

Integrated Analysis of Morphological and Reproductive Traits Across Reproductive Stages in Mallards (*Anas platyrhynchos*): Insights into Reproductive Ecology and Success

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Abstract: Seasonal progression of breeding activities in waterfowl is accompanied by marked adjustments in nest construction and reproductive allocation. In this study, I examine how breeding stages shape nest characteristics and reproductive performance in Mallards (*Anas platyrhynchos*) breeding on Oued Charef Dam Island, northeastern Algeria. Nest dimensions, egg traits, clutch composition, and reproductive success were monitored across successive breeding stages throughout the season. Temporal variation in these traits was analysed using univariate statistical tests (ANOVA with Tukey HSD) and multivariate approaches (Principal Component Analysis and non-metric multidimensional scaling (NMDS)). Results indicate a consistent increase in nest size, egg dimensions, and clutch size as the breeding season advanced. Egg volume and mass peaked during the incubation and brood-rearing stages, coinciding with higher hatching and overall reproductive success in later breeding phases. Multivariate analyses revealed that breeding stage strongly structured the observed patterns of reproductive investment, with PCA identifying a dominant gradient of allocation intensity and NMDS confirming its positive relationship with reproductive outcomes. These findings highlight a progressive and coordinated adjustment of reproductive traits in Mallards breeding under semi-arid Mediterranean conditions. The study provides new insights into the temporal organization of reproductive investment in waterfowl and offers a valuable baseline for evaluating the effects of environmental variability and human disturbance on breeding performance.

Keywords: breeding stages, reproductive allocation, nest structure, waterfowl ecology, principal component analysis (PCA), NMDS

Introduction

Reproductive performance is a central determinant of fitness in birds and plays a key role in shaping population trajectories. In waterfowl, breeding success depends on the coordinated expression of multiple morphological and reproductive traits, including nest structure, egg characteristics, clutch composition, and parental investment (Ankney & MacInnes 1978, Hansell, 2000). Rather than representing static attributes, these traits are inherently flexible and adjust throughout the breeding cycle as females balance energetic constraints, reproductive demands, and environmental conditions (Collias & Collias 1984, Metcalfe & Thorpe 1992). Despite the broad distribution and ecological importance of the Mallard (*Anas platyrhynchos*), research on its reproduction has often examined individual components of breeding biology in isolation, such as nest-site selection, egg size, or clutch size (Vergara 2010, Raveling et al. 2000). This fragmented approach has limited our ability to understand how multiple reproductive traits covary through time and collectively influence reproductive outcomes. An integrated perspective is therefore necessary to identify how reproductive investment is structured across successive stages of the breeding cycle. Nest construction represents a critical early investment in reproduction, as nest dimensions and structure directly influence insulation,

microclimatic stability, and vulnerability to predation (Collias & Collias 1984, Martin et al. 2000). Similarly, egg size, mass, and volume reflect maternal allocation of resources to offspring and are closely linked to embryonic development, hatchling quality, and early survival (Williams 1994, Nager et al. 2001). Variation in these traits has been associated with female condition, age, and environmental quality, underscoring the plasticity of reproductive strategies in response to ecological constraints (Borger et al. 2023, Högstedt 1980). However, the extent to which nest traits, egg characteristics, and clutch parameters change jointly across breeding stages remains poorly documented in waterfowl. The breeding cycle encompasses a sequence of distinct phases from nest establishment and egg laying to incubation and brood care each characterized by specific energetic costs and physiological trade-offs (Metcalf & Thorpe 1992, Swennen 1989). Examining reproduction through a stage-based framework allows for a more accurate assessment of temporal shifts in reproductive investment and helps identify periods when reproductive success may be most strongly constrained. Nevertheless, waterfowl studies have rarely adopted such an approach, relying instead on short-term or stage-specific observations (Vergara 2010, Raveling et al. 2000). In this context, the present study provides an integrated assessment of reproductive traits across successive breeding stages in a wild Mallard population breeding on Oued Charef Dam Island in northeast Algeria. This semi-arid Mediterranean wetland represents a poorly studied environment where ecological constraints may shape reproductive strategies differently from those documented in temperate systems. Four reproductive stages are distinguished early breeding, mid-breeding I, mid-breeding II, and late breeding corresponding to progressive phases of reproductive investment from nest construction to incubation and chick rearing. Using a combination of univariate and multivariate analyses (ANOVA, Tukey HSD, principal component analysis, and redundancy analysis), this study investigates how reproductive stage influences nest morphology, egg size and volume, clutch size, hatching success, and overall breeding performance. Specifically, the objectives are to: (1) characterize stage-specific variation in nest, egg, and clutch traits; (2) examine the covariation among morphological and reproductive parameters across the breeding cycle; and (3) assess the role of reproductive stage in mediating reproductive success under semi-arid conditions. I hypothesize that reproductive investment is reduced during early breeding and increases through subsequent stages as reproductive effort intensifies, reflecting changing energetic demands and environmental conditions. I further predict that larger and deeper nests and increased egg volume will be associated with higher hatching success and improved breeding performance, while variation in clutch size may reflect context-dependent reproductive strategies rather than fixed effects. Understanding how reproductive traits vary across clearly defined breeding stages is increasingly important in the context of climate change, which is expected to modify the timing, duration, and predictability of avian breeding cycles (Capilla-Lasheras et al. 2021b, McRae & Conway 2024). By adopting an integrated, stage-based framework, this study provides new insights into the reproductive ecology of Mallards in North African wetlands and establishes a valuable baseline for future comparative and long-term investigations.

