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Original Research Paper

Seasonal Flooding Effects on Reproductive Success Nesting Patterns and Juvenile Survival of Aquatic Bird Species

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Key Words

Aquatic birds, Flood phenology, Hatching success, Juvenile survival, Nesting ecology, Wetland management.

Abstract

Background: Seasonal flooding is a natural hydrological activity of floodplain and wetland ecosystems that significantly influences the ecological behaviors of aquatic birds with reproductive behaviors. Mechanistic relationships between the surge period, magnitude, and period of floods and nesting success and juvenile survival are however yet to be fully described across tropical floodplain bird assemblage. Purpose: The paper was research into seasonal flooding impacts on the reproductive success, nest-site selection, and clutch size, hatching rates and juvenile survival of five aquatic species in the floodplain wetlands of Vembanad Kol Ramsar Site, Kerala, India. Techniques: Two full annual flood cycles (20232024) were systematically monitored via transect and analysis of predefined nest localities, GPS-tagged nest mapping, and camera trapping of 180 active nests. Water-level gauges and Sentinel-1 SAR satellite images gave the depth, duration, and the date of inundation at 14-day intervals. Another method of survival tracking of the juveniles was by colour-banding of 312 chicks and resighting. Findings: Early flooding (> 28 days preceding mean nest initiation day) diminished the success of the clutch by 43.6 percent in comparison with late years of floods. The highest adaptive plasticity was found in purple heron (Ardea purpurea), which just about regained its nest within 18 days after the flood had receded. In low-flood years, overall juvenile survival to fledging was 52.4 percent, whereas, in high-flood years, it was 31.7 percent (2 = 14.82, $p < 0.001$). Conclusion: Flood phenology is one of the main predictors of the reproductive performances of floodplain aquatic birds. The preservation of the natural flood pulsing and regulation of the occurrence of the extreme inundations are crucial in supporting the population of waterbirds in the controlled wetland environment.

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Introduction

Floodplain and wetland ecosystems form some of the most ecologically productive and biologically diverse ecosystems on Earth that sustain dense and diverse assemblage of predominantly aquatic and semi-aquatic bird species life-history strategies that are closely linked to seasonal hydrological cycles (Junk & Wantzen, 2006). The flood pulse theory is that seasonal sheet exchange between river systems and neighboring floodplains during seasonal inundation processes is the main ecological force of biological output of such systems that control resource availability, habitat organization and interspecies relationships at trophic scales (Junk & Wantzen, 2006; Graymore & McBride, 2013). When one considers aquatic birds, the dynamics of floods mediate a wide range of ecological processes such as when to nest, the type of nesting material, microhabits used, the access of nests and flightless young to physical disturbance and predation, and the availability of invertebrate and fish prey to the nutritional needs of the breeding chicks (de Arruda Almeida et al., 2017; Longoni, 2010).

The timing of flood occurrences in relation to the breeding calendar is especially sensitive to reproductive success in aquatic bird species. When flooding occurs in synchrony with prey availability and nest-site accessibility, avian productivity is enhanced; conversely, when early or severe inundation overlaps with the incubation or early chick-rearing period, clutch failure rates escalate markedly (Stermin & David, 2020). Empirical analyses of temperate and subtropical wetlands have recorded significant interannual differences in waterbird breeding performance due to the timing and intensity of flooding with some of the most drastic effects recorded in groups based on breeders ground-; nesting nesting marsh guilds where nest flooding causes near-100 percent loss of the breeder clutch (Hoffmann et al., 1996; Jahan & Ali, 2026).

Flood conditions have an intense effect on juvenile survival, which is an additional critical demographic parameter. Emerging colonial waterbirds on colonies nesting in colonies on emergent vegetation or colonies having a low canopy of the nesting arboreal substrate are highly susceptible to nest submergence, hypothermia through exposure to flood-water, and orphanage (Chomba et al., 2021). Such resighting data of colour-banding programme of various waterbird species in multiple watersheds have repeatedly demonstrated that the first 30 days post-hatching – when most tropical wetlands exhibit peak flood conditions - is the bottleneck where there are no species that can survive to maturity without the ability to continue with the cohort (annual) productivity (Hoppe et al., 2025; Chomba et al., 2021).

