Zoology and Ecology, 2025, Volume 35, Number 2
Online ISSN: 2165-8013
https://doi.org/10.35513/21658005.2025.2.4

BREEDING BIOLOGY AND NESTING HABITAT OF SQUACCO HERON, LITTLE EGRET, AND WESTERN CATTLE EGRET AT LAKE TONGA (NORTH-EASTERN ALGERIA)

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Ouarti, L., Nouri, N., Lazli, A.,Samar, M.F., Hamdouche, M., Sahi, S., Khalfallah, M. 2025. Breeding biology and nesting habitat of Squacco Heron, Little Egret, and Western Cattle Egret at lake Tonga (North-eastern Algeria). *Zoology and Ecology* 35(2), 118–129. https://doi.org/10.35513/21658005.2025.2.4

Article history
Received: 26 July 2025;
accepted: 11 November 2025

Keywords:
Lake Tonga; Squacco Heron; Little Egret; Western Cattle Egret; breeding; nests; environmental factors

Abstract. The current study aimed to monitor three species of ardeids: Squacco Heron (*Ardeola ralloides*), Little Egret (*Egretta garzetta*), and Western Cattle Egret (*Bubulcus ibis*) at Lake Tonga (36°53′N, 08°31′E) through biweekly surveys over two years, from December 2021 to November 2023. During the breeding periods (April to August), weekly observations were conducted, which included the detailed measurements of nests, eggs, and nesting locations. The generalized linear models (GLM) and mixed data factor analysis (FAMD) were used to analyze the relationships between environmental factors and nesting characteristics. Population numbers for the three species fluctuated seasonally. In 2022, 108 nests were counted, while 104 in 2023. Little Egrets and Western Cattle Egrets typically laid 3 to 5 eggs per nest, whereas Squacco Herons 3 to 4 eggs. All species exhibited high hatching rates: 90.83% for Little Egrets, 97.09% for Cattle Egrets, and 89% for Squacco Herons in 2022. These rates remained similarly high in 2023, with 91.42% for Little Egrets, 93.24% for Cattle Egrets, and approximately 97% for Squacco Herons. Statistical analysis indicated that clutch size was the primary factor affecting reproductive success (p = 2.89e-10). The findings demonstrated that the focal species are highly sensitive to environmental characteristics, particularly vegetation height, water depth, and climate conditions. Nest distribution patterns were influenced by environmental factors such as temperature and humidity, affecting each species differently. Little Egrets and Western Cattle Egrets exhibited similar distribution patterns within the colony, while Squacco Herons tended to nest at higher elevations. This investigation highlights the impact of ecological conditions on Ardeidae reproduction and distribution at Lake Tonga.

INTRODUCTION

The study of colonial water birds requires a comprehensive examination of their nesting site preferences, seasonal dietary habits, reproductive biology, and behavioural traits (Hafner 1977; Hafner and Fasola 1992). Consequently, establishing systematic monitoring programmes in the Mediterranean region is essential for enhancing our understanding of ecological and behavioural changes, which are vital for developing effective conservation and management strategies (Lindenmayer and Likens 2010).

The breeding and foraging habitats of many bird species, particularly herons, are closely linked to wetland ecosystems. In north-eastern Algeria, the El Kala wetland complex and Lake Tonga provide optimal habitats for these bird groups and serve as important bioindicators of the ecological health of the region (Samraoui et al. 2012). This unique wetland environment characterized by its favourable conditions has been the subject of recent studies revealing crucial insights into the distribution and successful breeding of various heron species (Chettibi et al. 2019; Loucif et al. 2020; Gherib et al. 2021; Chedad et al. 2022; Bouzid et al. 2023; Ouarti et al. 2023).

The environmental factors in these wetlands significantly contribute to the flourishing of a substantial population of heron species in this unique habitat (Chedad et al. 2022; Ouarti et al. 2023). Heron populations exhibit distinct seasonal patterns closely correlated with climatic and aquatic conditions. Fluctuations in temperature, water levels, and the physicochemical characteristics of the lake including nutrient concentrations and salinity are crucial in determining the timing of the herons breeding and feeding activities (Draidi et al. 2023).

The reproductive success of herons depends on several factors, including suitable nesting sites, access to food resources, and overall environmental conditions (Ashoori and Barati 2013). The characteristics of nesting sites are particularly important in large colonies with diverse species, as factors such as vegetation type, spatial arrangement, and selection criteria significantly influence reproductive success (Uzun 2009).

Previous studies have demonstrated that the vertical stratification of nests within colonies can reduce interspecific competition and facilitate coexistence (Hafner et al. 1982; Fasola 1986), but the specific mechanisms may vary across geographical regions and ecological contexts.

Climate and hydrological conditions also play crucial roles in the breeding ecology of Ardeidae. Fluctuations in temperature, water levels, and the physicochemical characteristics of wetlands including nutrient concentrations and salinity can significantly influence the timing of breeding activities, food availability, and ultimately reproductive success (Kushlan 2011; Draidi et al. 2023). Climate change and anthropogenic alterations to hydrological regimes therefore pose significant threats to these species, particularly in Mediterranean wetlands that are already under considerable pressure (Ramirez et al. 2012; Samraoui et al. 2012).

This study aims to classify the temporal patterns of three heron species (i.e. Squacco Heron, Little Egret, and Western Cattle Egret) at Lake Tonga, gather data on nesting sites and breeding success, and analyze the colony's distribution while identifying the factors that influence the nesting behaviours of these species during 2022 and 2023 breeding seasons.

