



CLUTCH AND EGG SIZE IN MARINE AND FRESHWATER COMMON TERNS *STERNA HIRUNDO*

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Clutch and egg sizes in birds are affected by intrinsic and environmental factors. Clutch size is affected by food availability and predation risk, while egg size is influenced by parental age and environmental conditions during both the breeding and pre-breeding period. In the Common Tern *Sterna hirundo*, egg size decreases with the laying sequence, and the survival rate of the last-hatching chicks is lower than that of their siblings. We studied the differences in clutch size, egg volume, and egg volume reduction in Common Terns inhabiting marine and freshwater habitats. Clutch size varied in the studied regions. Egg size differed annually, but the greater volume reduction of second- and third-egg was found in marine habitats and among late clutches, regardless of the year. Egg volume and reductions were correlated with females' body characteristics.

Key words: egg volume reduction, habitat, female morphometry, Adriatic Sea, Croatia

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Na veličinu legla i jaja kod ptica utječu i unutarnji i okolišni čimbenici. Veličina pologa utjecana je dostupnošću hrane i rizikom od predacije, dok na veličinu jaja utječu dob roditelja i okolišni uvjeti tijekom sezone gniježdenja i predgniježdećeg razdoblja. U položima crvenokljune čigre *Sterna hirundo* veličina jaja se smanjuje s redoslijedom polaganja, a vjerojatnost preživljavanja posljednjeg izleženog ptica niža je nego kod ostalih ptica u leglu. Istražili smo razlike u veličini pologa, volumenu jaja i smanjenju volumena jaja kod čigri koje nastanjuju morska i slatkovodna staništa. Veličina pologa razlikovala se između proučavanih regija. Veličina jaja varirala je među godinama, a veće smanjenje volumena drugog i trećeg jaja utvrđeno je u morskim staništima i među kasnim položima, neovisno o godini. Volumen i smanjenje volumena jaja bili su u korelaciji s tjelesnim karakteristikama ženki.

Ključne riječi: smanjenje volumena jaja, stanište, morfometrija ženki, Jadransko more, Hrvatska

INTRODUCTION

The annual reproductive success of birds depends on the number of clutches laid, clutch size, and chick survival. Avian clutch size is heritable, although to some extent affected by environmental conditions, leading to intraspecific variability (CODY, 1966). The main factors affecting clutch size include food availability and predation risk (MARTIN, 1992). Food availability can vary depending on environmental productivity,

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seasonality, day length, and abundance of competitors (HOCKEY & WILSON, 2003). Reduced food availability and higher predation risk result in smaller clutch sizes (MARTIN, 1992; HOCKEY & WILSON, 2003).

In birds, as in many other oviparous animals, egg size affects offspring quality and survival during the early stages of life (KRIST, 2011). Morphological traits of offspring, particularly body mass at hatching, are positively correlated with egg size, and larger eggs tend to increase chick survival during the early chick-rearing period (WILLIAMS, 1994; KRIST, 2011). Egg size depends on various intrinsic and environmental factors, including the age of both parents (MILLS, 1979; KRIST, 2011; GENOVART *et al.*, 2022) and food availability (KRIST, 2011). The differences in egg size can also result from carry-over effects from previous seasons (HARRISON *et al.*, 2011; FAYET *et al.*, 2016). Intra-clutch variation in egg size is considered to have an adaptive value, with birds adopting the “brood-reduction strategy” laying smaller final eggs and birds adopting the “brood-survival strategy” having a relatively large final egg (SLAGSVOLD, *et al.* 1984).

The Common Tern *Sterna hirundo* is a colonial species that breeds across the Northern Hemisphere. It lays up to four eggs per clutch, with a three-egg clutch being the most common. Egg size decreases with laying sequence (MOORE *et al.*, 2000). Common Terns lay one clutch per year, but in the case of clutch or brood loss, replacement clutches may occur (BECKER & ZHANG, 2011). Studies on egg characteristics and their effect on chick survival in Common Terns have shown a positive correlation between egg mass and hatchling mass, as well as lower growing rates and lower chick survival in last-hatching chicks (BOLLINGER *et al.*, 1990; BOLLINGER, 1994; MOORE *et al.*, 2000; ARNOLD *et al.*, 2006). Common Terns inhabit both marine and freshwater habitats, which differ in spatial and temporal prey availability (BECKER *et al.*, 1997), potentially influencing their life-history traits.

