

Laying date, egg volumes and chick survival in Lapwing (*Vanellus vanellus* L.), Redshank (*Tringa totanus* L.), and Black-tailed Godwit (*Limosa limosa* L.)

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Egg laying date, egg volumes, hatching weight and guarding females in tending periods were recorded for Lapwing (*Vanellus vanellus* L.), Redshank (*Tringa totanus* L.) and Black-tailed Godwit (*Limosa limosa* L.) breeding on meadows in Kiskunsági National Park, 50 km south of Budapest (19° 07' E; 47° 08' N). The meadows were flooded artificially in autumn but no water management or agricultural activities were carried out during the period of the breeding season. Longest time interval and greatest nest distance between first and replacement clutches was 17 days and 94 m for Lapwing, 17 days and 85 m for Redshank and 20 days and 120 m for Godwit. Egg sizes were smaller in replacement clutches than in first clutches. Positive correlation was found between the egg volumes, hatching weight and chick survival.

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1. Introduction

Egg volume is generally held to be an important index of egg quality and is correlated with chick survival in many bird species. Egg size has been correlated with chick hatching weight, hatching size, growth rate, survival and fledgling weight in shags, (Amundsen & Stokland 1990), gulls (Persons 1970, Lundberg & Väisänen 1979, Bolton 1991), terns (Nisbet 1978), grouse (Moss *et al.* 1981), murrens (Birkhead & Nettleship 1982), skuas (Furness 1983) and tits (Schifferli 1973). In this study I focused on the rela-

tionship between the egg volumes and chick survival of three wader species.

To date little is known about the replacement clutches of waders, including egg parameters, female condition and the time interval and distance between nests for first and replacement clutches. In this study I marked individual females with painted patches, and was thus able to identify which birds laid replacement clutches after the destruction of their first clutch. I recorded the time intervals and distances between the two nests and measured egg volumes, egg weights and hatching weights of replacement clutches.

2. Study area and methods

The study area was chosen on a site where artificial fish ponds had been created in 1953 over 380 ha in Kiskunság National Park, 50 km south of Budapest (19° 07' E; 47° 08' N), and where fish breeding was abandoned in 1966. The fish ponds had dried up and were first flooded artificially in 1987. In each August the ponds dried up and were re-flooded every autumn during the study period from 1988-1995. No water management or agricultural activities were carried out in the area during the breeding season. A meadow of 210-240 ha was a suitable breeding habitat for ground nesting birds in the ponds; the rest of the area was covered by water. Surrounding area of the ponds was covered by arable field and dry meadow.

Nests were detected by observing the incubating parents either from a car parked on the banks or from hides where suitable nesting were far from the banks. About 70-80 ha could be viewed from the hides and 130-160 ha from the banks. Nests were marked with sticks placed a few meters from them, and their arrangement in the study area was mapped.

Nest identification started at the beginning of March. Each part of the study area was examined at 3-4 day intervals. The detected nests were also checked at 3-4 day intervals. Laying date was based on the interval during which the first egg was laid. When the first egg-laying, hatching or any event within the clutch occurred during the period between two checks, the day halfway between visits was recorded. After chicks hatched the area covered by arable field and dry meadow, with poor and short plants, was surveyed for a dis-

tance of 2 km around the breeding area. The area was divided into belts 500 m wide and surveyed by driving down the centre of the belt at 3-4 day intervals, observing parents guarding chicks.

Nest losses resulted from predation and other disturbances, including flooding following rainfall and inter- and intra-specific aggressive interactions. Predation was identified by the complete disappearance of the clutch or by the presence of partially eaten eggs in or near the nest. All losses not resulting from predation were considered as due to 'other disturbance'.

Marking of birds was carried out using the technique suggested by Paton & Park (1986). Dummy eggs were treated with a mixture of oil jelly and either Rhodamin B, anilin blue or xylinene orange. Beads of gel (5-10x3-5 mm) were placed along the length of the eggs, which were then substituted in the nests during the period of incubation. Combinations of the colours marked the birds in unique patterns on their abdomens and breasts so that they could be individually identified. Sexes were identified by display and copulatory behaviour. Parents from 7-11 nests were marked in each species in each year. Of the eggs that were painted, the first clutches of 19 pairs of Lapwings and 15 pairs of Godwits were destroyed but then replaced. Seven Lapwing nests and 6 Godwit nests were abandoned due to the painting procedure, over the 8 year study period; these were omitted from all analyses.

