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PREDICTORS OF HATCHING SUCCESS IN URBAN EURASIAN COOTS: ROLES OF BREEDING TIMING AND NEST CHARACTERISTICS

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Abstract. Nest-site conditions and breeding phenology may relate to reproductive success in marsh-nesting birds, but their relative importance remains unclear. We examined hatching success in the Eurasian Coot (*Fulica atra*) using 204 eggs from 43 nests in an urban wetland, integrating nest-scale habitat variables, initiation date, and egg volume. At the nest level, all 43 nests were analysed using a quasibinomial GLM because the initial binomial model showed substantial overdispersion. None of the four *a priori* nest-level predictors reached conventional statistical significance after accounting for overdispersion. Distance to open water showed the strongest negative association with hatching success (OR = 0.45, $p = 0.078$), whereas initiation date (OR = 0.69, $p = 0.341$), nest height above water (OR = 1.27, $p = 0.532$), and vegetation cover (OR = 1.64, $p = 0.242$) showed weaker evidence. At the egg level, a binomial GLMM based on 204 eggs from 43 nests showed a negative association between egg volume and hatching outcome (OR = 0.34, 95% CI: 0.12–0.92, $p = 0.033$), while the nest-level covariates did not reach conventional significance. Egg outcomes were strongly clustered within nests (ICC ≈ 0.78). Overall, evidence for consistent nest-level predictors was limited, whereas egg volume was negatively associated with hatching fate.

INTRODUCTION

Reproductive success in water birds is shaped by the interaction between breeding phenology and nest-site conditions in dynamic wetland environments (Rounds et al. 2004; Cheriet et al. 2015). Wetland breeding conditions can change rapidly as water levels fluctuate, vegetation develops, and exposure to disturbance or predation varies over time, requiring adaptive responses from breeding populations (Austin and Buhl 2011). The studies of water birds in north-eastern Algeria have shown that breeding performance may vary with both breeding timing and nest-site conditions, although the direction of these relationships differs among species. At Boussedra Pond, Common Moorhens *Gallinula chloropus* (Linnaeus, 1758) nested predominantly in dense stands of *Typha angustifolia*, and egg volume declined as the breeding season progressed (Samraoui et al. 2013). In Mallards *Anas platyrhynchos* (Linnaeus, 1758), breeding outcome declined with later egg laying (Fouzari et al. 2018), whereas nesting success in Little Grebes *Tachybaptus ruficollis* (Pallas, 1764) was related to water depth and nest size (Athamnia et al. 2015). In Common Moorhens, clutch success increased with both laying date and water depth, partly reflecting seasonal variation in predation and flooding (Meniaia et al. 2014).

In the Eurasian Coot *Fulica atra* (Linnaeus, 1758), as in its congener, the American Coot *F. americana* (Gmelin, 1789), breeding ecology is closely linked to habitat structure, nest-site selection, and seasonal timing (Hałupka et al. 2020). In *F. atra*, laying dates have advanced over recent decades in a Polish population (Hałupka et al. 2020), and weather effects on reproductive performance are modulated by breeding habitat (Chyb and Minias 2022). Both the timing of reproduction and parental age can influence breeding performance in coots (Ryan and Dinsmore 1980; Brinkhof et al. 2002). The experimentally altered timing of the first brood affects the probability of a second

brood and parental survival (Brinkhof et al. 2002), while habitat selection and breeding success are shaped by broader ecological conditions such as the availability of submerged macrophytes resistant to fish predation (Nieoczym and Kloskowski 2018). Regional studies have demonstrated considerable geographic variation in these relationships, with nest placement and initiation date depending strongly on wetland patchiness and vegetation structure, and clutch size exhibiting a seasonal decline (Samraoui and Samraoui 2007; Talbi et al. 2020).

Long-term studies have shown that breeding phenology in the Eurasian Coot can shift over time, with nesting occurring earlier in recent decades (Hałupka et al. 2020). Phenological changes may alter the match between breeding and food availability, as documented in water birds and passerines (Both et al. 2006; Renner and Zohner 2018) and may also affect processes such as brood reduction (Horsfall 1984). These broader patterns underscore the importance of understanding how breeding timing and local conditions are related to reproductive success at the population scale.

Despite this background, the relative contributions of seasonal progression and local nest-site characteristics remain difficult to disentangle, because vegetation structure and hydrological conditions around nest sites may change over the course of the breeding season (Samraoui and Samraoui 2007; Uzun 2012; Zhang et al. 2018), potentially affecting breeding performance (Brzeziński et al. 2013). This issue is especially relevant in coots whose nests are built in emergent vegetation at the water–vegetation interface (Nieoczym and Kloskowski 2018). In such settings, nests located farther from open water may occur in different vegetation settings and may require adults to move farther between the nest and open-water areas. In the Camargue, Eurasian Coots generally nested close to open water, which serves as a feeding area within the territory, and nest sites were constrained by emergent vegetation of a minimum height (Salathé 1986). In American Coots, nest-site characteristics such as water depth, vegetation height, concealment and distance to open water varied with local conditions, and the intermingling of open water and emergent cover influenced how many coots nested (Gorenzel et al. 1982). Later breeding attempts may also experience lower success as environmental conditions change through the season. In the Camargue, nesting success depended on the timing of marsh drying: the young fledged on only 8% of marshes that dried before the end of June, versus 83% of those that dried after early July (Salathé 1986). In the Eurasian Coot, the probability of a second brood also declined as the season progressed (Brinkhof et al. 2002).