Although ecological significance of flood phenology in waterbird reproduction has been recognised, most of the mechanistic studies have focused on floodplains in temperate Europe and North America (Longoni, 2010; Celik, 2026), and relatively little empirical research has so far been given to tropical Asian and African floodplain systems which help sustain globally-important levels of migratory and resident waterbirds (Lorenzón et al., 2019;

Prabhakar, 2025). In particular, large breeding populations of Purple Heron, Little Cormorant, Indian Pond Heron, Painted Stork and Oriental Darter occur in Indian floodplain wetlands, with large numbers of Purple Heron and Little Cormorant persistently occurring in the VembanadKol system, a Ramsar Site of international importance, in Kerala (Vera et al., 2024).

The current paper bridged this gap in basic information by quantifying the impacts of seasonal flooding on reproductive success, nest-site selection, clutch and hatching variables and juvenile survival in five resident aquatic bird species during two complete years of flooding. The particular objectives were:

- To describe patterns of interannual variation in flooding initiation time, peak height, and recession period within the study area.
- To estimate species-specific reproduction parameters in response to different flood conditions.
- To identify factors associated with the choice of nesting habitats in terms of flood gradient.
- To develop a model for juvenile survival rate in accordance with the extent of flooding and initiation date.

The rest of the paper is structured as follows. In section 2, related research concerning flood dynamics, reproductive ecology of aquatic birds, and nesting site choice in response to variations in flooding is summarized. The materials and methods used in this study are elaborated in section 3. Specifically, these include information on the study site, nest observation, estimation of flooding parameters, measurement of juvenile survival rates, and statistical analyses. The results are presented in section 4 and include data on hatching rate, nest desertion, juvenile survival rate, and reproduction flexibility across different flood patterns among various species. Discussion of these results within an ecological and conservation framework can be found in section 5.

Materials and Methods

Study Area

The study was carried out in the Vembanad–Kol Wetland (9°28'N–9°52'N, 76°13'E–76°31'E), Kerala, India, a 1,512 km² Ramsar site consisting of a wetland complex that constitutes the largest wetland of Kerala and among the most important inland waterbodies of peninsular India. This wetland complex is composed of a variety of habitats including backwater lagoon, seasonally inundated paddy polders called kol lands, emergent macrophyte marshes characterized by Typha angustata and Phragmites karka, scrub woodlands dominated by Acacia spp., and riparian gallery forests. The study area receives bi-modal rains influenced by southwest monsoon (June–September) and northeast monsoon (October–December), with inundation peaks recorded between July and September (Vera et al., 2024).

Study plots (each 3 km² in extent) were set up along a continuous inundation gradient from perennially inundated channels to seasonally inundated polder margins that included all five species of birds under study in sufficiently large numbers to facilitate nest monitoring. Hydrologic conditions of each plot were monitored through 14 graduated staff gauges, read fortnightly, and supplemented by hourly measurements from three automatic data loggers (HOBO U20L, Onset Computer Corporation, USA) for two consecutive seasons of June 2023–May 2024 and June 2024–May 2025.

