BioOne COMPLETE

Environmental variables predict timing of breeding in the polygynous Eurasian bittern Botaurus stellaris

Authors: Kasprzykowski, Zbigniew, and Polak, Marcin

Source: Folia Zoologica, 63(3) : 188-193

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/fozo.v63.i3.a6.2014

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Folia-Zoologica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Folia Zool. – 63 (3): 188–193 (2014)

Environmental variables predict timing of breeding in the polygynous Eurasian bittern *Botaurus stellaris*

Zbigniew KASPRZYKOWSKI[1]* and Marcin POLAK[2]

[1] *Department of Ecology and Environmental Protection, University of Natural Sciences and Humanities in Siedlce, Prusa 12, 08-110 Siedlce, Poland; e-mail: zbigniew.kasprzykowski@uph.edu.pl*
[2] *Department of Nature Conservation, Maria Curie-Skłodowska University, Akademicka 19, 20-033 Lublin, Poland*

Received 14 March 2014; Accepted 14 October 2014

Abstract. The timing of clutch initiation in migratory birds is determined by many factors and affects fitness. In polygynous species the date of egg laying may also be determined by mating status. In order to identify the habitat factors enabling Eurasian bittern females to breed early, a study was carried out on nine fishpond complexes in eastern Poland during 2003-2009. The habitat characteristics of the nesting sites, including fish stock type and the breeding success were recorded for 48 monogamous, 31 primary, 30 second and 12 third or fourth females. The analysis showed that early nesting females preferred a higher density of old reed stems and chose less attractive ponds with poorer food resources. Monogamous and primary females laid first eggs eight days earlier on average and had higher breeding success than the second, third and fourth females. The relationship between the fate of broods and the breeding success of neighbouring nests was found for second females. Our results suggest that Eurasian bittern females benefit from early nesting, provided they can find appropriate vegetation at the nesting site.

Key words: early nesting, fate of brood, fishpond, habitat quality, polygyny

Introduction

The timing of breeding can strongly affect fitness of many bird species (Lack 1968). Generally, early breeders enjoy a higher reproductive success than later ones (Price et al. 1988). The benefits and potential costs of early breeding may be especially pronounced in single-brooded birds (Svensson 1995). If birds start breeding too early, they run the risk of the eggs hatching before the food supply is optimal. In addition, laying eggs under harsh conditions early in the season increases energy costs (Perrins 1970). On the other hand, nest predation is another strong selection pressure forcing the early timing of reproduction, since re-nesting is then possible if the first clutch has failed (Svensson 1995). Moreover, many external factors, such as climate, territory quality and mating system, as well as internal ones like age, body condition and genetic differences among individuals, determine the date of egg laying (e.g. Sheldon et al. 2003, Gonzalez-Solis et al. 2004, Elmberg et al. 2005, Casagrande et al. 2006, Rubolini et al. 2007, Dobson et al. 2008).

The nesting of migratory birds in high latitudes should be relatively synchronous and peak when food conditions are optimal for chick rearing (Lack 1968). However, females generally turn up in the nesting areas in temporal waves after the males. Timing differences in the arrivals of females influence the start of nesting and may determine their status within a male territory (Orians 1969). Females sharing one male's territory often compete with each other for male parental care or resources, and such intrasexual competition may adversely affect reproductive output (Verner & Willson 1966, Lubjuhn et al. 2000, Moreno et al. 2002). Selective pressure on lower mating status females is particularly noticeable in species with biparental care of the young (Bensch 1996, Searcy & Yasukawa1996, Huk & Winkel 2006).

In the Eurasian bittern *Botaurus stellaris*, a polygynous species, parental care on the part of the male is occasional, if it occurs at all (Voisin 1991, Klejdus 2007). The long-range vocalisation of the male is thought to serve as an advertising call for territorial defence and mate attraction (White et al. 2006).

* *Corresponding Author*

Downloaded From: https://complete.bioone.org/journals/Folia-Zoologica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Booming season length is variable among sites, years and individuals (Gilbert et al. 1994, Puglisi et al. 2003) and could be an important indicator for females in mate choice (White et al. 2006). Consequently, the males best able to signal their presence to females may attract more mates (see Dale & Slagsvold 1990). However, no correlation has been found between booming parameters, and components of breeding success and harem size (Polak 2006).

