0	0	0

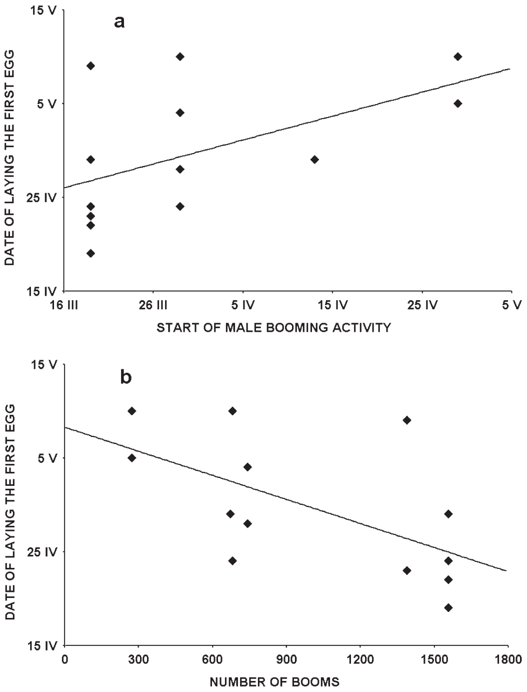

Fig. 3. Date of female's start nesting in relation to the first date of the booming activity (a) and number of all booms uttered by males in the pre-laying period (b).

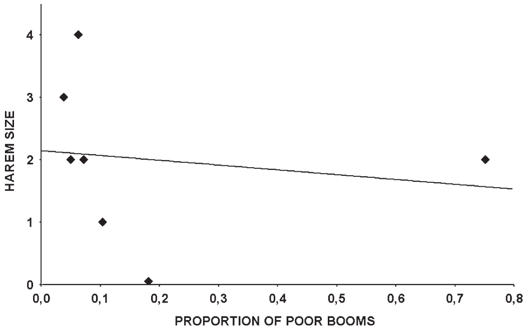

Fig. 4. Relationship between the male's proportion of poor booms and harem size.

study suggests a function related to mate attraction. It has been assumed that females are fertile during the laying period (Birkhead & Møller 1991). The booming rate and effort was highest in the pre-laying phase and decreased drastically after the start of egg-laying. In addition, females settled earlier in territories of males with an early start of booming activity and having a high vocalization rate. Males that started booming earlier had higher booming effort in the pre-laying period, probably because males need some time to modify the anatomical structures involved in sound production (see Puglisi *et al.* 2001).

This study presents the first evidence of a relationship between the booming activity and reproductive success of bitterns. The results should be used with caution due to the small sample size. It is possible, however, that female choice cannot be explained only by the differences among male vocalization rate, boom train length or poor boom occurrence. Females can choose nest sites as a function of habitat parameters such as prey availability or territory quality in terms of the risk of predation (a resource defense polygyny *sensu* Ostfeld 1987). Additionally, abundance of food near the nest site is very important for female bitterns during the whole breeding period although in the early phases of chick rearing the need to leave the brood unattended is particularly urgent. It was found that female bitterns can catch food directly from the nest (Adamo *et al.* 2004).

The high density of calling males could mask the honesty of vocalization as a possible signal of male quality for females. In a nocturnal species, the Eagle Owl *Bubo bubo*, the duration and rate of calling represents an honest signal of the phenotypic and genetic quality of individuals (Penteriani 2003). However, male-male vocal competition may be one of the confounding factors making it difficult to detect an effect of male quality. In Camargue (France) significant differences were found in the average length of boom trains and booming rates at sites with low and high bittern density (Poulin & Lefebvre 2003b).

The present study shows that early boomers with high vocalization rate attracted earlier laying females. This could be linked to the benefit of these males, because it is generally accepted that late breeding may reflect poor breeding performance resulting in few recruits (Barba *et al.* 1995).

The breeding biology of the bittern differs from other herons in that the male is emancipated from brood care and the lack of a pair bond. The mating system where a female feeds her brood alone may have evolved only in species inhabiting high-productivity habitat (Schulze-Hagen *et al.* 1999). Fishponds with reedbeds have very high productivity and contained almost unlimited feeding resources for the bittern. In relation to different habitats and parts of the species range, bitterns might choose between different strategies such as resource defense polygyny and an exploded lek mating system (see Jiguet *et al.* 2000). The differences in these reproductive strategies should reflect differences in booming male density and length of the booming season, which in turn correspond to limiting resources (food, safe nesting areas) and how they are distributed in time and space. In conclusion, this hypothesis should be tested in further studies carried out under different ecological situations.

Acknowledgements. I would like to thank Jola Polak and Adam Lesiuk for assistance in the field. My special thanks go to Luca Puglisi and Brigitte Poulin for useful comments on the manuscript.

