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Offspring sex ratio and partially asynchronous hatching in the Little Bittern (*Ixobrychus minutus*) population in south-western Slovakia

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Birds are one of the best-studied animal groups in Europe. Despite this, there are several bird species, including the Little Bittern (*Ixobrychus minutus*), of which the breeding biology is still little known. Here, I examine the sex of offspring in relation to hatching order, the degree of hatching asynchrony and some other aspects of nesting biology (such as breeding phenology, clutch size, egg and nestling survival) of the Little Bittern in the south-western Slovakian population. Egg-laying occurred from 5 May to 10 July, but the majority of clutches were initiated in May. Mean clutch size was 5.2 ± 0.92 (SD) eggs. Parents initiated full incubation predominantly after laying the third egg (86.4% of cases) of the clutch, which led to only partially asynchronous hatching of eggs. However, no evidence was found for offspring sex ratio adjustment according to hatching order. Nevertheless, survival rates of eggs and nestlings were relatively high (80.9% and 94.3 %, respectively). The possible causes of observed patterns are discussed.

1. Introduction

In a sexually size-dimorphic species where one sex is larger and thus costlier to rear than the other, females are predicted to adjust the sex ratio of their offspring according to local environmental or other conditions in order to maximize their own reproductive fitness (Trivers & Willard 1973). In many species, the offspring sex ratio varies with the hatching order (Krebs *et al.* 2002, Arnold & Griffiths 2003, Bowers *et al.* 2011) because producing the larger sex later in the hatching sequence decreases sibling rivalry and the probability of loss of the lowest ranked nestling (Carranza 2004, Moreno-Rueda *et al.* 2016). It is evident that such interactions between offspring sex and hatching order are more pronounced in species with higher degrees of hatching asynchrony (Szöllősi *et al.* 2007).

A suitable model species for testing the relationship between offspring hatching order and sex, in birds with asynchronous hatching, is one of the least studied heron species in Europe, the Little Bittern (*Ixobrychus minutus*). Although the breeding biology of the Little Bittern has been studied in more detail in recent decades in Spain (Pardo-Cervera *et al.* 2010), Poland (Flis 2016, Filipiuk & Kucharczyk 2016), Algeria (Samraoui *et al.* 2012) and in India (Fazili 2014), no study to date has examined the offspring sex ratio in relation to hatching order in this species, and existing studies have also produced mixed results regarding the onset of egg incubation (Witherby *et al*. 1937, Hudec 1994, Fazili 2014).

To extend our knowledge, this paper contributes the first data on the offspring sex ratio and data on hatching asynchrony of the Little Bittern in south-western Slovakia. Given that Little Bittern males are larger than females (Cramp & Simmons 1977), based on intra-brood competitive equilibrium hypothesis (Uller 2006), I predicted that nestlings that hatched later were more likely to be male than female.

2. Material and methods

2.1. Study species and study sites

The Little Bittern is a monogamous, non-colonial nesting species (Kushlan & Hancock 2005), which inhabits dense marsh vegetation (*Phragmites australis*, *Typha* spp.). It breeds typically once per year (but see Filipiuk & Kucharczyk 2016). After breeding failure, replacement nests are located close to a previously failed nest (Cramp & Simmons 1977). The number of eggs per clutch ranges from 3 to 7 and eggs are incubated by both parents for 16 to 19 days. Nestlings generally fledge 16–18 days after hatching, but from the age of about seven days, if disturbed, they may temporarily leave the nest and disperse into the adjacent vegetation (Cramp & Simmons 1977).

Data on the breeding biology and hatching of Little Bitterns was gathered from two breeding sites approximately 54 km apart (fishponds near Ľubá and Jatov, 47°51′ N 18°36′ E and 48°08′ N, 18°01′ E respectively, located in south-western Slovakia) over a period of 5 years (2015–2019). The total number of breeding pairs at both study sites was 15–23 pairs.

2.2. Field procedures

I systematically searched for Little Bittern nests at 3- to 5-day intervals from early May to late July to detect them during the nest-building period. Each nest was labelled with a unique code and then checked daily from the beginning of egg laying until clutch completion. I also numbered eggs as laid with a waterproof pen to determine egg sequence. The onset of full incubation was defined as the date when warm eggs were first detected in the nest. The relative temperature of eggs was measured, by holding them to cheek, and then subjectively categorised as warm (they were warm to the touch), intermediate (colder to the touch than eggs from the previous category) or cool (cold to the touch) (see also Rowe & Weatherhead 2009, Arnold 2011). Only nests for which I was able to determine the exact date on which parents started full incubation were included in subsequent analysis.