A further challenge is that these factors are not fully independent. Seasonal changes in vegetation, water conditions, and nest accessibility can make it difficult to determine whether reproductive outcomes are associated primarily with the time of nest initiation or nest location. Previous studies have associated breeding timing with reproductive performance (Hałupka et al. 2020) and nest-site selection with vegetation structure and the spatial arrangement of nesting habitat (Samraoui and Samraoui 2007; Squalli et al. 2020), providing the basis for the hypotheses tested in this study.

The present study examined variation in hatching success in the Eurasian Coot at both nest and egg levels. We tested two main predictions. First, we predicted that hatching success would decline with later nest initiation, based on previous evidence that breeding timing is associated with reproductive performance in coots (Brinkhof et al. 1993; Hałupka et al. 2020). Second, we predicted a higher hatching success in nests positioned at a greater height above water surface and closer to open water, based on previous evidence that nest placement and habitat structure are associated with breeding performance in coots (Samraoui and Samraoui 2007; Squalli et al. 2020; Nieoczym and Kloskowski 2018). At the egg level, we also examined whether egg volume was associated with hatching outcome. We aimed to evaluate associations between breeding timing, nest-site characteristics, and egg-level variation in hatching success.

MATERIALS AND METHODS

Study area

The study was conducted at Boussedra Pond near El Bouni, north-eastern Algeria (36.846551° N, 7.727835° E). Boussedra is a small, unprotected freshwater wetland of approximately 55 ha within the Annaba region (Figure 1). The site is of considerable ornithological importance and supports a diverse breeding water bird community, including species of conservation concern such as the Ferruginous Duck *Aythya nyroca* (Güldenstädt, 1770) and White-headed Duck *Oxyura leucocephala* (Scopoli, 1769), reported as Near Threatened and Endangered, respectively, in the regional assessment of Samraoui and Samraoui (2008). Boussedra was also identified as one of the noteworthy breeding wetlands of north-eastern Algeria (Aouadi et al. 2021). The wetland is surrounded by an increasingly urbanised landscape and has been strongly affected by land-filling; earlier surveys documented a substantial loss of its surface area, and this pressure has continued in recent decades (Aouadi et al. 2021).

Vegetation at the site is dominated by the stands of *Bolboschoenus maritimus* (L.) Palla, 1905, *Typha angustifolia* L., 1753, and *Schoenoplectus lacustris* (L.)

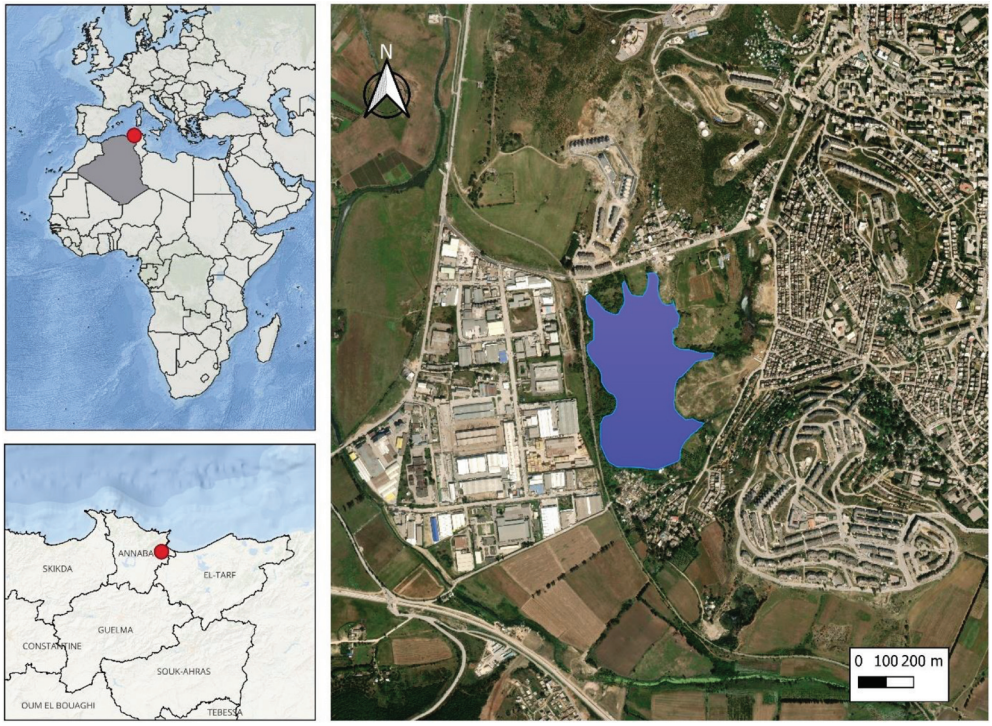


Figure 1. Study area at Boussedra Pond, north-eastern Algeria (North Africa).

Palla, 1888, while dense *Tamarix gallica* L., 1753 occurs mainly along the southern margin. Despite strong anthropogenic pressure, Boussedra Pond remains of high ecological value. It is recognised as an Important Bird Area (Aouadi et al. 2021) and supports both breeding and wintering water birds, including the White-headed Duck, Ferruginous Duck, Little Bittern *Ixobrychus minutus* (Linnaeus, 1766), and Great Bittern *Botaurus stellaris* (Linnaeus, 1758). The wetland also provides habitat for the endemic and threatened newt *Pleurodeles poireti* (Gervais, 1835).

Study methods

Fieldwork was carried out twice per week from the beginning of March to the end of June 2025, encompassing the breeding season. Each nest was assigned a unique code, and the location of most nests was recorded using a handheld GPS. For each nest, we measured nest height above water surface, internal and external nest diameters, water depth at the location of the nest, and surrounding vegetation height. Vegetation cover was visually estimated in the field by the observers as a percentage of vegetation cover within a 4 × 4 m plot centred on each nest; no photographic or drone-based assessment was used. Distance to open water was analysed as a single nest-level covariate recorded in centimetres. The field records indicate one value per nest and do not specify whether this measure represented the shortest linear distance to the nearest open-water patch, distance to a channel, or a threshold-based definition of open water.

