

Seasonality predicts egg size better than nesting habitat in a precocial shorebird

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Kubelka V., Sládeček M., Zámečník V., Vozabulová E. & Šálek M. 2019. Seasonality predicts egg size better than nesting habitat in a precocial shorebird. *Ardea* 107: 239–250. doi:10.5253/arde.v107i3.a4



Egg size represents a fundamental predictor of chick mass and body condition. Chicks from bigger eggs have significantly increased survival, especially in precocial species, where chicks must forage for themselves and cope with environmental threats, such as bad weather or predators. Therefore, our understanding of the factors influencing egg size is crucial both from the perspective of their breeding ecology as well as of their conservation. However, studies simultaneously addressing multiple factors and quantifying their influence on egg size in large samples are rare. Here, we test the effect of seasonality, clutch size and nesting habitat on egg size, measured as volume, in a ground-nesting shorebird, the Northern Lapwing *Vanellus vanellus*, using a sample of 4384 eggs from 1125 clutches in South Bohemia, Czech Republic, during the period between 1988 and 2018. We report a significant decline in egg size over the breeding season, on average bigger eggs in larger clutches with a significant difference between 2-egg and 4-egg clutches, and no direct effect of nesting habitat. From our review of the same predictors across 15 Northern Lapwing populations throughout Europe it is apparent that replacement or late clutches have on average 3–7% smaller eggs than first or early clutches. Nesting habitat only rarely affects egg size and there are no significant differences in egg size between 3-egg and 4-egg clutches. Earlier studies showed that chicks hatching from bigger eggs early in the breeding season performed better, and that there was higher food abundance available for chicks at that time. This fact, together with the documented seasonal decline in egg size, sends an important message to conservationists and policymakers that early breeding attempts may play a pivotal role in safeguarding shorebird breeding productivity.



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Key words: clutch size, chick survival, egg size, nesting habitat, Northern Lapwing, precocial offspring, predation, seasonal timing, *Vanellus vanellus*, wader

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Egg size in birds is not only a measure of parental investment, but also represents an important predictor of chick growth and survival (Williams 1994, Christians 2002, Krist 2011). In general, egg size is more impor-

tant for precocial birds, where chicks must forage for themselves soon after hatching and are more exposed to harsh climatic conditions or predators in comparison with altricial nestlings (Starck & Ricklefs 1998). Pre-

social birds enhance survival of their chicks by investing more in eggs, which are, on average, proportionally more energy-rich and larger than eggs of altricial birds (Carey *et al.* 1980, Sotherland & Rahn 1987, Starck & Ricklefs 1998, Deeming 2007, Stoddard *et al.* 2017). Shorebirds belong to the bird clades with the proportionally largest eggs (Rahn *et al.* 1975).

The positive relationship between egg size and chick size, measured usually as, respectively, volume and mass, has been found in many bird species (Martin 1987, Christians 2002, Krist 2011) including shorebirds (Byrkjedal & Kålås 1985, Galbraith 1988a, Grant 1991, Thompson & Hale 1991, Hegyi 1996, Blomqvist *et al.* 1997, Hegyi & Sasvari 1998, Dittmann & Hötker 2001, Sheldon 2002, Larsen *et al.* 2003). Bigger chicks are in better body condition, are capable of longer-lasting self-thermoregulation, are more effective at searching for prey and can escape from predators easier. This advantage of hatching from a bigger egg can positively influence chick survival until fledging (Davis 1975, Galbraith 1988a, Bolton 1991, Grant 1991, Sheldon 2002, Eglinton *et al.* 2010, Krist 2011).

Variability in egg size is higher among clutches than within a clutch (Nol *et al.* 1984, Redmond 1986, Thompson & Hale 1991, Blomqvist & Johansson 1995, Dittmann & Hötker 2001, Parish *et al.* 2001). Egg size thus seems to be a consistent maternal trait, because eggs in a female's consecutive clutches are more similar in size than the eggs of different females, and intrinsic factors of particular females, such as protein storage or ovary size, probably play an important role (Christians 2002). Nevertheless, older, more experienced and heavier females lay bigger eggs than younger and lighter individuals of the same species (Nol *et al.* 1984, Thompson & Hale 1991, Parish *et al.* 2001, Christians 2002). Despite the generally assumed pivotal role of female intrinsic characteristics (Christians 2002), environmental factors, e.g. food availability during the egg formation period, can influence egg size (Lank *et al.* 1985, Perrins 1996, Nol *et al.* 1997). As food availability can differ among nesting habitat types (e.g. Galbraith 1988b, Blomqvist & Johansson 1995), habitat quality may influence not only the food availability for chicks (Devereux *et al.* 2004, Kentie *et al.* 2013), but also the egg size via the food supply for females prior to the egg-laying period. Furthermore, eggs in replacement or seasonally later clutches tend to be smaller than in the first ones (Byrkjedal & Kålås 1985, Redmond 1986, Galbraith 1988a, Šálek 1995, Hegyi 1996, Grønstøl 1997, Hegyi & Sasvari 1998, Sandercock *et al.* 1999, Sharpe 2006), possibly suggesting combined effects of intrinsic as well as several envi-

ronmental factors. Therefore, a possible seasonal change in egg size could have important consequences for chick survival.