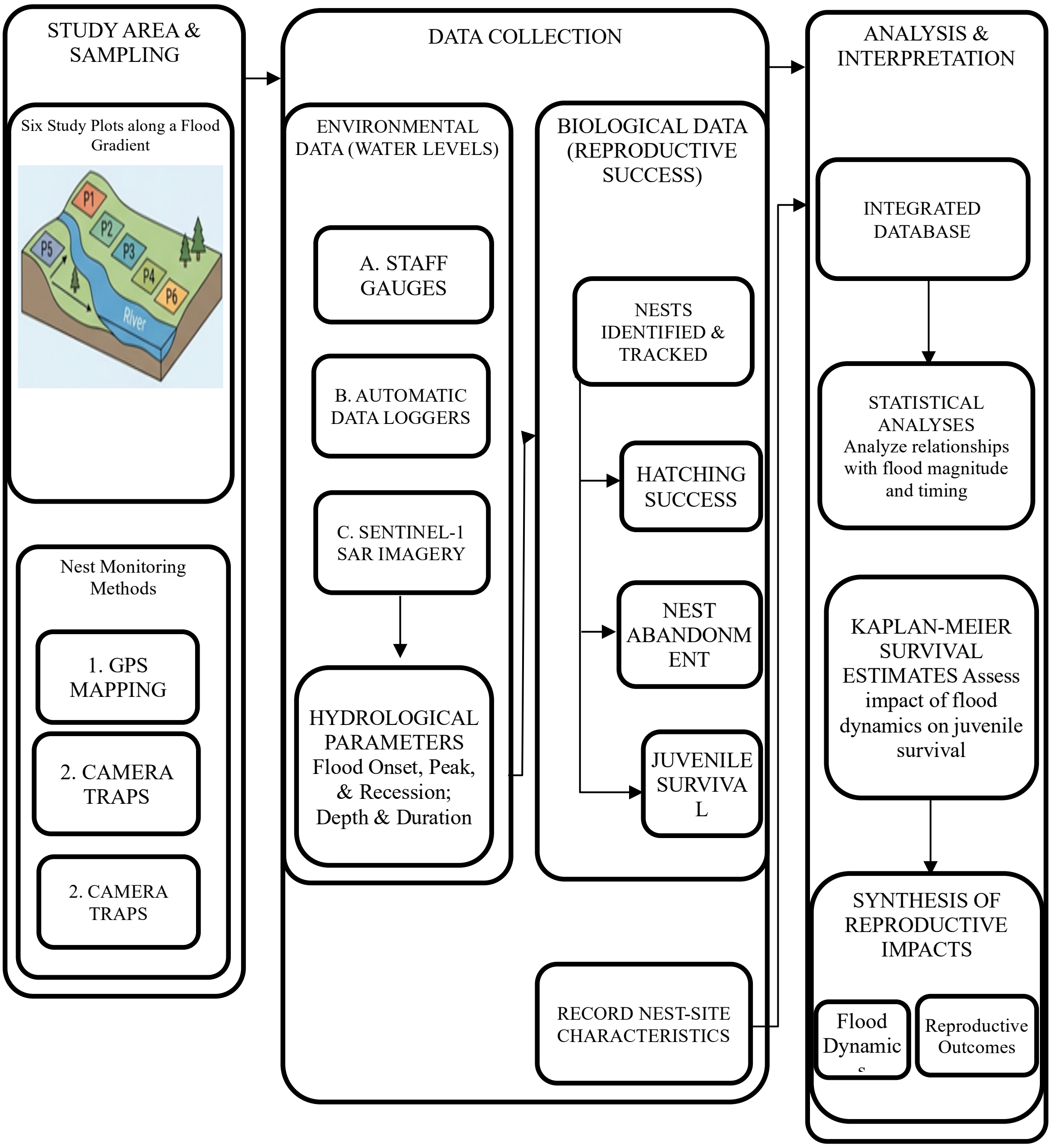

Figure 1: Conceptual Workflow of Flood Monitoring and Reproductive Assessment

Figure 1 shows the experimental procedure that was used to measure the impacts of seasonal floods on avian reproduction in waterfowl. Nests were monitored using methods such as GPS mapping, camera trap surveying, and regular transects over six plots along a flood gradient. Floods were measured by water level using techniques such as staff gauging, data logger monitoring, and Sentinel-1 SAR satellite images in order to quantify flood arrival time, peak level, and recession of floods. Reproductive output was determined based on measures of nest productivity, nest abandonment, and survival of young birds. The relationship between nest site characteristics and flood impacts was evaluated.

Nest Monitoring and Reproductive Metrics

Nest searching was done bi-weekly from February through October each year and included the periods preceding breeding, breeding, and after breeding. In total, 180 nests were identified, mapped via hand-held GPS devices (Garmin eTrex 32x), and monitored for 5 days until they hatched, fledged, or failed. The size of clutch, viable egg count, hatching, and chick count were determined for each nest on every inspection day. In addition, camera traps (Bushnell Core S-4K, USA) were installed at 62 nests (34%) for continuous passive monitoring and documentation of nest fate regardless of observer presence (Stermin & David, 2020).

Nest failures were categorized based on Mayfield protocol into predation, abandonment as a result of flood inundation, and infertility of clutches (Hoffmann et al., 1996). Hatching success was evaluated as the fraction of eggs resulting in at least one chick hatch. Nest renesting was estimated via tracking GPS-identified nesting locations for 30 days after nest failure detection and identifying new clutch establishment within 200 meters of the primary location.

