The length of breeding season in two populations of the Common Kingfisher (*Alcedo atthis*)

Délka hnízdní sezóny u dvou populací ledňáčka říčního (Alcedo atthis)

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In Central Europe, the breeding season of the Common Kingfisher (Alcedo atthis) extends from late March to the second half of September, during which a pair can successfully rear up to four broods. Intensity of reproduction may vary depending on the parents' condition and territory quality. In the seasons 2014-2018, we monitored breeding of 95 Kingfisher pairs at the Danube river system in south-western Slovakia (hereafter "Danubian population") and 121 pairs in the Central Bohemian, South Bohemian and Vysočina regions of the Czech Republic ("central Bohemian population"). We estimated the total length of the breeding season for the study populations as the time period between the first egg laying date and the fledging date of the last young in the population, regardless the pair identity. The length of the breeding season was estimated also for individual pairs. In the Danubian population, we estimated the mean length of the breeding season at 172 days for the whole population and 101 days for individual pairs. In the central Bohemian population, we estimated the mean length of the breeding season at 165 days for the whole population and 89 days for individual pairs. In both populations, most pairs bred two times. In the Danubian population, three or four breeding attempts per season were recorded more often than in the central Bohemian population. Moreover, we documented five breeding attempts per season in one pair from the Danubian population. Despite the different number of broods per pair per season, the mean length of the breeding season of the individual pairs did not differ between the populations, which was a result of larger overlaps of consecutive breeding attempts in the Danubian pairs.

Hnízdní sezóna ledňáčka říčního (Alcedo atthis) ve střední Evropě trvá od pozdního března do druhé poloviny září a jednotlivé páry během ní mohou úspěšně vychovat mláďata až ze čtyř snůšek. Počet hnízdění přitom může záviset na kondici rodičů a kvalitě jejich teritorií. V období 2014–2018 jsme sledovali hnízdění 95 párů ledňáčků říčních v soustavě ramen Dunaje na jihozápadním Slovensku ("dunajská populace") a 121 párů ve Středočeském, Jihočeském kraji a v kraji Vysočina ("středočeská populace"). Průměrná délka hnízdní sezóny dunajské populace činila 172 dní pro celou populaci (datum prvního sneseného vejce až datum posledního vyvedeného mláděte v populaci bez ohledu na identitu páru) a 101 dní pro jednotlivé hnízdní páry. Průměrná délka hnízdní sezóny "středočeské" populace

činila 165 dní pro celou populaci a 89 dní pro jednotlivé hnízdní páry. Nejvíce párů v obou populacích hnízdilo dvakrát za sezónu, třikrát a čtyřikrát za sezónu hnízdila větší proporce párů z dunajské oproti "středočeské" populaci a u jednoho páru z dunajské populace bylo dokonce zdokumentováno pět hnízdění za sezónu. Rozdíl v průměrné délce hnízdní sezóny jednotlivých párů mezi srovnávanými populacemi nebyl i přes zjištěný rozdíl v počtu hnízdění za sezónu statisticky významný, což bylo způsobeno delšími časovými překryvy následných hnízdění u párů z dunajské populace.

Keywords: Central Europe, number of broads per year, population, timing of breeding season

INTRODUCTION

The Common Kingfisher (Alcedo atthis) is a species with an extremely long breeding season, which lasts from March to July in the Great Britain or in Sweden (Woodall 2001). In Central Europe, the breeding season lasts from the end of March or beginning of April to July (Hudec & Šťastný 2005), August (Kucharski & Čech 2009), or, ultimately, to mid-September (Čech 2010, Turčoková et al. 2016). The length of the breeding season at the population level (i.e., from the first egg laying date until the fledging date of the last young in the population) varies between 136 days (Poland) and 171 days (Czech Republic; Kucharski & Čech 2009, Čech 2010).

Kingfisher pairs regularly breed two times per season, but exceptionally up to four times, while their consecutive breeding attempts usually overlap (Morgan & Glue 1977, Cramp 1985, Woodall 2001). In cases of overlapping broods, the male continues feeding and brooding the young in the earlier nest, while the female starts incubating a new clutch in another nest. Moreover, when attaining polygyny, one male may attend up to six nests per season (Cramp 1985, Woodall 2001, Čech 2016). The fluctuating reproductive success reflects differences in Kingfisher condition, which strongly depends on the necessity of short/long distance movements in the winter (Ansorge 2017). Another important factor is territory quality, particularly the availability of small (5–8 cm) fish, given that the parents have to provide their young with a huge amount of such food (Čech & Čech 2011, Vilches et al. 2012, 2013, Čech & Čech 2017).