In different European populations of the Eurasian bittern, from one to five female nests have been found within male territories (Puglisi & Bretagnolle 2005). On the fishponds of eastern Poland, in contrast to other habitats, clumped nesting is a common strategy and more than half the females nest in harems (Kasprzykowski & Polak 2013). In single nests (monogamous females), the first eggs were laid earlier than in the clustered nests (polygynous females), and the first-egg laying period was longer in nest clusters than in single nests (Kasprzykowski & Polak 2013). However, there were no differences in other reproductive parameters between these two categories of female. Owing to the severe winter in eastern Poland, first-egg laying is somewhat delayed and better synchronised than in west European populations; it is also correlated with the start of the booming period (Polak & Kasprzykowski 2010). Other factors favouring early nesting have not yet been analysed, however.

The aims of this study are to identify the factors allowing a female to breed early and to examine the effects of early nesting. One of our hypotheses is that the first-egg laying date depends on habitat quality. We expect that some habitat parameters could accelerate the onset of breeding. Because nesting time determines mating status of females in the polygynous system, we also include this aspect in the analysis. The second hypothesis is that the success of nests is linked with female category and the fate of neighbour females. We expect that late secondary females have lower success corresponding to the success of neighbouring nests.

Material and Methods

Study area and field procedures

The study was carried out in eastern Poland on nine fishpond complexes stocked with common carp *Cyprinus carpio*. The ponds varied in area from 15 to 203 ha; their combined area was 815 ha. Most ponds were extensively managed and partially covered by discrete stands of vegetation dominated by common reed *Phragmites australis*, lesser bulrush *Typha angustifolia* and sedges *Carex* sp. The mean density of the bittern breeding populations on these ponds ranged between 4.6 ind./100 ha for males and 5.2 ind./100 ha for females (Polak & Kasprzykowski 2009). The study areas were surveyed from the beginning of March to early July from 2003 to 2009. Nests were located by systematic walking through the emergent vegetation, not only in the booming males' territories. Special efforts were made to find nest clusters, and the surroundings of every nest found were searched. In a large reedbed, this was an area within a radius of 100 m from the nest. The positions of all the nests found were recorded on a 1:5000 scale sketch map of the area, and the coordinates of all the nests were obtained by GPS. During the chick-rearing period five inspections of the nest contents were usually made within the first 20 days of hatching. In the majority of nests the first-egg date was established by backdating, assuming 25-26 days for incubation (Mallord et al. 2000, Demongin et al. 2007, Longoni et al. 2007). To eliminate the year effect, the data were standardised against the median of the first egg date in the population in each year. Because two-week-old bitterns can disperse from the nest into the dense vegetation, nests were defined after Puglisi & Bretagnolle (2005) as being successful when at least one young bird had survived up to 15 days old. Females were assigned to four categories: monogamous (single female without cluster effect), primary (the first females hatching and feeding nestlings in cluster), second (females hatched later than primary) and third/fourth (females hatched later than the second ones) (see Sejberg et al. 2000, Huk & Winkel 2006, Kasprzykowski & Polak 2013). We collected data on the breeding parameters of 48 monogamous, 31 primary, 30 second and 12 third/fourth females. The distances between the nearest active nests were measured using a tape or GPS and the nests closest each other were treated as neighbouring. Five habitat parameters which may govern the nesting of females on a specific semi-natural habitat like fish ponds were recorded (Polak 2007, Polak et al. 2008, Table 1). We used the methodology applied in studies of the Eurasian bittern in the UK (Tyler et al. 1998, Gilbert et al. 2005) with some modifications (Kasprzykowski & Polak 2013). The microhabitat variables, i.e. water depth and the number of dry and green reed stems, were measured in 126 quadrats (50 × 50 cm) placed around the nests. The macrohabitat parameters, i.e. distance to open water and distance to the fishpond dyke were measured from aerial photographs (GEOPORTAL, www.geoportal.gov.pl). All the measurements were made from the end of April to the end of May. Due to seasonal variation in water level, water depth