During the hatching period, I visited nests daily to determine hatching order and hatching interval, *i.e.* the span of time that elapsed between hatching of the first and last egg. Immediately after hatching, each chick was individually marked with coloured tape attached around the tarsus and, later (at 5–7 days of age), ringed with a standard aluminium ring. Each nest was then monitored every 3–5 days until all surviving nestlings reached at least ten days of age. This was because older nestlings leave the nest as soon as they perceive the approach of an intruder and disperse into the surrounding vegetation (see also Trnka 2020). Nestling survival was then calculated as the proportion of hatchlings that were still alive on day 10 in or near the nest.

Blood samples for sex determination were collected during the breeding seasons of 2016 and 2017. I took 3–5 drops of blood from each nestling within two days after hatching by means of metatarsal-vein puncture and preserved it in 70% ethanol. The sex of hatchlings was determined by polymerase chain reaction (PCR) amplification of introns in two homologous genes CHD-Z and CHD-W in the private accredited genetic laboratory Genomia (https://www.genomia.cz/en). This technique was verified as reliable by the correct sexing of two male and two female adults coming from the fishponds near Ľubá.

To estimate the primary sex ratio of Little Bittern hatchlings accurately, I considered for analysis only nests in which all eggs hatched and no egg or nestling was lost before I could sample it, which accounts for 95% of all found nests. I did not know the identity of all nest owners; however, there should be low probability of pseudoreplication due to repeated sampling of the same Little Bittern pair as the species breeds only once per year in the study area and replacement nests are located close to the first nests (Cramp & Simmons 1977). In 2016 and 2017 only four nests (10%) were predated.

According to my previous experience (*e.g.* Trnka 2015, 2020), I am also sure that my field study did not negatively affect the nesting success of Little Bitterns. Despite the species' shy and secretive habits, the Little Bittern is highly tolerant of research activities and during my study no chick died and no nest was abandoned during the two days after nest checking and blood sampling.

2.3. Data analyses

The overall population sex ratio was analysed using the binomial test. The effect of hatching order (early, middle, late) on the sex of an offspring (binary; male or female) was tested using a generalised linear mixed models (GLMM) with binomial distribution in the package lme4 (see also Bates *et al.* 2015). Because clutch sizes varied from 3 to 7 eggs, chicks were categorised as being hatched in the first, middle or last third of the hatching order (cf. Krebs *et al.* 2002). In cases when equal number of chicks could not be assigned to each category, those ambiguous instances were assigned to "early" or "middle" categories because the species starts the incubation when already 2–4 eggs are laid and usually, these eggs hatch synchronously (see Results). The full statistical model contained fixed predictors of hatching order (early, middle, late), locality (binary; Jatov or Ľubá), date of the first egg laid (continuous; 1 = 1 May), final clutch size (continuous), year (categorical, 2016 and 2017) and hatching interval (continuous; in days). Repeated sampling from every brood was controlled for with the random effect of brood identity. Importantly, when data were reanalysed using direct hatching sequence (following Kasprzykowski *et al.* 2014), the same conclusion was reached (non-significant hatching order effect: $\chi^2 = 3.23$, $df = 6$, $P = 0.780$).

Akaike information criterion corrected for small sample sizes (AIC_c) was used to find the best model (Burnham & Anderson 2002). The model selection was performed using R package MuMIn (v. 1.43.17; Barton 2020). Because the effect of hatching order was a predictor of key interest, it was retained in all models regardless of its significance. All analyses were performed using the software R v. 3.5.0 (R Core Team 2020).

3. Results

3.1. General breeding biology

A total of 95 active Little Bittern nests were monitored in 2015–2019. The majority of clutches (60%) were initiated in May (mean = 28.5 ± 14.76 (SD), 1 = 1 May, n = 95). The earliest recorded date of egg laying was 5 May (2018), and the latest 10 July (2019). Clutch size varied from 3 to 7 eggs with an average of 5.2 ± 0.92 (SD) eggs per nest (n = 93). Out of 478 laid eggs, 387 (80.9%) successfully hatched. Predation was responsible for 11.6% of failed clutches. Nestling survival was generally high (94.3%, n = 365), and all chicks that died were the last or penultimately hatched in their broods.

3.2. Initiation of egg incubation and hatching asynchrony

In the study population of Little Bitterns, parents initiated full incubation mainly after laying the third egg of the clutch (86.4% of cases, mean = 2.96 ± 0.37 (SD), n = 44, 2015–2019), and only rarely after the second (9.1% of cases) or the fourth (4.5% of cases) egg was laid. All eggs laid before the onset of incubation hatched synchronously, *i.e.* within 24 h. Remaining eggs hatched asynchronously in the order in which they were laid. The hatching interval varied, according to clutch size, from 1 to 4 days (mean = 2.50 ± 0.78 (SD), n = 40, 2015–2019).