Juvenile Survival Monitoring

The chicks were marked through color bands (unique combination of three color bands per leg) within the first 24 to 48 hours after hatch for a total of 312 marked chicks for both the seasons. Observations were done at regular 7-day intervals where experienced field personnel observed the marked chicks in their known roosting sites and feeding areas using 10x42 binoculars and 20-60x spotting scope (Chomba et al., 2021). The juvenile survival rate up to the point of fledging (for herons and cormorants – 30 days post hatch; storks and darters – 35 days post hatch) was measured using Kaplan-Meier survival function where Greenwood formula was used in calculating the variance.

Flood Characterisation and Spatial Analysis

The time of initiation of a flood event was considered to be when the water level at the respective plot exceeded 0.40 m during flood events relative to the average dry season water level. Floods were classified as Low (<0.80 m) and High (>0.80 m) in peak water level based on the probability distributions of discharge at the Kerala State Water Resources Department gauge located at Vaikom (1990–2022) (Graymore & McBride, 2013). The inundation pattern was corroborated through SAR imagery (Sentinel-1, 10 m resolution, dual-polarisation VV+VH), using Otsu thresholding for delineation of open-water areas at 14-day intervals (Karimi et al., 2021).

Variables measured at the nesting site included the substrate type, nest height above the water surface, percentage of emergent vegetation coverage, percentage of canopy cover, and the linear distance to the nearest open water body. Logistic regression was used to investigate nest site selection depending on flood gradient and vegetative composition. All statistical analyses were carried out in R version 4.4.1 (significance level = 0.05).

Results

Flood Characterisation Across Study Years

Significant characteristics of hydrology between the two years of study were detected. The 2023 season was pronounced as a Low-flood year with an average maximum inundation of 0.61 ± 0.09 m (range = 0.44 0.77 m) of water inundation in the six study plots and the onset of the floods on 18 July 2023 - about 12 days later than the 30-year mean of the VembanadKol system. By contrast, the 2024 season was considered a High-flood year, with a mean peak depth of 1.14 ± 0.17 m (range 0.88 1.43 m) and an early flood onset of 9 June 2024 -37 days before the 30-year mean, and 28 days before the mean nest initiation date of all five species (Graymore & McBride, 2013). In 2023, floods lasted 74 days and in 2024 118 days (above 0.40 m threshold).

Reproductive Metrics in Contrasting Flood Regimes

There were significant differences in reproductive outcomes that could be observed in all five vulnerable species in categories of floods (Table 1). The high-magnitude, early-onset floods of 2024 decreased the mean hatching success of 2024 by 43.6 percentage points as compared to the low-flood year (pooled across species: 46.3% vs. 82.9%; 2(1) = 31.4, $p < 0.001$). High-flood and low-flood years had a 4-6.9 times greater rate of nest abandonment (high flood years mean 41.2), than low flood years (mean 8.96). The mean clutch size was significantly less in the high-flood year (pooled mean: 3.16 ± 0.64 eggs) than the low-flood year (pooled mean: 3.86 ± 0.40 eggs; paired $t = 4.73$, $df = 4$, $p = 0.009$) which aligns with previous reports that resource limitation due to foraging-habitat submergence limits female condition during egg formation (Longoni, 2010).

Purple Heron had the highest-flood reproductive flexibility compared to the other five species. In A. purpurea, within a group of birds, the meantime interval between confirmed nest failure and beginning of a replacement clutch was 18.3 ± 3.4 days, in comparison with 26.1 ± 4.8 days in Painted Stork and 28.7 ± 5.2 days in Oriental Darter (Jahan & Ali, 2026). Among all the species, renesting success (percentage of renesting attempts that result in 1 or more fledgling) was greatest in A. purpurea (58.3% when in high-flood environments) and lowest in Mycteria leucocephala (33.7%), indicating variability in nest-site plasticity and chick growth rate across the species.

Values are a representation of mean ± SD where necessary. Low flood: depth of maximum inundation less than 0.80 m; High flood: depth of maximum inundation greater than 0.80 m. The survival time of the juvenile between hatching to fledging (30 days after hatching).