From interspecific comparison it is apparent that many bird species trade-off the number of eggs in the clutch against egg size (Blackburn 1991, Figuerola & Green 2006, Martin *et al.* 2006). However, this pattern has not been found in shorebirds (Olsen *et al.* 1994), which usually have clutches of four eggs (Lack 1947, Arnold 1999), although there is some inter and intraspecific variability in the number of eggs in complete clutches (del Hoyo *et al.* 2018). Studies on the trade-off between egg size and clutch size at the intraspecific level are less common (e.g. Rohwer 1988, Hořák *et al.* 2008, Pellerin *et al.* 2016, Song *et al.* 2016).

The Northern Lapwing *Vanellus vanellus*, a precocial shorebird, breeds in agricultural landscapes using diverse nesting habitats with variable availability of different foraging opportunities (Cramp & Simmons 1983, Shrubbs 2007). This species probably aggregates energetic reserves for egg production particularly after



Northern Lapwing *Vanellus vanellus* chicks facing a difficult future while hatching late in the breeding season from smaller eggs in a maize field, which is often hot and dry with scarce food supply (photo V. Kubelka, 26 May 2012, Češňovice, South Bohemia, Czech Republic).

arrival to its breeding grounds, as suggested by indirect evidence (Galbraith 1989, Blomqvist & Johansson 1995, Shrubbs 2007), lays a varying number of eggs in the clutch (Cramp & Simmons 1983, Shrubbs 2007) despite a predominant clutch size of four eggs (Klomp 1970), and thus represents a suitable model species for investigating environmental or physiological factors affecting egg size (Galbraith 1988a).

Our aim is to assess and quantify the role of factors influencing egg size in Northern Lapwings and discuss the implications for conservation practices. We are using a long-term data set to ask the following questions. (1) Do seasonal timing (seasonality), nesting habitat and/or clutch size influence egg size? (2) Is chick size after hatching predicted by egg size in our study area? In addition, by reviewing the existing literature, we investigate (3) variation in the effect size of seasonality, nesting habitat and clutch size across Northern Lapwing populations, and discuss possible consequences for chick performance.

METHODS

Study area and field measurements

We searched for Northern Lapwing (Lapwing from hereon) nests near České Budějovice, Czech Republic, during 17 breeding seasons: 1988–1989, 1991, 1993–1994, 1996–1997, 2008–2009, 2011–2018. The study area (centre: 49.0°N, 14.4°E) consists of approximately 60 km² of agricultural landscape with prevailing arable land at an altitude of 380–420 m (for more details see Šálek & Šmilauer 2002, Zámečník *et al.* 2018). Lapwings breed in the whole area in small aggregations (rarely more than 25 pairs) or less commonly as individual pairs. We searched for nests using binoculars and telescopes, or by direct nest searching in denser breeding colonies during the breeding season. The peak of the start of incubation was usually during the first two weeks in April with the overall median on 7 April,

the earliest clutch incubation started on 19 March in 2017 and the latest on 15 June in 2013.

We recorded nest locations and assigned nesting habitat into one of six categories (Table 1). We determined the first day of incubation for each nest using the flotation method (van Paassen *et al.* 1984) or using the observed egg-laying dates of first or sequential eggs. The incubation start represents a day when the third egg was laid (Shrubbs 2007). For two egg clutches the laying date of the second egg was used. We took egg measurements (length, width) to the nearest 0.05 mm using vernier calipers. Due to possible egg size differences with the laying sequence within clutches (Lislevand *et al.* 2005), only complete clutches were included. Nests where not all eggs were measured and also two-egg or three-egg clutches found at a later incubation stage were excluded to eliminate a possible effect of partial predation on clutch size and mean within-clutch egg size in a clutch. The final dataset contained 1125 clutches with all eggs measured, specified known nesting habitat and defined first day of incubation. During 2013–2014 we also weighed chicks in or close to the nest at the day of hatching, using electronic scales with an accuracy of 0.01 g. The fate of chicks was not determined in this study. Additionally, we collected data following the same procedures in East Bohemia (50.18°N, 15.61°E; more detail on study site in Zámečník *et al.* 2018), at c. 200 km from the South Bohemian study site. These data were used only in the comparison among European populations.

Data processing

From the egg measurements, we estimated egg volume according to Galbraith's (1988) formula: $V = 0.457 \times L \times W^2$, where V is egg volume in mm³, L is length of the egg in mm and W is width of the egg in mm. We converted the values to cm³ and calculated the mean egg volume for each clutch as the targeted response variable. Similarly, we computed mean body mass of freshly hatched chicks from each clutch. We coded the

Table 1. Description of nesting habitat categories in South Bohemia, Czech Republic, and relative proportion (%) of these habitats among 1125 clutches.