In this study, we compared clutch and egg sizes in Common Terns in freshwater and marine colonies in Croatia, with special emphasis on the relative size of the last egg in the clutch. We tested whether different environments affect clutch size, egg size, and egg size reduction in Common Terns. We also compared female body measures with their clutch size and egg characteristics.

MATERIALS AND METHODS

Study area

The study was conducted in two freshwater and two marine areas between 2021 and 2024 (Fig. 1). Freshwater study areas were located in NW Croatia: the Sava river basin near Zagreb (three colonies: the Rakitje gravel pits 45.797° N, 15.840° E, Blato 45.780° N, 15.881° E, and Siromaja 45.779° N, 16.137° E), and the Drava river basin near Koprivnica (one colony, the Šoderica gravel pit 46.227° N 16.909° E). The colonies in the Sava river basin belong to the same population, with birds moving among colonies each year depending on the water levels. The colony at Siromaja was located on a breeding raft, while the two other colonies were located on gravel islands. The number of pairs per colony varied across the years due to fluctuating water levels: 0–115 at Rakitje, 26–67 at Siromaja, and 0–100 at Blato. The colony at Šoderica gravel pit (Drava river basin) was active only two years, with 66 pairs in 2021 and 35 in 2023; all clutches were laid in June. In 2023, the highly pathogenic avian influenza outbreak caused mortality in Common Terns and a decrease in number of clutches in freshwater habitats.

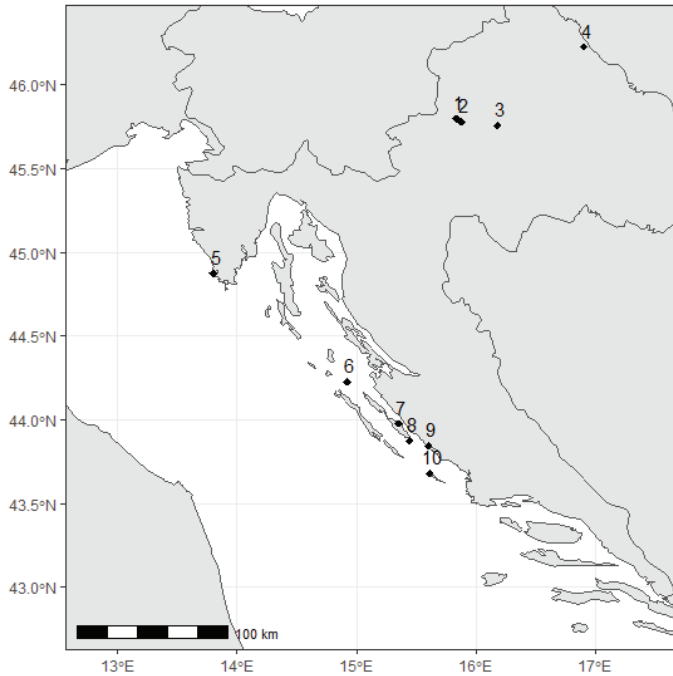


Fig. 1. Studied colonies of the Common Tern in Croatia. 1- Rakitje, 2- Blato, 3 – Siromaja, 4 – Šoderica, 5 – Pula, 6 – Bivošćak, 7 – Školjić, 8 – Ošljak Mali, 9 – Splićak, 10 – Mikavica.

