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Population Dynamics, Breeding Success, and Conservation Implications of *Crocodylus palustris* in Captive and Semi-Natural Systems across India

Dinámica poblacional, éxito reproductivo e implicaciones para la conservación de *Crocodylus palustris* en sistemas cautivos y seminaturales en la India

Dinâmica populacional, sucesso reprodutivo e implicações para a conservação de *Crocodylus palustris* em sistemas cativos e seminaturais na Índia

Fellows S.[1]

[1] Deputy Director, Madhya Pradesh State Forest Research Institute, Jabalpur, Madhya Pradesh, India

Correo electrónico: sandeepfellows2016@gmail.com

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Abstract

The mugger crocodile (*Crocodylus palustris*), classified as Vulnerable by the IUCN and protected under Schedule I of the Wildlife (Protection) Act, 1972, functions as a keystone wetland predator across the Indian subcontinent. A comprehensive analysis of 2024 Central Zoo Authority (CZA) records from 45 facilities across 12 Indian states (n = 1,187 individuals) revealed an average annual captive population growth of 18.5%, driven primarily by inter-facility transfers rather than natality (78% transfer contribution). Overall mortality was 2.53%, with juveniles (<2 years) accounting for 65% of all deaths, and captive populations exhibited persistent male-biased sex ratios (1.14:1 M:F) with 12.4% unsexed individuals. Facilities employing naturalistic enclosure designs demonstrated significantly higher hatching success than standard concrete enclosures (25.1% vs. 11.6%; $F = 6.82$, $p = 0.02$), attributable to thermal gradients (28–34°C), sandy nesting substrates, and seasonal hydrological variation essential for oviposition and temperature-dependent sex determination. Because temperature-dependent sex determination is conserved across multiple reptilian taxa in South and Southeast Asia, these findings have broader regional relevance beyond *C. palustris*. Evidence-based recommendations include standardized genetic sex determination protocols, ecological enclosure redesign, improved juvenile rearing systems, and integrated captive–wild conservation frameworks to ensure long-term demographic viability and genetic health of this ecologically critical species

Keywords: *Crocodylus palustris*, captive breeding, Temperature-dependent sex determination, Juvenile mortality

Resumen

El cocodrilo de los pantanos (*Crocodylus palustris*), clasificado como Vulnerable por la UICN y protegido bajo el Anexo I de la Ley de Protección de la Vida Silvestre de 1972 en la India, cumple una función ecológica clave como depredador de humedales en el subcontinente indio. El análisis de los registros de la Autoridad Central de Zoológicos (CZA, 2024) de 45 instalaciones en 12 estados de la India (n = 1.187 individuos) mostró un crecimiento anual promedio de la población cautiva de 18,5%, impulsado principalmente por transferencias entre instalaciones más que por natalidad (78% del incremento). La mortalidad general fue de 2,53%, con los juveniles (<2 años) representando el 65% de las muertes, y se observó una razón sexual sesgada hacia machos (1,14:1) junto con 12,4% de individuos sin sexar. Las instalaciones con recintos naturalistas presentaron un éxito de eclosión significativamente superior al de los recintos estándar de concreto (25,1% vs. 11,6%; F = 6,82; p = 0,02), asociado con gradientes térmicos (28–34 °C), sustratos arenosos para nidificación y variación hidrológica estacional. Se recomienda la estandarización de métodos de determinación sexual, el rediseño ecológico de recintos, la mejora del manejo juvenil y la integración de estrategias de conservación ex situ e in situ.

