BREEDING PARAMETERS OF THE GULL-BILLED TERN *GELOCHELIDON NILOTICA* IN BOUGHRARA LAGOON, SOUTHEAST TUNISIA

AMEL NEB* & SLAHEDDINE SELMI

Ecology & Environment Laboratory (LR24ES17 – CDR2024ES04), Faculty of Sciences, Gabès University, Zrig 5072, Tunisia
**(ennebamel88@yahoo.fr)*

Received 19 October 2025, accepted 26 December 2025

ABSTRACT

Neb, A., & Selmi, S. (2026). Breeding parameters of the Gull-billed Tern *Gelochelidon nilotica* in Boughrara Lagoon, southeast Tunisia. *Marine Ornithology, 54*(1), 171–175. http://doi.org/10.5038/2074-1235.54.1.1689

We provide, for the first time, data on the breeding parameters of the Gull-billed Tern *Gelochelidon nilotica* in Tunisia, at Boughrara Lagoon. From May to July 2024, we monitored a breeding colony located on a small islet in the northern part of the lagoon. In total, 112 nests were monitored: 71 nests initiated in mid-May (early clutches) and 41 in early June (late nests). Clutch size ranged from one to four eggs (mean ± standard deviation [SD] = 2.51 ± 0.06), with no significant difference between early and late nesters. Egg volume ranged from 14.65 to 49.23 cm^3 (mean ± SD = 27.56 ± 4.03) and did not vary with laying date. However, egg volume decreased significantly with laying order across all nests. Last-laid eggs were smaller than first-laid eggs, consistent with a brood reduction strategy, which is a common breeding strategy in terns. Only 15% of nests failed to produce chicks, but the causes of failure could not be determined precisely. No evidence of egg predation was recorded, and failures were likely due to conflicts between neighboring pairs. Early nests were more successful than late nests (94% vs. 76%). This seasonal decline in reproductive success is consistent with general trends in waterbirds and may reflect either lower intrinsic quality of late breeders or deterioration of environmental conditions late in the breeding season.

Key words: breeding parameters, brood reduction, *Gelochelidon nilotica*, nesting phenology, Tunisia

INTRODUCTION

Investigating the environmental and ecological factors that affect the breeding success of birds is essential for understanding population dynamics and informing conservation efforts. This is particularly relevant for waterbirds, which are experiencing ongoing population declines, especially in the Black Sea-Mediterranean region (Agreement on the Conservation of African-Eurasian Migratory Waterbirds, 2022; Birdlife International, 2008; International Wader Study Group, 2003; Qualli et al., 2024; SEO/BirdLife, 2025). The Gull-billed Tern *Gelochelidon nilotica* has a near-global distribution, ranging from the Americas through parts of Europe and North Africa to Central Asia and Australia (del Hoyo & Collar, 2014; Molina, Pérez-Gil, & Martínez, 2020). The only known breeding colonies on the African continent, totaling 1,800 pairs, have been documented for the northwest African countries (Sánchez et al., 2004).

In Tunisia, the Gull-billed Tern has long been recognized as a regular breeder in the Ichkeul wetland complex in northern Tunisia, as well as on the islands of Chikli (Lake of Tunis) and Kneiss (Gulf of Gabès) (Isenmann et al., 2005). It has also been recorded breeding at the Thyna salina, located in the suburbs of Sfax in the Gulf of Gabès (Chokri et al., 2010). At the latter site, egg laying occurred in early May, and clutch size ranged from one to three eggs. However, most breeding attempts failed due to predation by stray dogs *Canis familiaris* (Chokri et al., 2010).

Nesting has also been reported on the islets of the Boughrara Lagoon, in the southern Gulf of Gabès (Isenmann et al., 2005; Neb & Selmi, 2019), although no information on reproductive parameters has been documented. The present study examines variation in the reproductive parameters in this understudied population, including breeding phenology, nesting behavior, egg and clutch size, and hatching success, all of which have not previously been reported for this population. In contrast to the nearest breeding colony (i.e., Thyna salina in the suburbs of Sfax), the study colony is subject to minimal human disturbance, as it is located on an isolated and rarely visited islet. Nest predators, especially stray dogs, are absent, and waterbird nests are subject to low predation pressure (Neb & Selmi, 2019). Under these conditions, reproductive success is expected to be high.