In this study we compared the length of the breeding season, the number of broods per season and the time interval between the consecutive broods in two populations living in different altitudes and environments – Danubian (lowland) and central Bohemian (rather highland) population. We analysed the relationships between the length of the breeding season, number of broods, and year.

METHODS

The Common Kingfisher breeding biology was studied from March to September 2014-2018 in the Danube river system in the Slovak Republic (altitude 110-200 m a. s. l.), particularly between 1868.7 (Bratislava; 48°06'13.5"N, 17°09'31.3"E) 1819.0 river km (Gabčíkovo; 47°52'32.1"N, 17°31'18.0"E). In total, 55 km of river branches were regularly checked for occupied nests. The Kingfisher population inhabiting this area is further mentioned as "Danubian". Concurrently, the fieldwork was also carried out in the Central Bohemian, South Bohemian and Vysočina regions of the Czech Republic (400-770 m a. s. l.). In total,

230 km of 26 streams or rivers together with two water reservoirs were monitored (49°35'53"– 49°40'46"N, 15°11'38" – 14°17'39"E). The Kingfisher population inhabiting this area is further mentioned as "central Bohemian".

In late April, when the Common Kingfishers incubate the first clutch, we checked newly found or previously known burrows for the presence of active nests. The nests were inspected weekly using a miniature camera (Probe Maxivideo MV 201). The laying date of the first egg in the clutch was determined directly or assessed backwards from the nestling's appearance, assuming the length of the incubation period to be 21 days (Cramp 1985) and the laying interval to be one day (Čech 2009). At the time of the nestling period, parent birds were mist-netted in front of the breeding bank and ringed using aluminium rings. Using a special tool without damaging the burrow, nestlings were extracted from the nesting chamber and ringed at the age of 14-18 days. We continued to check the nest burrows after chick ringing for possible repeated breeding attempts in the same burrows. We also checked potential breeding banks with the aim of finding the new nests. Chicks usually leave the nest at the age of 23–25 days (Cramp 1985). To determine the fledging date, we assumed that chicks leave the nest at the age of 25 days.

We calculated the length of the breeding season for the whole population, expressed as the time (in days) between the first egg laying date and the fledging date of the last young in the population, regardless the pair identity. Yearly estimates were averaged from the five years, separately for particular populations. Moreover, we estimated the length of the breeding season for individual pairs (Danubian population: n = 95 pairs, central Bohemian population: n = 121 pairs). Using the generalized linear model (GLM) we tested 1) the influence of population, year (both categorical variables), interaction between population and year, and number of broods per year (ordinal variable) on the length of the breeding season of individual pairs (continuous variable), and 2) the influ-

Table 1. Numbers of the Common Kingfisher (*Alcedo atthis*) breeding pairs used for data analysis.

Tab. 1. Počet hnízdních párů ledňáčka říčního (Alcedo atthis) vstupujících do ar	do analyz
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variable / <i>proměnná</i>	value / hodnota	n_{1+2}	n_1	n_2
population / populace	1 (Danubian / <i>dunajská</i>)	_	95	_
	2 (central Bohemian / "středočeská")	-	-	121
year / rok	2014	49	17	32
	2015	45	18	27
	2016	50	26	24
	2017	37	17	20
	2018	35	17	18
number of broods /	1	70	22	48
počet hnízdění	2	99	43	56
	3	34	18	16
	4	12	11	1
	5	1	1	0
total / celkem		216	95	121

ence of the same explanatory variables on the number of broods per year (ordinal variable; for dataset structure see Table 1).

For the pairs that bred at least twice during the season, we estimated the time interval between the consecutive broods as the time period (in days) between the fledging date of young from the previous brood and the date of laying of the first egg in a consecutive nest. If there was a lag, we took a positive value, while a negative value was taken in cases of overlapping consecutive broods. When the pair bred at least three times per season, we used

the mean interval between consecutive broods in the analysis. We specified the time interval between the consecutive broods for 61 pairs of the central Bohemian population and 54 pairs of the Danubian population. We were not able to determine the time interval between the consecutive broods in 12 pairs of the central Bohemian population and 19 pairs of the Danubian population, since their nesting was interrupted for various reasons (i.e., predation, bank collapse, flooding of a burrow) before we determined the first egg laying date. We compared the time interval between the consecutive

Table 2. GLM model testing the influence of explanatory variables – population, year (both categorical variables), and number of broods (ordinal variable) on the length of breeding season of individual Kingfisher pairs (continuous variable). In total, 95 breeding pairs from the Danubian and 121 pairs from the central Bohemian population were included in the analysis. Significant results are shown in bold.