Palabras claves: *Crocodylus palustris*, Cría en cautiverio, Determinación sexual dependiente de la temperatura, Mortalidad juvenil

Resumo

O crocodilo-dos-pântanos (*Crocodylus palustris*), classificado como Vulnerável pela IUCN e protegido sob o Anexo I da Lei de Proteção da Vida Selvagem de 1972 na Índia, atua como um predador-chave de áreas úmidas no subcontinente indiano. A análise dos registros de 2024 da Central Zoo Authority (CZA) de 45 instalações em 12 estados da Índia (n = 1.187 indivíduos) revelou um crescimento médio anual da população cativa de 18,5%, impulsionado principalmente por transferências entre instituições e não pela natalidade (78% do aumento). A mortalidade geral foi de 2,53%, com juvenis (<2 anos) representando 65% das mortes, e observou-se uma razão sexual persistentemente enviesada para machos (1,14:1), além de 12,4% de indivíduos sem sexagem. Instalações com recintos naturalísticos apresentaram sucesso de eclosão significativamente superior em comparação com recintos padrão de concreto (25,1% vs. 11,6%; F = 6,82; p = 0,02), devido à presença de gradientes térmicos (28–34 °C), substratos arenosos para nidificação e variação hidrológica sazonal. Recomenda-se a padronização de protocolos de determinação sexual, o redesenho ecológico dos recintos, o aprimoramento do manejo de juvenis e a integração entre conservação ex situ e in situ.

Palavras-chave: Crocodylus palustris, Reprodução em cativeiro, Determinação sexual dependente da temperatura, Mortalidade juvenil

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Introduction

Ecological Significance and Distribution

The mugger crocodile (*Crocodylus palustris*; Lesson, 1831) occupies a broad range of freshwater habitats across the Indian subcontinent, including rivers, reservoirs, irrigation canals, marshes, oxbow wetlands, temple tanks, village ponds, and other anthropogenically modified aquatic systems. Within India, the species is reported from at least 16 states and persists in both protected and human-dominated landscapes, reflecting remarkable ecological plasticity. As an apex predator and ecosystem engineer, *C. palustris* regulates fish, amphibian, and waterbird populations, scavenges carrion, influences trophic interactions, and creates wallows and basking sites that contribute to sediment turnover, nutrient redistribution, and localized enhancement of benthic productivity.

The ecological role of the mugger extends beyond predation. By shaping aquatic edge habitats through nesting, basking, and territorial behavior, the species contributes to microhabitat heterogeneity that may indirectly benefit sympatric fauna. Its persistence in agro-wetland mosaics, reservoir landscapes, and peri-urban wetlands further highlights its relevance as an indicator of freshwater ecosystem integrity. However, coexistence with humans also elevates the probability of conflict, particularly in regions where fishing, livestock watering, bathing, and agricultural use overlap with crocodile habitat.

A defining reproductive characteristic of *C. palustris* is temperature-dependent sex determination (TSD), whereby incubation temperature influences hatchling sex ratios. This mechanism is not unique to the species and is documented across several reptilian taxa native to South Asia, including *Gavialis gangeticus*, *Chelonia mydas*, *Batagur baska*, and *Nilssonia gangetica*. Consequently, thermal ecology insights derived from mugger crocodiles have broader implications for reptile conservation biology in the Indian subcontinent, particularly under contemporary climate variability and long-term warming scenarios.

Conservation History and Status

Historical exploitation for the skin trade, coupled with habitat degradation, egg collection, wetland drainage, and persecution, caused severe declines in mugger crocodile populations during the mid-20th century. By the early 1970s, wild populations were estimated to have declined by more than 90% across large portions of their range. In response, India initiated the landmark Crocodile Conservation Project (commonly referred to as Project Crocodile) in 1975, emphasizing captive breeding, ranching, habitat protection, and strategic reintroduction. This program, supported by state forest departments and zoological institutions, represented one of the earliest structured crocodilian recovery initiatives in Asia.

The species is currently classified as Vulnerable on the IUCN Red List and receives the highest level of statutory protection under Schedule I of the Wildlife (Protection) Act, 1972. Despite substantial recovery relative to historical lows, current population estimates of approximately 10,000–15,000 adults remain unevenly distributed, with strongholds concentrated in select river basins, reservoirs, and protected wetland networks. Recovery remains constrained by continuing habitat fragmentation, altered hydrological regimes, illegal fishing practices, entanglement, pollution, retaliatory killing, nest disturbance, and escalating climate-related pressures that may influence nesting phenology and TSD outcomes.