Habitat category	Description	Number (%)
Ploughed field	Ploughed fields, stubble fields with partial ploughing	32
Meadow	Meadows and pastures	13
Winter crops	Winter wheat, oil-seed-rape fields	15
Spring crops	Harrowed fields, spring crops, maize fields, spring beans	33
Clover	Clovers and temporary grass planting on arable land	1
Other	Fallow lands, dry fishpond bottoms, other marshlands, potatoes	6

first day of incubation for each clutch as the number of days since the start of the calendar year, but without taking into account leap years, for easier comparability of data; thus 91 always equals 1 April and 152 equals 1 June, etc. Because a warmer winter or wetter spring can accelerate the start of the Lapwing breeding season (Both *et al.* 2005, Musters *et al.* 2010) and the timing of the breeding season was unique every year in our study population, we also computed standardized first days of incubation expressed as a number of days prior to or after the median first day of incubation for each year separately. There was no temporal trend in egg size variation for the 1125 clutches over the 17 breeding seasons of 1988–2018 (General Linear Model: slope = -0.009 , $F_{1,1123} = 1.12$, $P = 0.282$), which is important when addressing the questions in this study.

Literature review and effect size assessment

We searched for relevant publications using the keywords 'Northern Lapwing' or '*Vanellus vanellus*' in the electronic databases Web of Science, Searchable Ornithological Research Archive and Google Scholar, or via reference works (Cramp & Simmons 1983, Shrubb 2007, del Hoyo *et al.* 2018) and references in relevant publications. We found 13 publications which held information on egg size and at least one predictor that is also used in this study, in combination with our two data sets, this accounts to 15 Lapwing populations in our review study.

For better comparison among populations, we expressed the effect size of each predictor as a relative percentage difference between mean values of the tested categories and the overall mean egg size in a particular dataset. The reasons for this standardization was a possible geographical variation in egg size, as seen in shorebirds (Väisänen 1977) and in Lapwings particularly (Chylarecki *et al.* 1997), and the fact that some studies used different egg volume computations or used egg mass instead of egg volume. Seasonality was reported in two ways: (1) comparison between first and replacement clutches as assessed in individually marked birds; (2) comparison between early and late clutches using the regression line of egg size against incubation start days over the two-month breeding season. In the cases where the breeding season was a little bit longer (Sheldon 2002, this study), the effect size was adjusted for a two months period only. Note that in two studies (Sheldon 2002, Sharpe 2006), the date was not standardized according to the yearly median of the first day of incubation, and therefore the seasonal change in egg size could be less apparent in these cases.

When reporting the influence of nesting habitat on egg size, only Galbraith (1988a) had a proportionally balanced distribution of first and replacement clutches between two tested prevalent habitat categories, and Murton & Westwood (1974) had similar sample sizes between habitats for different months during the breeding season. Other studies did not account for the possible different proportions of first and replacement clutches between two tested habitats and one study (Cherkaoui & Hanane 2011) even acknowledges the possible impact of this disbalance on egg size. No study accounted for a possible influence of a change in clutch size over the breeding season (Shrubb 2007). It is therefore necessary to interpret the significance of reported values and the comparison of effect sizes of clutch size and nesting habitat among studies with caution.

We incorporated data in the comparative analyses only if more than ten clutches were available per category, otherwise, we assigned them as NA: no data available. In the case of Klabník (1984), we calculated egg volumes from the mean egg measurements according to the given formula (Galbraith 1988a) and then calculated egg size differences for particular categories from egg volumes. For the estimates of predictor effect sizes, in four studies (Murton & Westwood 1974, Galbraith 1988a, Baines 1990, Blomqvist & Johansson 1995) we calculated mean egg volumes for each category from the given subset values (e.g. per year or habitat) using a weighted mean according to sample size (number of clutches) in each subset. We used these values for the predictor effect size estimates by calculating the percentage difference between the mean values of tested categories and the overall mean egg size in the particular dataset of the given Lapwing population. Overall values of predictor effect sizes were calculated as the mean weighted by sample size (number of clutches) across all studies that reported the relationship and its quantification.

Statistical analyses

All statistical analyses were performed with R v. 3.3.3 (R Core Team 2017). We performed general linear models (GLM) using the 'lm' function or general linear mixed-effects models (GLMM) fitted with the 'lmer' function from the 'lme4' package (Bates & Maechler 2012). Apart from models with one dependent variable only, we performed two models to assess simultaneously the effect of seasonality, habitat and clutch size on egg size. The first model included all three possible two-way interactions between variables but because none of them were significant, the model presented

here included only fixed effects of the three dependent variables with year as a random intercept. Models were estimating the effect of particular variables while controlling for all other variables in the model (Table 3). Individual categories of nest habitat and clutch size were compared using post-hoc multiple comparisons of means (Tukey contrasts) in the ‘multcomp’ package (Hothorn *et al.* 2017). Model assumptions, such as normality and homoscedasticity of residuals, were checked visually from diagnostic plots (Crawley 2013). To visualize uncertainty in our model estimates in plots, we added the 95% credible intervals based on the joint posterior distribution of 5000 simulated values based on model outputs as generated by the ‘sim’ function in R (Gelman *et al.* 2016). Data and R codes for this study are available at Open Science Framework (<https://osf.io/zxbhs/>).