After the chicks had been hatched 10-15 days (in early tending period) and between 25-30 days after hatching (in late tending period) I recorded the presence or absence of females in the study area. When females tending were recorded their broods were considered to be alive, when

females disappeared before 30 days after their chicks had hatched, their young were considered to be died. One Lapwing and three godwit males tended alone because the females deserted, they were omitted from all analyses.

The eggs were measured with a sliding calliper with an accuracy of ± 0.1 mm. Both maximum length (L) and breadth (B) were measured, and egg volume (V) was calculated using the formula, $V=0.51 \times L \times B^2$ (Hoyt 1979). Weights of freshly laid eggs (weighted no later than the second day after laying) and freshly hatched chicks were weighted with Pesola spring balances. Egg sizes and hatching weights were averaged for each clutch and the mean used for further calculations.

Weight measurements were made using electronic balances (± 1 g) set below the nests in a hollow so that the nest sitting on top of the balance was at its original height. Balances were placed below the nests and taken out after each measurement of parents. Cables from the balances were connected to the displays that could be seen clearly from the car and the hide. Balances were calibrated using known weights each time a measurement was taken after resiting the nest with eggs on the balance. Parents were weighted in the first and fourth week of incubation period for both the first and replacement clutches.

Statistical analyses were carried out using the SPSS statistical package.

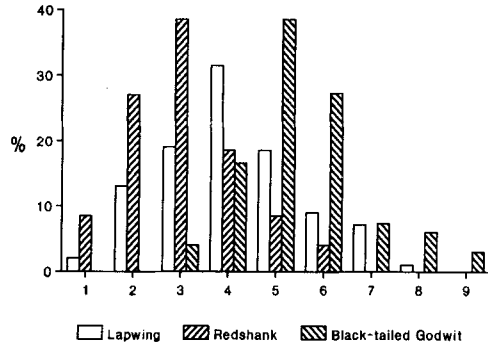


Fig. 1. Laying date distribution of the first clutches of three wader species. The numbering of the horizontal axis refers to the nine 10 day periods from 1st of March to the end of May.

3. Results

3.1. Laying date and egg volumes

Laying date for 244 female Lapwings, 214 Redshanks and 171 Black-tailed Godwits were recorded over a period of 8 years. I defined nine 10-day intervals within the egg laying period between March 1st and May 29th and calculated the percentage distribution of clutches laid during each interval. Figure 1 shows that Lapwings laid their eggs earliest and Godwits laid their eggs latest ($\chi^2=233.0$, $P<0.001$). When laying date were calculated using a series number where 1 denoted 1st March, the differences in the mean laying date between Lapwing, Redshank and Godwit were significant. (Lapwing: $n=244$ $\bar{x}=22.42$, $SD=19.62$; Redshank: $n=214$

Tab. 1. Egg volumes (cm^3) laid in early, peak or late laying period for three wader species.

		Lapwing			Redshank			Black-tailed Godwit		
		n	\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	SD
Laying period	Early	78	24.97	1.18	90	19.74	0.95	45	43.80	1.32
	Peak	91	25.70	0.93	67	20.83	0.71	82	45.46	1.54
	Late	75	25.08	0.80	57	19.95	0.94	44	44.04	1.16

\bar{x} =36.17, SD=20.06; Godwit: n=171
 \bar{x} =47.12, SD=22.17: ANOVA:
 F_{2,629}=8.29, P<0.001.)

I identified three periods within the egg laying season for each species. The peak period was when most clutches were laid, the early period contained all the 10 day intervals before that and the late period all the 10 day intervals after it. I found the highest egg volumes in the peak period for all three species, but the differences in volume between eggs laid in the early and late periods were not significant (Tab. 1). (Between peak and early period for Lapwing, Redshank and Black-tailed Godwit: t=4.70, t=5.75 and t=5.82, P<0.001 in each occasion; between peak and late period: t=4.32, t=8.13 and t=6.36, P<0.001 in each occasion; between early and late period: t=0.67, t=1.30 and t=0.91, NS in each occasion.)