Captive Conservation Imperative

Captive populations of *C. palustris* in India serve multiple conservation functions: demographic insurance against local extirpation, maintenance of founder lineages, educational outreach, rescue and rehabilitation support, and potential augmentation of wild populations through head-starting or release-based programs. Approximately 45 Central Zoo Authority (CZA)-recognized zoological facilities collectively maintain 1,187 mugger crocodiles, making this one of the most substantial ex situ holdings for a native Indian reptile.

However, numerical abundance in captivity does not necessarily translate into demographic resilience. Captive populations often exhibit low breeding participation, reduced hatchling success, juvenile mortality bottlenecks, and skewed sex ratios. Standardized concrete enclosures, inadequate nesting substrate, poor thermal heterogeneity, overcrowding, suboptimal water quality, and inconsistent husbandry protocols may compromise reproductive physiology and early-life survival. In crocodilians, these deficiencies can have cascading consequences because the earliest life stages are disproportionately sensitive to temperature fluctuation, nutritional stress, pathogen exposure, and social aggression.

Research Objectives

The present study was designed to evaluate the demographic structure and reproductive performance of *C. palustris* maintained in Indian captive and semi-natural systems using a national-scale institutional dataset. Specific objectives were to:

1. Assess captive population demographics using 2024 CZA inventory data across recognized facilities.
2. Examine the influence of enclosure design on hatching success and early-life survival.
3. Characterize age-specific mortality patterns and identify probable causal factors.
4. Compare captive demographic trends with broad wild population expectations.
5. Develop evidence-based recommendations for integrated captive–wild conservation planning, with particular relevance for management standardization in states such as Madhya Pradesh.

Materials and Methods

Data Acquisition and Facility Classification

Primary data were obtained from the Central Zoo Authority Captive Inventory of Scheduled Animals (2024), encompassing records from 45 zoological facilities distributed across 12 Indian states and comprising 1,187 individuals of *Crocodylus palustris*. Extracted variables included age class, sex, sex determination status, natality, mortality, inter-zoo transfers, acquisitions, and breeding records for the period 2020–2024.

Facilities were classified into two operational enclosure categories based on documented husbandry characteristics and breeding infrastructure:

1. **Naturalistic enclosures (n = 18):**
 These facilities maintained habitat features approximating ecological nesting conditions, including thermal gradients of 28–34 °C, sandy nesting substrates

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elevated approximately 1–2 m above water level, basking zones with partial shade, and seasonal hydrological variation simulating natural wetland cycles.

2. **Standard enclosures (n = 27):**
   These facilities primarily consisted of concrete pools or simplified holding systems with limited thermal heterogeneity, reduced nesting substrate availability, and minimal seasonal environmental modulation.

The described incubation and breeding conditions correspond largely to central and peninsular Indian climatic regimes characterized by tropical semi-arid to sub-humid conditions with relatively stable dry-season thermal windows during the primary nesting and incubation period.

Population and Reproductive Metrics

The following demographic and reproductive indicators were assessed:

- Apparent annual population growth rate across facilities
- Proportional contribution of natality versus inter-facility transfer to net population increase
- Annual mortality rate
- Age-specific mortality distribution (juvenile, subadult, adult)
- Sex ratio (male:female), with χ^2 goodness-of-fit testing against an expected 1:1 distribution
- Proportion of unsexed individuals
- Breeding participation across facilities
- Total egg production and comparative hatching success by enclosure type

Age classes were defined as follows:

- **Juvenile:** <2 years
- **Subadult:** 2–5 years
- **Adult:** >5 years

Comparisons between enclosure types were undertaken to evaluate whether naturalistic systems were associated with improved reproductive outcomes relative to standard enclosures.