MATERIALS AND METHODS

Study Site

This study was conducted on a small islet located at the northern part of the Boughrara Lagoon, between Djerba Island and El-Jorf Peninsula, in south-eastern Tunisia (33°43′55″N–10°42′56″E). This islet covers an area of approximately 1 km^2 and rises no more than 10 m above sea level. It is covered with low perennial vegetation dominated by *Salicornia*, with sparse nitre bushes *Nitraria retusa*.

Besides the Gull-billed Tern, this islet hosts nesting colonies of five other colonial waterbird species: Slender-billed Gull *Chroicocephalus genei*, Yellow-legged Gull *Larus michahellis*, Common Tern *Sterna hirundo*, Little Tern *Sternula albifrons*, and Little Egret *Egretta garzetta* (Neb & Selmi, 2019).

Data Collection

Fieldwork was conducted during the 2024 breeding season. The islet was visited from mid-May to the end of July at a frequency of two to

three visits per week. Each discovered nest was monitored until the end of the incubation period, defined as either the hatching of at least one egg (successful nests) or hatching failure (nest abandonment or egg disappearance). In cases of failure, the nest and its surroundings were carefully inspected for evidence to help identify the cause.

Upon discovery, each nest was marked with a numbered wooden pole placed nearby. The following parameters were recorded: nest diameter (cm) and distance (m) to the nearest nest. Clutch date (i.e., the date of first egg-laying) and clutch size were also determined. Clutch size was determined only for nests in which laying was complete. Thus, any clutch lost during the egg-laying phase was not considered. Each newly laid egg was marked with a permanent, non-toxic marker at the time of discovery to determine laying order.

Once a clutch was complete and before incubation progressed, the length (L) and width (l) of each egg were measured using a digital caliper (precision: ± 0.1 mm). These data were subsequently used to determine egg volume, following Oro (2001): $V\ (cm^3) = 0.000485 \times L\ (mm) \times l^2\ (mm)$. Total egg volume was also calculated for each nest.

Data Analysis

Data were first used to describe nesting phenology by plotting the number of initiated nests as a function of date (Julian date), allowing identification of the two nesting peaks (early vs. late nests; see Results). We then used the non-parametric Mann-Whitney test to assess whether nest diameter, distance to the nearest neighbor, clutch size, and total egg volume (i.e., the sum of egg volumes in a clutch) differed between early and late nests. We also assessed whether (1) hatching success (proportion of nests that hatched at least one chick), and (2) the proportion of hatched eggs per nest (number of hatched eggs divided by the number of eggs laid) differed between early and late nests, using a χ^2 test and Mann-Whitney test, respectively.

Moreover, a Generalized Linear Mixed Model (GLMM) was conducted to check whether egg volume (response variable) differed between early and late clutches and among egg laying orders (first, second, and third and later eggs), included as fixed effects. Nest identity was included as a random effect to account for possible non-independence among eggs from the same clutch. In this model, the interaction between fixed effects was also tested to assess whether the magnitude and/or direction of intra-clutch variation in egg volume varied with nesting phenology. All statistical analyses were carried out using SAS software (SAS Institute, 2008). Values are expressed as mean ± standard deviation (SD).

RESULTS

Nesting Phenology and Nest Measurements

The terns exhibited two distinct nesting periods: 15–21 May (71 nests) and 03–05 June (41nests; Fig. 1). Earlier breeders constructed significantly larger nests (Fig. 2; Mann-Whitney test: $Z = -1.895$; $p = .058$), and nearest neighbor distance (0.2–7 m) was significantly larger in late nests (Fig. 2; Mann-Whitney test: $Z = 6.088$; $p < .001$).

Clutch Size and Egg Size

Clutch size ranged from one to four eggs (modal clutch = 3 eggs; median = 3 eggs; mean = 2.509 ± 0.057 eggs). Total egg volume per clutch ranged from 17.72–121.30 cm^3 (mean = 68.41 ± 19.03 cm^3). Neither variable differed significantly between early and late clutches (Mann-Whitney test: $Z = 0.206$, $p = .837$ for clutch size; $Z = -0.190$, $p = .849$ for total egg volume; Fig. 2).