MATERIALS AND METHODS

Study area

The study was conducted at Lake Tonga (36°53′N, 08°31′E), a freshwater lake that supports some of the richest avian communities along the southern shore of the Mediterranean Basin (Benyacoub et al. 2011; Loucif 2020; Gherib et al. 2021). The lake covers an area of 2,600 hectares with an average depth of 1.20 m. The Messida, an artificial waterway, serves as a link between the Mediterranean Sea and the northern section of the Lake (Chettibi et al. 2019) (Figure 1). The designation of Lake Tonga as a Ramsar site is a testament to its global importance in terms of wetland conservation. It serves as a sanctuary for numerous species of migratory birds and provides a variety of vital habitats for biodiversity (Lemmoui et al. 2024). Aquatic plant abundance plays a crucial role in shaping resource allocation and providing essential habitats for various birds populations. *Typha angustifolia* stands are particularly important in sustaining avian diversity. The ecosystem also includes other plant species such as *Iris pseudoacorus*, *Scirpus lacustris*, *Scirpus maritimus, Phragmites australis*, *Salix pedicellata*, and *Sparganium erectum*. Springtime brings increased activity as numerous flowering plants emerge. *Nymphaea alba*, a perennial water plant, is known for its aggressive spread across open water surfaces, necessitating careful monitoring and control to preserve ecological equilibrium (Kadid 1999; Saifouni et al. 2020).

Data collection

Our study was rigorously designed to capture the seasonal dynamics and breeding activities of Ardeids populations. To achieve this, a systematic monitoring programme was implemented from December 2021 to November 2023, spanning two complete annual cycles and structured around the species' breeding and non-breeding periods.

During non-breeding periods, we conducted biweekly visits to closely track population fluctuations. For the identification of Ardeids species in the field, we relied on the Heinzel Guide to European Birds, utilizing a Konus-Spot 20 × 60 telescope and KERN 8 × 30 binoculars (Ouarti et al. 2023).

As the breeding season approached (April to August), we increased our sampling intensity to weekly visits. This heightened frequency enabled us to precisely document breeding phenology and measure success metrics at a finer scale.

Each visit was strictly limited to a maximum of three hours within the colony, aiming to minimize our impact. Finally, we systematically recorded weather conditions (temperature, humidity, precipitation, and wind speed) using a portable weather station Renke (RS-HSQXZ-

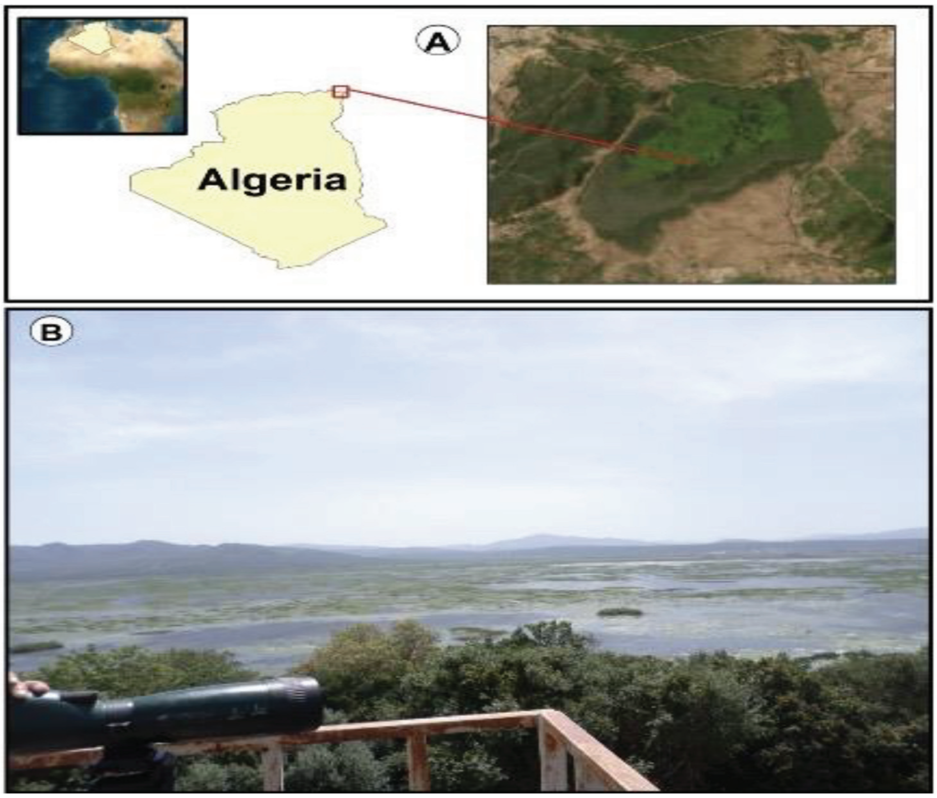

Figure 1. Geographic location of Lake Tonga (A) and panoramic view of the lake (B).

USB-2-5S-EX), providing essential context for our observations.

Each sampled nest was marked with a small, numbered tag placed beneath it. All nests were constructed in *Tamarix* trees. For each nest, we recorded the following parameters:

-Nest structure measurements: External diameter (mm), internal diameter (mm), and depth (cm) were measured using a measuring tape**.** Nest volume was calculated using the formula for a truncated cone: $V = (1/3) * \pi * h * (r^2 + r * R + R^2)$, where R and r are the external and internal radii (i.e. half of the measured diameters), and h is the nest depth (Przymencki et al. 2022).

- Nest position measurements: Elevation (height from water/ground surface to nest bottom (cm)) was measured using a telescopic measuring rod. Geographic coordinates were recorded using a handheld GPS device Garmin (eTrex 10).