Statistical Analysis

Statistical analyses were performed in **R version 4.3.2**. Data normality was evaluated using the **Shapiro–Wilk test**, and homogeneity of variances was examined using **Levene's test.** Comparative analysis of hatching success between enclosure types was conducted using **one-way analysis of variance (ANOVA)**. Sex ratio deviation from parity was assessed using **χ^2 goodness-of-fit tests**. Correlation analyses, where applicable, were examined using **Pearson's correlation coefficient**. Statistical significance was set at **$\alpha = 0.05$**. Descriptive values are presented as percentages and, where appropriate, with 95% confidence intervals.

Results

Population Dynamics

Across the 45 surveyed facilities, the mean apparent annual population growth rate was **18.5%** (95% CI: **12.3–24.7%**). However, this increase was driven predominantly by **inter-facility transfers**, which accounted for **78%** of net numerical growth, rather than by intrinsic reproductive recruitment. This finding indicates that apparent expansion of captive holdings reflects administrative redistribution more than sustainable captive natality.

The overall annual mortality rate averaged **2.53%** across the study period, with a cumulative **240 deaths** recorded between 2020 and 2024. Although this mortality level may appear modest at the aggregate level, mortality was disproportionately concentrated in early life stages.

Table 1. Age-Specific Mortality Distribution (2020–2024)

Age Class	**Deaths (n)**	**% Total Mortality**	**% Total Mortality**
Juvenile (<2 years)	156	65.0	Thermal stress, ammonia toxicity, conspecific aggression
Subadult (2–5 years)	52	21.7	Territorial conflict, nutritional deficiency
Adult (>5 years)	32	13.3	Senescence, chronic disease
Total	204	100.0	$\chi^2 = 45.2$, df = 2, $p < 0.001$

Legend: Mortality data were derived from Central Zoo Authority (2024) captive inventory records and categorized using standard crocodilian age-class definitions.

Demographic Composition and Sex Ratios

The overall sex ratio of captive *C. palustris* populations was significantly **male-biased** at **1.14:1 (M:F)** (**χ^2 = 18.4, p < 0.001**), deviating significantly from the expected 1:1 ratio. Additionally, **12.4%** of individuals remained unsexed, reflecting either incomplete diagnostic assessment or uncertainty in younger cohorts. Facilities with active breeding programs showed only marginal improvement, with a sex ratio of **1.08:1**, yet still failed to achieve parity.

This male bias is biologically meaningful because in crocodilians, modest deviations in hatchling sex ratios may amplify over time in managed populations, especially where breeding adults are few or founder lineages are unevenly represented.

Reproductive Performance

Breeding activity was documented in only **28%** of surveyed facilities, indicating that the majority of institutions maintaining *C. palustris* were not contributing substantially to reproductive recruitment. Across all facilities, total egg production was reported as **531 clutches/egg units** (as recorded in institutional summaries), yielding an overall hatching success of **18.3%**.

Facilities with naturalistic enclosures outperformed standard enclosures by a substantial margin. Naturalistic systems achieved **25.1% hatching success**, whereas standard concrete enclosures yielded only **11.6%**. This difference was statistically significant (**ANOVA: F = 6.82, p = 0.02**), supporting the hypothesis that enclosure design strongly influences reproductive success.

Table 2. Comparative Breeding Success by Enclosure Design

Enclosure Type	**Facilities (n)**	Eggs Laid (n)	Hatching Success (%)	ANOVA F(P)
Naturalistic	18	342	25.1	6.83(0.02)
Standard	27	189	11.6	-
Total	45	531	18.3	-

Legend: Values represent original analyses conducted in the present study using CZA (2024) inventory data and are not directly reproduced from prior publications.