Material and methods

Study area

The study was carried out on a small rocky island (approximately 150 ha) located within the Oued Charef Dam (36°5'22.91"N, 7°23'20.78"E; altitude: 920 m; reservoir surface area: 1010 ha), near the town of Souk Ahras, in northeastern Algeria.(Boukrouma et al. 2021) (Fig. 1). The area experiences a semi-arid Mediterranean climate characterized by an annual precipitation ranging from 158 mm to 480 mm, with over 70% of rainfall occurring during the winter months (October to March). Mean annual temperatures fluctuate between 11.9 °C and -22 °C, with hot dry summers and cold winters. Seasonal variation is pronounced, with a dry period lasting from late spring through early autumn. (Boukrouma et al., 2021)

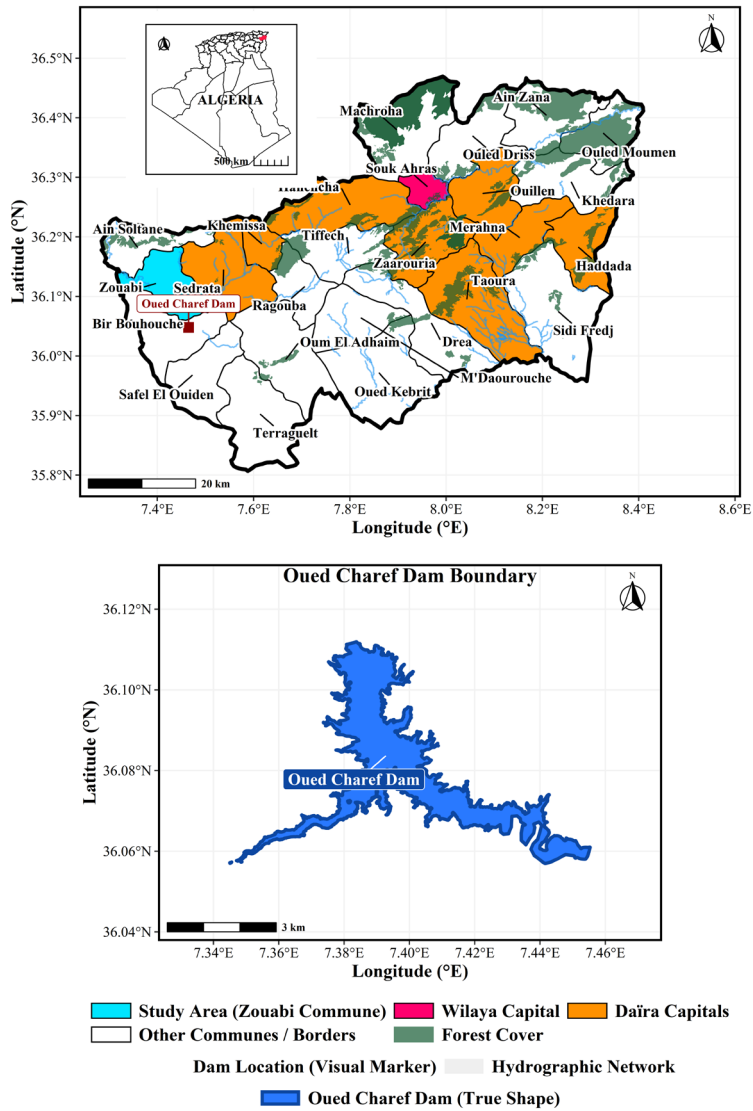


Fig. 1: (A) Map showing the location of the study area: a small rocky island within the Oued Charef Dam, located near the Province of Souk Ahras, Northeastern Algeria. (Established By Boukroum, 2026)