Tab. 2. Zobecněný lineární model testující vliv vysvětlujících proměnných populace, rok (kategorické proměnné) a počet zahnízdění (ordinální proměnná) na délku hnízdní sezóny (kontinuální proměnná) jednotlivých párů ledňáčka říčního. Celkem bylo do analýzy zahrnuto 95 hnízdních párů dunajské populace a 121 párů "středočeské" populace. Statisticky významné výsledky jsou tučně zvýrazněny.

predictor / prediktor	df	F	p
intercept	1	632.60	<0.001
number of broods / počet hnízdění	4	85.43	<0.001
population / populace	1	0.13	0.715
year / rok	4	5.66	<0.001
population × year / populace × rok	4	3.22	0.014

Table 3. GLM model testing the influence of explanatory variables – population and year (categorical variables) on the number of broods per year recorded in Kingfisher pairs (ordinal variable). In total, 95 breeding pairs from the Danubian and 121 pairs from the central Bohemian population were included in the analysis. Significant results are shown in bold.

Tab. 3. Zobecněný lineární model testující vliv vysvětlujících proměnných populace a rok (kategorické proměnné) na počet zahnízdění (ordinální proměnná) jednotlivých párů ledňáčka říčního. Celkem bylo do analýzy zahrnuto 95 hnízdních párů dunajské populace a 121 párů "středočeské" populace. Statisticky významné výsledky jsou tučně zvýrazněny.

predictor / prediktor	df	F	р
intercept	1	1159.87	< 0.001
population / populace	1	15.61	<0.001
year / rok	4	0.86	0.490
population × year / populace × rok	4	0.61	0.660

broods between the populations by means of t-test.

All statistical analyses were carried out in SPSS version 23. Each breeding pair was included in the analyses only once.

RESULTS

The length of the breeding season in the Danubian population varied among years between 141 and 185 days with the mean of 172 days (± 8 SE), while in the central Bohemian population it varied between 149 and 186 days with the mean of 165 days (± 6 SE). The length of the breeding season of individual pairs from the Danubian population varied between 51 and 184 days with the mean of 101 days (± 4 SE), while for the central Bohemian population it varied between

44 and 186 days with the mean of 89 days (± 3 SE; Fig. 1). Although the length of the breeding season of individual pairs did not statistically differ between the Danubian and central Bohemian populations, the year played a significant role (different in each population) along with the brood number (Table 2).

The number of broods significantly differed between the two populations (Table 3). In both populations, the majority of pairs bred two times per year (Fig. 2) – particularly between 18% (2017) and 67% of breeding pairs (2015) in the Danubian population and between 41% (2014) and 59% of breeding pairs (2015) in the central Bohemian population. Pairs from the Danubian population had three or four broods per season more often than pairs from central Bohemia. In the

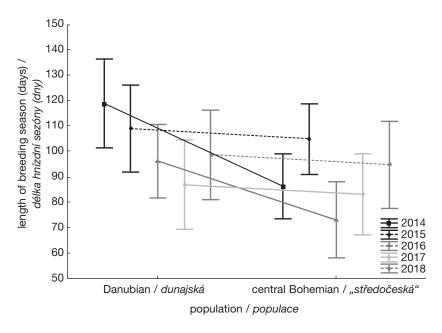


Fig. 1. Differences in the length of breeding season of individual Kingfisher pairs between the Danubian and central Bohemian populations in the years 2014–2018. Means (points) and 95% confidence intervals (whiskers) are given. Yearly sample sizes for particular populations are presented in Table 1.

Obr. 1. Rozdíly v délce hnízdní sezóny jednotlivých hnízdních párů mezi dunajskou a "středočeskou" populací ledňáčka říčního v letech 2014–2018. Znázorněny jsou průměry (body) a 95% konfidenční intervaly (úsečky). Počet párů z jednotlivých populací zahrnutý do analýz v konkrétním roce je prezentován v tab. 1.