Comparative Captive–Wild Metrics

Captive populations exhibited higher apparent numerical growth than wild populations; however, this difference was largely administrative rather than biological, given the dominant role of inter-zoo transfers. In contrast, wild populations across India appear comparatively stable in recognized strongholds, but the absence of standardized, national-scale, repeated monitoring limits precise inference regarding demographic trends, recruitment, and regional sex structure.

The discrepancy between captive numerical increase and uncertain wild demographic data underscores the risk of overestimating conservation security on the basis of institutional abundance alone.

Discussion

Drivers of Demographic Imbalance

The male-biased sex ratio observed in captive populations is consistent with the thermal sensitivity of crocodilian sex determination. In *C. palustris*, incubation temperatures above approximately **33 °C** are associated with a higher probability of male hatchling production, whereas incubation within the **28–32 °C** range tends to favor increased female output. When captive systems lack thermal heterogeneity or expose nests to uniformly elevated temperatures—common in concrete-dominated enclosures with high solar absorption—sex ratio distortion becomes more likely.

Naturalistic enclosures mitigate this problem by providing variable microclimates, shaded nesting zones, sandy substrates with differential thermal conductivity, and more realistic moisture regimes. These features likely explain the observed improvement in hatching success and may also contribute to more balanced sex outcomes, although direct hatchling sex validation was not uniformly available across all institutions.

Juvenile Mortality Bottleneck

Juveniles accounted for **65%** of all recorded deaths, making early-life mortality the single most critical demographic bottleneck in captive mugger management. The principal contributing factors—thermal stress, ammonia toxicity, and conspecific aggression—indicate that mortality is driven less by unavoidable biological fragility and more by modifiable husbandry conditions.

Thermal instability can impair feeding, growth, immune competence, and metabolic regulation. Poor water quality, particularly elevated ammonia concentrations in poorly filtered or overcrowded pools, increases the risk of chronic physiological stress, dermal pathology, and opportunistic infection. Aggressive interactions among juveniles, especially under high stocking density or inadequate refuge provision, can lead to injury, suppressed feeding, and death.

Isolation rearing of vulnerable hatchlings, cohort size management, automated thermal monitoring, structured basking access, and continuous water-quality surveillance are therefore likely to produce immediate gains in survival.

Interstate Management Variation

Facilities in **Gujarat** and **Madhya Pradesh** demonstrated comparatively superior outcomes where naturalistic enclosure standards were more consistently adopted. This suggests that management success is not merely a function of species biology but also of institutional design philosophy, technical capacity, and state-level implementation quality. For Madhya Pradesh in particular, where major river systems and reservoir complexes support both captive and wild conservation opportunities, integration of standardized ex situ protocols with in situ monitoring could create a model framework for other states.

National standardization under CZA guidance is therefore warranted. Without uniform minimum standards for nesting substrate, thermal profiling, water quality, hatchling isolation, and reproductive record-keeping, inter-institutional variation will continue to undermine overall program efficiency.

Captive–Wild Conservation Disconnect

Although captive holdings are numerically substantial, the present analysis indicates that much of the observed growth is administrative rather than reproductive. If transfers dominate apparent expansion and breeding participation remains limited, then ex situ populations may be demographically fragile despite high census counts. Furthermore, without coordinated pedigree tracking, founder representation assessment, and molecular genetic monitoring, captive populations risk progressive loss of heterozygosity, cryptic inbreeding, and reduced adaptive potential.

This disconnect is particularly concerning because captive populations are often assumed to provide long-term insurance for wild populations. Such assumptions are valid only when ex situ populations are reproductively viable, genetically managed, and strategically linked to field-based conservation goals.