Internal and external nest diameters were measured in the field. Each egg was individually marked with a permanent marker. Egg mass was measured to the nearest 0.1 g using a Pesola spring balance, and egg length and breadth were measured to the nearest 0.1 mm using vernier callipers. Egg volume (cm³) was calculated following Hoyt (1979) as:

$$V = 0.000509 \times L \times B^2,$$

where V is egg volume (cm³), L is egg length (mm), and B is maximum egg breadth (mm).

Laying chronology was analysed using first-egg date. When direct egg laying observations were unavailable, first-egg dates were estimated assuming a laying interval of one egg per day and 28 days between first egg and hatching (Lack 1950). Clutches were considered complete when egg number remained unchanged between two consecutive visits. Predation was identified visually in the field from characteristic signs of egg damage or disappearance. Nest fate and predation events were recorded separately. For failed nests, predation was assigned as the cause when field evidence indicated that predation was responsible for the failure.

Statistical analyses

The full dataset comprised 43 monitored nests, all of which had complete data for the hatching-success response and the four focal nest-level predictors; therefore, all 43 nests were included in the primary nest-level analysis. Failed nests, including depredated nests, were

Table S1. Summary of the nest-level and egg-level statistical models used to analyse hatching success in Eurasian Coots.

Model	Response variable	Predictors/covariates	Random effect	Sample size
Nest-level quasibinomial GLM	Number of hatched *vs.* unhatched eggs per nest	Initiation date; distance to open water; nest height above water; vegetation cover	None	43 nests
Egg-level binomial GLMM	Individual egg hatching outcome	Egg volume; initiation date; distance to open water; nest height above water; vegetation cover	Nest identity	204 eggs from 43 nests

Note: All continuous predictors were z-standardised before modelling. The quasibinomial model was used at the nest level because the initial binomial GLM showed substantial overdispersion.

retained because nest failure contributes directly to the hatching-success response. Analyses were conducted at two complementary biological levels to reflect the hierarchical structure of the dataset, with multiple eggs nested within nests, and to avoid pseudoreplication (Hurlbert 1984; Sokal and Rohlf 1995; Zar 2010). At the nest level, hatching success was modelled as the number of hatched versus unhatched eggs per nest. The primary model included initiation date, distance to open water, nest height above water, and vegetation cover as predictors specified *a priori*. All continuous predictors were z-standardised before modelling (Dytham 2011). Because the initial binomial GLM showed substantial overdispersion (Pearson dispersion = 3.37), inference was based on a quasibinomial GLM, with odds ratios reported for a one-standard-deviation increase in each predictor.

At the egg level, individual hatching outcome was analysed using a binomial generalized linear mixed model (GLMM) based on 204 eggs from 43 nests. The model included egg volume as an egg-level predictor and initiation date, distance to open water, nest height above water, and vegetation cover as nest-level predictors. All continuous predictors were z-standardised before modelling. Nest identity was included as a random intercept to account for the non-independence of eggs within nests. The intraclass correlation coefficient (ICC) was calculated on the latent logistic scale as $ICC = \sigma^2_{nest} / (\sigma^2_{nest} + \pi^2/3)$ and interpreted as residual among-nest heterogeneity after accounting for the fixed predictors. A summary of nest-level and egg-level statistical models is provided in Table S1.

Because the initiation date and distance to open water could covary seasonally, their association was examined using both Pearson and Spearman correlation coefficients. Effect sizes are reported as odds ratios with 95% confidence intervals and *p*-values.

Model adequacy was evaluated separately for the two analytical frameworks. For the nest-level analysis, overdispersion was assessed using the Pearson dispersion statistic and the ratio of residual deviance to residual degrees of freedom. The binomial GLM showed substantial overdispersion (Pearson dispersion = 3.37; deviance/df = 3.52); therefore, inference was based on a quasibinomial GLM. Variance inflation factors (VIFs) were used to assess collinearity among predictors (Fox and Weisberg 2019). For the egg-level GLMM, convergence, singularity of random-effect structure, optimizer behaviour, and potential complete or quasi-complete separation were examined before inference. All tests were two-sided with $\alpha = 0.05$. Statistical analyses were conducted in R (R Core Team 2025). Nest-level GLMs were fitted using the stats package and egg-level GLMMs using lme4 (Bates et al. 2015).

RESULTS

Clutch size and nest characteristics

A total of 43 nests were monitored, and all 43 were included in the nest-level analysis. Unless otherwise stated, descriptive values are presented as mean ± SD. Mean clutch size was 4.74 ± 1.50 eggs, and mean hatching proportion per nest was 0.743 ± 0.370. Mean egg length, breadth, and volume per nest were 54.29 ± 2.11 mm, 36.50 ± 1.20 mm, and 36.90 ± 3.08 cm³, respectively. Full descriptive statistics are presented in Table 1. Nest fate was classified as successful, failed, or unknown (Table 2). Among the nine failed nests, predation accounted for eight failures (88.9%), whereas flooding accounted for one (11.1%; Table 2).

Breeding phenology and microhabitat predictors of hatching success

In the nest-level quasibinomial GLM, none of the four focal predictors showed a clear association with hatching success (Table 3). Distance to open water showed the strongest negative pattern: nests farther from open water tended to have lower hatching odds, although the confidence interval included unity (OR = 0.45, 95% CI: 0.18–1.10, $p = 0.078$; Figure 2). Initiation date also showed a negative pattern (OR = 0.69, 95% CI: 0.32–1.51, $p = 0.341$; Figure 3). Vegetation cover showed no clear association with hatching success (OR = 1.64, 95% CI: 0.70–3.84, $p = 0.242$; Figure 4), and nest height above water was likewise not clearly associated with hatching success (OR = 1.27, 95% CI: 0.58–2.78, $p = 0.532$; Figure 5).