Total egg volume per clutch ranged from 14.65–49.23 cm^3 (mean ± SD = 27.55 ± 4.03), with no significant difference between early and late clutches (GLMM: $F_{1,143} = 0.210$, $p = .650$). However, within a nest, egg volume decreased significantly with laying order (GLMM: $F_{2,143} = 11.54$, $p < .001$; Fig. 3) for both early and late nesters, (GLMM: $F_{2,143} = 0.100$, $p = .906$).

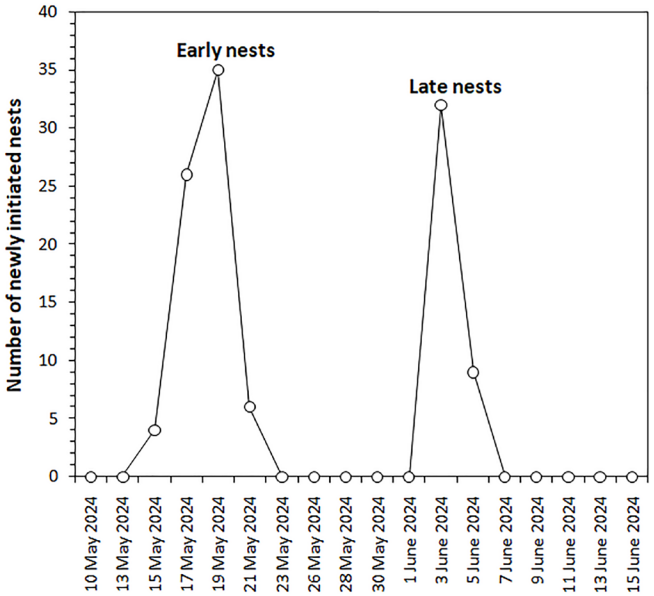

Fig. 1. Number of newly initiated nests of Gull-billed tern *Gelochelidon nilotica* plotted as a function of date, showing two distinct nesting periods (early vs. late nests).

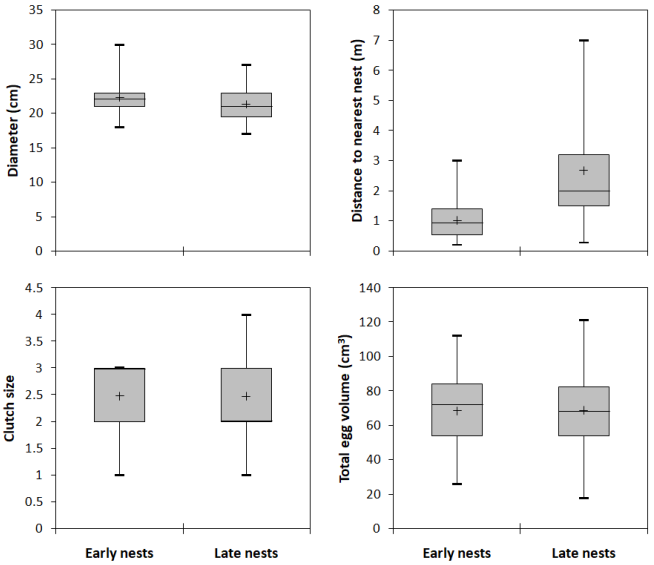

Fig. 2. Boxplots of nest diameter, distance to nearest neighbor, clutch size, and total egg volume in early and late nests. Means are indicated by plus symbols, median values by solid lines, inter-quartile range by gray rectangles, and extreme values by whiskers.