- Microhabitat characteristics: Vegetation height (cm) around the nest was measured at four cardinal points and averaged. Water depth (cm) beneath the nest was measured using a graduated pole.

- Reproductive parameters: Clutch initiation date, clutch size, egg biometrics (length, width, and weight), hatching date, and number of chicks surviving to 21 days post-hatching were recorded. Egg measurements were taken using digital calipers and recorded their weight using a 500-gram Pesola scale. Egg volume was calculated using the formula: $V = 0.51 \times$ egg length $\times$ egg width 2 (Hoyt 1979).

A clutch was considered complete when three consecutive inspections at 48-hour intervals showed no changes in egg number. We defined hatching success as the proportion of eggs that hatched successfully from the total number of eggs laid in completed clutches. Fledging success was operationally defined as survival to 21 days post-hatching, as monitoring beyond this age becomes challenging due to chick mobility and interference. This operational definition is consistent with previous studies on Ardeidae (Tourenq et al. 2004; Kazantzidis et al. 2013).

Data Analysis

In our evaluation of species fluctuations in Lake Tonga, we employed the total bird species abundance, represented as N. Hatching success for each species was determined by calculating the ratio of successfully hatched eggs. R software was used for statistical computations. We employed generalized linear models (GLM function from R\'s stats package) to examine (i) egg length, (ii) egg width, (iii) egg weight, (iv) year 2022 and 2023, and (v) the species (WCE: Western Cattle Egret, LE: Little Egret, SH: Squacco Heron) on hatching rate. Species was included as a categorical explanatory variable to account for interspecific variation in egg characteristics and to avoid data pooling across species. Model significance was assessed using p-values, with the alpha level set at 0.01.

Additionally, we performed a Factorial Analysis of Mixed Data (FAMD). This analytical method combined Principal Component Analysis (PCA) for continuous variables and Multiple Correspondence Analysis (MCA) for categorical variables, allowing us to identify correlations among the different factors under study (Audigier et al. 2016). For cartographic representation and spatial analysis, we utilized ESRI ArcMap version 10.7.1.

RESULTS

Monitoring and abundance of Ardeids species

Our field observations confirmed the year-round presence of the Western Cattle Egret (*Bubulcus ibis*). From December to early February, their numbers were relatively low, but they increased in May 2022 (Figure 2A), reaching a maximum of 494 individuals, and peaked at 550 individuals in July 2023 (Figure 2B).

Monitoring the abundance of heron species at Lake Tonga revealed monthly variations. The highest number of Little Egrets (*Egretta garzetta*) was recorded in the second half of August, with 103 individuals observed in 2022 (Figure 2A) and 112 in 2023 (Figure 2B).

During the study period, Squacco Heron (*Ardeola ralloides*) numbers ranged from 21 to 65 individuals in 2022 (Figure 2A) and from 8 to 41 in 2023 (Figure 2B), with the largest counts occurring from May to July in both years.

Breeding biology

In total, we identified 108 accessible nests in 2022: 43 belonging to Western Cattle Egrets, 35 to Squacco Herons, and 30 to Little Egrets. In 2023, we recorded 37 nests of Western Cattle Egrets, 32 of Squacco Herons, and 35 of Little Egrets, bringing the overall total to 104 nests. The average clutch size for Western Cattle Egrets was 4 ± 0.58 eggs in 2022 and 3.81 ± 0.40 eggs in 2023. For Little Egrets, the average clutch size was 3.97 ± 0.57 eggs in 2022 and 3.83 ± 0.38 eggs in 2023. The average clutch size for Squacco Herons was 3.8 ± 0.47 eggs in 2022 and 3.84 ± 0.37 eggs in 2023 (Table 1).

During the 2022 breeding season, most nestlings were observed in the latter half of April for Western Cattle Egrets and in May for both Little Egrets and Squacco Herons. The egg-laying began in the second half of May. The first nestlings hatched on June for all species. However, in 2023, a delay in the start of the breeding season was noted for these species, attributed to heavy rainfall in the El Tarf region from late May to early June.

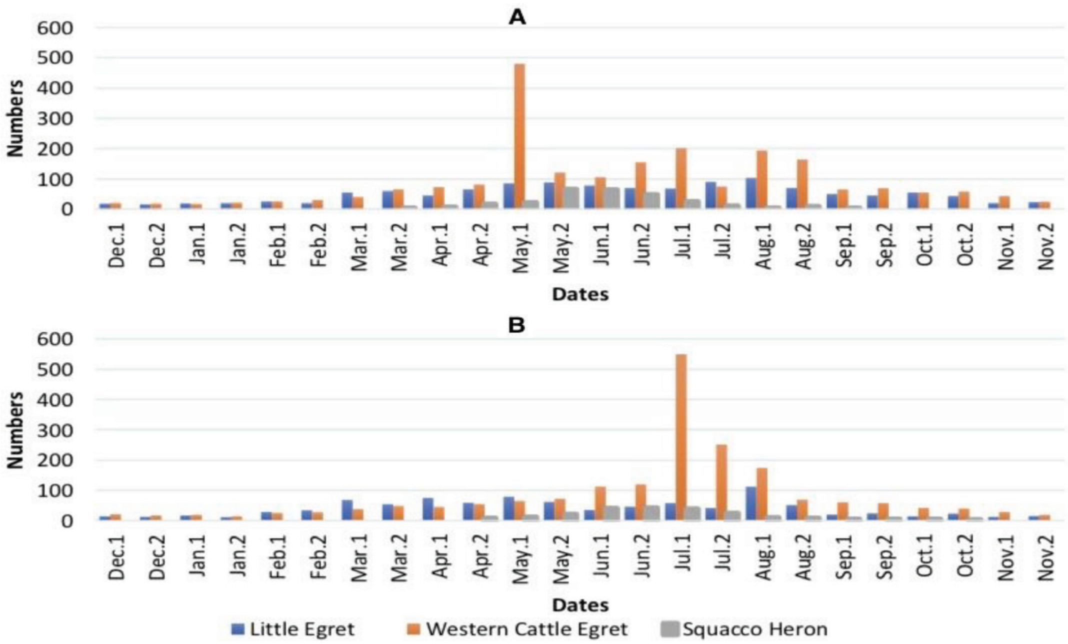

Figure 2. Abundance variation of the focal species at Lake Tonga during the study period, 2021–2022 (A) and 2022–2023 (B).