Initiation date and distance to open water were moderately negatively correlated (Pearson $r = -0.45$,

Table 1. Descriptive statistics of nesting sites, nest measurements, clutch traits, and mean egg measurements per nest of Eurasian Coot at Boussedra Pond (N = 43).

Variable	Mean ± SD	Minimum	Maximum
Distance to open water (cm)	25.63 ± 8.57	0.00	40.00
Water depth (cm)	60.14 ± 15.56	30.00	90.00
Vegetation height (cm)	129.07 ± 21.36	50.00	160.00
Vegetation cover (%)	32.84 ± 17.06	10.00	100.00
External nest diameter (cm)	31.21 ± 3.79	25.00	41.00
Internal nest diameter (cm)	20.80 ± 3.69	13.00	28.00
Nest height (cm)	18.67 ± 4.80	6.00	28.00
Clutch size (eggs)	4.74 ± 1.50	1.00	7.00
Total clutch volume (cm^3)	174.84 ± 57.31	40.45	297.33
Hatching proportion per nest	0.743 ± 0.370	0.000	1.000
Mean egg length per nest (mm)	54.29 ± 2.11	49.50	60.82
Mean egg breadth per nest (mm)	36.50 ± 1.20	31.89	38.75
Mean egg volume per nest (cm^3)	36.90 ± 3.08	28.21	42.48

Table 2. Fate of Eurasian Coot nests monitored at Boussedra Pond in 2025 (N = 43).

Year	N	Fate unknown, n (%)	Successful, n (%)	Failed, n (%)	Predated, n (%)*	Flooded, n (%)*	Unknown causes, n (%)*
2025	43	1 (2.3)	33 (76.7)	9 (20.9)	8 (88.9)	1 (11.1)	0 (0.0)

*Percentages for predation, flooding, and unknown causes were calculated among failed nests only (n = 9).

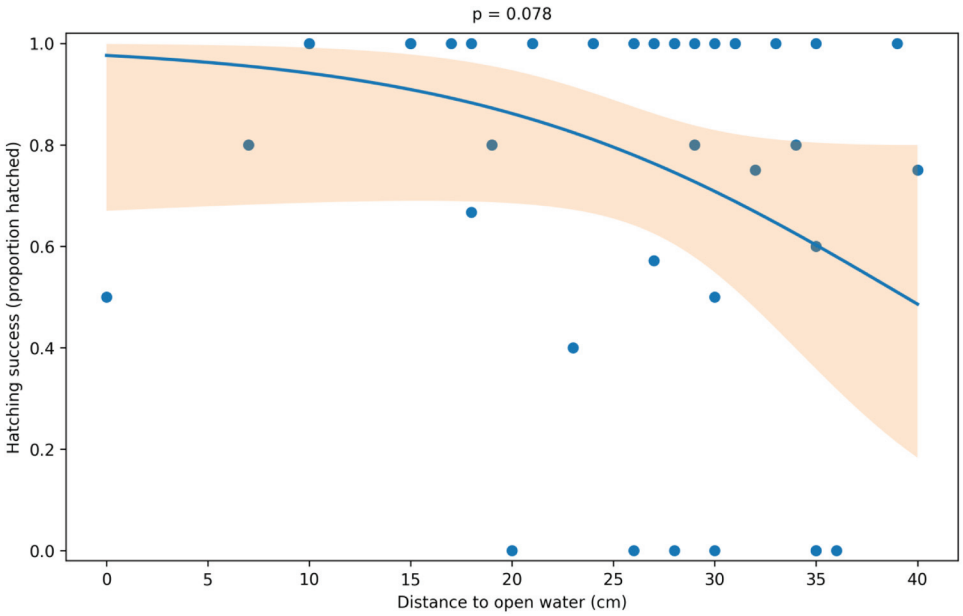


Figure 2. Predicted hatching success as a function of distance to open water. Solid line shows fitted values from the nest-level quasibinomial GLM, and the shaded band represents the pointwise 95% confidence interval adjusted for overdispersion.

Table 3. Quasibinomial GLM parameter estimates for hatching success in Eurasian Coot nests in 2025 (n = 43).

Predictor	β	SE	*t*	*p*	OR	95% CI for OR
Intercept	1.30	0.34	3.79	< 0.001	3.66	1.83–7.33
Vegetation cover (%)_z	0.50	0.42	1.19	0.242	1.64	0.70–3.84
Distance to open water (cm)_z	−0.81	0.45	−1.81	0.078	0.45	0.18–1.10
Nest height above water (cm)_z	0.24	0.39	0.63	0.532	1.27	0.58–2.78
Initiation date_z	−0.37	0.39	−0.96	0.341	0.69	0.32–1.51

Note: Continuous predictors were z-standardised. Standard errors, *t* tests, and 95% confidence intervals account for extra-binomial variation.