RESULTS

Effect of seasonality, clutch size and nesting habitat on egg size in South Bohemia

The mean egg volume in the clutch varied from 19 to 28 cm³ (mean: 23.40 cm³ ± 1.38 SD, median: 23.44 cm³) and declined significantly over the breeding season, using the first day of incubation for individual clutches (Figure 1, Table 2). Also clutch size was significantly related to mean egg size (Table 2). Mean egg volume in 2-eggs clutches was 4.1% smaller than in 4-eggs clutches (Tukey contrasts: $z = 2.77$, $P = 0.021$); other clutch sizes did not differ significantly, although

Table 2. Effect of seasonality, clutch size and nesting habitat on mean egg size in the clutch. Linear mixed effect models with the random intercept effect of year, all variables were controlled for the effect of remaining ones (type III analysis controlling for the effect of all remaining predictors, $n = 1125$ clutches). Two-way interactions and single terms are included in the first model. Seasonality is expressed as standardized first day of incubation, see Methods for more details.

Model	Predictor	<i>F</i>	<i>df</i>	<i>P</i>
First	Seasonality	2.57	1,1101	0.110
	Clutch size	5.27	3,1100	0.001
	Habitat	1.77	5,1076	0.012
	Seasonality×Clutch size	1.85	2,1096	0.160
	Seasonality×Habitat	1.32	5,1073	0.250
	Habitat×Clutch size	1.30	7,1098	0.250
Second	Seasonality	68.79	1,7640	<0.001
	Clutch size	3.25	3,1112	0.020
	Habitat	1.27	5,7990	0.270

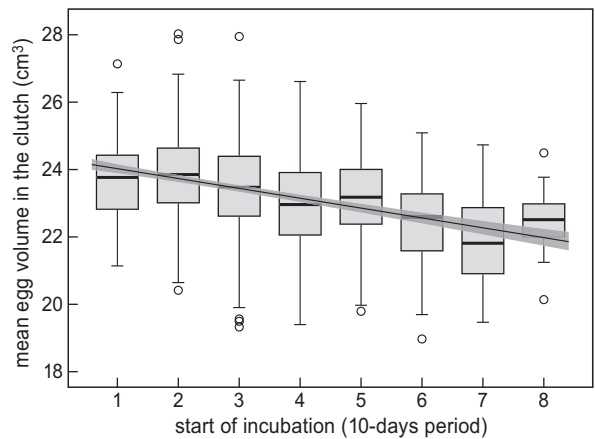


Figure 1. Mean egg volume in clutches in relation to standardized first day of incubation ($n = 1125$ clutches in 17 breeding seasons during 1988–2018 in South Bohemia, Czech Republic). Line with shaded area indicates model prediction with 95% credible intervals based on the joint posterior distribution of 5000 simulated values based on model outputs (Table 2) and generated by the ‘sim’ function in R (Gelman *et al.* 2016). Box-plots represent two 10-day periods before and six 10-day periods after the median of the first incubation day each year. Medians are denoted by thick lines, 25% and 75% quartiles by boxes, whiskers denote minimum and maximum values (when these do not expand beyond the ± 1.5 times inter-quartile range), or 1.5 inter-quartile range with outliers denoted with open circles.

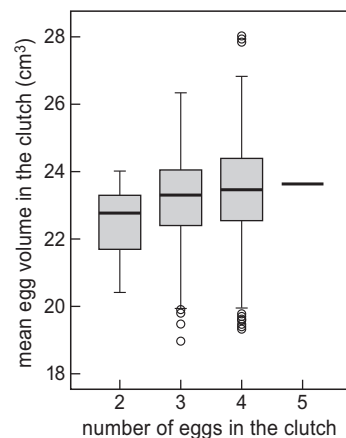


Figure 2. Mean egg volume in the clutch in relation to the clutch size. See Figure 1 for an explanation of the box plots. Overall $n = 1125$ clutches, 4 eggs = 987 clutches, 3 eggs = 121 clutches, 2 eggs = 16 clutches, 5 eggs = 1 clutch) during 1998–2018 in South Bohemia, Czech Republic.

egg size tended to increase with clutch size (Figure 2). There was no effect of nesting habitat after controlling for seasonality and clutch size (Table 2). Nesting habitat was significant only on its own (GLMM: $F_{5,794} = 11.67$, $P < 0.001$), with on average smaller eggs in spring

crops later in the season (Table 3), than in ploughed fields, meadows and winter crops (Tukey contrasts: all P -values < 0.001). In the comparison of three main habitats with similar mean first day of incubation, i.e. ploughed field, meadow and winter crop (Table 3), the habitat category did not influence the mean egg volume in the clutch (GLMM: $F_{2,281} = 1.65$, $P = 0.190$, $n = 676$ clutches).