Data collection and nest monitoring

Field surveys on the Mallard (*Anas platyrhynchos*) were conducted from early October 2018 to early June 2019. Nest structure was measured, including internal and external diameters and nest depth, using a measuring tape, and weekly nest checks were performed to monitor clutch progress, chick productivity, and nesting success. To account for temporal variation, the reproductive period was divided into four stages early breeding (early October–mid-December), mid-breeding I (mid-December–early March), mid-breeding II (early March–late April), and late breeding (late April–early June) each representing roughly one-fourth of the fieldwork period. While this classification is based on calendar dates rather than direct physiological or behavioral markers, it provides a practical framework to analyze temporal changes in reproductive traits. Nest success was determined from direct observations of hatching or the presence of eggshell fragments and down feathers, and nests were considered failed if all eggs disappeared or were damaged before hatching (Boukrouma et al. 2021). Chick productivity was monitored up to 20 days post-hatching. Cases of egg loss due to cannibalism were identified through direct observation or the presence of peck marks and yolk traces near nests. Each egg was individually marked, weighed using a Pesola spring scale (0–500 g, precision 1 g), and measured for length and width to the nearest 0.1 mm, with egg volume calculated as:

$$\text{Volume (cc)} = \frac{(0.476 \times \text{length} \times \text{width}^2)}{1000}$$

where length and width are measured in millimeters (mm), and the constant 0.476 is a species-specific shape coefficient commonly used for gull eggs (Hoyt, 1979).

The laying date of a nest was defined as the date the first egg was laid, consistent with methodologies commonly applied in contemporary research on gull reproductive timing (Chokri et al. 2023). For nests first discovered during the incubation stage, to estimate laying dates a 28-day incubation duration was subtracted from the calculated hatching dates. Hatching success was determined by counting the number of hatched eggs during the final monitoring visit before nest termination. Nest outcomes were categorized as: (1) successful, if at least one egg hatched; (2) abandoned, when no activity was noted and eggs were cold or disappeared before expected hatching; and (3) predated, where evidence of egg or chick predation was found.

Statistical analysis

All statistical analyses were carried out using R software, version 4.5.0 (R Core Team 2025). Prior to analysis, data were checked for normality using the Shapiro–Wilk test in order to determine the appropriate statistical approach for each variable. To evaluate the influence of breeding stage on morphological and reproductive traits, one-way ANOVA was employed when the data met assumptions of normality and homogeneity of variances. This allowed for the comparison of means across the different ecological seasons. Post-hoc Tukey’s HSD tests were then used to identify which specific Reproductive Stages differed significantly, offering detailed insights into temporal patterns. To examine broader patterns and interactions among multiple variables simultaneously, multivariate analyses were also conducted. Principal Component Analysis (PCA) was used to reduce dimensionality and identify the main axes of variation in the dataset, helping to visualize how nest and reproductive traits varied across ecological seasons. Additionally, non-metric multidimensional scaling (NMDS) was implemented to assess the extent to which breeding stage explains variation in the multivariate structure of the data. These methods together provided a comprehensive understanding of how seasonality shapes reproductive strategies and nest morphology. Violin Boxplots were generated using R packages “ggplot2” selected for his capacity to produce high-quality and interpretable figures suited to ecological data.

RESULTS

Reproductive stages effects on morphological and reproductive parameters

Reproductive stages, defined by environmental conditions such as temperature, food availability, and water levels, were associated with significant variation in nest characteristics (dimensions) and reproductive parameters (egg size, volume, weight, hatching success, and breeding success), indicating that these traits differed across reproductive events. Post-hoc Tukey HSD tests revealed specific pairwise differences. For external nest diameter (cm, N = 20 per stage), values increased progressively across the reproductive season, being smallest during Early Breeding and largest during Late Breeding (diff = 7.40, $p < 0.001$) (Figure 2A).