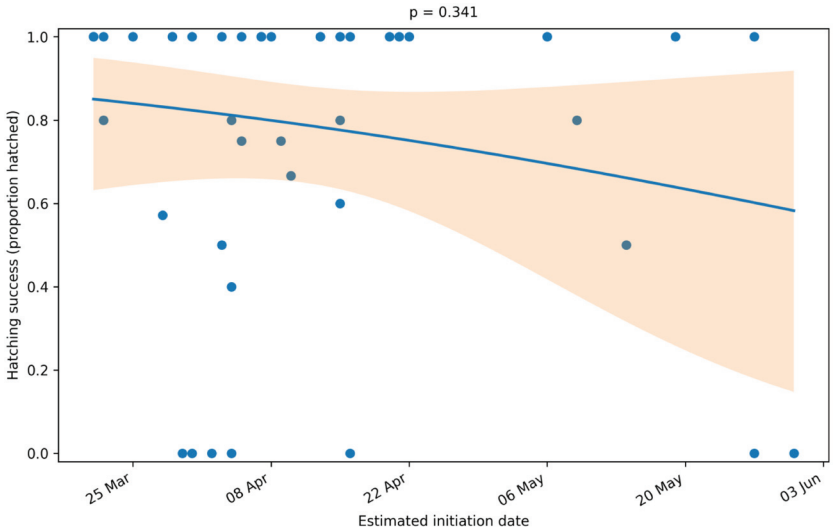


Figure 3. Predicted hatching success as a function of estimated initiation date. Solid line shows fitted values from the nest-level quasibinomial GLM, and the shaded band represents the pointwise 95% confidence interval adjusted for overdispersion.

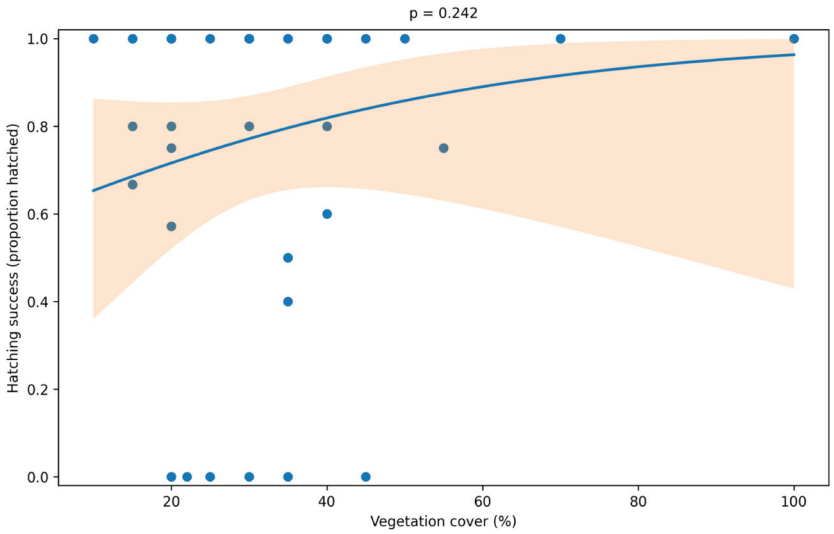


Figure 4. Predicted hatching success as a function of vegetation cover. Solid line shows fitted values from the nest-level quasibinomial GLM, and the shaded band represents the pointwise 95% confidence interval adjusted for overdispersion.

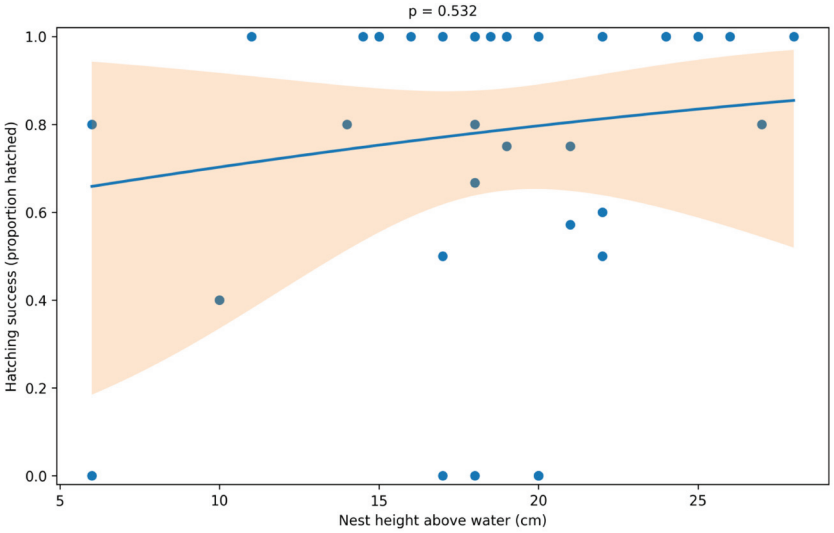


Figure 5. Predicted hatching success as a function of nest height above water. Solid line shows fitted values from the nest-level quasibinomial GLM, and the shaded band represents the pointwise 95% confidence interval adjusted for overdispersion.

Table 4. Egg-level GLMM parameter estimates for hatching fate in Eurasian Coot eggs in 2025 (204 eggs from 43 nests).

Predictor	β	SE	z	*p*	OR	95% CI
Intercept	2.79	0.84	3.34	< 0.001	16.32	3.17–83.91
Egg volume (z)	−1.09	0.51	−2.13	0.033	0.34	0.12–0.92
Initiation date (z)	−1.09	0.88	−1.24	0.216	0.34	0.06–1.89
Distance to open water (z)	−1.37	0.79	−1.73	0.083	0.25	0.05–1.20
Nest height above water (z)	0.53	0.81	0.65	0.513	1.70	0.35–8.33
Vegetation cover (z)	1.31	0.94	1.39	0.163	3.69	0.59–23.17

Note: Nest identity was included as a random intercept (variance = 11.92, SD = 3.45). The latent-scale ICC was 0.78 and was calculated as ICC = $\sigma^2_{nest}/(\sigma^2_{nest} + \pi^2/3)$. All continuous predictors were z-standardised before modelling.

p = 0.002; Spearman ρ = −0.43, p = 0.004; n = 43), indicating that later nests tended to be recorded closer to the measured open-water edge. Collinearity between these two predictors was low (VIF = 1.52 for initiation date and 1.30 for distance to open water).