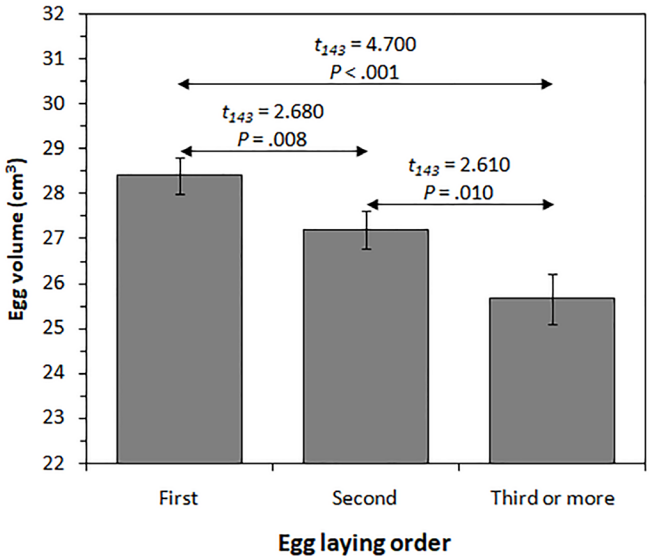

Fig. 3. Estimated least-square means (± SE) of egg volume (in cm^3) by laying order, based on Generalized Linear Mixed Model (GLMM). The model included nesting phenology (two classes: early vs. late nests) and egg laying order (three classes: first, second, and third or later eggs) as fixed effects, and nest identity as a random factor.

Hatching Success

Hatching success, defined as the proportion of nests that hatched at least one chick, was high (85%). It was significantly higher in early nests than in late nests: 94% (67/71) and 76% (31/41), respectively (χ^2_1 = 8.360, p = .004). The proportion of hatched eggs per nest (range = 0–1 eggs; median = 1 egg in both groups; mean ± SD = 0.887 ± 0.256 for early nests and 0.675 ± 0.421 for late nests) decreased significantly with laying date (Mann-Whitney test: Z = -2.887, p = .002). The causes of hatching failure could not be determined, as no evidence of predation was found. In most cases, eggs were found intact or slightly damaged outside the nest. Less frequently, eggs were found in the nest, damaged but not consumed. These failures were likely due to aggressive interactions between neighboring pairs, as such behavior was commonly observed.

DISCUSSION

This study aimed to provide data to improve understanding of the breeding ecology and population dynamics of the Gull-billed Tern in North Africa. To our knowledge, the colony examined here has never been the subject of detailed research or monitoring, which also applies to the majority of colonial waterbirds nesting in the Boughrara Lagoon (but see Neb & Selmi, 2019). The differences reported here relative to other Gull-billed Tern colonies could reflect the combined influence of abiotic and biotic factors.

Compared with Gull-billed Terns in other North African countries, birds at Boughrara Lagoon started egg laying relatively late (15–21 May). In a previous study at a nearby Tunisian breeding colony, in the Thyna-Sfax salina, egg laying began at the end of April (Chokri et al., 2010), whereas it occurred in early May in Morocco (Radi et al., 2004) and in Denmark (Moller, 1981). In Algeria and at Lake Nasser, Egypt, egg laying began in the first or second week of April (Bouzid et al., 2019; Jens Hering et al., 2021). It remains unclear whether this spatial variation reflects a difference in breeding phenology resulting from population-specific migration strategies or variation in local environmental conditions, particularly weather. Supporting the latter hypothesis, we observed a delay in nesting of all waterbird species breeding on the islet during the 2024 season, likely due to unusually high rainfall in late April and early May. Given the clay-rich nature of the island's soil, the rainfall resulted in persistent sticky mud which took time to dry out, delaying nest establishment relative to typical breeding dates.

Mean clutch size at Boughrara Lagoon (2.5 eggs) was similar to values reported for other North African colonies: 2.1 in Algeria (Bouzid et al., 2019), 2.2–2.6 in Tunisia (Chokri et al., 2010), and 2.4 in Morocco (Radi et al., 2004). Most clutches (63%) were initiated during May, but a second, smaller peak occurred during the third week of June. It remains unclear whether these later clutches represent replacement clutches or are attributable to inexperienced young individuals. In waterbirds, younger and/or low-quality individuals are known to breed later in the season than older, more experienced birds (Brinkhof et al., 1993; Johns et al., 2017; Parsons, 1975; Ryder, 1975). However, in the present study, we lack information on the quality or age of late breeders.

Incubation began with the first laid egg and lasted an average of 22 days, consistent with values reported for other populations (Inoue, 1985; Wolford, 1971). Hatching rate exceeded 85%. This high hatching success is most likely due to low predation pressure, consistent with our expectation. Stray dogs, which are the primary predators of waterbird nests at the Thyna-Sfax breeding site (Chokri & Selmi, 2019), have not been recorded on this isolated islet. Moreover, natural oophagous predators, such as rats or snakes, appear to be absent. These species were never observed, and no evidence of their presence (e.g., burrows, tracks, or moults) was found despite targeted searches. The few egg losses recorded were likely due to aggressive conflicts between neighboring breeding pairs. However, although aggression between breeding birds was common, we never observed birds damaging the eggs of neighboring nests.