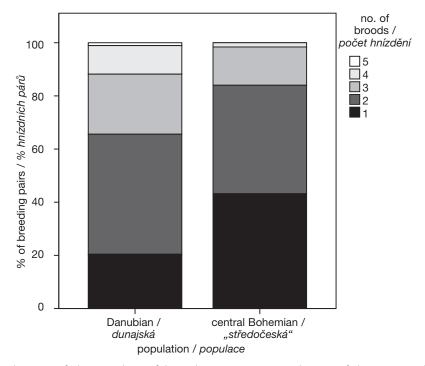


Fig. 2. Distribution of the number of broods per season in the Kingfisher pairs of the Danubian (n = 95 pairs) and central Bohemian population (n = 121 pairs). Pooled data for the period 2014–2018 (each pair was included only once).

Obr. 2. Počet hnízdění jednotlivých párů ledňáčka říčního za sezónu v dunajské (n = 95 párů) a "středočeské" populaci (n = 121 párů). Sloučená data z let 2014–2018 (každý hnízdní pár byl do analýz zahrnut jenom jednou).

Danubian population, we documented one pair that bred five times. In both populations, the number of broods did not differ among years (Fig. 3).

The studied populations significantly differed in the time interval between the consecutive broods (t-test: t = -2.68, p = 0.004, n for Danubian population = 54 pairs, n for central Bohemian population = 61 pairs). The time interval between the consecutive broods was shorter in pairs from the Danubian population (mean = -1.4 days \pm 1.9 SE) than in pairs from the central Bohemian population (mean = 6.6 days \pm 2.2 SE).

DISCUSSION

Breeding seasons of the studied Common Kingfisher populations lasted on average 172 days in the Danubian and 165 days in the central Bohemian population as a whole. Breeding seasons of individual pairs lasted on average 101 days in the Danubian population and 89 days in the central Bohemian population. Pairs from the Danubian population had more breeding attempts per season, but the length of their breeding season did not differ from that of the central Bohemian pairs, because there were larger overlaps of consecutive breeding attempts in the Danubian pairs than in the Central Bohemian pairs.

The length of the breeding season revealed in the present study is consistent with the previous research from the Czech Republic (172 days; Kucharski & Čech 2009), but differs from the results from Poland (136 days; Kucharski

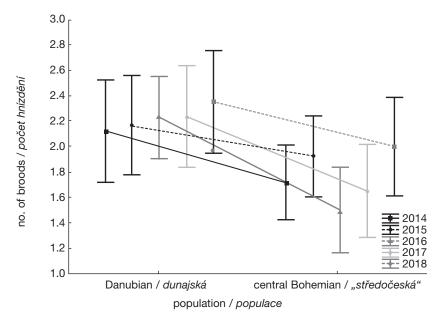


Fig. 3. Differences in the number of broods between the Danubian and central Bohemian Kingfisher populations in the years 2014–2018. Means (points) and 95% confidence intervals (whiskers) are given. Yearly sample sizes for particular populations are presented in Table 1. **Obr. 3.** Rozdíly v počtu hnízdění jednotlivých párů ledňáčka říčního za sezónu mezi dunajskou a "středočeskou" populací v rozmezí let 2014–2018. Znázorněny jsou průměry (body) a 95% konfidenční intervaly (úsečky). Počet párů z jednotlivých populací vstupující do analýz v konkrétním roce je prezentován v tab. 1.

& Čech 2009). The shorter breeding season in Poland may be explained by a lower number of broods. A certain part of both populations in the present study bred four times per season, while in Poland no fourth brood was documented (Kucharski & Čech 2009). Moreover, we recorded a unique case of five breeding attempts of one pair in the Danubian population, leading to the 185-day breeding season and altogether 19 raised chicks from three successful broods (Rubáčová & Melišková 2020).

The length of the breeding season of individual pairs was correlated with the number of broods, while it differed among years but not between the studied populations. In both populations, the majority of pairs was found to breed two times per year, even though more pairs from the Danubian population had three

or four broods per season. However, this result was not caused by a higher nest failure rate that would lead to more replacement clutches in the Danubian population, given that our data show similar nesting success for both populations (83.6% in Danubian population vs. 85.7% in central Bohemian population; unpublished data). The length of the breeding season did not differ between the two populations, because there was a larger overlap of consecutive breeding attempts in the Danubian pairs than in the central Bohemian pairs. Kingfisher females may leave the nests with nestlings after they develop thermoregulation at the age of approximately six days and start another brood (Cramp 1985), while males continue feeding the nestlings alone (Čech 2009, Turčoková et al. 2016). In some cases, the female lays eggs in the nest with old nestlings (own unpublished data). The overlap length varied considerably between pairs, reaching between 6 and 20 days. This may depend on food supply and male hunting ability (Cramp 1985).