Egg-level hatching outcome and among-nest heterogeneity

The egg-level GLMM included 204 eggs from 43 nests (Table 4). Egg volume was negatively associated with hatching probability (OR = 0.34, 95% CI: 0.12–0.92, p = 0.033). By contrast, initiation date (OR = 0.34, 95% CI: 0.06–1.89, p = 0.216), distance to open water (OR = 0.25, 95% CI: 0.05–1.20, p = 0.083), nest height above water (OR = 1.70, 95% CI: 0.35–8.33, p = 0.513), and vegetation cover (OR = 3.69, 95% CI: 0.59–23.17, p = 0.163) showed no clear associations with individual egg hatching outcome.

Egg outcomes were strongly clustered within nests. The nest random-intercept variance was 11.92 (SD = 3.45), corresponding to a latent-scale ICC of 0.78. This indicates substantial residual among-nest heterogeneity after accounting for the fixed predictors.

DISCUSSION

Patterns in hatching success across nest- and egg-level predictors

The nest-level analysis provided limited evidence that the breeding timing or the measured nest-site variables explained variation in hatching success. Distance to open water showed the strongest negative pattern, but its confidence interval included unity, while initiation date, nest height above water, and vegetation cover showed no clear relationship with hatching success. At the egg level, egg volume was negatively related to hatching probability, whereas the nest-level covariates included in the GLMM showed no clear relationships with individual egg fate. Egg outcomes were strongly clustered within nests (ICC = 0.78), indicating substantial residual variation among nests beyond that accounted for by the measured predictors.

Ecological interpretation of nest-site patterns

Nest height above water showed no clear relationship with hatching success in the nest-level analysis. Predation accounted for eight of the nine failed nests, whereas flooding accounted for only one. Previous work at Boussedra Pond documented predation by the viperine snake *Natrix maura* (Linnaeus, 1758) on the Common Moorhen *Gallinula chloropus* (Linnaeus, 1758) nests, indicating that this species occurs as a nest predator at the site (Talbi et al. 2021). Predator identity was not systematically determined for individual nest failures in the present study; therefore, the observed variation in hatching success cannot be attributed to any particular predator species. The influence of nest elevation and surrounding water conditions on predator access may differ among predator groups and requires direct observation to evaluate.

Nest height above water and seasonal water-level change represent different aspects of nest-site conditions. Because nest height was measured relative to the water surface at a single point in time, the study does not allow reconstruction of how this distance changed during the breeding season. If water levels declined while nest elevation remained fixed, the vertical distance between the nest and the water surface would increase. Lower water levels could also alter the degree of aquatic isolation around nests, but predator responses to such changes were not measured. Flooding, by contrast, would result from subsequent increases in water level or other inundation events. Given that only one failed nest was attributed to flooding, flooding was a minor source of nest failure in this population.

Mean nest height above water was 18.7 cm in the present study, compared with 14.5 cm reported for a Moroccan population (Squalli et al. 2020). This comparison is descriptive because hydrological conditions, reference levels, and nest-height measurement procedures may differ among studies and were not evaluated directly here.

Distance to open water showed the strongest negative pattern among the nest-level predictors, although the evidence remained limited and the confidence interval included unity. Nests farther from open water therefore

tended to have lower hatching odds, but this relationship should be interpreted cautiously. Proximity to open water could influence predator detection, escape behaviour, or access to foraging areas, but none of these processes was measured directly. These mechanisms remain plausible explanations rather than demonstrated benefits of nesting close to open water. Future work combining repeated habitat measurements with direct observations of predator activity and adult movements would help determine whether proximity to open water has a consistent biological role in hatching success.

Breeding phenology and hatching success

Hatching success showed no clear association with initiation date. Seasonal declines in reproductive success have been documented in free-living birds (Verhulst and Nilsson 2008), including Eurasian Coots (Brinkhof et al. 1993) and Mallards *Anas platyrhynchos* in north-eastern Algeria (Fouzari et al. 2018). In Collared Flycatchers *Ficedula albicollis* (Temminck, 1815), within-season variation in temperature and precipitation has also been associated with reproductive outcomes (Arct et al. 2025), illustrating that environmental conditions can vary within the breeding season and influence reproductive performance. However, a seasonal decline in hatching success was not statistically supported in the present study.

Previous work has shown that declining water depth can delay breeding in Eurasian Coots (Zhang et al. 2018), but our data do not indicate that later breeding was accompanied by lower hatching success. Vegetation cover was included together with initiation date in the nest-level model, and neither variable showed a clear association with hatching success. Vegetation height was measured as an additional habitat descriptor but was not included in the primary model, and seasonal changes in vegetation structure were not monitored repeatedly. Consequently, possible seasonal changes in habitat conditions, predator exposure, or differences among breeding individuals cannot be distinguished with the present data.

Seasonal vegetation development could covary with breeding phenology, as reported for nest-site use in North African rallids (Samraoui et al. 2015), but this mechanism was not tested directly in the present study.

Egg-level traits and residual among-nest heterogeneity

Egg volume was negatively associated with individual hatching outcome in the egg-level GLMM, with larger eggs showing lower hatching odds. The biological basis of this pattern remains unclear. Whole-nest failure, particularly predation, affected several eggs simultaneously and may therefore have influenced egg-level outcomes independently of individual egg characteristics. A strong clustering of hatching outcomes within nests further suggests that nest-level conditions or other unmeasured differences among nests may have contributed to this relationship. Accordingly, the negative association with egg volume should not be interpreted as evidence that larger eggs themselves reduce hatching probability. The effects of hatching order on brood reduction and chick survival have been documented in Coots (Horsfall 1984), but hatching order and post-hatching survival were not assessed in the present study.