Table 3. Mean egg volumes and mean clutch incubation start date in six nesting habitats ($n = 1125$ clutches) in South Bohemia during 1988–2018. For more detailed habitat descriptions see Table 1.

Habitat	Mean egg volume (cm ³)	SE	Mean incubation start	SE (days)	n
Ploughed field	23.71	0.07	6 April	0.59	362
Meadow	23.56	0.11	2 April	0.55	147
Winter crops	23.49	0.10	4 April	0.59	167
Spring crops	22.97	0.07	27 April	0.94	367
Clover	23.85	0.30	8 April	3.75	15
Other	23.43	0.18	11 April	1.88	67

Egg size and chick size in South Bohemia

The mean chick mass in a clutch right after hatching was significantly related to the mean egg volume in the clutch (GLM: slope = 0.701, $F_{1,44} = 99.32$, Adjusted $R^2 = 0.69$, $P < 0.001$) with heavier chicks hatching from bigger eggs (Figure 3).

Comparison among European populations

There was a significant effect of seasonality (first clutches vs. replacements, or regression of egg size over the two-month breeding season) on egg size in 7 out of the 11 reviewed studies (Table 4). All 10 studies that reported relationships were negative: generally, clutches laid later in the season consisted of smaller eggs than clutches from the first part of the breeding season. On average there was a 5.6% decline (range 0.1–11.8%, $n = 10$ studies, 2389 clutches) of egg size in the course of the breeding season. When the two approaches assessing seasonality were treated separately, the average decline for known first and replacement clutches was 2.9% (0.1–11.8%, $n = 5$ studies, 612 clutches), and the regression over the two-month breeding season showed a mean decline of 6.5% (5.9–7.3%, $n = 5$ studies, 1777 clutches).

Table 4. Review of seasonality, nesting habitat and clutch size effect on egg size in different Northern Lapwing populations. NA = no data available, ns = no significant relationship. NA/ ns = reporting non-significant relationship but without exact data for the effect size estimate. Two main habitat categories are compared in each study. Only 3-eggs and 4-eggs clutches are compared. Relationships are expressed in percentage of the difference between mean values of tested categories from the overall mean egg size in the particular dataset (see Methods for details) and are directional for seasonality and clutch size but not for nesting habitat. Significant relationships (given by test presented in each study) are highlighted in **bold**.

Source	Location	Study period	Number of clutches (eggs)	Seasonality ^a (% change)	Habitat	Clutch size 3–4
this study, Šálek 1995	S Bohemia (CZ)	1988–2018	1125 (4384)	(–6.8%)	0.4% (ns)	+1.1% (ns)
our unpubl. data	E Bohemia (CZ)	2013–2018	119 (467)	(–6.1%)	1.3% (ns)	+0.3% (ns)
Baines 1990	N England (GB)	1986–1987	386	NA	0.2% (ns)	NA
Bellebaum & Dittberner 2001	NE Germany	2000	69 (252)	(–3.5%)	NA	NA
Blomqvist & Johansson 1995	SW Sweden	1987–1990	216 (787)	–0.1%	2.9%	NA
Cherkaoui & Hanane 2011	N Morocco	2003–2010	69 (255)	NA	3.1%	NA
Galbraith 1988a	S Scotland (GB)	1984–1986	220 (790) ^b	–2.3%	2.9%	+1.0% (ns)
Grønstøl 1997	W Norway	1991–1994	72 (288) ^b	–11.8%	NA	NA
Hart <i>et al.</i> 2002	SE England (GB)	1997	61 (226)	NA/ ns	NA/ ns	+0.9% (ns)
Hegyí 1996	C Hungary	1988–1995	34 ^b	–3.8%	NA	NA
Klabník 1984	N Bohemia (CZ)	1975–1981	83 (318)	NA	NA	–0.8% (ns)
Murton & Westwood 1974	E England (GB)	1971–1973	55 (205)	NA	6.0%	NA
Parish <i>et al.</i> 2001	NE England (GB)	1992–1995	702	–4.0%	NA	NA
Sharpe 2006	N Wales (GB)	2003–2004	274	(–7.3%)	NA/ ns	NA/ ns
Sheldon 2002	C England (GB)	1999–2000	190	(–5.2%)	NA/ ns	NA/ ns

^afirst vs. replacement clutches, or the regression line through the whole season (in parentheses)

^bmarked/individually recognized females – Seasonality means first vs. replacement clutches of the same females