3.3. Offspring sex ratio and hatching order

A total of 219 hatchlings (122 males, 97 females) from 40 clutches were sexed, and there was no significant bias in the overall sex ratio (exact binomial test: $P = 0.105$). Similarly, the sex ratio of earlier synchronously hatched chicks did not differ significantly from the parity (67 males, 53

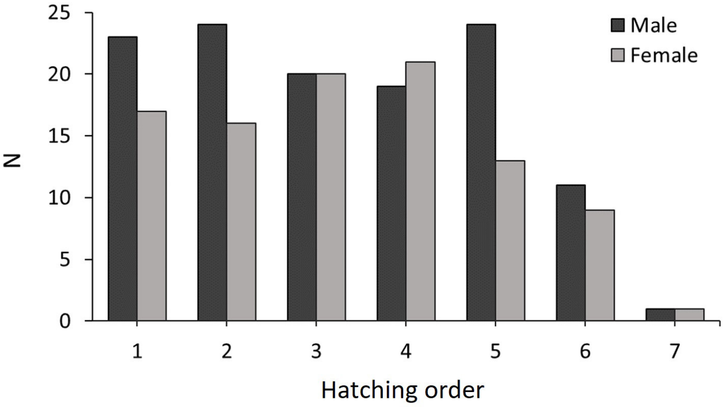

Fig 1. The number of male and female Little Bittern chicks per hatch order value

females; exact binomial test: $P = 0.122$, Fig. 1), and the same proportion of males (21) and females (19) were produced from last-laid eggs. Also no difference was found in the proportion of males and females between synchronously and asynchronously hatched chicks ($\chi^2 = 0.002$, $df = 1$, $P = 0.967$). Model selection procedure indicated that no effect significantly explained variation in the offspring sex (Table 1) and detailed GLMM outputs confirmed this (Table 2).

4. Discussion

Contrary to the general predictions, results of this study showed no evidence for offspring sex ratio adjustment according to hatching order in the Little Bittern. Despite increased probability of death due to starvation (Holmes & Hatchwell 1991, this study), no bias was found in the sex ratio of last-hatched chicks either. This is in contrast to studies of other taxonomically related species, such as Cattle Egrets (*Bubulcus ibis*) and White Storks (*Ciconia ciconia*), where males dominated amongst the first hatched chicks (Voltura 1998, Tryjanowski *et al.* 2011, but see Aguirre & Vergara 2007). In spite of this, the survival of nestlings in successful nests was relatively high, as in other Little Bittern populations (*e.g.* Martínez-Abraín 1994, Samraoui *et al.* 2012).

The lack of offspring sex-ratio change with hatching order could be due to the fact that females compensate for the potential disadvantage of later-hatched chicks by other mechanisms. For example, females could differentially allocate maternal resources to eggs according to the laying order and the sex of the embryo, instead of using sex manipulation (*e.g.* Blanco *et al.* 2002, Ferrari *et al.* 2006, Saino *et al.* 2011). Further research should therefore test potential causal links between egg content, laying order and other post-hatching behavioural provisioning mechanisms in this species.

An additional explanation may lie in the partially asynchronous hatching strategy used by the Little Bittern population in this study. I found that the first two to four laid eggs in a clutch hatched synchronously (*i.e.* within 24 h of one another), and the remaining eggs hatched asynchronously (*i.e.* one young hatched per day) (see also Lloyd & Martin 2003). This type of egg incubation also contrasts with the assumption that Little Bitterns start to incubate after the first or second egg is laid (Witherby *et al.* 1937, Fazili 2014). Differences in the onset of egg incubation between this and other Little Bittern populations could reflect different environmental conditions in the study areas. Indeed, major determinants of the degree of hatching asynchrony, such as the food abundance and the intensity of nest predation (Clark & Wilson 1981, Barrientos *et al.* 2016), may markedly differ across the species' breeding range.

The partial hatching asynchrony that I identified in the south-western Slovakian population fits the nest failure hypothesis (Clark & Wilson 1981). According to this hypothesis, the degree of hatching asynchrony is related to nest mortality early and late in the nesting cycle, when higher mortality during the egg-laying and incubation periods leads to asynchronous hatching; and

Table 1. Model selection output based on Akaike information criterion corrected for small sample sizes (AIC_c). Shown are best five models testing effects (see Methods) on the offspring sex. Effect of hatching order was retained in all models as predictor of the key interest. Degrees of freedom (*df*), model log-likelihood (LL), corrected AIC criterion (AIC_c), the difference between AIC_c of the focal model and the best model (ΔAIC_c) and Akaike weight (weight; the relative likelihood of a model) for each model are shown.