Egg hatching outcomes were strongly clustered within nests (ICC = 0.78). Eggs from the same nest therefore tended to have more similar outcomes than eggs from different nests. This clustering does not indicate that the measured nest-site characteristics were responsible for the among-nest variation. The nest random effect may reflect unmeasured parental attributes, local environmental conditions, nest-specific events, or whole-nest failure.

Limitations

Several limitations should be considered. The study covered a single breeding season and therefore cannot quantify interannual variation in breeding conditions or reproductive performance. Water-level dynamics, human disturbance, predator identity, and predator activity were not monitored continuously, and nest height above water and distance to open water were recorded as single nest-level measurements. In addition, the field records do not provide a more detailed operational definition of the open-water boundary. Future studies should define this boundary in advance, repeat hydrological and nest-to-water measurements through the season, and identify nest predators directly where possible.

Implications for habitat management

Despite these limitations, the findings have implications for urban wetland management. Predation was the dominant recorded cause of nest failure, but the predator-specific mechanisms linking nest position to failure were not established; management should therefore avoid assuming that a single intervention will reduce predator access. Maintaining a heterogeneous mosaic of open-water patches, emergent vegetation, and ecotones may preserve a range of nesting conditions. Reed-bed management, including selective mowing, can alter habitat use and may benefit some larger-bodied water birds while disadvantaging smaller reed-associated species, so such interventions should be applied cautiously and at a fine spatial scale (Giordano et al. 2024). Maintaining relatively stable water conditions may also

help preserve nesting habitat, but flooding was uncommon in this study and hydrological dynamics were not monitored continuously. These recommendations should therefore be treated as provisional and evaluated through site-specific monitoring.

CONCLUSION

At the nest level, hatching success varied substantially, but none of the four measured predictors showed a clear association after accounting for overdispersion. Distance to open water showed the strongest negative pattern. At the egg level, egg volume was negatively associated with hatching probability, although the mechanism underlying this relationship remains uncertain and egg outcomes were strongly clustered within nests. These results indicate substantial residual variation among nests and support a cautious interpretation of associations between breeding phenology, nest-site characteristics, egg volume, and hatching success in this single-season study.

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Statements and Declarations

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Conflict of Interest Disclosure

The authors declare no conflicts of interest.

Data Availability Statement

The data supporting this study (field notes and photographic records) are available from the corresponding author upon reasonable request.

Ethics Approval Statement

This study was approved by the Algerian Ministère de l'Enseignement Supérieur et de la Recherche Scientifique.

Author contribution

NB. Investigation, Review & Editing

FS. Conceptualization, Methodology, Data Curation, Writing – Original Draft

SC. Investigation, Review & Editing

BS. Visualization, Resources, Review & Editing

REFERENCES

Aouadi, A., Samraoui, F., Touati, L., Nedjah, R., Souiki, L., & Samraoui, B. 2021. Close to the madding crowd: Waterbird responses to land use conversion in and around a Mediterranean urban wetland. *Wetlands* 41, 85. https://doi.org/10.1007/s13157-021-01484-9

Arct, A., Martyka, R., Miler, K., Skorb, K., Gustafsson, L., & Drobniak, S.M. 2025. The impact of weather conditions on avian breeding performance: Insights from a long-term study. *Frontiers in Zoology* 22, 23. https://doi.org/10.1186/s12983-025-00569-z

Athamnia, M., Samraoui, F., Kelailia, B., Rouabah, A., Alfarhan, A.H., & Samraoui, B. 2015. Nest-site selection and reproductive success of the Little Grebe *Tachybaptus ruficollis* in northeast Algeria. *Ardeola* 62, 113–124. https://doi.org/10.13157/arla.62.1.2015.113

Austin, J.E., & Buhl, D.A. 2011. Nest survival of American Coots relative to grazing, burning, and water depths. *Avian Conservation and Ecology* 6, 1. https://doi.org/10.5751/ACE-00472-060201

Bates, D., Mächler, M., Bolker, B., & Walker, S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67, 1–48. https://doi.org/10.18637/jss.v067.i01

Both, C., Bouwhuis, S., Lessells, C.M., & Visser, M.E. 2006. Climate change and population declines in a long-distance migratory bird. *Nature* 441, 81–83. https://doi.org/10.1038/nature04539

Brinkhof, M.W.G., 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, 577–587.

Brinkhof, M.W.G., Cavé, A.J., Daan, S., & Perdeck, A.C. 2002. Timing of current reproduction directly affects future reproductive output in European Coots. *Evolution* 56, 400–411. https://doi.org/10.1111/j.0014-3820.2002.tb01349.x

Brzeziński, M., Jedlikowski, J., & Żmihorski, M. 2013. The effect of nest site on the nesting success of the Coot *Fulica atra*. *Ornis Fennica* 90, 57–64. https://doi.org/10.51812/of.133822

Cheriet, S., Samraoui, F., Al-Farhan, A.H., & Samraoui, B. 2015. Factors affecting nesting success in the Great-crested Grebe *Podiceps cristatus* at Lake Tonga, north-east Algeria. *Ostrich* 86, 239–245. https://doi.org/10.2989/00306525.2015.1067932

Chyb, A., & Minias, P. 2022. Complex associations of weather conditions with reproductive performance in urban population of a common waterbird. *International Journal of Biometeorology* 66, 1163–1172. https://doi.org/10.1007/s00484-022-02266-6

Dytham, C. 2011. *Choosing and Using Statistics: A Biologist's Guide*, 3rd edition. Wiley-Blackwell.

Fouzari, A., Samraoui, F., & Samraoui, B. 2018. The bree-

ding ecology of Mallard *Anas platyrhynchos* at Lake Tonga, north-eastern Algeria. *Ostrich* 89, 315–320.