Table 1. Average ± SD of eggs traits of Squacco Heron, Little Egret and Cattle Western Egret at the Lake Tonga colony (2022–2023).

Species	N	L (mm)	W (mm)	V (cm3)	Wt (g)	Clutch size
Western Cattle Egret	313	37.60 ± 4.53	26.73 ± 2.15	0.14 ± 0.02	24.52 ± 0.91	3.91 ± 0.49
Little Egret	253	38.76 ± 4.05	26.79 ± 1.46	0.14 ± 0.02	24.98 ± 1.13	3.90 ± 0.48
Squacco Heron	256	38.32 ± 3.96	25.96 ± 1.23	0.13 ± 0.02	24.50 ± 0.87	3.82 ± 0.42

N: number of eggs, L: egg length, W: eggs width, V: eggs volume, Wt: eggs weight.

Hatching success

Across the 2022 and 2023 breeding seasons, we observed a remarkably high hatching success rates in the nests of the focal species. On average, about 91.1% of Little Egret eggs successfully hatched, compared to 95.2% for Western Cattle Egrets and nearly 93% for Squacco Herons.

Our analyses, conducted using GLM 1 and GLM 2 models, revealed a crucial point: among all the factors we examined in this study, only the clutch size in each nest significantly influenced both the number of eggs laid and, consequently, the number of chicks that perished (with a very low *p*-value of 2.89e-10). While egg length had a marginally significant impact on hatching rates and a notable effect on mortality, the other parameters we investigated did not show statistically significant effects in either model (Figure 3).

Nests distribution and mapping

The aquatic environment of Lake Tonga distinguishes the heron colony, which is home to multiple species. Within Lake Tonga, the Western Cattle Egret nests alongside the Little Egret and Squacco Heron in a mixed colony (Figure 4).

The studied species primarily occupied shallow areas of Lake Tonga, with a mean water depth of 51.3 ± 9.19 cm, characterized by dense vegetation. All three species nested in *Tamarix* trees, using dead eucalyptus branches, and formed densely packed colonies. Squacco Herons nested at higher elevations (124.21 ± 43.40 cm in 2022 and 127.09 ± 36.19 cm in 2023) compared to Little Egrets (121.43 ± 39.49 cm in 2022 and 121.26 ± 46.38 cm in 2023) and Western Cattle Egrets (110.8 ± 34.90 cm in 2022 and 119.51 ± 45.75 cm in 2023) (Table 2).

We have proposed several hypotheses to elucidate the

Table 2. Average ± SD of nests surveyed of Squacco Heron, Little Egret, and Western Cattle Egret at the Lake Tonga colony (2022–2023).

Species	N	Ext. D (cm)	Int. D (cm)	N. dpt. (cm)	N. V (cm^3)	N. E (cm)	H. vg. (cm)
Western Cattle Egret	80	35.5 ± 2.92	25.3 ± 2.70	1.6 ± 0.46	1576.99 ± 533.49	115.16 ± 40.37	82.20 ± 6.97
Little Egret	65	36.2 ± 2.69	26.5 ± 2.28	1.5 ± 0.43	1588.24 ± 532.28	121.35 ± 42.94	83.00 ± 7.35
Squacco Heron	67	33.8 ± 2.56	24.7 ± 2.82	1.3 ± 0.33	1197.27 ± 332.99	125.65 ± 39.80	82.53 ± 6.74

N: number of nests, Ext. D: external diameter, Int. D: internal diameter, N. dpt.: nest depth, N. V: nest volume, N. E: nest elevation, H. vg.: vegetation height.