Downloaded From: https://complete.bioone.org/journals/Folia-Zoologica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

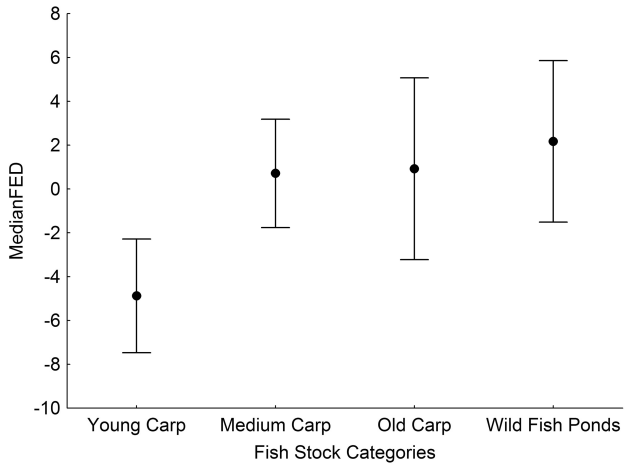


Fig. 1. Standardised median first-egg date (points) with 95 % CI (whiskers) in ponds with three common carp age classes: young-of-year (N = 16), medium carp (N = 73), 2-year old carp (N = 13) and wild fish pond (N = 23).

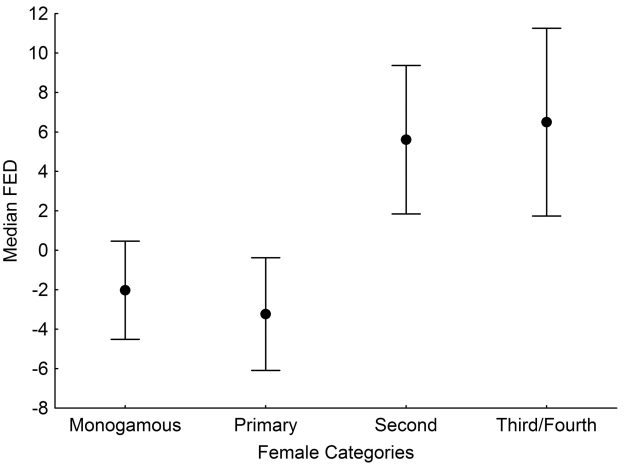


Fig. 2. Standardised median first-egg laying date (points) with 95 % CI (whiskers) in monogamous (N = 48), primary (N = 31), second (N = 30) and third/fourth females (N = 12).

Table 1. Mean, standard deviation (SD) and the range of habitat variables measured at Eurasian bittern nests (n = 126).

Variable	Mean	SD	Min-max
Water depth (cm)	45.0	16.92	9-97
Number of dry reed stems (n)	18.8	15.15	0-85
Number of green reed steams (n)	10.7	10.83	0-42
Distance to open water (m)	30.8	22.64	4-114
Distance to fishpond dyke (m)	29.2	26.19	6-138

under nests was recorded during the first visit at the beginning of breeding period. In a specific habitat type like fishpond complexes, an important factor related to food resources is the common carp year-class (Kasprzykowski & Polak 2013). Therefore, the fish stock in the separate ponds with active nests was used as a proxy of food abundance. After Kloskowski (2009), we divided common carp into three year-classes: young-of-year carp with individual weights of 1.5-3.0 mg, to reach 8-15 g in early July; medium carp after first wintering at 30-50 g, 2-year-old-carp at 150-240 g and wild fish ponds, with different species and different age categories.

Statistical analysis

General Linear Model (GLM) with identity link function and normal error distribution was used to test first hypothesis stated in the introduction (Crawley 1993). The standardised first-egg laying date was treated as a dependent variable. Five continuous habitat parameters and four categories of fish stock were used as independent variables. Multi-co-linearity of variables was checked and correlations between them were < 0.6. To verify the second hypothesis, Generalized Linear Model (GLZ) with logit link function and binomial distribution was used (McCullagh & Nelder 1989). The fate of brood (1 – success, 0 – loss) was dependent variable in the model and female mating status and success of neighbouring nest were the

Table 2. General Linear Model test of the influence of environmental parameters on the standardised first-egg laying date of Eurasian bittern females.