There was significant variation in breeding success with the advancement of the nesting season. Late nests (late June) were characterized by significantly lower hatching rates than early nests (late May), a pattern widely reported in terns and other waterbirds across diverse geographic areas (Arnold et al., 2006; Hafner, 1977; Hochachka, 1990; Klomp, 1970; Perrins & McCleery, 1989; Pratt & Winkler, 1985; Ranglacket al., 1991; Rodgers Jr, 1987). This pattern may reflect lower intrinsic quality of late breeders compared to early breeders. Alternatively, the decline in breeding success may result from deteriorating environmental conditions as the nesting season progresses. Food availability often decreases later in the breeding season (Arnold, et al., 2004, 2006; Christian et al., 2001; Eriksson, 1978; Korpimäki & Wiehn, 1998; Verhulst & Tinbergen, 1991), although we lack direct data on the temporal variation of food resources at the study site to verify this hypothesis. In addition to the decline in food resources, increasing temperatures late in the season may elevate the risk of dehydration, thereby making egg incubation and chick rearing conditions more challenging. These factors could partly explain the decline in the reproductive performance of individuals. Therefore, the poor performance of late breeders may result from a combination of abiotic (weather) factors and food scarcity.

Egg volume decreased significantly within laying order. Such variation in egg size within a clutch is a common reproductive strategy in birds, particularly in species prone to brood reduction (Amundsen & Stokland, 1990). In many terns and other waterbirds, the first egg laid is typically larger in volume and hatches earlier than subsequent eggs, giving the first chick a consistent size and developmental advantage (Dunn, 1975; Fasola & Saino, 1995; Neb et al., 2019). This creates a hierarchy within the brood, especially when food availability is unpredictable. Chicks originating from smaller, later-laid eggs typically have lower competitive ability and are therefore more vulnerable to starvation or parental neglect when food is scarce (Stienen & Brenninkmeijer, 2006). This strategy likely represents an evolutionary adaptation whereby parents produce more eggs than they can typically raise, ensuring that only the most viable chicks—often those from larger, earlier-laid eggs—will survive under suboptimal conditions (Amundsen & Stokland, 1990). In the present study, egg volume was lower in late-laid eggs; however, the underlying cause of this pattern remains unclear and may reflect variation in food availability or other unmeasured factors.

Future research should address the issues highlighted above. In particular, it would be valuable to examine whether reproductive investment, specifically clutch size and egg volume, depends on food availability. This would require sampling potential prey and monitoring their abundance in the foraging areas of breeding pairs throughout the breeding season.

CONCLUSION

This study provides new insights into the reproductive ecology of the Gull-billed Tern in Tunisia, where only one previous study has been conducted. These findings enhance our understanding of the species' status across the Mediterranean basin and may inform the implementation of effective conservation strategies.

DECLARATION OF CONFLICTS OF INTEREST

The author declares no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

ACKNOWLEDGMENTS

This work was carried out in partnership with the Association Jlij pour l'Environnement Marin (AJEM), as part of the Mobilité des Docteurs (MOBIDOC) program funded by the European Union through the Science With And For Youth (SWAFY) project, and managed by the Agence Nationale de Promotion de la Recherche (ANPR). This study complies with Tunisian laws and ethical standards for wildlife research, as it was based solely on observation without capture or handling of the species studied. We thank M. Mohamed Neb and M. Sami Abdeljaoued for their invaluable help in the field, as well as Dr. Khaled Chouikhi for the various interactions during the early stages of this work. We thank the reviewers for their constructive comments, which improved the manuscript.

AUTHOR CONTRIBUTIONS

AN: Conceptualization, investigation, methodology, writing—original draft. SS: Supervision, formal analysis, writing—review & editing.