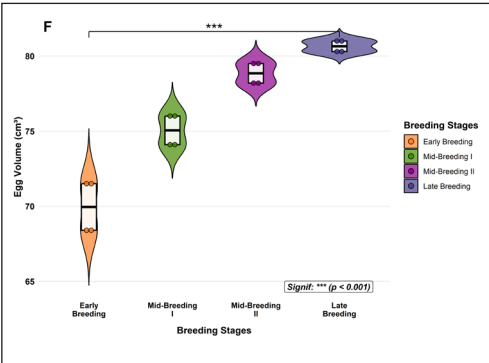
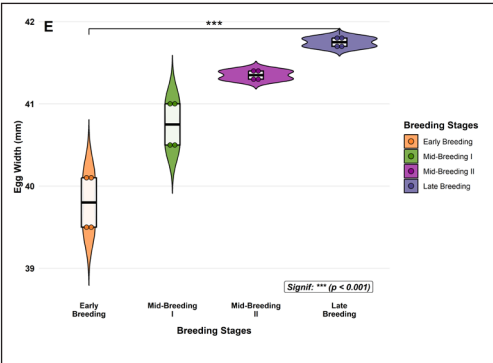
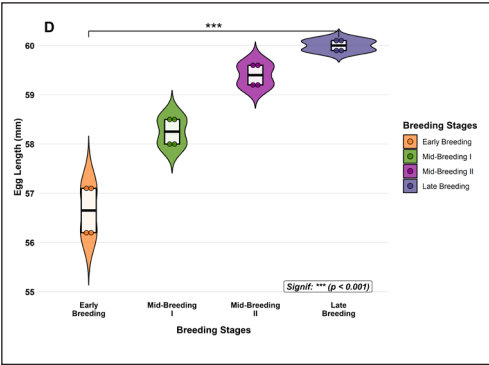
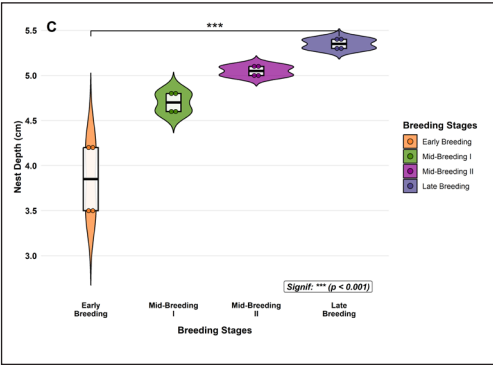
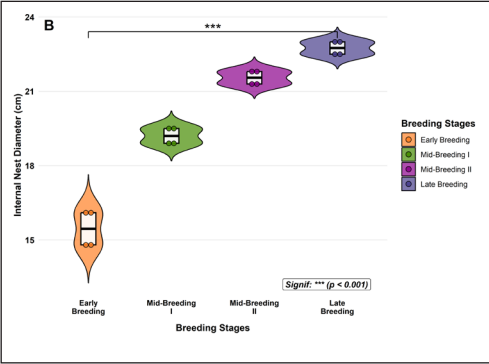
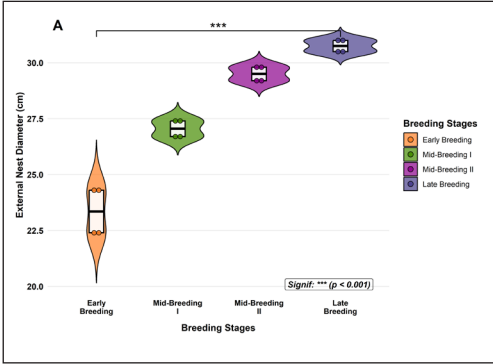
Significant differences were also found between Mid-Breeding I and Late Breeding (diff = 3.70, $p = 0.00001$) and between Mid-Breeding II and Late Breeding (diff = 1.25, $p = 0.064$, trend). Similarly, internal nest diameter was significantly smaller during Early Breeding compared to later stages (Mid-Breeding I, diff = 3.75, $p < 0.001$; Mid-Breeding II, diff = 6.10, $p < 0.001$; Late Breeding, diff = 7.30, $p < 0.001$) (Figure 2B). This indicates that nests gradually became larger over the reproductive season, reaching maximum dimensions during Late Breeding. Nest depth also showed a significant effect of reproductive stage, being lowest during Early Breeding and highest during Late Breeding (diff = 1.50 cm, $p < 0.001$) (Table 1, Figure 2C; $N = 20$). For egg traits, egg length increased significantly across reproductive stages, being smallest during Early Breeding (diff = 1.60–3.35 mm, $p < 0.001$) (Table 1, Figure 2D; $N = 20$) and largest during Late Breeding. Egg width followed a similar pattern, with significantly lower values during Early Breeding compared to Mid-Breeding I, Mid-Breeding II, and Late Breeding (diff = 0.95–1.95 mm, $p < 0.001$) (Figure 2E). As a result, egg volume increased progressively across the season (diff = 5.1–10.7 cm³, $p < 0.001$) (Figure 2F), as did egg weight (diff = 3.30–5.45 g, $p < 0.001$) (Figure 2G; $N = 20$), indicating increasing maternal investment as the breeding season progressed. Hatching success also varied significantly among reproductive stages, being lowest during Early Breeding and highest during Late Breeding (diff = 46.25–58.20 %, $p < 0.05$) (Table 1, Figure 2H; $N = 20$). Similarly, breeding success increased significantly across the stages (diff = 34.75–48.90 %, $p < 0.01$) (Figure 2I; $N = 20$). These patterns suggest that the Early Breeding stage is characterized by lower nest quality and reduced reproductive performance, whereas the Late Breeding stage represents the most favorable conditions for successful reproduction.