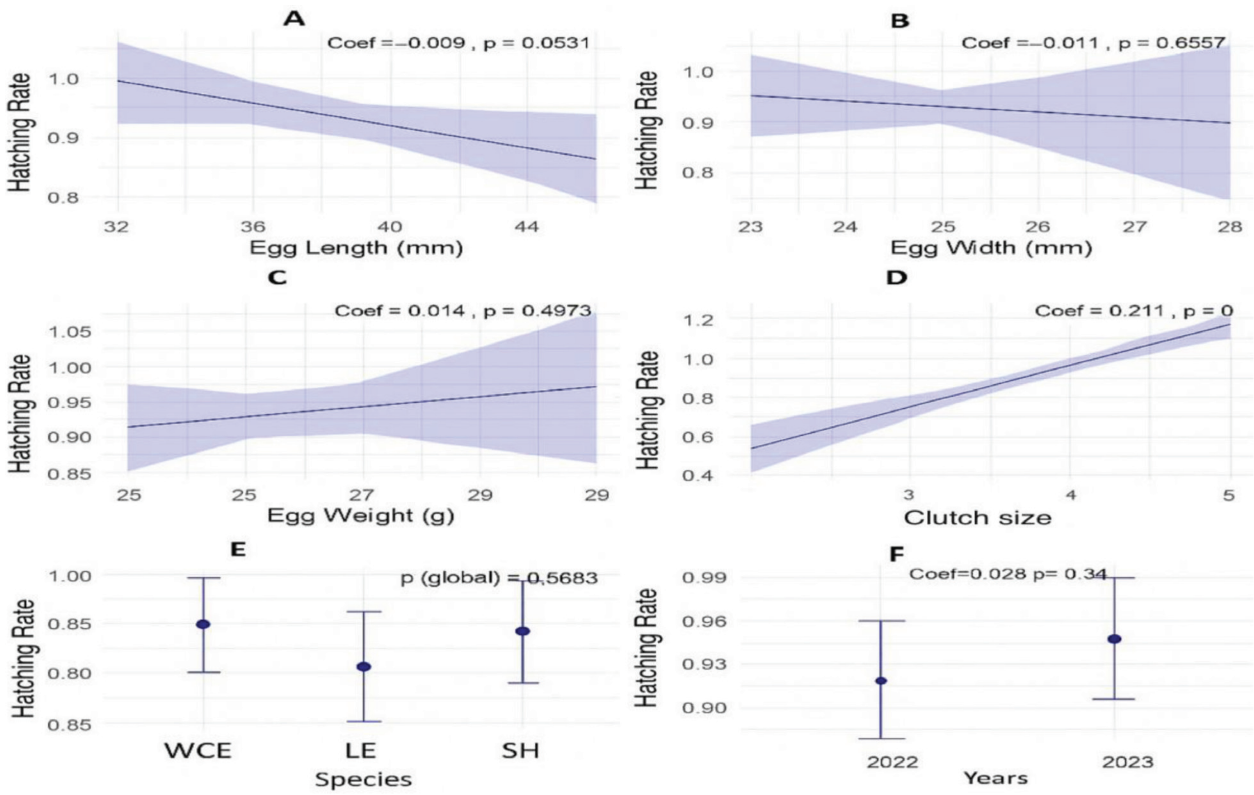

Figure 3. Variation in hatching success among three heron species: Western Cattle Egret (WCE), Little Egret (LE), and Squacco Heron (SH) at Lake Tonga in relation to (A) egg length, (B) egg width, (C) egg weight, (D) clutch size, (E) species, and (F) years (2022 and 2023).

nesting patterns and mechanisms within the mixed colony at Lake Tonga. Little Egrets and Western Cattle Egrets exhibit a similar horizontal nest distribution (Figure 5), forming the colony's core.

Analysis of nesting patterns of the studied species

The data analysis employed the Factorial Analysis of Mixed Data (FAMD) to investigate the relationships between various environmental factors and nesting characteristics. The results revealed significant interspecific differences in nesting preferences, with notable correlations observed between spatial coordinates, temperature, humidity, and other environmental variables. The application of the FAMD demonstrated that each species exhibits a distinct distribution and varying contributions to the principal components, thereby underscoring the ecological dynamics at play within this habitat (Figure 6).

Table 3 shows the correlation between both quantitative and qualitative variables, and their contributions in 5 dimensions. The spatial distribution of nests is influenced by location within the study area, as evidenced by a strong correlation between spatial coordinates (X, Y) and Dim.1. Climatic factors, particularly temperature (T) and humidity (Humd), were linked to Dim.2, suggesting their impact on nest site selection, especially for Squacco Herons. Vegetation structure and nest size played crucial roles in nest site choice, particularly for

Figure 4. Breeding sites of Ardeids in Lake Tonga (copyright Ouarti L., 2022).