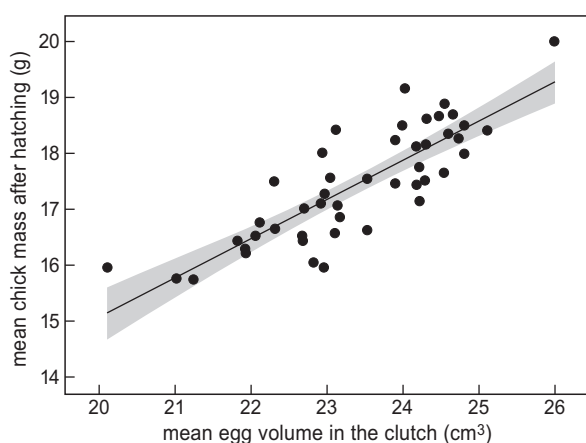


Figure 3. Relationship between mean chick mass at the day of hatching and mean egg volume. Line with shaded area indicates model prediction with 95% credible intervals based on the joint posterior distribution of 5000 simulated values based on model outputs (Table 2; see caption Figure 1). As we were not aware of the hatching order of chicks, the mean chick body mass from all chicks in the clutch and the mean egg volume of all eggs in the clutch were used, each dot in the figure represents one family/clutch ($n = 46$ clutches comprising 161 chicks during 2013–2014) in South Bohemia, Czech Republic.

The influence of nesting habitat, measured as the difference between the two most prevalent habitat categories, was significant in four out of ten cases. On three occasions, eggs were bigger in arable land than in coastal pastures, rough grazed pastureland or heathland. In one case, eggs were bigger in wet meadows than in saline grasslands. In all four cases, the study sites were dominated by a uniform habitat type. The effect size was between 0.2–6.0% ($n = 7$ studies, 2190 clutches; Table 4), but note different habitat categories. There were no significant differences in egg size between clutches of three or four eggs in any of the seven studies. The effect size was on average 0.9% (–0.8–1.1%, $n = 5$ studies, 1608 clutches) of the mean egg size (Table 4).

DISCUSSION

We have investigated the relative importance of three factors – seasonality, nest habitat and clutch size – potentially influencing egg size in Northern Lapwings in Europe. By using a long-term dataset from South Bohemia and reviewing literature we estimated, for the first time, effect sizes across multiple populations. We targeted our research on egg size with several possible response variables (seasonality given by egg-laying

date, nesting habitat, clutch size or habitat), but directly studied other parameters of reproductive investment, such as clutch size (Shrubb 2007) and egg-laying date (e.g. Both *et al.* 2005, Brandsma *et al.* 2017).

Seasonality

Seasonal timing has the biggest effect on egg size in Lapwings, with first clutches at the beginning of the breeding season containing on average 5.6% larger eggs in comparison with late and probable replacement clutches. This finding is in line with studies of other shorebirds (Byrkjedal & Kålås 1985, Redmond 1986, Hegyi 1996, Hegyi & Sasvari 1998, Sandercock *et al.* 1999).

We identify three main, but not mutually exclusive, factors that can be responsible for this phenomenon: (1) depleted energy reserves during laying of a replacement clutch (Hegyi & Sasvari 1998), (2) younger females producing smaller eggs and laying generally later in the season (Christians 2002), and (3) lower food availability for females laying later in the breeding season. There are several indications that the females' food supply influences egg size and that energetically rich earthworms play an important role (Baines 1990, Grønstøl 1997). For example, in South Sweden, Lapwings arrived at their breeding grounds at the same time, but females at the sites with more earthworms started laying earlier (Högstedt 1974). The more time spent before egg-laying on arable land with better availability of earthworms, the bigger eggs produced (Blomqvist & Johansson 1995). Earthworms become less available later in the season as they retreat deeper into the soil, particularly during dry weather conditions (Baines 1990, Beintema *et al.* 1991), or, they may be less easily found in compacted soil under growing crops. Warmer winters and wetter springs can accelerate the start of the Lapwing breeding season (Both *et al.* 2005, Musters *et al.* 2010), however, more rain early in the spring could also mean more easily available prey for females (Ausden *et al.* 2001), which could be used to gather more energy and produce larger eggs than during dry conditions.

Habitat

The effect of habitat on egg size was only significant in four out of ten studies. All these four studies share a feature of landscape uniformity and polarization. This 'landscape polarization' (Wilson *et al.* 2001, Siriwardena *et al.* 2012), defined as the presence of different but uniform habitats at various parts of the study area, probably limits feeding possibilities of an individual

Lapwing, because there are less or no other different habitats around the nest site. In three studies, eggs were found to be always bigger in arable land than in coastal pastures (Blomqvist & Johansson 1995), rough grazed pastureland (Galbraith 1988a) or heathland (Murton & Westwood 1974), which is in accordance with better earthworm availability in arable land (Blomqvist & Johansson 1995). Two studies (Blomqvist & Johansson 1995, Cherkaoui & Hanane 2011) reported smaller eggs in the habitat with higher proportions of replacement clutches, and only two studies (Murton & Westwood 1974, Galbraith 1988a) could be partially controlled for seasonality (see Methods). Therefore, the overall effect of habitat on egg size must be interpreted with caution; it can be over-estimated and be more driven by seasonality, similarly to the findings in South Bohemia.