Tab. 1: Summary of statistical analyses examining the effect of reproductive stages on nest morphology, egg traits, and reproductive performance in Mallards (*Anas platyrhynchos*) at Oued Charef Dam (Algeria).

Variable	N	Test	df	F / χ^2	p-value	Post-hoc / Significant differences	Significance
External Nest Diameter (cm)	20	ANOVA	3, 16	108.3	5.9e-09	LB > EB***, MBII > EB***, MBI > EB***, LB > MBI*	***
Internal Nest Diameter (cm)	20	ANOVA	3, 16	194.7	1.93e-10	LB > EB***, MBII > EB***, MBI > EB***, LB > MBI**, LB > MBII*, MBII > MBI**	***
Nest Depth (cm)	20	ANOVA	3, 16	36.71	2.53e-06	LB > EB***, MBII > EB***, MBI > EB*, LB > MBI**	***
Egg Length (mm)	20	ANOVA	3, 16	82.83	2.75e-08	LB > EB***, MBII > EB***, MBI > EB***, LB > MBI*, LB > MBII, MBII > MBI*	***
Egg Width (mm)	20	ANOVA	3, 16	54.78	2.83e-07	LB > EB***, MBII > EB***, MBI > EB*, LB > MBI**, LB > MBII*, MBII > MBI**	***
Egg Volume (cm ³)	20	ANOVA	3, 16	69.81	7.26e-08	LB > EB***, MBII > EB***, MBI > EB*, LB > MBI***, LB > MBII*, MBII > MBI**	***
Egg Weight (g)	20	ANOVA	3, 16	123	2.82e-09	LB > EB***, MBII > EB***, MBI > EB*, LB > MBI***, LB > MBII*, MBII > MBI**	***
Clutch Size	20	ANOVA	3	6.882	0.0719	EB < LB (ns), others ns (Dunn test)	ns

Hatching Success (%)	20	ANOVA	3, 16	7.882	0.0036	LB > EB**, MBII > EB**, MBI > EB*, LB > MBI**, LB > MBII*, MBII > MBI*	**
Breeding Success (%)	20	ANOVA	3, 16	12.28	0.000573	LB > EB***, MBII > EB***, MBI > EB**, LB > MBI***, LB > MBII**, MBII > MBI**	***

Legend: N = total number of nests observed (N = 20), LB = Late Breeding, EB = Early Breeding, MBI = Mid-Breeding I, MBII = Mid-Breeding II, Significance codes: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. Post-hoc / Significant differences indicate pairwise comparisons between reproductive stages (Tukey HSD for ANOVA).