REFERENCES

Agreement on the Conservation of African-Eurasian Migratory Waterbirds. (2022). *Managing waterbird disturbance: A short guide for wetland managers (Draft 2).* https://www.unep-aewa.org/document/managing-waterbird-disturbance-short-guide-wetland-managers-draft-2

Amundsen, T., & Stokland, J. N. (1990). Egg size and parental quality influence nestling growth in the Shag. *The Auk*, *107*(2), 410–413. https://doi.org/10.2307/4087629

Arnold, J. M., Hatch, J. J., & Nisbet, I. C. T. (2004). Seasonal declines in reproductive success of the common tern *Sterna hirundo*: Timing or parental quality? *Journal of Avian Biology*, *35*(1), 33–45. https://doi.org/10.1111/j.0908-8857.2004.03059.x

Arnold, J. M., Hatch, J. J., & Nisbet, I. C. T. (2006). Effects of egg size, parental quality and hatch-date on growth and survival of Common Tern *Sterna hirundo* chicks. *Ibis*, *148*(1), 98–105. https://doi.org/10.1111/j.1474-919X.2006.00487.x

BirdLife International. (2008). *State of the world's birds: Indicators for our changing world*. BirdLife International. https://www.birdlife.org/

Bouzid, A., Bouchekera, A., Samraoui, F., & Samraoui, B. (2019). Breeding of the gull-billed tern in the Sahara and an update on its distribution in Algeria. *Zoology and Ecology*, *29*(1), 1–10. https://doi.org/ 10.35513/21658005.2019.1.10

Brinkhof, M. W., Cavé, A. J., Hage, F. J., & Verhulst, S. (1993). Timing of reproduction and fledging success in the coot *Fulica atra*: Evidence for a causal relationship. *Journal of Animal Ecology*, *62*(3), 577–587. https://doi.org/10.2307/5206

Chokri, M. A., Selmi, S., Sadoul, N., & Béchet, A. (2010). Nidification des Sternes naine *Sterna albifrons*, pierregarin *Sterna hirundo* et Hansel *Sterna nilotica* dans le salin de Sfax, Tunisie: Chronologie, effectif et succès reproducteur [Nesting of Little Tern *Sterna albifrons*, Common Tern *Sterna hirundo* and Gull-billed Tern *Sterna nilotica* in the Sfax salina, Tunisia: Chronology, abundance and breeding success]. *Alauda*, *78*, 51–60.

Christians, J. K., Evanson, M., & Aiken, J. J. (2001). Seasonal decline in clutch size in European starlings: A novel randomization test to distinguish between the timing and quality hypotheses. *Journal of Animal Ecology*, *70*(6), 1080–1087. https://doi.org/10.1046/j.0021-8790.2001.00566.x

del Hoyo, J., & Collar, N. J. (2014). *HBW and BirdLife International illustrated checklist of the birds of the world. Volume 1: Non-passerines*. Lynx Edicions.

Dunn, E. K. (1975). The role of environmental factors in the growth of tern chicks. *Journal of Animal Ecology*, *44*(3), 743–754. https://doi.org/10.2307/3574

Eriksson, M. O. (1978). Lake selection by golden eye ducklings in relation to the abundance of food. *Wildfowl*, *29*, 103–109.

Fasola, M., & Saino, N. (1995). Sex-biased parental-care allocation in three tern species (*Laridae*, *Aves*). *Canadian Journal of Zoology*, *73*(8), 1461–1467. https://doi.org/10.1139/z95-172

Hafner, H. (1978). Le succès de reproduction de quatre espèces d'Ardeidés *Egretta g. garzetta* L., *Ardeola r. ralloides* Scop., *Ardeola i. ibis* L., *Nycticorax n. nycticorax* L. en Camargue. *La Terre et la Vie*, *32*, 279–289. *[Article in French]*

Hochachka, W. (1990). Seasonal decline in reproductive performance of song sparrows. *Ecology*, *71*(4), 1279–1288. https://doi.org/10.2307/1938265

International Wader Study Group. (2003). Waders are declining worldwide. *Wader Study Group Bulletin*, *101*, 8–12.

Isenmann, P., Gaultier, T., El Hili, A., Azafzaf, H., Dlensi, H., & Smart, M. (2005). *Oiseaux de Tunisie* [Birds of Tunisia]. Société d'Etudes Ornithologiques de France.