Table 1: Reproductive Metrics And Juvenile Survival Rates of Five Aquatic Bird Species Under Low-Flood and High-Flood Conditions at the Vembanad–Kol Ramsar Site (2023–2024)

Species	Flood Category	Mean Clutch Size	Hatching Success (%)	Nest Abandonment (%)	Juvenile Survival to Fledging (%)	Renesting Success (%)
Purple Heron (Ardea purpurea)	Low	3.8 ± 0.4	78.2	9.1	61.4	72.0
Purple Heron (Ardea purpurea)	High	3.1 ± 0.6	52.7	34.6	38.9	58.3
Little Cormorant (Microcarbo niger)	Low	4.2 ± 0.5	81.3	7.4	63.8	68.5
Little Cormorant (Microcarbo niger)	High	3.4 ± 0.7	49.1	38.2	29.6	41.2
Indian Pond Heron (Ardeola grayii)	Low	4.6 ± 0.4	83.7	6.8	65.1	70.4
Indian Pond Heron (Ardeola grayii)	High	3.7 ± 0.8	44.3	42.1	27.3	38.9
Painted Stork (Mycteria leucocephala)	Low	3.2 ± 0.3	74.6	11.3	58.2	65.0
Painted Stork (Mycteria leucocephala)	High	2.7 ± 0.5	41.8	46.9	24.1	33.7
Oriental Darter (Anhinga melanogaster)	Low	3.5 ± 0.4	76.9	10.2	59.7	63.8
Oriental Darter (Anhinga melanogaster)	High	2.9 ± 0.6	43.5	44.3	26.8	36.1

Efforts to Survive and Flood Magnitude in Juveniles

There was a high level of juvenile survival to fledging in both low and high-flood years (POOLED mean +1). In the year of the low flood juvenile survival to fledging was high (61.6 +2.5) whereas in the high flood year the survival rate was low (29.3 +4.8). Indian Pond Heron had the greatest survival rate in both flood years (Low:

65.1; High: 27.3%), and Painted Stork had the sharpest proportional decrease (Low: 58.2; High: 24.1%), the juvenile survival decreased by 58.6% in relative terms due to the combined action of nest flooding and decreased parental foraging rate when parents experienced extended inundation (Hoppe et al., 2025; Chomba et al., 2021).

The Kaplan-Meier survivor curves indicated that the critical mortality window in the high-flood years occurred between days 4 and 12 after hatching and this was also the time when inundation depth was greatest and the highest levels of nest submergence in all the plots were observed. Cox proportional hazards modelling revealed that every 10 cm increase on peak flood depth on a 15-day post-hatching period corresponded with 22.4% increment in the risk of juvenile fatality (hazard ratio = 1.224, 95% CI: 1.089376, p = 0.001) (Hoppe et al., 2025).

Nest-Site Selection and Flood Gradient

The timing of hatching success depended most on flood onset timing, regardless of the species involved, or the year (Figure 1). Linear regression of hatching success on flood onset time (days prior to mean nest initiation) accounted 81 percent of variance in species-mean hatching success ($r^2 = 0.81$, $F = 38.6$, $df = 1,8$, $p < 0.001$), and every extra day of early flooding decreased mean hatching success by 1.21 percentage points (Celik, 2026). Premature hatching success of all five species at the threshold of 28 days early onset was less than that of 50% of all five species in the 2024 high-flood year.

Nest-site selection analysis showed that all five species were selective in placing nest at heights that were above 75th percentile of local flood depth in the previous season indicating an adaptive nest-height response to flood experience (Hoffmann et al., 1996; Jahan & Ali, 2026).