Variable	Parameter estimate	SE	t	P
Intercept	18.20	3.06	5.94	< 0.001
Young carp	–4.77	1.87	2.55	0.012
Medium carp	1.60	1.23	1.31	0.194
Old carp	–0.11	2.14	0.04	0.961
Wild pond	0	0	0	-
Water depth	–0.07	0.04	1.38	0.169
Number of dry reed stems	–0.19	0.06	3.15	0.002
Number of green reed steams	0.10	0.08	1.25	0.213
Distance to open water	0.04	0.04	0.88	0.381
Distance to fishpond dyke	–0.04	0.03	1.07	0.286

Downloaded From: https://complete.bioone.org/journals/Folia-Zoologica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Table 3. Generalized Linear Model test of the influence of female mating status, the fate of neighbour nest and their interaction on success of Eurasian bittern females.

Variable	Parameter estimate	SE	Wald statistic	P
Intercept	–0.47	0.27	3.09	0.078
Monogamous females (M)	–0.41	0.35	1.34	0.246
Primary females (P)	–0.39	0.42	0.88	0.349
Second females (S1)	1.02	0.49	4.28	0.039
Third and fourth females (S2)	0	0	0	-
Success of neighbouring nests (SN)	0.67	0.27	6.22	0.013
Loss of neighbouring nests (LN)	0	0	0	-
M * SN	–0.64	0.35	3.27	0.071
P * SN	0.33	0.42	0.62	0.432
S1 * SN	0.98	0.49	3.90	0.048

predictors. In addition, ANOVA was used to compare first-egg laying date in four categories of female mating status. Statistical processing was performed using the STATISTICA 10.0 package (Statsoft Inc. 2011).

Results

The first analysis showed that the first-egg laying date was negatively related with the number of old reed stems (Table 2). The other four habitat parameters: water depth, the number of green reed stems, the distance to open water and the distance to fishpond dyke did not have a significant effect. However, ponds with young-of-year carp negatively affected the onset of reproduction in female bitterns. The other three categories of fish stock: medium carp, 2-year-old-carp and wild fish ponds were not related with the first-egg laying date. In nests situated on ponds with the youngest fish, the first eggs were laid five days earlier on average than in the other ones (Fig. 1).

Accounting for female mating status showed that monogamous and primary females laid first eggs eight days earlier on average than the second, third and fourth females (ANOVA $F_{3,118} = 8.60$, $P < 0.001$, Fig. 2). Moreover, the breeding success in monogamous and primary nests was higher (70.8 %, 71.0 % respectively) than in those of second (53.3 %) and third/fourth females (58.3 %). These differences between female categories were supported by GLZ analysis (Table 3). The success of nest was found to be associated with the breeding success of neighbouring nests. However, the interaction between both predictors was significant and positive only for second nest category but no such relationship was recorded for monogamous and primary females.

Discussion

Although the Eurasian bittern inhabits a wide spectrum of habitats, reedbeds are still the most important nesting sites (White et al. 2006). Evolutionary adaptation to breeding in this kind of habitat is manifested by the perfect camouflage of the female plumage. Therefore, old (dry) reed stems play an important role in choosing nesting sites (Polak et al. 2008). The present study shows that this habitat parameter is also associated with early breeding. In the second part of April, when Eurasian bittern females begin nesting, water bodies are devoid of green emergent vegetation and, crucially, have just the right density of dry stems to mask the female on the nest. Water depth and other macrohabitat parameters appear to have a lesser effect on the timing of breeding. In turn, the richness of food resources, analysed as a qualitative factor of fish stock, affected the females' timing of breeding. We found a negative relation between the first-egg laying date and young-of-year common carp. Ponds with fish of this age class are unattractive compared to the one-year class (medium) and were sparsely populated by clustering females, because of the very small weight of the fish (Kasprzykowski & Polak 2013). On the other hand, one quarter of the monogamous females nested on this category of pond. This negative preference could be explained by the fact that solitary females belong to the group of early breeders, together with primary females. The late-nesting group included females of lower mating status in the polygynous system. Second, third and fourth females laid their first eggs relatively simultaneously and significantly later after the monogamous and primary females. These results suggest that Eurasian bittern females start breeding in two waves. When choosing nesting sites, early females are guided mostly by the densities of old stems and settle in less attractive habitats. In contrast, late females build nests on ponds offering a more suitable category of fish stock. Some late females may re-lay after a failed first clutch. Replacement clutches seem to be a fairly common behaviour in the Eurasian