The marine colonies were located in the Adriatic Sea. In the northern Adriatic, one colony was situated on man-made structures (docks) in the bay of Pula, Istria (44.875° N 13.802° E). This colony was established in 2022 and studied in 2023 and 2024, with 39 and 33 breeding pairs, respectively. In Dalmatia (central Adriatic), colonies were located on small uninhabited islands in Zadar and Knin-Šibenik Municipalities: Školjić east of the island of Pašman (43.977° N 15.356° E), Ošljak Mali south of Pašman (43.876° N 15.447° E) and Splićak near Prosika (43.844° N 15.606° E), Bivošćak near Molat (44.228° N 14.925° E) and Mikavica near Žirje (43.679° N 15.615° E). The number of breeding pairs varied across the years: 6–32 at Školjić, 0–24 at Splićak, 18 at Ošljak Mali, 12 at Bivošćak, and 19 at Mikavica.

DATA COLLECTION

Clutches were monitored from early May to early July during breeding seasons from 2021 to 2024. The mean clutch size was calculated from all nests in the colonies. At each colony, a sample of at least 50 eggs was measured (or all eggs if fewer than 50), including clutches from the colony edge as well as the central ones. Clutches with more than four eggs and clutches containing eggs with obviously different coloration were omitted from the analysis, as they were considered to have been laid by two females. Clutches containing atypical eggs (dwarf or elongated) were included in the clutch size analysis but excluded from the egg size analysis.

The maximum length and maximum breadth of each egg were measured with callipers to the nearest 0.01 mm. All measurements were made by the second author. Between 2021 and 2024, 975 eggs from 388 clutches were measured.

We captured adult terns at nests with measured eggs using walk-in traps during the late incubation stage, in late May and early June in order to compare female body measures with clutch size and egg characteristics. Birds were fitted with plastic and steel rings, measured, weighed, and released at the same site. Head-and-bill lengths, lengths of bill to skull, and bill depths and widths at the distal edge of nostrils were measured using callipers with 0.1 mm precision (Eck *et al.*, 2011; Demongin, 2016). Wing and tail lengths were measured using a stopped ruler with 1 mm precision, but were not used in this study because wingtips and tail feathers in many individuals were already worn. Body mass was obtained using a digital scale with 0.5 g precision. Blood samples for sex determination were taken from the ulnar or metatarsal vein (FRIDOLFSSON & ELLEGREN, 1999).

DATA ANALYSES

We calculated egg volume using the equation [$V = L \times B^2 \times k$], where V is egg volume (mm^3), L is egg length (mm), B is egg breadth (mm), and k is a species-specific constant (Hoyt, 1979). We used $k = 0.502$, according to MOORE *et al.* (2000). We separately analysed egg variables in three-egg clutches ($N_{\text{clutches}} = 211$, as some of the clutches were excluded due to the small sample size for certain regions and years). The largest egg was referred to as A-egg, the middle one as B-egg, and the smallest one as C-egg. The same notation was used for one- and two-egg clutches. The fourth egg in the clutch was not analysed, as the sample size was too small. Clutches laid in May were considered early clutches and those laid in June late clutches. The laying date was determined using the egg flotation method (HAYS & LECROY, 1971).

We calculated the average value and standard deviation of egg volume for all measured eggs per study area and season. We also calculated these values separately for A-, B- and C-eggs as well as for eggs from early and late clutches. Additionally, we calculated the egg volume reduction, as the percentage of B- and C-eggs volumes compared to A-egg volume within each clutch. We built generalised linear mixed-effect models to analyse the effect of the habitat (freshwater vs. marine), region (Sava, Drava, Istria, and Dalmatia), year, and month on clutch size and egg variables. As the variable region was nested in the variable habitat, we used in the models only the one that performed better. In the models with clutch size as the dependent variable, the colony size (number of nests in the given year) was included among the variables. ANOVA and t-test were used to calculate the significance between the egg measures from different clutches or habitats.

Clutch size and egg variables of early and late clutches from the same year and colony were compared only for the two colonies at which numbers of late clutches were high enough: Školjić (Dalmatia) in 2021 ($N_{\text{early}} = 29$, $N_{\text{late}} = 28$) and Pula (Istria) in 2023 ($N_{\text{early}} = 42$, $N_{\text{late}} = 37$) using the two-tailed t-test.