The higher reproductive effort of Kingfishers from the Danubian population may be caused by better condition of the parents and/or territory quality, as was documented in other bird species (e.g., Bryant 1975, Nilsson & Svensson 1993, Moreno at al. 1998, Tremblay et al. 2003). The Danubian Kingfishers could benefit from milder winters with non-freezing water that support the resident population (own observations). Residents may reduce energy expenditure and save time by avoiding long distance movements. Consequently, their survival may increase and the saved energy may be invested into reproduction (Newton 2008, Payevsky 2016). Second, the Danubian breeders may profit from high-quality foraging habitats of a large lowland river with a high diversity of fish prey (Kováč 2015). A diverse fish-community, particularly with cyprinids spawning several times a year, allows birds to continually forage on fish of a preferred size. A combination of better body condition of breeders together with high quality territories enables the Danubian pairs overlap consecutive broods for a longer time period than the Central Bohemian pairs. That could be the reason why Kingfishers from the Danube produce more broods per season than those from central Bohemia, although the length of breeding season is the same.

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SOUHRN

Ledňáček říční (Alcedo atthis) patří k druhům s dlouhou hnízdní sezónou. Ve střední Evropě hnízdí ledňáčci od konce března do druhé poloviny září a během jedné sezóny může jeden pár úspěšně odchovat mláďata až ze čtyř snůšek (Cramp 1985). Počet snůšek může být ovlivněn např. kondicí rodičů a/nebo kvalitou teritoria. V této studii porovnáváme délku hnízdní sezóny pro celou populaci a také délku hnízdní sezóny, počet snůšek a čas mezi dvěma následnými hnízděními během sezóny u jednotlivých párů mezi dunajskou (1868,7.-1819,0. říční km, celkem 55km toku a jeho ramen, nadmořská výška 110-200 m n. m.) a "středočeskou" populací (Středočeský a Jihočeský kraj, kraj Vysočina, celkem 230km toků a dvě nádrže, nadmořská výška 400-770m n. m.).

Hnízdní biologie ledňáčka říčního byla studována od března do září 2014–2018. Hnízdní nory byly kontrolovány přibližně jednou týdně a průběžně byly vyhledávány nové nory. Dospělí ptáci byli u hnízdních nor odchytáváni a kroužkováni či později v sezóně kontrolováni. Mláďata byla ve věku od 14 do 18 dní opatrně vyjmuta z nory pomocí speciálního nástroje a po okroužkování šetrně vrácena zpátky. Poté jsme pokračovali v kontrole nor s cílem dohledat opakovaná hnízdění stejného páru. Za období 2014–2018 bylo

zdokumentováno hnízdění 95 párů dunajské populace a 121 párů "středočeské" populace (tab. 1).

Délka hnízdní sezóny u dunajské populace činila v průměru 172 dní (± 8 SE) pro celou populaci (datum prvního sneseného vejce až datum posledního vyvedeného mláděte v populaci bez ohledu na identitu páru) a 101 dní (± 4 SE) pro jednotlivé hnízdní páry. Délka hnízdní sezóny u "středočeské" populace činila 165 dní (± 6 SE) pro celou populaci a 89 dní (± 3 SE) pro jednotlivé hnízdní páry. Délka hnízdní sezóny jednotlivých hnízdních párů se nelišila mezi populacemi (tab. 2), avšak u obou populací meziročně kolísala (obr. 1). Populace se však lišily v počtu hnízdění za sezónu. Nejvíce párů, a to shodně u obou populací, hnízdilo dvakrát za sezónu, přičemž tři a čtyři hnízdění ročně byly častější u dunajské populace (obr. 2, tab. 3). U jednoho páru z dunajské populace bylo dokonce zaznamenáno pět snůšek za sezónu (detailní popis viz Rubáčová & Melišková 2020). Počet hnízdění se u obou populací statisticky nelišil mezi jednotlivými roky (obr. 3, tab. 3).

Přestože se populace lišily v počtu započatých hnízdění, nebyl mezi nimi zjištěn rozdíl v délce hnízdní sezóny. Vysvětlením je čas uplynulý mezi dvěma následnými hnízděními stejného páru, který byl u dunajské populace kratší. Páry v dunajské populaci si dokonce mohly dovolit delší překryv mezi následnými hnízděními, tj. samice dříve opouštěla mláďata, aby započala novou snůšku, přičemž o mláďata se nadále staral jen samec. Důvodem mohlo být to, že ramena Dunaje – velké nížinné řeky – poskytují větší potravní nabídku.

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