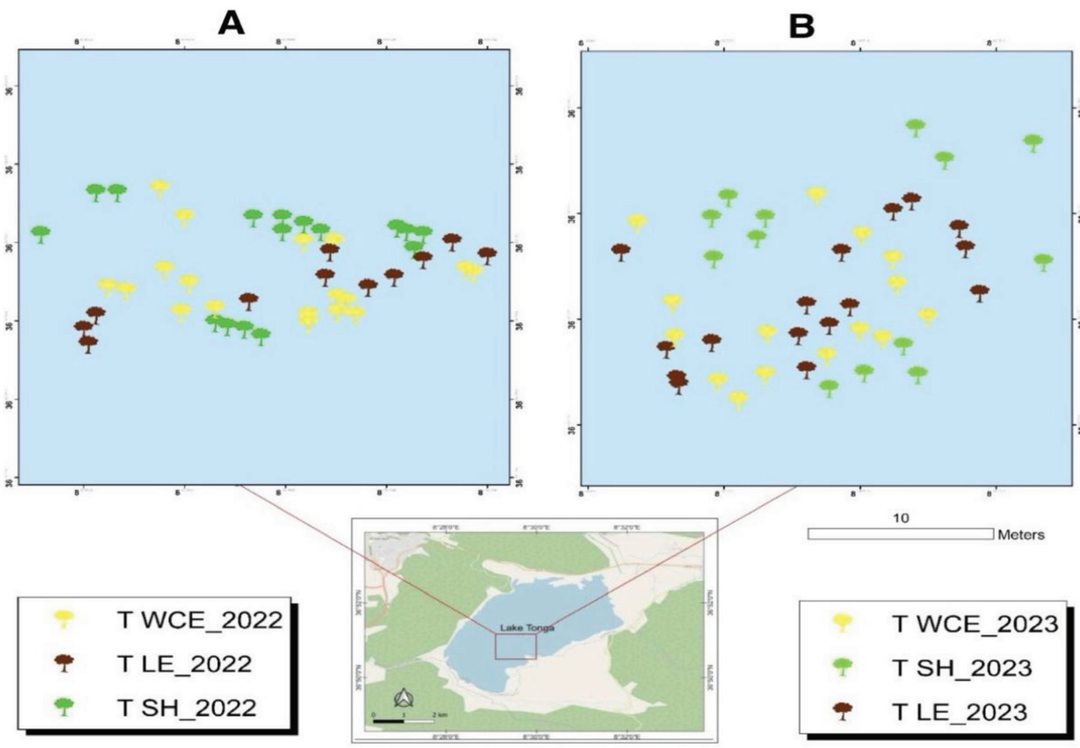

Figure 5. The distribution of nests of three heron species in Lake Tonga during the 2022 (A) and 2023 (B) breeding seasons. TWCE: trees that house nests of Western Cattle Egret, TLE: trees that house nests of Little Egret, TSH: trees that house nests of Squacco Heron.

Table 3. Coordinates of the variables with the factors of the FAMD.

	Dim.1	Dim.2	Dim.3	Dim.4	Dim.5
Cumulative % of variance	19.47	36.41	49.79	58.29	66.43
X (spatial coordinates x)	0.91	0.01	0.16	0.14	0.22
Y (spatial coordinates y)	0.92	-0.01	0.16	0.13	0.21
T (Temperature)	-0.30	0.75	-0.38	0.09	0.12
Humidity	0.20	0.66	0.04	-0.45	-0.12
Wind	0.49	-0.65	0.12	-0.10	-0.01
Precipitation	-0.24	-0.50	-0.11	0.54	0.21
External diameter of nest	0.03	0.64	0.52	0.22	0.13
Internal diameter of nest	-0.38	0.05	0.15	-0.23	0.70
Volume of nest	-0.03	0.33	0.65	0.28	-0.04
Height of Vegetation	-0.03	0.20	0.10	0.49	-0.44
Z (elevation of nest)	-0.15	0.05	0.24	0.39	0.21
Water depth	-0.62	-0.10	-0.05	0.20	0.07
Chronology of installation of nests	0.45	0.55	-0.57	0.22	0.20

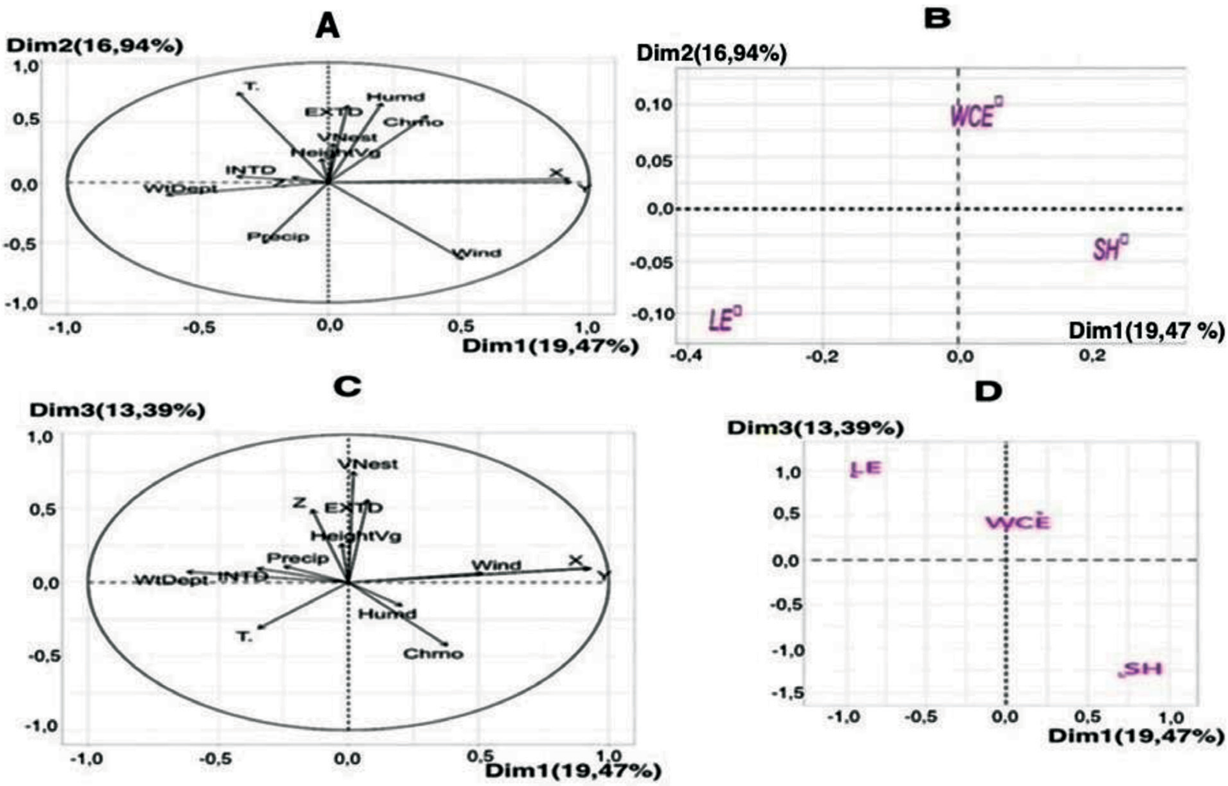

Figure 6. Distribution of variables and individuals in the first three components of FAMD (see parameter names in Table 3): (A) Correlation circle of variables on FAMD dimensions 1 and 2; (B) Projection of individuals on FAMD dimensions 1 and 2; (C) Correlation circle of variables on FAMD dimensions 1 and 3; (D) Projection of individuals on FAMD dimensions 1 and 3. WCE: Western Cattle Egret, LE: Little Egret, and SH: Squacco Heron.