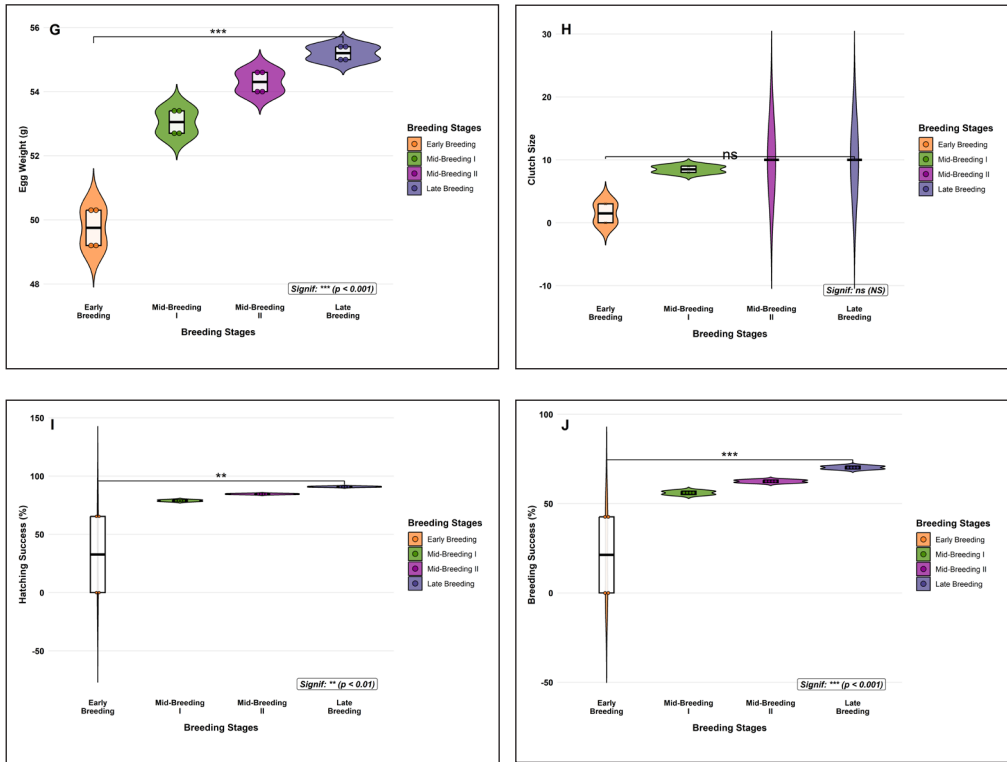


Fig. 2: Seasonal effects on nest characteristics, egg traits, and reproductive success with corresponding figures: external nest diameter (Fig. 2A), internal nest diameter (Fig. 2B), nest depth (Fig. 2C), egg length (Fig. 2D), egg width (Fig. 2E), egg volume (Fig. 2F), egg weight (Fig. 2G), clutch size (Fig. 2H), hatching success (Fig. 2I), and breeding success (Fig. 2J), at the small island of Oued Charef Dam, northeast Algeria.

Multivariate analysis of nesting and reproductive parameters across Breeding Stages

The multivariate analysis of Mallard reproductive and nesting parameters revealed strong associations between reproductive stages, nest characteristics, and reproductive output. The Principal Component Analysis (PCA) indicated that the first two dimensions captured the majority of the variation in the dataset. PC.1 was strongly correlated with most quantitative variables, including Nest Depth ($R^2 = 0.998$, $p < 0.001$), Egg Width ($R^2 = 0.994$, $p < 0.001$), Egg Volume ($R^2 = 0.993$, $p < 0.001$), External Nest Diameter ($R^2 = 0.993$, $p < 0.001$), Egg Length ($R^2 = 0.993$, $p < 0.001$), Egg Weight ($R^2 = 0.990$, $p < 0.001$), Internal Nest Diameter ($R^2 = 0.987$, $p < 0.001$), Clutch Size ($R^2 = 0.982$, $p < 0.001$), Breeding Success ($R^2 = 0.959$, $p < 0.001$), and Hatching Success ($R^2 = 0.920$, $p < 0.001$), highlighting PCA.1 as an overall gradient of reproductive investment and nest productivity (Fig.3). The categorical variable Breeding Stage was also significantly associated with PCA.1 ($R^2 = 0.995$, $p < 0.001$), with early breeding stage negatively associated and Mid breeding I positively associated, reflecting a progressive increase in nest size, egg characteristics, and reproductive success along the breeding cycle. PCA.2 explained additional variability primarily linked to differences between early and mid-breeding stages ($R^2 = 0.980$, $p < 0.001$), with Nest Building positively associated

and early breeding negatively associated, suggesting that PCA.2 captures transitional changes rather than overall reproductive output. Complementing these results, Non-metric Multidimensional Scaling (NMDS) further corroborated these findings, demonstrating a clear and sequential segregation of breeding stages in ecological space (Fig. 4). The group centroids revealed a distinct successional trajectory along the first axis (NMDS1), shifting from Early Breeding (mean: -4.58) through Mid-Breeding I (-0.44) and Mid-Breeding II (2.22), to Late Breeding (2.80). This ordination aligns with the PCA results, illustrating a progressive modification of nesting parameters throughout the season. Notably, the Mid-Breeding I stage was sharply differentiated along the second axis (NMDS2 = -2.37), suggesting a unique ecological signature or transitional state during this specific phase. Together, PCA and NMDS reveal that reproductive success metrics drive the primary variation across breeding stages, while nest and egg morphology vary more subtly, providing novel insights into the progression of Mallard reproductive ecology and representing the first comprehensive study linking these variables across the entire breeding cycle.