Conservation and Management Framework

Priority Captive Interventions

The present findings support several immediate institutional interventions:

1. **Standardized sex determination protocols:** Implementation of molecular sexing, ultrasonography, and age-appropriate morphological confirmation to reduce the proportion of unsexed individuals and improve demographic planning.
2. **Ecological enclosure redesign:** Replacement or retrofitting of simplified concrete systems with ecologically functional enclosures incorporating sandy nesting banks, shaded basking mosaics, graded water depths, and monitored thermal gradients.
3. **Enhanced juvenile rearing systems:** Density-controlled hatchling units, water-quality automation, ammonia threshold monitoring, compartmentalized rearing, and aggression-minimizing cohort management.
4. **Centralized digital monitoring:** A CZA-linked national demographic dashboard integrating breeding, mortality, transfers, sex structure, and pedigree-level metadata for adaptive management.

Integrated Captive–Wild Conservation Model

Long-term conservation of *C. palustris* requires explicit linkage between ex situ and in situ systems. Captive facilities should not function solely as display institutions; rather, they should serve as managed demographic and genetic repositories that complement field conservation. An integrated model should include:

- Standardized wild population surveys
- Nest monitoring and hatch success assessment in key river basins and reservoirs
- Habitat Suitability Index (HSI) mapping for strongholds and conflict-prone zones
- Rescue-to-rehabilitation pipelines with genetic documentation
- Head-starting or release programs only where ecological and genetic criteria are met
- Post-release monitoring using telemetry or mark–recapture frameworks

Such a model would be especially relevant for states such as **Madhya Pradesh**, where reservoir and riverine systems can support landscape-scale conservation planning.

Conclusion

The present national-scale analysis of Central Zoo Authority (2024) records demonstrates that captive populations of *Crocodylus palustris* in India exhibit numerical growth but remain constrained by significant reproductive and demographic limitations. Apparent increases in captive abundance are driven largely by inter-facility transfers rather than sustainable natal recruitment. Persistent male-biased sex ratios, incomplete sex determination, low breeding participation, poor hatching success in standard enclosures, and pronounced juvenile mortality collectively undermine long-term demographic stability.

Among the management variables examined, **naturalistic enclosure design** emerged as the most consistently beneficial intervention, significantly improving hatching success and likely reducing thermal distortion of reproductive outcomes. The study therefore supports a shift away from purely containment-based husbandry toward ecologically informed captive management systems.

Ultimately, the conservation future of *C. palustris* depends not on captive census size alone but on the establishment of **integrated captive–wild management**, including genetic stewardship, standardized husbandry, robust field monitoring, and strategic alignment between zoological institutions and forest/wildlife agencies. Such an approach is essential for maintaining the long-term viability, ecological function, and adaptive resilience of this keystone wetland crocodilian.

Recommendations

Given the strong ecological and management relevance of *Crocodylus palustris* in central India, particularly in reservoir and riverine systems of **Madhya Pradesh**, the following actions are recommended:

1. **Annual standardized field surveys** integrating basking counts, nest-site documentation, juvenile recruitment assessment, and habitat occupancy records.
2. **Habitat Suitability Index (HSI) mapping** across rivers, reservoirs, marshes, and anthropogenic wetlands to identify conservation priority zones and conflict hotspots.
3. **Community awareness and coexistence programs** focused on fishing communities, riparian villages, temple-tank users, and wetland-dependent households.
4. **Ecotourism frameworks** that are regulated, non-invasive, and conservation-linked, particularly in reservoir landscapes where crocodile visibility is high.
5. **CZA minimum enclosure standards** mandating thermal gradients, nesting substrate, and hatchling rearing protocols for all breeding-holding institutions.
6. **National crocodilian demographic database integration** linking captive records with state forest department field observations.
7. **Genetic management and founder representation audits** prior to any interstate transfer or conservation breeding expansion.
8. **Pilot captive–wild linkage models in Madhya Pradesh and Gujarat**, where enclosure performance and habitat availability suggest strong implementation potential.

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The research team contributed through field-level data support, technical assistance, literature collation, analytical inputs, and continuous collaborative feedback, collectively enhancing the scientific rigor, clarity, and conservation relevance of the manuscript.