Johns, M. E., Warzybok, P., Bradley, R. W., Jahncke, J., Lindberg, M., & Breed, G. A. (2017). Age, timing, and a variable environment affect double brooding of a long-lived seabird. *Marine Ecology Progress Series*, *564*, 187–197. https://doi.org/10.3354/meps11988

Klomp, H. (1970). The determination of clutch-size in birds: A review. *Ardea*, *58*(1), 1–124. https://doi.org/10.5253/arde.v58.p1

Korpimäki, E., & Wiehn, J. (1998). Clutch size of kestrels: Seasonal decline and experimental evidence for food limitation under fluctuating food conditions. *Oikos*, *83*(2), 259–272. https://doi.org/10.2307/3546837

Molina, B., Pérez-Gil, M., & Martínez, R. (2020). *Conservación de aves acuáticas en Europa* [Conservation of waterbirds in Europe]. Ediciones Ambientales.

Møller, A. P. (1981). Breeding cycle of the Gull-billed *Tern Gelochelidon nilotica* Gmel., especially in relation to colony size. *Ardea*, *69*, 193–198.

Neb, A., & Selmi, S. (2019). Breeding parameters of the Little Egret (*Egretta garzetta*) in Boughrara Lagoon, South-eastern Tunisia. *Waterbirds*, *42*(3), 328–332. https://doi.org/10.1675/063.042.0309

Oro, D., & Ruxton, G. D. (2001). The formation and growth of seabird colonies: Audouin's Gull as a case study. *Journal of Animal Ecology*, *70*(4), 527–535. https://doi.org/10.1046/j.1365-2656.2001.00517

Parsons, J. (1975). Seasonal variation in the breeding success of the Herring Gull: An experimental approach to pre-fledging success. *Journal of Animal Ecology*, *44*, 553–573. https://doi.org/10.2307/3590

Perrins, C., & McCleery, R. (1989). Laying dates and clutch size in the Great Tit. *The Wilson Bulletin*, *101*(2), 236–253.

Pratt, H. M., & Winkler, D. W. (1985). Clutch size, timing of laying, and reproductive success in a colony of Great Blue Herons and Great Egrets. *The Auk*, *102*(1), 49–63. https://doi.org/10.2307/4086822

Radi, M., Qninba, A., Rguibi-Idrissi, H., & Dakki, M. (2004). Reproduction de la Sterne Hansel *Sterna nilotica* à la Sebkha Zima (région de Marrakech – Maroc) [Breeding of the gull-billed tern *Sterna nilotica* in the Zima salina (area of Marrakech, Morocco)]. *Alauda*, *72*, 201–209.

Ranglack, G. S., Angus, R. A., & Marion, K. R. (1991). Physical and temporal factors influencing breeding success of Cattle Egrets (*Bubulcus ibis*) in a West Alabama colony. *Colonial Waterbirds*, *14*, 140–149. https://doi.org/10.2307/1521466

Rodgers, J. A., Jr. (1987). Breeding chronology and reproductive success of Cattle Egrets and Little Blue Herons on the west coast of Florida, USA. *Colonial Waterbirds*, *10*, 38–44. https://doi.org/10.2307/1521282

Ryder, J. P. (1975). Egg-laying, egg size, and success in relation to immature-mature plumage of Ring-billed Gulls. *Wilson Bulletin*, *87*, 534–542.

Sánchez, J. M., Muñoz del Viejo, A., Corbacho, C., Costillo, E., & Fuentes, C. (2004). Status and trends of gull-billed tern *Gelochelidon nilotica* in Europe and Africa. *Bird Conservation International*, *14*, 335–351. https://doi.org/10.1017/S095927090400036X

SAS Institute. (2008). *SAS/STAT user's guide*. SAS Institute.

SEO/BirdLife. (2025, February 12). *26th Spanish Ornithology Congress (SEO2025) highlights urban biodiversity and phenotypic development*. https://seo.org/programa-provisional-26-congreso-espanol-de-ornitologia-valencia/

Stienen, E. W. M., & Brenninkmeijer, A. (2006). Effect of brood size and hatching sequence on prefledging mortality of Sandwich terns: Why lay two eggs? *Journal of Ornithology*, *147*(5), 520–530. https://doi.org/10.1007/s10336-006-0075-3

Verhulst, S., & Tinbergen, J. M. (1991). Experimental evidence for a causal relationship between timing and success of reproduction in the Great Tit *Parus m. major*. *The Journal of Animal Ecology*, *60*(1), 269–282. https://doi.org/10.2307/5459