Fox, J., & Weisberg, S. 2019. *An R Companion to Applied Regression*, 3rd edition. Sage.

Giordano, J., Moretti, F., & Battisti, C. 2024. Pattern in water-related birds reveals a shift in biomass between mature and mowed reedbeds: evidence from a coastal wetland. *Ethology Ecology & Evolution* 36, 679–696. https://doi.org/10.1080/03949370.2024.2411508

Gorenzel, W.P., Ryder, R.A., & Braun, C.E. 1982. Reproduction and nest site characteristics of American Coots at different altitudes in Colorado. *The Condor* 84, 59–65.

Hałupka, L., Czyż, B., & Macias Dominguez, C.M. 2020. The effect of climate change on laying dates, clutch size and productivity of Eurasian Coots *Fulica atra*. *International Journal of Biometeorology* 64, 1857–1863. https://doi.org/10.1007/s00484-020-01972-3

Horsfall, J.A. 1984. Brood reduction and brood division in coots. *Animal Behaviour* 32, 216–225. https://doi.org/10.1016/S0003-3472(84)80340-1

Hoyt, D.F. 1979. Practical methods of estimating volume of bird eggs. *The Auk* 96, 73–77.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54, 187–211.

Lack, D. 1950. The breeding seasons of European birds. *Ibis* 92, 288–316. https://doi.org/10.1111/j.1474-919X.1950.tb01753.x

Meniaia, Z., Samraoui, F., Alfarhan, A.H., & Samraoui, B. 2014. Nest-site selection, breeding success and brood parasitism in the Common Moorhen *Gallinula chloropus* in Algeria. *Zoology and Ecology* 24(4), 305–313. https://doi.org/10.1080/21658005.2014.959281

Nieoczym, M., & Kloskowski, J. 2018. Habitat selection and reproductive success of Coot *Fulica atra* on ponds under different fish size and density conditions. *Hydrobiologia* 820, 267–279. https://doi.org/10.1007/s10750-018-3664-2

R Core Team. 2025. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Renner, S.S., & Zohner, C.M. 2018. Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annual Review of Ecology, Evolution, and Systematics* 49, 165–182. https://doi.org/10.1146/annurev-ecolsys-110617-062535

Rounds, R.A., Erwin, R.M., & Porter, J.H. 2004. Nest-site selection and hatching success of waterbirds in coastal Virginia: some results of habitat manipulation. *Journal of Field Ornithology* 75, 317–329.

Ryan, M.R., & Dinsmore, J.J. 1980. The behavioral ecology of breeding American Coots in relation to age. *The Condor* 82, 320–327. https://doi.org/10.2307/1367401

Salathé, T. 1986. Habitat use by Coots nesting in a Mediterranean wetland. *Wildfowl* 37, 136–171.

Samraoui, F., & Samraoui, B. 2007. The reproductive ecology of the Common Coot *Fulica atra* in the Hauts Plateaux, northeast Algeria. *Waterbirds* 30, 133–139. https://doi.org/10.1675/1524-4695-(2007)030[0133:TREOTC]2.0.CO;2

Samraoui, B., & Samraoui, F. 2008. An ornithological survey of Algerian wetlands: Important Bird Areas, Ramsar sites and threatened species. *Wildfowl* 58, 71–96.

Samraoui, F., Alfarhan, A.H., & Samraoui, B. 2013. Status and breeding ecology of the Common Moorhen *Gallinula chloropus* in Algeria. *Ostrich* 84, 137–144. https://doi.org/10.2989/00306525.2013.823130

Samraoui, F., Nedjah, R., Alfarhan, A.H., & Samraoui, B. 2015. An overview of the Rallidae of Algeria with particular reference to the breeding ecology of the Purple Swamp-Hen *Porphyrio porphyrio*. *Wetlands Ecology and Management* 23, 505–517. https://doi.org/10.1007/s11273-014-9404-0

Sokal, R.R., & Rohlf, F.J. 1995. *Biometry: The Principles and Practice of Statistics in Biological Research*, 3rd edition. W.H. Freeman.

Squalli, W., Mansouri, I., Dakki, M., & Fadil, F. 2020. Nesting habitat and breeding success of *Fulica atra* in tree wetlands in Fez's region, central Morocco. *Journal of Animal Behaviour and Biometeorology* 8, 282–287. https://doi.org/10.31893/jabb.20037

Talbi, A., Samraoui, F., Samraoui, B., Zullo, F., & Battisti, C. 2020. Habitat selection of Coot *Fulica atra* and Moorhen *Gallinula chloropus* in a remnant Mediterranean wetland (Italy): implications for conservation. *Lakes & Reservoirs: Research & Management* 25, 413–418. https://doi.org/10.1111/lre.12347

Talbi, A., Touati, L., Athamnia, M., Samraoui, F., Battisti, C. & Samraoui, B. 2021. The synanthropic Common Moorhen *Gallinula chloropus* in North Africa: the impact of habitat degradation on breeding performances. *Zoology and Ecology* 31, 15–23. https://doi.org/10.35513/21658005.2021.1.4

Uzun, A. 2012. The effect of vegetation and water depth on nest patterns of the Eurasian Coot *Fulica atra*. *Turkish Journal of Zoology* 36, 820–823. https://doi.org/10.3906/zoo-1109-23

Verhulst, S., & Nilsson, J.A. 2008. The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363, 399–410. https://doi.org/10.1098/rstb.2007.2146

Zar, J.H. 2010. *Biostatistical Analysis*, 5th edition. Pearson.

Zhang, W., Liu, T., Cheng, K., & Rummy, P. 2018. Declining water depth delayed the breeding time of *Fulica atra*, not human disturbance. *PLoS ONE* 13, e0202684. https://doi.org/10.1371/journal.pone.0202684