Downloaded From: https://complete.bioone.org/journals/Folia-Zoologica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

bittern, especially when nest failure occurs before the end of May (Dmitrenok et al. 2005).

Avoidance of aggression could explain the significant differences in the first-egg laying date between primary females and second, third and fourth ones that settled at the same time in a male territory (Slagsvold & Lifjeld 1994). Secondary females should benefit from the reduction in breeding overlap with primary females because resident females are usually the most aggressive during the early stages of breeding. Generally, aggression towards a female intruder is a reaction to the theft of materials, the displacement of the resident female from the nesting site and mate, the destruction of eggs or young, nest parasitism, increased nest predation as well as reduced investment in nest guarding by the male parent (Slagsvold & Lifjeld 1994). However, during our research we did not observe any aggression between females.

Our study shows that early nesting monogamous and primary females have higher breeding success. The greater total losses in polygynous bird species are most plausibly explained by the males' withholding paternal care from secondary broods and the frequently suboptimal food conditions available to late-breeding secondary females (Lubjuhn et al. 2000). These two factors may be of much less importance to a bittern population nesting on fishponds. Extensive fish management and abundant food resources were most likely responsible for the good breeding parameters obtained for this population and favoured the polygynous system of reproduction (Polak & Kasprzykowski 2010, Kasprzykowski & Polak 2013). Moreover, because bittern females do not normally receive help from males in the care of the young (Puglisi & Bretagnolle 2005), intrasexual competition appears to be reduced.

We found that the fate of secondary broods was linked with the breeding success of neighbouring nests, but no such relationship was recorded for primary nests. These results suggest increasing predation pressure during the lengthening breeding period when secondary females are nesting in a cluster. Another study showed that nearest-neighbour nests of waterfowl tended to share the same fate, suggesting that cluster nests either survived or were depredated as a group (Ringelman et al. 2012). Therefore, early and solitary (before cluster formation) bittern females seem to be less exposed to failure resulting from predation. For cryptically coloured birds such as Eurasian bittern females, nest dispersion has been proposed as an important mechanism for counteracting density-dependent predation (Tinbergen et al. 1967, Andren 1991). However, studies on waterfowl report different levels of relationship between nest density and predation, which are associated with different factors like nest type (artificial *vs.* natural), predator community or spatial scale (Ackerman et al. 2004, Gunnarsson & Elmberg 2008, Ringelman et al. 2012).

To conclude, our study shows that early nesting females are more closely associated with appropriate vegetation at the nesting site than late nesters. On the other hand, early females choose less attractive habitats with poorer food resources. Later second, third and fourth females have lower breeding success, which shows the benefits of early nesting.

Acknowledgements

We would like to thank Janusz Kloskowski, Jarosław Krogulec, Marek Nieoczym, Ewa Zębek, Rafał Kuropieska and Marta Szaniawska for their help with the fieldwork and Peter Senn for correcting the English. We also thank the two anonymous referees for their helpful comments on the manuscript.