For 43 measured females (16 from freshwater and 27 from marine colonies) captured between 2021 and 2023, we recorded clutch and egg size characteristics to compare female morphometric characteristics with clutch size and egg variables. As egg volumes varied among years (see Results), we calculated the deviation from the mean value for each egg variable within each colony, month, and year. We ran

several linear models with clutch size, the deviation of the volume of the first egg, and the deviation of the reduction of the volume of the B- and C-egg in a clutch as dependent variables and year, habitat (freshwater or marine) as categorical variables and head-and-bill length, bill length, width and depth, and body mass as continuous variables.

Statistical analyses were performed in R 4.4.0 (R CORE TEAM, 2023) using *lme4* and *MuMIn* packages (BATES *et al.*, 2015; BARTOŃ, 2024).

RESULTS

Clutch size

The average clutch size varied annually between 2.1 and 2.8 eggs in freshwater and between 2.2 and 2.8 marine colonies (Tab. 1). Linear models showed that the most important factor for clutch size was the region, with the largest clutches in the Sava river and the Istria colonies and the smallest in the Drava river colony. Late clutches were significantly smaller than early ones by -1.9 eggs in the Pula colony (Istria) in 2023 ($t_{77} = 3.830$, $p < 0.001$), but not in the Školjić colony (Dalmatia) in 2021 ($t_{55} = 0.657$, $p = 0.51$).

Tab. 1. The average annual clutch size of Common Terns in four regions in Croatia. The number of clutches is provided in parentheses.

	2021	2022	2023	2024
Freshwater				
Sava river basin	2.3 ± 0.85 (158)	2.6 ± 0.66 (189)	2.4 ± 0.87 (67)	2.8 ± 0.43 (26)
Drava river basin	2.1 ± 0.81 (66)		1.7 ± 0.61 (14)*	
Marine				
Istria			2.8 ± 0.61 (42)	2.5 ± 0.62 (33)
Dalmatia	2.2 ± 0.76 (81)	2.4 ± 0.81 (35)	2.3 ± 0.65 (23)	2.2 ± 0.73 (55)

*heavily predated colony

Egg size

A total of 975 eggs were measured, including 26 from single-egg clutches, 264 from two-egg clutches, 657 from three-egg clutches, and 28 from four-egg clutches. Egg length ranged from 32.8 to 46.6 mm and egg width from 25.8 to 32.6 mm, with mean values of 40.76 ± 1.87 and 30.11 ± 0.98 mm, respectively.

In three-egg clutches, the total volume and the volume of the first egg were mostly affected by the year (Tab. 2). Both the total volume and the volume of the first egg were significantly larger in 2023 and 2024 than in 2021 (total volume 2023, $t = 1.795$, $p < 0.05$; 2024, $t = 2.012$, $p < 0.05$; A-egg 2023, $t = 1.845$, $p < 0.05$; 2024, $t = 1.657$, $p < 0.05$). However, the reduction of B- and C-egg was affected by habitat and month, rather than year (Tab. 3). Greater reduction of both B- and C-eggs was found in marine habitats and among late clutches (B-egg: $t = 2.123$, $p < 0.05$; C-egg: $t = 2.131$, $p < 0.05$). Additionally, the reduction of C-egg was greater in clutches with a larger volume of the first egg ($t = -2.983$, $p < 0.005$).

The A-egg volume was related to clutch size: in single-egg clutches, the eggs were smaller than the first eggs in two- and three-egg clutches in both freshwater ($F_{2,185} = 5.137$, $p < 0.01$) and marine habitats ($F_{2,187} = 3.023$, $p = 0.05$), as well as in all early clutches ($F_{2,236} = 4.755$, $p < 0.01$).

Female body measures

The average head-and-bill length in 43 measured adult females was 76.07 ± 2.33 mm, bill length was 44.70 ± 1.92 mm, bill depth 7.25 ± 0.58 mm, bill width 4.66 ± 0.65 mm, and body mass 116.98 ± 7.90 g. Birds from marine colonies were slightly larger, but the difference was significant only for the body mass (t -test $t = 1.875$, $p < 0.05$; Tab. 4). Among measured females, four had one-egg clutches, 16 had two-egg clutches, and 23 had three-egg clutches.