On the other hand, no egg size differences among habitats were found in studies without 'landscape polarization' within the study area, i.e. consisting of grassland only (Baines 1990, Hart *et al.* 2002) or arable land only (Sharpe 2006, East Bohemia in this study), probably only with subtle qualitative differences between prevailing nesting habitat categories. Furthermore, the effect of habitat on egg size in Lapwing was also not visible in a mosaic agriculture landscape consisting of a heterogeneous mixture of arable fields with different crop types, meadows, pastures and fish ponds (South Bohemia, this study, Sheldon 2002), where females can easily feed nearby in different habitats, which is a common behaviour in Lapwings (Baines 1990, Berg 1993, Blomqvist & Johansson 1995), thereby removing any effect of nesting habitat on egg size. Although egg sizes differed among some habitats within arable land in South Bohemia (this study), this was in fact caused by seasonality (here the incubation start date), and not by habitat. The smaller eggs in replacement clutches later in the season in spring cereals, after mechanical damage of first clutches during agricultural activities such as harrowing of ploughed fields, is the most probable explanation of this pattern. This finding implies that future studies should address all possible relevant predictors simultaneously in one model to be able to distinguish their relative importance.

Clutch size

There were no significant differences in egg size between the 3- and 4-egg clutches based on the literature review. However, there was a slight tendency to bigger eggs in larger clutches, with eggs of 4-egg clutches being on average 0.9% larger than 3-egg

clutches. The significantly smaller eggs in 2-egg clutches in South Bohemia fits this pattern. Similarly, also Galbraith (1988a) found smaller egg volumes in 2-egg clutches in comparison with larger clutches. However, apart from the South Bohemian study locations, none of the other studies accounted for the possible change in clutch size over the season (Shrubb 2007), therefore it is important to treat the comparison among studies with caution. Nevertheless, any difference in egg size between 3-egg and 4-egg clutches is small, probably with only minor biological relevance.

The data gathered here suggest that Lapwings that produce smaller clutches do not have more energy to increase egg size, following the trade-off principle. On the contrary, the egg size is generally smaller in these smaller clutches, especially in South Bohemia (Šálek 1995, this study), demonstrating that Northern Lapwings do not trade-off clutch size against egg size among individuals. But this may of course be different within individuals. This finding corresponds to interspecific comparisons among shorebirds (Olsen *et al.* 1994) and intraspecific studies in some waterfowl species (Rohwer 1988, Hořák *et al.* 2008).

Chick survival and conservation implications

The well-studied advantage of heavier shorebird chicks hatched from bigger eggs (Byrkjedal & Kålås 1985, Galbraith 1988a, Grant 1991, Thompson & Hale 1991, Hegyi 1996, Blomqvist *et al.* 1997, Hegyi & Sasvari 1998, Dittmann & Hötter 2001, Sheldon 2002, Larsen *et al.* 2003) was confirmed also for Northern Lapwings breeding in South Bohemia. Besides the quality of parents (Blomqvist *et al.* 1997), any initial advantage of a larger size can have significant effects on body condition, growth and survival (Galbraith 1988a, Sheldon 2002). In Scotland, chicks hatched from eggs bigger than 23 cm³ were twice as likely to survive until fledging as chicks from smaller eggs (Galbraith 1988a). A similar advantage for higher chick survival was apparent also in Sweden (Blomqvist *et al.* 1997). Our finding of on average 5.6% larger eggs and subsequently bigger chicks at the beginning of the breeding season compared to the end of the season, will probably provide an important advantage to early hatching Lapwing chicks. In addition, availability of food and water for chicks is also known to often deteriorate at the end of the breeding season (Matter 1982, Galbraith 1988c, Beintema *et al.* 1991). Chicks can try to compensate for decreased food availability by increasing foraging activity; however, this means a higher exposure to potential predators (Evans 2004) and likely an increase in the chick predation rate (Mason *et al.*

2018). Maintaining high food availability for adults and chicks could be stimulated by a high-water table during the breeding season (e.g. Eglington *et al.* 2010), and could be an important conservation measure for shorebirds breeding in agricultural grasslands.

The Northern Lapwing has undergone a significant decline throughout Europe (BirdLife International 2004, Delany *et al.* 2009) and despite extensive efforts to change this trend (e.g. Tucker *et al.* 1994, Wilson *et al.* 2009), the species is still declining (BirdLife International 2015). The majority of Lapwing populations, either on grassland or in regions with predominantly arable fields, are not able to produce a sufficient number of fledglings to compensate for year-round adult mortality (Peach *et al.* 1994, French *et al.* 2000, Sheldon 2002, Sharpe 2006, Roodbergen *et al.* 2012) and chick survival may play a pivotal role (Roodbergen *et al.* 2012).