Literature

Ackerman J.T., Blackmer A.L. & Eadie J.M. 2004: Is predation on waterfowl nests density dependent? Tests at three spatial scales. *Oikos 107: 128–140.*

Andren H. 1991: Predation: an overrated factor for overdispersion of birds' nests? *Anim. Behav. 41: 1063–1069.*

Bensch S. 1996: Female mating status and reproductive success in the great reed warbler: is there a potential cost of polygyny that requires compensation? *J. Anim. Biol. 65: 283–296.*

Casagrande S., Dell'Omo G., Costantini D. & Tagliavini J. 2006: Genetic differences between early- and late-breeding Eurasian kestrels. *Evol. Ecol. Res. 8: 1029–1038.*

Crawley M.J. 1993: GLIM for ecologists. *Oxford, Blackwell.*

Dale S. & Slagsvold T. 1990: Random settlement of female pied flycatchers, *Ficedula hypoleuca*: significance of male territory size. *Anim. Behav. 39: 231–243.*

Demongin L., Dmitrenok M. & Bretagnolle V. 2007: Determining great bittern *Botaurus stellaris* laying date from egg and chick biometrics. *Bird Study 54: 54–60.*

Dmitrenok M., Demongin L. & Zhurauliov D. 2005: Three cases of replacement clutches in the great bittern *Botaurus stellaris*. *Ardea 93: 271–274.*

Dobson F.S., Nolan P.M., Nicolaus M., Bajzak C., Coquel A. & Jouventin P. 2008: Comparison of color and body condition between early and late breeding king penguins. *Ethology 114: 925–933.*

Elmberg J., Nummi P., Poysa H., Gunnarsson G. & Sjoberg K. 2005: Early breeding teal *Anas crecca* use the best lakes and have the highest reproductive success. *Ann. Zool. Fenn. 42: 37–43.*