Tab. 2. Linear models of the total egg volume and the volume of the first egg in three-egg clutches of the Common Tern in Croatia. The last model is the full model.

Variables	np	Dev	AICc	Δ AICc	Wi
Total egg volume					
Year	5	2970793374	4082.2	0	0.589
Habitat + Year	6	2970784372	4084.3	2.12	0.204
Habitat + Month	4	3042865305	4085.2	2.96	0.134
Year + Month + Habitat	7	2969809347	4086.4	4.19	0.073
First egg volume					
Year	5	375442164	3645.7	0	0.663
Year + Region	6	372289963	3647.7	1.95	0.250
Year + Month	8	375138480	3650.4	4.64	0.065
Year + Month + Region	9	372273420	3652.6	6.81	0.022

Tab. 3. Linear models of the reduction in the volume of the second and third egg in three-egg clutches of the Common Tern in Croatia. The last model is the full model.

Variables	np	Dev	AICc	Δ AICc	Wi
Second egg volume reduction					
Habitat * Month	5	1403.722	1008.9	0	0.702
Habitat + Month	4	1434.293	1011.4	2.45	0.206
Month * Year	8	1395.661	1014.1	5.20	0.052
Year + Month + Habitat	7	1413.540	1014.7	5.73	0.040
Third egg volume reduction					
Habitat * Month	5	4104.148	1235.3	0	0.745
Habitat + Month	4	4194.171	1237.8	2.48	0.216
Month * Year	8	4117.892	1242.4	7.13	0.021
Year + Month + Habitat	7	4166.734	1242.8	7.45	0.018

Clutch size was not related to any of the female body traits. However, the deviation in the volume of the first egg was positively correlated with body mass ($t = 2.162$, $p < 0.05$), while the deviation in the reduction of B- and C-egg was smaller in females with longer head-and-bill (B-eggs $t = 2.354$, $p < 0.05$; C-eggs $t = 2.296$, $p < 0.05$).

Tab. 4. Body measurements of incubating female Common Terns in freshwater and marine colonies. Differences between habitats were tested using a t-test. * $p < 0.05$

	Freshwater N= 16	Marine N = 27	t-value
Head-and-bill /mm	75.98 ± 2.39	76.13 ± 2.34	0.202
Bill length /mm	44.16 ± 2.46	45.02 ± 1.48	1.431
Bill width /mm	4.58 ± 0.54	4.71 ± 0.71	0.631
Bill depth /mm	7.31 ± 0.45	7.21 ± 0.65	-0.570
Body mass /g	114.13 ± 8.91	118.67 ± 6.86	1.875*

DISCUSSION

The clutch size varied from region to region, but was not influenced by habitat or colony size. The largest clutches were recorded along the Sava river and in Istria, while the smallest were along the Drava river. Common Terns bred at the colony at Šoderica gravel pit near the Drava river in 2021 and 2023, and in both years, breeding started in June. As our study indicated that late clutches might be smaller than the early ones (as found in Istria), the smaller clutch size at Šoderica could be the result of the inclusion of late clutches in the analysis. Smaller size of late clutches was already recorded in some Common Terns (BECKER & LUDWIGS, 2004) and Black-legged Kittiwakes *Rissa tridactyla* (COULSON & PORTER, 1985).

The egg volume varied significantly between years. It is known to be affected by the female's condition and resource allocation (KRIST, 2011), which may be constrained by nutritional limitations (CHRISTIANS, 2002). Thus, the annual differences in egg volume may be affected by environmental factors, especially food abundance, during both the breeding and the pre-breeding period. The effect of the laying month on the egg volume had lower significance in our sample, although it was shown that in Common Terns, earlier clutches may contain larger eggs (MOORE & MORRIS, 2005; ARNOLD *et al.*, 2006)