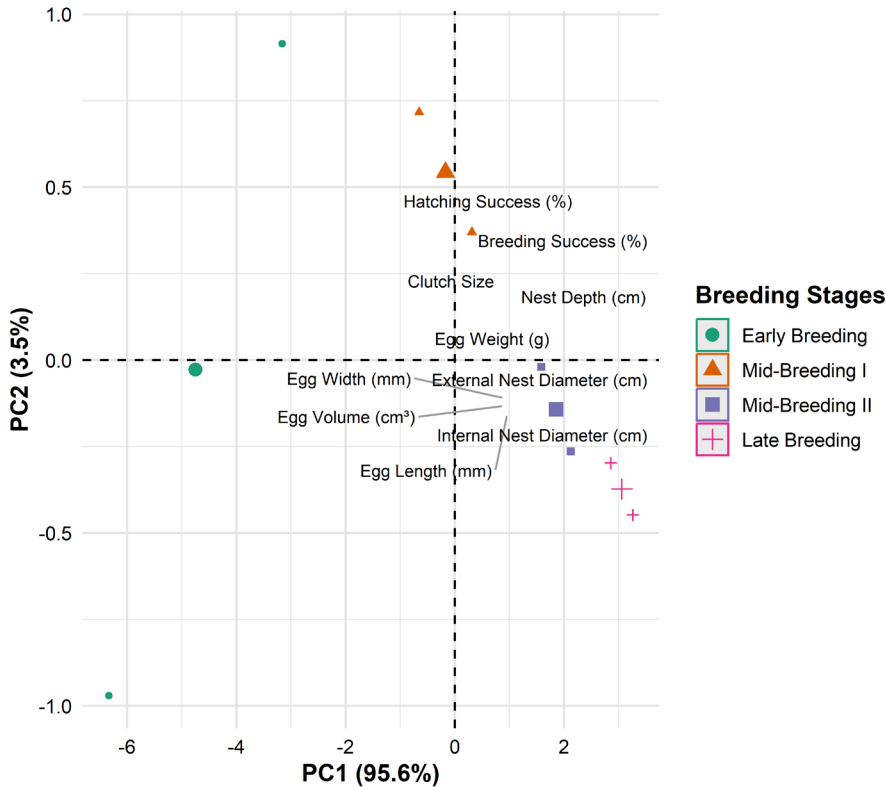


Fig. 3: Principal Component Analysis (PCA) of nesting and reproductive traits across Breeding Stages at the small island of Oued Charef dam, northeast Algeria.

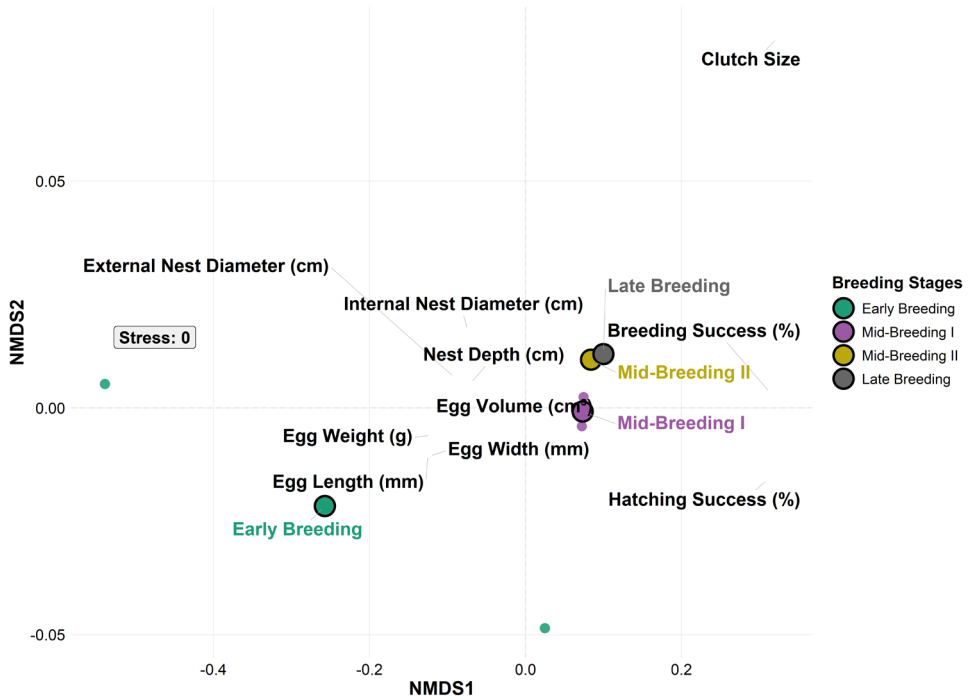


Fig. 4: Non-metric Multidimensional Scaling (NMDS) plot of Mallard (*Anas platyrhynchos*) reproductive and nesting parameters across the breeding stages at the small island of Oued Charef dam, northeast Algeria.