Little Egrets, as shown by a strong association of nest volume (VNest) and vegetation height (HeightVg) with Dim.3. Hydrological conditions, including water availability and depth, affected nest distribution, particularly for Western Cattle Egrets, as indicated by the association of precipitation (Precip) and water depth (Wt Dept) with Dim.4 and Dim.5. Little Egrets and Squacco Herons tend to have the most centralized nest elevations, while Western Cattle Egrets typically nest at lower levels.

DISCUSSION

The temporal typology of the focal species results from a complex interaction between regional, ecological and anthropogenic factors. Preserving the natural habitats of various populations worldwide is crucial for upholding their diversity and overall hearth, especially considering recent findings on habitat availability decline for water birds in sensitive wetlands (De la Cruz and Numa 2024).

The present study provides comprehensive insights into the breeding biology and nesting habitat selection of three sympatric Ardeidae species at Lake Tonga, revealing complex patterns of resource partitioning that facilitate coexistence. Our findings support the theoretical framework of niche differentiation (MacArthur and Levins 1967) and demonstrate how multiple niche dimensions (spatial, temporal and behavioural) interact to reduce interspecific competition in a mixed-species colony.

The year-round presence of Western Cattle Egrets with bimodal abundance peaks contrasts with a more restricted seasonal occurrence of Little Egrets and especially Squacco Herons, suggesting differential migration strategies that may reduce interspecific competition during critical periods. Our findings on the sequential timing of breeding (Western Cattle Egrets first, followed by Little Egrets and then Squacco Herons) are consistent with patterns observed in other Mediterranean wetlands. In Camargue (southern France), Hafner et al. (1982) documented similar breeding chronology among these species, with an average lag of 7–10 days between species. This temporal offset may reduce competition for food resources during the critical chick-rearing period when energy demands are the highest (Kushlan 2011). The interannual variation in breeding phenology, particularly the delay observed in 2023 following heavy spring rainfall, demonstrates the plasticity of these species in response to environmental conditions, a trait that may become increasingly important under climate change scenarios (Ramirez et al. 2012).

The seasonal fluctuations in Ardeidae populations at Lake Tonga reflect complex interactions between regional migration patterns, local breeding activities, and resource availability. Similar seasonal dynamics have been reported from other North African wetlands, including sites in Tunisia (Nefla et al. 2015), suggesting consistent regional patterns. However, the peak abundance of Western Cattle Egrets at Lake Tonga (550 individuals) is substantially higher than reported from comparable wetlands in Tunisia (Nefla et al. 2015) and Egypt (Hering et al. 2020), highlighting the exceptional importance of Lake Tonga for this species in the region.

Our results strongly support the vertical stratification hypothesis, with significant differences in nest height among the three species that inversely correlate with body size. This pattern, with smaller Squacco Herons nesting higher than larger Western Cattle Egrets and Little Egrets, has been documented in other mixed Ardeidae colonies (Fasola and Alieri 1992; Kazantzidis et al. 2013) and represents a classic example of spatial niche partitioning. The mechanism likely involves a combination of physical constraints (larger species may avoid higher, more precarious positions) and competitive interactions (smaller species may be excluded from preferred lower positions).

The vertical stratification observed at Lake Tonga was more pronounced in areas with higher nesting densities, suggesting that interspecific competition intensifies resource partitioning, as predicted by ecological theory (MacArthur and Levins 1967). Similar density-dependent strengthening of niche differentiation has been reported in heron colonies in Italy (Fasola 1986) and Greece (Kazantzidis et al. 2013), supporting the view that competition is a key driver of community structure in colonial water birds.

The horizontal distribution patterns revealed by our spatial analyses provide additional evidence for niche partitioning. The clustering of Western Cattle Egrets and Little Egrets in the colony core, which contrasted with the more dispersed distribution of Squacco Herons, suggests different social preferences or tolerance thresholds for conspecific and heterospecific neighbours. Comparable patterns have been documented in mixed colonies in the Camargue (Hafner et al. 1982) and the Po Plain of Italy (Fasola and Alieri 1992), indicating consistent spatial organization principles across Mediterranean Ardeidae colonies.

The FAMD results revealed complex relationships between environmental variables and species-specific nest site selection, supporting our microhabitat selection hypothesis. A strong association of Western Cattle Egrets with shallower areas aligns with their foraging ecology, as this species frequently feeds in terrestrial habitats and agricultural landscapes (Kushlan and Hancock 2005). In contrast, the preference of Squacco Herons for areas with denser vegetation and higher sensitivity to climatic variables reflects their more specialized aquatic foraging strategy and potentially greater vulnerability to predation due to their smaller size (Kazantzidis et al. 2013).

These findings extend beyond previous studies that often focused on single environmental variables by demonstrating how multiple factors interact to shape habitat selection in these species. The multivariate approach employed here reveals that nest site selection is influenced by a complex interplay of spatial location, vegetation structure, hydrological conditions, and climatic factors, with species-specific responses to these variables facilitating coexistence through niche differentiation.

An exceptionally high reproductive success at Lake Tonga suggests particularly favourable conditions, including abundant food resources, limited predation pressure, and minimal human disturbance. The minimal egg loss observed during the study period is further evidence that predation pressure was minimal.

The identification of clutch size as the primary factor affecting reproductive success, with larger clutches showing slightly lower per-egg hatching rates, is consistent with life-history theory predictions about trade-offs between offspring number and quality (Hillesheim and Stearns 1992). Similar negative relationships between clutch size and per-egg success have been reported in other Ardeidae studies (Cezilly et al. 1995; Tourenq et al. 2004), suggesting a common biological constraint across populations.