In light of the current results it is obvious that conservation measures for Lapwings should involve support for the first breeding attempts by preventing clutch losses due to destruction by agricultural activities, in particular during the early breeding season. This can be achieved via nest protection (Kragten *et al.* 2008, Zámečník *et al.* 2018), or on a larger scale, with the use of effective agri-environmental schemes (Eglington *et al.* 2010, Smart *et al.* 2014, Schmidt *et al.* 2017). However, nest predation seems to be in general the most common case of shorebird nest failure (MacDonald & Bolton 2008) and an increase in nest predation rates has been recorded throughout Europe (Roodbergen *et al.* 2012, Kubelka *et al.* 2018). Therefore, the use of predator exclusion by nest enclosures (Isaksson *et al.* 2007), habitat management (Laidlaw *et al.* 2017) or predator control (Bolton *et al.* 2007) might be also essential for the multifaceted support of Lapwing breeding success at sites with high predation pressure.

Taken together, the literature review and our own field data show that in Lapwings bigger eggs, together with food being more readily available for chicks at the beginning of the breeding season, is a double advantage for chicks hatching from the first breeding attempt. Protection of first clutches together with safeguarding or restoring food availability via a higher water table should be an important target in conservation measures for shorebirds breeding in the agricultural landscape.

ACKNOWLEDGEMENTS

We would like to thank many researchers who helped us in the field on a regular basis, and especially R. Piálková, V. Štorek, K. Chmel, J. Vlček, B. Pešek, V. Janatová, V. Dočekalová, K. Žohová, K. Brynychová, Z. Karlíková, T. Kejzlarová, H. Vitnerová and M. Bulla for sharing the dataset of 42 clutches from 2008–2009 in South Bohemia. V. Dočekalová, D. Kubelková and K. Mášková helped us with transcribing the field data into an electronic form and H. Hötker helped us with the grey literature from Germany. We thank K. Žohová for the cover drawing, P. Wiersma, J. Ouwehand and two anonymous referees for their critical comments that improved the manuscript and C.E. Tanner from University of Bath for the linguistic assistance. V.K. was supported by the Charles University Grant Agency (GAUK 927516), ÉLVONAL-KKP 126949 of the Hungarian government and Ministry of Education, Youth and Sports of Czech Republic (grant No. LO1415). V.Z. and M.Š. were supported by grant IGA FŽP (project No. 20174231). M.S., E.V. and M.Š. were supported by the CIGA (project No. 20164209) and IGA FŽP (project No. 20164218) grants.

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SAMENVATTING

De grootte van een ei voorspelt in hoge mate het gewicht en de lichaamsconditie van het kuiken dat uiteindelijk uit het ei kruipt. Grote eieren bieden een aanzienlijk betere overlevingskans voor de nakomelingen dan kleine, vooral bij nestvlieders (waarvan de kuikens na het uitkomen zelf moeten foerageren,

bestand moeten zijn tegen soms barre weersomstandigheden en op hen loerende roofdieren). Daarom is het belangrijk om te begrijpen welke factoren de grootte van eieren beïnvloeden, zowel vanuit een broedecologisch perspectief alsook vanuit vogelbeschermingsoogpunt. Het komt echter niet veel voor dat in een studie meerdere factoren tegelijkertijd worden gemeten om zo hun invloed op de grootte van eieren te kwantificeren. In dit onderzoek testten we het effect van de tijd in het seizoen, de legselgrootte en de nesthabitat op het volume van eieren bij de Kievit *Vanellus vanellus* in Zuid-Bohemen (Tsjechië). Tussen 1988 en 2018 werden in totaal 4384 eieren (1125 legsels) gemeten. Het volume van de eieren nam gedurende het broedseizoen significant af. Gemiddeld waren de eieren in grote legsels groter dan in kleine legsels (verschil tussen tweelegsels en vierlegsels significant). We vonden geen direct effect van de nesthabitat op het volume van de eieren. Uit ons overzicht van dezelfde variabelen in 15 kievitpopulaties in Europa die eerder waren onderzocht, blijkt dat vervangende of late legsels gemiddeld 3–7% kleinere eieren hebben dan eerste of vroege legsels. De nesthabitat beïnvloedde in deze studies de grootte van de eieren niet of nauwelijks. En er waren geen significante verschillen in de grootte van de eieren tussen legsels met drie en vier eieren. Vroegere studies hebben laten zien dat kuikens uit grote eieren vroeg in het broedseizoen het beter doen dan kleine eieren later in het seizoen en dat de voedselbeschikbaarheid vroeg in het seizoen beter is. Dit gegeven, samen met de gedocumenteerde seizoenafname van de grootte van de eieren, is ook belangrijk voor natuurbeschermers en beleidsmakers. Vroege broedpogingen kunnen een cruciale rol spelen bij het verbeteren van het broedsucces van steltlopers.

Corresponding editor: Janne Ouweland

Received 23 August 2018; accepted 22 May 2019