3.2. Replacement clutches

In total 67 female Lapwings 51 female Redshanks and 65 female Godwits were marked by paint patches during the breeding season over the 8 year study period. Twenty-six Lapwings, 27 Redshanks and 37 Godwits suffered failure of their first clutches, and 17 Lapwings, 14 Redshanks and 15 Godwits laid a replacement clutch.

The mean distance between first and replacement clutches was greatest for Godwit and shortest for Redshank (ANOVA: F_{2,43}=8.57, P<0.001; Tab. 2). The time interval between first and replacement clutches were not significant among the species (ANOVA: F_{2,43}=2.24, P=0.171).

Egg volume was smaller in replacement clutches than in first clutches for each species (Lapwing: t=2.30, P<0.05; Redshank: t=3.14, P<0.001; Godwit: t=2.61, P<0.02). Calculations of the relationship between interval separating first and replacement clutches and mean egg volume in the replacement clutches showed a positive correlation for all three species, i.e. the longer the time waited after the first clutch, the larger the egg volumes in the replacement clutch. (Lapwing: r=0.846, P<0.001; Redshank: r=0.632, P<0.02; Godwit: r=0.773, P<0.001.)

3.3. Egg volumes, hatching weight and chick survival

Observations were made on the hatching day for 31 Lapwing clutches, 22 Redshank clutches and 26 Godwit clutches, with chicks being weighted during the first few hours of life. (Mean for Lapwings: \bar{x} =16.32g, SD=1.09; for Redshank:

Tab. 2. Comparison of first and replacement clutches for three wader species.

	Lapwing			Redshank			Black-tailed Godwit		
	n	\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	SD
Distance from the first nest (m)	17	76.88	6.64	14	69.73	5.96	15	98.40	9.32
Time between first and replacment clutches (day)	17	10.86	0.78	14	11.90	0.61	15	12.27	0.98
Egg volume (cm ³) in the first clutch	17	24.74	1.03	14	20.42	1.08	15	45.37	1.30
Egg volume (cm ³) in the replacement clutch	17	23.82	1.37	14	19.23	0.92	15	44.21	1.16

Tab. 3. Egg volumes (cm³) of females of three wader species that were observed or not observed in the tending period.

	Lapwing			Redshank			Black-tailed Godwit		
	n	\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	SD
Early tending period									
Females observed	24	26.00	0.87	21	21.11	0.71	33	46.47	1.14
Females not-observed	43	24.70	1.04	28	20.04	0.75	32	44.92	1.18
Late tending period									
Females observed	12	26.06	0.84	14	21.46	0.66	27	46.89	1.10
Females not-observed	55	24.91	1.06	35	20.16	0.77	38	44.91	1.24

\bar{x} =14.80g, SD=1.86, for Godwits: \bar{x} =27.55g, SD=1.21, combined data of first and replacement clutches.) A positive correlation was found between mean hatching weight and mean egg volume within a clutch for all species (Lapwing: $r=0.815$, $P<0.001$; Redshank: $r=0.640$, $P<0.001$; Godwit: $r=0.717$, $P<0.001$).

The duration of incubation for those clutches where chicks were weighed neonatally was \bar{x} =27.76 days, SD=1.52 for Lapwings, \bar{x} =25.61 days, SD=1.26 for Redshanks and \bar{x} =28.54 days, SD=1.30 for Godwits.

Tab. 3. shows the number of females observed or absent in the early and late tending periods and their egg volumes. In all species, egg volumes of females that were present are larger than those of females absent in the early and late tending periods. (Early period for Lapwing: $t=5.44$, $P<0.001$, Redshank: $t=5.09$, $P<0.001$, Godwit: $t=5.40$, $P<0.001$; late period for Lapwing: $t=4.08$, $P<0.01$, Redshank: $t=5.94$, $P<0.001$, Godwit: $t=6.78$, $P<0.001$.)