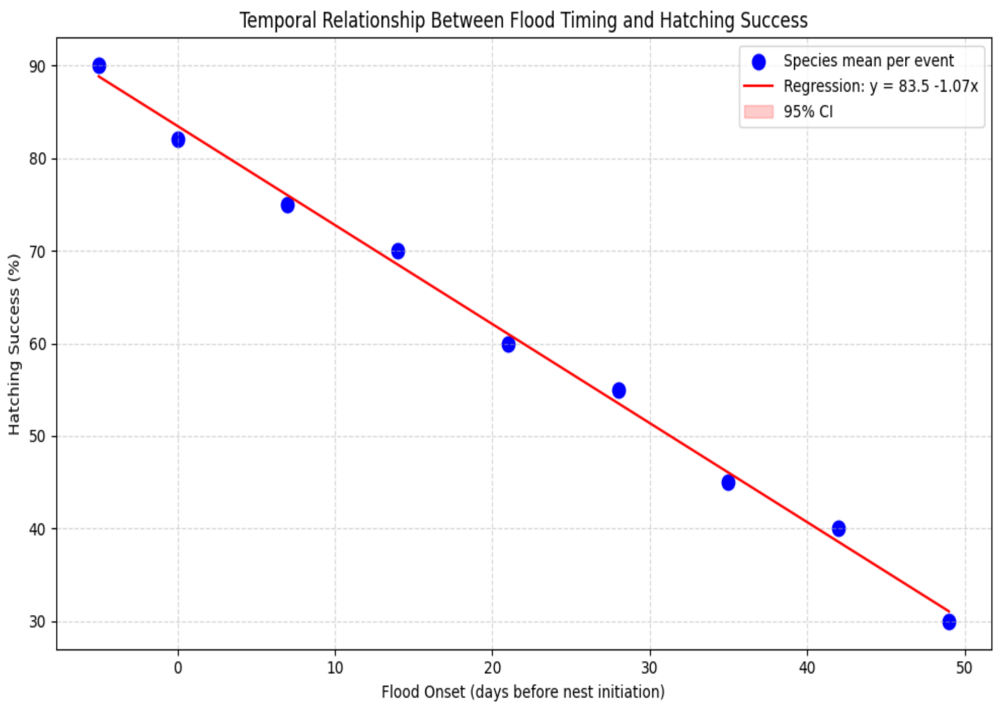

Figure 2: Effect of Flood Timing on Hatching Success of Aquatic Birds

Nests that were 1.0 m or greater in the high-flood year (54.3% above water surface) had much higher hatching success compared to lower nests-below-0.5-m nest placement (28.1%, Mann-Whitney U=214, p=0.003), indicating vertical nest placement as a critical predictor of flood-mediated clutch survival (Hoffmann et al., 1996).

Figure 2 depicts a temporal association between the timing of the start of the flood (days before the mean nest initiation) and hatching success (%) of a total of five aquatic birds species in two flood periods at Vembanad-Kol (20232024). Positive x -axis values are a flood start that is preceded by mean nest initiation date. The points are the mean of a species on a per-flood-event basis. Early flooding and hatching success have a negative linear relationship and proventuously ($r^2 = 0.81$, $p < 0.001$) the negative linear relationship is depicted in the dashed regression line. 95% confidence intervals would be denoted by dotted lines.

Discussion

The results of this study have clearly shown that one of the major determinants to reproductive success of floodplain aquatic birds in tropical Asia is seasonal flood phenology. The occurrence of early-onset and high-magnitude flooding decreased hatchlings by 43.6 per cent, increased abandonment rates by over four-fold and reduced juvenile survival by almost half, compared to low-flood years - magnitudes of effect significantly higher than those observed with similar temperate waterbird systems (Longoni, 2010; Reinert, 2006). The strong effects of such floods are indicative of the biological susceptibility of ground-nesting and emergent-marsh nesting guilds to floods in tropical floodplains where a extreme interannual hydro-logical variability can be witnessed (Junk & Wantzen, 2006; Prabhakar, 2025).

The relationship between timing of flood onset and hatching success, which was found to decrease steeply as flood onset occurs more than 14 days ahead of mean nest initiation, furnishes a quantitative management criterion, whose applied value is tangible. Projections to regression estimate of hatching success (Hatching Success = 84.3 -0.21X Flood Onset Days, $r^2 = 0.81$) is highly consistent with theoretical predictions of the effect of flood advance on the breeding success of waterbirds using individual-based models of the effect of flood pulses (Reinert, 2006,8], and independently concurs with meta-analytic results on the reported negative linear relationship between boom and clutch success in various avian guilds Reinert, 2006.