Downloaded From: https://complete.bioone.org/journals/Folia-Zoologica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Gilbert G., McGregor P.K. & Tyler G. 1994: Vocal individuality as a census tool: practical considerations illustrated by a study of two rare species. *J. Field Ornithol. 65: 335–348.*
Gilbert G., Tyler G.A., Dunn C.J. & Smith K.W. 2005: Nesting habitat selection by bitterns in Britain and the implications for wetland management. *Biol. Conserv. 124: 547–553.*
Gonzalez-Solis J., Becker P.H., Jover L. & Ruiz X. 2004: Individual changes underlie age-specific pattern of laying date and egg-size in female common terns (*Sterna hirundo*). *J. Ornithol. 145: 129–136.*
Gunnarsson G. & Elmberg J. 2008: Density-dependent nest predation – an experiment with simulated Mallard nests in contrasting landscapes. *Ibis 150: 259–269.*
Huk T. & Winkel W. 2006: Polygyny and its fitness consequences for primary and secondary female pied flycatchers. *Proc. R. Soc. Lond. B 273: 1681–1688.*
Kasprzykowski Z. & Polak M. 2013: Habitat quality and breeding parameters in relation to female mating status in the polygynous Eurasian bittern *Botaurus stellaris*. *J. Ornithol. 154: 403–409.*
Klejdus J. 2007: Notes on breeding biology and behaviour of the great bittern (*Botaurus stellaris*) on the Šumický upper fishpond in 2001-2007. *Sylvia 43: 139–153.*
Kloskowski J. 2009: Size-structured effects of common carp on reproduction of pond-breeding amphibians. *Hydrobiologia 635: 205–213.*
Lack D. 1968: Ecological adaptations for breeding in birds. *Chapman & Hall, London.*
Longoni V., Rubolini D. & Bogliani G. 2007: Delayed reproduction among great bitterns *Botaurus stellaris* breeding in ricefields. *Bird Study 54: 275–279.*
Lubjuhn T., Winkel W., Epplen J.T. & Brun J. 2000: Reproductive success of monogamous and polygynous pied flycatchers (*Ficedula hypoleuca*). *Behav. Ecol. Sociobiol. 48: 12–17.*
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.*
McCullagh P. & Nelder J.A. 1989: Generalized linear models. *Chapman & Hall, London.*
Moreno J., Veiga J.P., Romasanta M. & Sanchez S. 2002: Effects of maternal quality and mating status on female reproductive success in the polygynous spotless starling. *Anim. Behav. 64: 197–206.*
Orians G.H. 1969: On the evolution of mating systems in birds and mammals. *Am. Nat. 103: 589–602.*
Perrins C.M. 1970: Timing of birds breeding seasons. *Ibis 112: 242–255.*
Polak M. 2006: Booming activity of male bitterns *Botaurus stellaris* in relation to reproductive cycle and harem size. *Ornis Fenn. 83: 27–33.*
Polak M. 2007: Nest-site selection and nest predation in the great bittern *Botaurus stellaris* population in eastern Poland. *Ardea 95: 31–38.*
Polak M. & Kasprzykowski Z. 2009: Numbers and density of the bittern *Botaurus stellaris* on selected fishponds in the Lublin and Podlasie Południowe regions. *Not. Ornitol. 50: 155–164.*
Polak M. & Kasprzykowski Z. 2010: Reproduction parameters of the great bittern *Botaurus stellaris* in the fishponds of eastern Poland. *Acta Ornithol. 45: 75–81.*
Polak M. & Kasprzykowski Z. 2013: The effect of weather conditions on the breeding biology of the Eurasian bittern *Botaurus stellaris* in eastern Poland. *Ethol. Ecol. Evol. 25: 243–252.*
Polak M., Kasprzykowski Z. & Kucharczyk M. 2008: Micro-habitat nest preferences of the great bittern, *Botaurus stellaris*, on fishponds in central-eastern Poland. *Ann. Zool. Fenn. 45: 102–108.*
Price T., Kirkpatrick M. & Arnold S.J. 1988: Directional selection and the evolution of breeding date in birds. *Science 240: 798–799.*
Puglisi L., Adamo C. & Baldaccini N.E. 2003: Spatial behaviour of radio-tagged Eurasian bitterns *Botaurus stellaris*. *Avian Sci. 3: 133–143.*
Puglisi L. & Bretagnolle V. 2005: Breeding biology of the bittern. *Waterbirds 28: 392–398.*
Ringelman K.M., Eadie J.M. & Ackerman J.T. 2012: Density-dependent nest predation in waterfowl: the relative importance of nest density versus nest dispersion. *Oecologia 169: 695–702.*
Rubolini D., Ambrosini R., Caffi M., Brichetti P., Armiraglio S. & Saino N. 2007: Long-term trends in first arrival and first egg laying dates of some migrant and resident bird species in northern Italy. *Int. J. Biometeorol. 51: 553–563.*
Searcy W.A. & Yasukawa K. 1996: The reproductive success of secondary females relative to that of monogamous and primary females in red-winged blackbirds. *J. Avian Biol. 27: 225–230.*
Sejberg D., Bensch S. & Hasselquist D. 2000: Nestling provisioning in polygynous great reed warblers (*Acrocephalus arundinaceus*): do males bring larger prey to compensate for fewer nest visits? *Behav. Ecol. Sociobiol. 47: 213–219.*
Sheldon B.C., Kruuk L.E.B. & Merila J. 2003: Natural selection and inheritance of breeding time and clutch size in the collared flycatcher. *Evolution 57: 406–420.*
Slagsvold T. & Lifjeld J.T. 1994: Polygyny in birds: the role of competition between females for male parental care. *Am. Nat. 143: 59–94.*
Statsoft Inc. 2011: Statistica for windows (data analysis system), version 10. *www.statsoft.com*
Svensson E. 1995: Avian reproductive timing: when should parents be prudent? *Anim. Behav. 49: 1569–1575.*
Tinbergen N., Impekoven M. & Franck D. 1967: An experiment on spacing-out as a defence against predation. *Behaviour 28: 307–321.*
Tyler G.A., Smith K.W. & Burges D.J. 1998: Reedbed management and breeding bitterns *Botaurus stellaris* in the UK. *Biol. Conserv. 86: 257–266.*
Verner J. & Willson M.F. 1966: The influence of habitats on mating systems in North American passerine birds. *Ecology 47: 143–147.*
Voisin C. 1991: The herons of Europe. *Poyser, London.*
White G., Purps J. & Alsbury S. 2006: The bittern in Europe: a guide to species and habitat management. *The RSPB, Sandy.*

Downloaded From: https://complete.bioone.org/journals/Folia-Zoologica on 28 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use