4. Discussion

Different trends of seasonal variation in egg size are seen for different species of birds. For some species, egg size

increased as the breeding season progressed (Perrins 1970, Pikula 1971, Svensson 1978), whereas for others egg size decreased (Coulson 1963, Nelson 1966, Coulson *et al.* 1969, Parsons 1975, Birkhead & Nettleship 1982) and some species showed no seasonal variation in egg size (Coleman 1972, Pikula 1974, Bryant 1975, Miller 1979, Rofstad & Sandwik 1985). In this study the largest egg volumes were recorded during the peak period. The smaller egg size during both early and late laying periods may have two different explanations. Small egg size during the early laying period may be due to a reduced food availability to the females whereas late in the laying season it may be due to egg laying by the younger females (Perrins 1996).

Berg *et al.* (1992) studied the replacement clutches of Lapwing with colour-ringed birds and found that females nested again within two weeks and did so within 100m of their first clutch. My study confirms this observation with the furthest replacement clutch laid 94m from the first and the longest interval between clutches 17 days.

Previous report of the distance between first and replacement nests for Black-tailed Godwits estimated range from 80-640m (Balen 1959). I found that the distance in my study never exceeded

120 m and the time interval was never greater than 20 days. The high differences in the distances between first and replacement nests may be due to the various spatial disturbance of suitable nesting habitat.

I did not find reference about the replacement clutches of Redshanks. I recorded 85 m as greatest nest distance and 17 days as longest time interval between first and replacement clutches.

As the size of the chick is closely related to the size of the egg, larger eggs result in larger hatchings (Ricklefs *et al.* 1978). This relationship was recorded for both Lapwings and Black-tailed Godwits in both first and replacement clutches. Parsons (1970) suggested that large eggs produced more viable chicks in the semi-precocial Herring Gull because they hatched with larger yolk reserves. The larger energy store ensured the survival of chicks during the crucial first few days of life, when there is a high mortality rate for chicks. Several authors have demonstrated the importance of large egg size and high yolk content for chick survival (Bancroft 1985, Alisauskas 1986, Hepp *et al.* 1987, Meathrel & Ryder 1987, Meathrel *et al.* 1987), although several others have shown that large eggs contain proportionally less yolk than small ones (Parsons 1970, Ricklefs 1984, Meathrel & Ryder 1987, Meathrel *et al.* 1987). I have confirmed the survival value of large eggs for both Lapwings and Black-tailed Godwits. Females laying and hatching large eggs guarded their chicks during the tending period, but those producing smaller, lighter eggs were not observed to guard the young even during the early tending period, suggesting that the chicks were already dead.

Nevertheless, I conclude that the higher survival value of large eggs may only operate after hatching, because successful incubation was independent of egg size.

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Összefoglalás

A bÍbic (*Vanellus vanellus* L.), a pÍroslÁbú cankó (*Tringa totanus* L.), és a nagy goda (*Limosa limosa* L.) tojÁsrakÁsi ideje, tojÁstÉrfogata és fiÓka tÚlélése

A bÍbic (*Vanellus vanellus* L.), a pÍroslÁbú cankó (*Tringa totanus* L.) és a nagy goda (*Limosa limosa* L.) tojÁsrakÁsi ideje, a tojÁsok tÉrfogata, a fiÓkák kelési sÚlya és a fiÓka-gondozói periÓdusban a fiatalok tÚlélése került elemzésre a KiskunsÁgi Nemzeti Park területén, Apaj térségében (Budapesttől délre 50 km-re) gyűjtött adatok alapján. A vizgÁlati területet ősZel lekasZálás után mesterségesen elÁrasztották, költésidőben azonban semmiféle beavatkozás, illetve egyéb mezőgazdasági tevékenység nem volt a térségben. A bÍbic rakta le legkorábban tojÁsait, a nagy goda legkésőbb. Mindhárom faj a legnagyobb tÉrfogatú tojÁsokat a tojÁsrakÁsi idősZak középső szakaszában rakta. A leg-hosszabb időköz és a legnagyobb fészekközti távolság az első és a pótköltés között a bÍbiceknél 17 nap és 94 m, a pÍroslÁbú cankónál 17 nap és 85 m, a nagy godáknál 20 nap és 120 m volt. A pótköltések tojÁstÉrfogata kisebb volt, mint az első költések tojÁstÉrfogata. SzignifikÁns pozitív korreláció volt a tojÁstÉrfogat, az utódok kelési sÚlya és fiÓka-kori tÚlélés között.

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