Predictors	*df*	LL	AIC_c	ΔAIC_c	weight
Intercept + hatching order	4	−150.0	308.2	0.00	0.143
Intercept + hatching order + locality	5	−149.1	308.5	0.28	0.124
Intercept + hatching order + FEG	5	−149.5	309.4	1.18	0.079
Intercept + hatching order + FEG + locality	6	−148.6	309.7	1.49	0.068
Intercept + hatching order + year	5	−149.7	309.7	1.52	0.067

Table 2. Summary of a generalised linear mixed models testing the effect of hatching order and other potential factors on the brood sex ratio in the Little Bittern. The best model was created by backward elimination of non-significant terms whilst retaining the major variable of interest (hatching order).

Predictor	Full model			Best model		
	χ^2	*df*	*P*-value	χ^2	*df*	*P*-value
Hatching order	0.88	2	0.643	0.73	2	0.694
Locality	1.33	1	0.250	–	–	–
Year	1.30	1	0.255	–	–	–
First egg laid	1.24	1	0.266	–	–	–
Clutch size	0.12	3	0.733	–	–	–
Hatching interval	1.71	3	0.643	–	–	–

higher mortality in the nestling and fledging stages favours more synchronous hatching (Lee & Lima 2017). As the eggs of the Little Bittern are conspicuously white and more vulnerable to predation than cryptically coloured and mobile nestlings, parents can start incubating before clutch completion in order to protect the hatchability of their eggs (Arnold *et al*. 1987, Veiga 1992, Szöllősi *et al*. 2007). Additionally, later asynchronously hatched eggs may serve as insurance against mortality of earlier synchronously hatched “core” offspring (Forbes *et al*. 1997). On the other hand, Little Bittern incubation behaviour could also be interpreted as a strategy for testing actual nest-site safety where temporarily unincubated eggs may represent bait for potential nest predators. Similar behaviour has also been documented in Great Crested Grebes (*Podiceps cristatus*) (Goc 1986) and Grey Partridges (*Perdix perdix*) (Černý *et al.* 2018). Note that there is relatively high predation of nests during the egg stage (Trnka 2020). However, these explanations are speculative and need to be tested experimentally.

Several breeding parameters of the studied Little Bittern population did not differ from those of other populations (*e.g.* Pardo-Cervera *et al*. 2010, Samraoui *et al*. 2012, Fazili 2014). Notably, smaller clutches were only found in Spain (mean 4.0 ± 0.9 eggs per nest, Pardo-Cervera *et al*. 2010). However, considering the marked variation in the clutch sizes within and between seasons in this species (Fazili 2014), this variation could be due to differences in environmental conditions such as climatic factors and food supply; similar to the seasonal variation in the onset of egg laying. Generally, Little Bitterns in south-western Slovakia start to breed slightly earlier than Little Bitterns from Spain and North Africa (Pardo-Cervera *et al*. 2010, Samraoui *et al*. 2012).

To conclude, the results of this study suggest that the offspring sex ratio of the Little Bittern does not change in relation to their position in the hatching order. Little Bitterns generally hatched the first three laid eggs synchronously, whereas hatching of other eggs was asynchronous. This, together with the relatively high rate of chick survival found in the study population may indicate that partially asynchronous hatching (together with some other yet to be determined factors) may also be an effective way to reduce nestling mortality and sibling rivalry in this species. Nevertheless, more experimental studies with larger sample sizes and on different Little Bittern populations in various environmental conditions are required before a general conclusion can be drawn.

Poikasten sukupuolijakauma ja osittaisen kuoriutumisen epäsynkronia pikkuhaikarapopulaatiossa Lounais-Slovakiassa

Linnut ovat yksi parhaiten tutkittuja eliöryhmiä Euroopassa. Silti esimerkiksi pikkuhaikarasta ja sen lisääntymisbiologiasta on vähän tietoa. Tutkin pikkuhaikaran poikasten sukupuolijakaumaa suhteessa kuoriutumisjärjestykseen, kuoriutumisen synkroniaa ja lisääntymisbiologiaa (lisääntymisen ajankohta, munaluku, poikasten selviäminen). Tutkimus suoritettiin Lounais-Slovakian tutkimuspopulaatiossa. Muninta ajoittui pääosin toukokuulle, 5.5.–10.7. välille. Keskimääräinen munaluku oli 5.2 ± 0.92 (keskivirhe) munaa. Emot aloittivat haudonnan yleisimmin (86.4% emoista) kolmannen munan muninnan jälkeen, mikä johti osittain epäsynkroniseen kuoriutumiseen. Munien ja poikasten selviäminen oli suhteellisen korkea (80.9% ja 94.3%).

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