DISCUSSION

This study demonstrates that breeding stage shapes both morphological and reproductive traits in Mallards (*Anas platyrhynchos*), with nest dimensions, egg characteristics, and reproductive success showing systematic changes across the breeding cycle. External and internal nest diameters and nest-cup depth increased progressively from early to late breeding, indicating that nest construction is a flexible, stage-dependent process. Such progressive adjustments likely enhance thermal regulation, reduce predation risk, and support offspring survival (Hansell, 2000; Collias & Collias, 1984), consistent with patterns observed in other waterfowl species (Vergara 2010; Ankney & MacInnes 1978). These results emphasize the dynamic nature of nest traits, as females modulate investment according to both ecological conditions and reproductive demands.

Egg traits also varied across stages, with length, width, and volume generally increasing over the season. This pattern suggests that females adjust reproductive allocation to maximize offspring fitness, as larger eggs provide more nutrients and energy for developing embryos, enhancing hatching success and early duckling survival (Williams 1994, Nager et al. 2001). While clutch size tended to increase in mid- and late-breeding stages, it did not show statistically significant differences in univariate analyses. We therefore interpret changes in clutch size as non-significant trends, highlighting the need to distinguish between observable tendencies and statistically supported effects. These patterns align with life-history theory, where females face

trade-offs between egg number and quality depending on physiological state and environmental conditions (Borger et al. 2023, Metcalfe & Thorpe 1992). Reproductive success, measured as hatching success and overall breeding success, peaked during incubation and chick-rearing stages. This alignment suggests that maximal reproductive output coincides with periods of greatest nest investment and larger egg production, supporting the idea that successful reproduction relies on integrated strategies combining multiple traits rather than individual features alone (Martin et al. 2000, Rohwer & Freeman 1989). Such stage-specific allocation of resources underscores the importance of temporal dynamics in Mallard reproductive ecology. Multivariate analyses further clarified the relationships among nest morphology, egg traits, and reproductive output. PCA revealed that the first principal component, strongly associated with nest depth, egg traits, clutch size, and reproductive success, explained most of the variation across stages. These high correlations reflect biological integration of reproductive effort rather than redundancy among variables. The second PCA axis captured subtler variation associated with early breeding, reflecting transitional adjustments in nest construction before peak reproductive output. Non-metric multidimensional scaling (NMDS) supported these findings, showing that reproductive success metrics primarily drive variation across stages, whereas nest and egg traits contribute moderately and sometimes negatively along the main gradient. The calendar-based classification of reproductive stages is justified because these stages closely corresponded to observed shifts in reproductive behaviour, including nest construction, egg laying, and incubation. The calendar-based classification of reproductive stages is justified because these stages closely corresponded to observed shifts in reproductive behaviour, including nest construction, egg laying, and incubation. This framework allows for meaningful comparisons of stage-specific reproductive investment, while acknowledging that precise timing may vary among individuals. I also recognize key limitations: data were collected at a single site over one breeding season, which may constrain generalization. Nevertheless, the study provides a valuable baseline for future comparative or long-term research in semi-arid Mediterranean wetlands. Further investigations incorporating environmental covariates (e.g., temperature, rainfall, food availability) or experimental manipulations could strengthen causal inferences about the mechanisms driving observed patterns. Overall, our results demonstrate that reproductive investment in Mallards is highly dynamic and integrated. Females adjust nest construction, egg traits, and reproductive effort across breeding stages in a coordinated manner to optimize offspring survival under ecological constraints. Understanding these temporal patterns is critical for both ecological and conservation applications, as maintaining suitable nesting habitats and monitoring stage-specific reproductive traits can support population management and early detection of environmental impacts (Raveling et al. 2000, Swennen 1989). This stage-based, integrative approach provides a comprehensive understanding of Mallard reproductive ecology and establishes a foundation for future studies exploring how environmental variability, anthropogenic pressures, and climate change may affect reproductive strategies and success in wild waterfowl populations.

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