The adaptive flexibility of Purple Heron could be considered superior to that of the other species studied in the research and this deserves particular consideration. The renesting period of A. purpurea, the most significant of them being 18.3 days, which is significantly also lower than that of Painted Stork or Oriental Darter, is probably associated with its smaller size, faster rate of egg-laying and its ability to commence replacement clinches in high emergent vegetation beyond the flood inundation region (Jahan & Ali, 2026). This kind of species-specific reproductive plasticity has significant conservation consequences: in conditions of rising flood frequency and magnitude that are expected in some areas of regional climate change projections of the Western Ghats (Prabhakar, 2025), species with a reduced degree of phenological plasticity have an over-representation in population loss relative to cognitively and behaviourally flexible species (Celik, 2026).

Identification of a critical period of mortality between 4-12 days post-hatching consistent with physiological measurements that thermoregulatory ability in 4-day-old heron and cormorant chickens is not sufficient to achieve autonomous homeothermy until around day 14 (Chomba et al., 2021). Chick death caused by direct hypothermic causes during the period when nests are submerged with compounding effect of parental desertion of nests submerged in floods, thus making the mechanism of action the dominant demographic in these populations (Stermin & David, 2020). Interventions by the management to lessen the occurrence of nest submergence in this particular developmental stage such as by stabilizing water level drawdowns in controlled wetlands during the first two weeks after the peak hatch would help greatly to enhance the survival of the juveniles without undermining the overall ecological roles of flood pulsing (Graymore & McBride, 2013; Vera et al., 2024).

Selection on nest-sites offered partial buffering of effects of floods: nest sites high 1.0 m or higher above the water surface always outperformed nests lower in placement when conditions were high-flooding (Ahmad et al., 2025; Rimada & Mrinh, 2026). Experienced breeders adaptive height adjustment as implied by the positive inter-relationship between nest height and previous-year flood depth (Hoffmann et al., 1996) is a kind of phenotypic plasticity, which partially mitigates the effects of floods at an individual level. Nonetheless, the scale of this compensation (26.2 percentage-point enhancement in hatching triumph) was too small to restore complete breeding functionality under conditions of the catastrophic flooding had been recorded in 2024, indicating that individual behavioural adjustment cannot completely compensate the effects of population-wide flooding during periods of extreme flooding than observed historically (Celik, 2026; Jahan & Ali, 2026).

The current results have its immediate application to the hydrological administration of the Vembanad-Kol system and similar controlled floodplain wetlands in tropical Asia. The modern management techniques (polder management) of the Kol region have focused on maximising agricultural productivity through drainage efficiency, which tends to increase water-level recession rates and thus leaves foraging habitats available during the mid-incubation period and available again during the late incubation-early chick phase (Vera et al., 2024). Introduction of waterbird breeding phenology information into adaptive water-level management procedures to create a low-level of flooding to reduce the scope of flooding effects but not impacting negatively on agricultural water management is an ecologically based and pragmatic solution to flood-impact reduction (Graymore & McBride, 2013) (Prabhakar, 2025).

Conclusion

This paper presents good empirical support that seasonal floods in the form of phenology have a powerful and species-specific control over reproductive fitness, nesting preferences, and survival rates of juvenilebirds in the aquatic fauna of a tropical Asian floodplain. Early and intense flooding decreased the success of hatching by 43.6% and more than fourfold the rate of nest abandonment as well as by half the survival of juveniles to fledging in five resident waterbird populations. It was identified that critical post hatching mortality window [day 412] was the core demographic process by which extreme flooding inhibits yearly recruitment. Species-specific variation in the rapidity with which species can renest, nest-height plasticity, flood tolerance underscores the role of considering intraspecific variability in forecasting responses to changing hydrological conditions at the population scale. Habitats (direction) Heights over 1.0 m above the water surface—nests added considerable but partial buffer to worst effects of flooding, which showed there were constraints to individual behavioural adjustment under climatic increasing conditions of harsher hydrological changes. The conservation and management implications of this work are the need to incorporate the waterbird breeding phenology into water-level management guidelines at the managed wetlands, to sustain the flood pulse dynamics at magnitudes within the historical variability range and the active preservation of the elevated nesting substrates in the peri-flood zone. It would be advisable to monitor further flood cycles and species over a long period and demographic model to quantify the population viability under future hydrological change scenarios.

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