The subtle but significant effect of nest elevation on fledging success, particularly for Squacco Herons, provides empirical support for the adaptive value of vertical stratification in mixed colonies. Higher nests may offer better protection from ground predators or flooding events, benefits that may be especially important for smaller species with limited defensive capabilities. This finding aligns with studies from China (Rui et al. 2019) and Greece (Kazantzidis et al. 2013) that have documented the height-dependent variation in reproductive success in Ardeidae colonies.

The FAMD results highlight the multidimensional nature of environmental influences on colony structure and dynamics. The identification of distinct environmental gradients associated with different species provides a nuanced understanding of habitat selection processes that goes beyond simple presence/absence patterns. A strong influence of spatial coordinates and water depth (Dimension 1) on Western Cattle Egret distribution aligns with findings from South Africa (Chetty et al. 2025) and India (Abbasi and Khan 2023) that emphasize the importance of hydrological conditions for this species.

The association of climatic variables (temperature, humidity, wind) with Squacco Heron distribution (Dimension 2) suggests greater sensitivity to weather conditions in this smaller species. This finding is consistent with energetic constraints related to body size and may explain a more restricted seasonal presence of Squacco Herons compared to the larger species. Similar climate sensitivity has been documented in Spanish colonies (Forti et al. 2021), where Squacco Heron abundance showed stronger correlations with temperature anomalies than larger Ardeidae species did.

The correlation between nest structural characteristics and Little Egret distribution (Dimension 3) highlights the importance of construction parameters in habitat selection. Little Egrets invested more in nest construction (larger external and internal diameters) than the other species, potentially reflecting different predation pressures or structural requirements. This pattern differs somewhat from findings in Asian colonies (Ashoori and Barati 2013), where Little Egrets built smaller nests than Cattle Egrets, suggesting regional variation in nest construction strategies.

The influence of hydrological and vegetation characteristics (Dimensions 4 and 5) on colony structure underscores the importance of these factors for wetland-dependent species. The positive correlation between precipitation and vegetation height in Dimension 4 reflects seasonal dynamics in wetland productivity that may influence resource availability for breeding birds. Similar relationships between precipitation patterns and breeding parameters have been documented in Spanish Ardeidae colonies (Forti et al. 2021).

Our findings from Lake Tonga both align with and diverge from patterns observed in other Mediterranean wetlands, reflecting both regional consistency in ecological processes and local adaptation to specific environmental conditions. The species composition and breeding phenology at Lake Tonga are similar to those reported from the Camargue (Hafner et al. 1982), Greek wetlands (Kazantzidis et al. 2013), and other North African sites (Nefla et al. 2015), suggesting consistent regional patterns in Ardeidae ecology across the Mediterranean Basin.

However, the exceptionally high reproductive success rates at Lake Tonga exceed those reported from most other Mediterranean sites. For example, the hatching success for Squacco Herons at Lake Tonga (89–97%) substantially exceeds the 85% reported from the Camargue (Hafner 1978) and the 76% reported from Greek wetlands (Kazantzidis et al. 2013). This difference may reflect particularly favourable conditions at Lake Tonga, including abundant food resources, limited predation pressure, and effective protection measures within the El Kala National Park.

The vertical stratification pattern observed at Lake Tonga, with Squacco Herons nesting higher than the larger species, is consistent with patterns reported from Italian (Fasola 1986), French (Hafner et al. 1982), and Greek (Kazantzidis et al. 2013) colonies. However, the magnitude of height differentiation at Lake Tonga (mean difference of 13.4–18.7 cm between Squacco Herons and Western Cattle Egrets) is less pronounced than in some European colonies, where differences of 30–50 cm have been reported (Fasola 1986). This reduced stratification may reflect the specific vegetation structure at Lake Tonga, where Tamarix trees provide more homogeneous nesting substrates compared to the diverse vegetation types available in some European wetlands.

A strong influence of water depth on Western Cattle Egret distribution at Lake Tonga aligns with findings from the Ebro Delta in Spain (De la Cruz and Numa 2024) and coastal wetlands in the Bohai Rim region of China (Fu et al. 2025), highlighting the consistent importance of hydrological conditions for this species across its range. However, the specific depth preferences may vary regionally based on local foraging opportunities and competitive interactions.

CONCLUSION

This research offers a thorough evaluation of the temporal patterns and breeding ecology of Ardeidae species at Lake Tonga. The results reveal clear seasonal fluctuations in population numbers, with each species showing adaptations to local environmental conditions. Although clutch sizes differ among species, overall reproductive success remains high.

Nest site selection is influenced by water conditions, vegetation structure, and climatic factors. Using the Factorial Analysis of Mixed Data (FAMD), strong relationships were identified between spatial distribution, nesting characteristics, and environmental variables.

Understanding these ecological patterns is essential for conserving wetland habitats and ensuring the long-term sustainability of Ardeidae populations. Future research should examine how environmental changes affect breeding success and species interactions to support effective conservation strategies for wetland-dependent birds.

ACKNOWLEDGEMENTS

We want to thank the El Kala National Park officers, who accompanied and helped us throughout our field investigations.

This research was supported by the Algerian Ministry of Higher Education and Scientific Research (MESRS) and the General Directorate for Scientific Research and Technological Development (DGRSDT).

Conflict of interests

The co-authors report no conflicts of interest.

Funding

This research did not receive any financial support.

Data availability

The data used to support the findings of this study can be made available on reasonable request from the corresponding author.

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