Independently of the egg volume in the given year, the reduction of the second and third egg was greater in marine habitats. In general, larger differences in egg size should be expected in more variable environments (CREAN & MARSHALL, 2009; KRIST, 2011). It was shown that in Croatia, Common Terns in marine habitats forage over larger areas (KRALJ *et al.*, 2025) and have lower nest attendance (VODOPIJA *et al.*, 2024) than in freshwater habitats, which indicated lower food availability or predictability. Therefore, more predictable foraging opportunities in freshwater habitats might be related to smaller egg reduction in the clutch. The brood-reduction strategy, characterised by a smaller final egg, is common in larger species (SLAGSVOLD *et al.*, 1984). The reduction of egg volume along the laying order was recorded among other tern species (ØSTNES *et al.*, 1997; ZUARTH *et al.*, 2016) Although in the Common Tern the egg size decreases with the laying order, experimental studies of hatching asynchrony with manipulated broods have questioned the brood-reduction strategy in this species (BOLLINGER, 1994). It was suggested that smaller final egg size might even increase the survival of the last chick, as smaller eggs have shorter incubation periods and thus reduce the hatching asynchrony in the clutch (PARSONS, 1976).

Late clutches, with larger egg volume reduction, were either replacement clutches or clutches from birds that started breeding late in the season. Younger birds that

started laying eggs later often lay smaller eggs (CHRISTIANS, 2002). However, as the majority of birds were not colour-ringed, we could not determine the age of females or record replacement clutches of the same individual. Nisbet (2019) showed that in Common Terns, replacement clutches are smaller and contain lighter eggs. The greater reduction of the last egg in late clutches was found in other tern and gull species (SOLDATINI *et al.*, 2008; ZUARTH *et al.*, 2016).

As the age of parent birds was unknown, we could not account for the effect of age. In German Common Terns, the egg volume increased with age until birds reached five years, when the trend stabilised until the age of 13 years, when egg volume slightly decreased (GONZÁLEZ-SOLIS *et al.*, 2004). In contrast, in a North American Common Tern population, clutch size increased with age, but egg size was not affected (ARNOLD *et al.*, 2006; NISBET, 2020). The effect of parental age has been studied in other seabirds. Both younger and older Audouin's Gull *Larus audouinii* individuals laid smaller clutches and smaller eggs than middle-aged individuals (GENOVART *et al.*, 2022). In Red-billed Gulls *Larus novaehollandiae* the egg size increases not only with the female's age, but also with the male's (MILLS, 1979).

The range of the clutch size recorded between 2021 and 2024 in Croatia is consistent with previous studies along the Drava river in Slovenia: 2.3–2.6 eggs per clutch with median value 3 (JANŽEKOVIČ *et al.*, 2003), and 2.7 ± 0.71 eggs (VOGRIN, 1998), as well as with the general range of clutch size in this species (see data in KHEMIS *et al.*, 2021). Different patterns in annual variations of the clutch size in freshwater and marine colonies of Common Terns in Croatia could be the result of the differences in population dynamics of their prey. However, carry-over effects can also cause seasonal differences in fitness; for example, in birds, fat reserves at the end of non-breeding season can affect the clutch size (HARRISON *et al.*, 2011). Therefore, the use of different flyways and wintering areas by the freshwater and marine Common Terns from Croatia (PAVLINEC *et al.*, 2025) could also contribute to the differences in those patterns.

In Common Terns, egg size shows some variation among populations (VOGRIN, 1998; KHEMIS *et al.*, 2021). Oological data from the Adriatic population collected in the 1970s on 64 eggs, showed the length between 31.5 mm and 45.0 mm, and width between 26.3 and 36.2 mm (ŠTROMAR, 1972). The Common Tern eggs in NE Slovenia were somewhat larger, with the mean length of 41.23 mm, and the mean breadth of 30.07 mm (VOGRIN, 1998).

In our study, the clutch size was not related to any female body traits. However, our results indicate that females with larger body mass laid larger A-eggs and that females with longer head-and-bill showed a smaller reduction of B- and C-eggs. The relationship between female body mass and size and egg size has been studied in several species, but the results were not consistent (CHRISTIANS, 2002). Further studies on egg characteristics and female morphometry on the larger sample, preferably with known female age and supplemented with the study of females' adaptive genetic diversity could provide deeper insights into these relationships.

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