Ääntelyn aktiivisuus suhteessa lisääntymiseen ja haaremin kokoon kaulushaikaralla (*Botaurus stellaris*).

Moniavioisen kaulushaikaran ääntelyaktiivisuuden suhdetta lisääntymiseen tutkittiin Itä-Puolassa. Yksilöiden törähdysten pituudessa oli eroja ja koiraat, jotka olivat aktiivisimpia päästivät myös pisimmät törähdykset. Ääntelyaktiivisuus tai törähdysten pituus eivät kuitenkaan korreloineet lisääntymismenestyksen tai haaremikoon kanssa. Naaraat asettuivat kuitenkin aiemmin aktiivisesti ääntelevien ja ääntelyn aikaisemmin aloittavien yksilöiden reviireille. Ääntelyaktiivisuuden huippu ajoittuu naaraiden hedelmälliselle jaksolle. Tulokset viittaavat siihen, että ääntelyn aktiivisuus vaihtelee suhteessa pesinnän ajoittumiseen ja että sillä on lähinnä merkitystä sukupuolten välisessä kanssakäymisessä.

References

Adamo, M.C., Puglisi, L. & Baldaccini, N.E. 2004: Factors affecting Bittern Botaurus stellaris distribution in a Mediterranean wetland. — Bird Conservation International 14: 153–164.

Barba, E., Gil-Delgado, J. & Monrós, J.S. 1995: The costs of being late: consequences of delaying great tit Parus major first clutches. — Journal of Animal Ecology 64: 642–651.

Birkhead, T.R. & Møller A.P. 1991: Sperm competition in birds. Evolutionary causes and consequences. — Academic Press. London.

Catchpole, C.K. & Slater, P.J.B. 1995: Bird Song. — University Press, Cambridge.

Cramp, S. & Simmons, K.E.L. 1977: The Birds of the Western Palearctic, Vol.1. — Oxford University Press, Oxford.

Gilbert, G., McGregor, P.K. & Tyler, G. 1994: Vocal individuality as a census tool: practical considerations illustrated by a study of two rare species. — Journal of Field Ornithology 65: 335–348.

Jiguet, F., Arroyo, B. & Bretagnolle V. 2000: Lek mating systems: a case study in the Little Bustard Tetrax tetrax. — Behavioural Processes 51: 63–82.

Kenward, R.E. 1987: Wildlife radio-tagging: equipment, field techniques and data analysis. — Academic Press, London.

Mallord, J.W., Tyler, G.A., Gilbert, G. & Smith, K.W. 2000: The first case of successful double brooding in the Great Bittern Botaurus stellaris. — Ibis 142: 672–675.

McGregor, P.K. & Byle, P. 1992: Individually distinctive bittern booms: potential as census tool.—Bioacoustics 4: 93–109.

Ostfeld, R. S. 1987: On the distinction between female defense and resource defense polygyny. — Oikos 48: 238–240.

Penteriani, V. 2003: Breeding density affects the honesty of bird vocal displays as possible indicators of male/territory quality. — Ibis 145 (on-line), E127–E135.

Poulin, B. & Lefebvre, G. 2003a: Optimal sampling of booming Bitterns Botaurus stellaris. Ornis Fennica 80: 11–20.

Poulin, B. & Lefebvre, G. 2003b: Variation in booming among Great Bitterns Botaurus stellaris in the Camargue, France. —Ardea 91: 177–182.

Puglisi, L., Cima, O. & Baldaccini, N.E. 1997: A study of the seasonal booming activity of the Great Bittern Botaurus stellaris; what is the biological significance of the booms? —Ibis 139: 638–645.

Puglisi, L., Pagni, M., Bulgarelli, Ch. & Baldaccini, N. E. 2001: The possible functions of calls organization in the bittern (Botaurus stellaris). — Italian Journal of Zoology 68: 315–321.

Puglisi, L., Adamo, C. & Baldaccini, N.E. 2003: Spatial behaviour of radio-tagged Eurasian bitterns Botaurus stellaris.—Avian Science 3: 133–143.

Puglisi, L. & Adamo, C. 2004: Discrimination of individual voices in male Great Bitterns (Botaurus stellaris) in Italy. — Auk 121(2): 541–547.

Schulze-Hagen, K., Leisler, B., Schäfer, H.M. & Schmidt, V. 1999: The breeding system of the Aquatic Warbler Acrocephalus paludicola – a review of new results. — Vogelwelt 120: 87–96.

Tyler, G.A., Smith, K.W. & Burges, D.J. 1998: Reedbed management and breeding Bitterns Botaurus stellaris in the UK. — Biological Conservation 86: 257–266.

Voisin, C. 1991: The herons of Europe. — Poyser, London.