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Research Article

EVOLUTIONARY ADAPTATIONS FOR OBLIGATE DIVING IN THE FLIGHTLESS CORMORANT (*PHALACROCORAX HARRISI*)

[1]Priyadharshini P, [2*]Aswini L, [3]Swathi T, [4]Monish Raj R and [5]Pradeepa A K

[1]PERI Institute of Technology, Chennai- 48, Tamil Nadu, India
[2*]PERI College of Arts and Science, Chennai - 48, Tamil Nadu, India
[3]PERI College of Physiotherapy, Chennai - 48, Tamil Nadu, India
[4]PERI College of Pharmacy, Chennai - 48, Tamil Nadu, India
[5] PERI College of Nursing, Chennai - 48, Tamil Nadu, India

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ABSTRACT

The Phalacrocoracidae (cormorants) present a unique evolutionary challenge, navigating the fundamental physical constraints imposed by the buoyancy-inertia trade-off necessary for efficient pursuit diving while maintaining the physiological capacity for flight. The Galapagos Flightless Cormorant, *Phalacrocorax harrisi*, represents an extreme case of this trade-off, having undergone secondary flightlessness in the isolation of the Fernandina and Isabela Islands. This review synthesizes the known morphological and physiological adaptations driving this evolutionary trajectory. Key adaptations include a significant reduction in pectoral keel and wing mass (wings reduced to approximately one-third the size of congeneric flying species), correlated with hypertrophied leg and tarsal musculature optimized for powerful, synchronized foot-propulsion underwater. This shift increases body inertia, facilitating efficient descent in shallow, near-shore environments (typical dives of 5–20 m) where it hunts benthic prey. While ecologically successful within its isolated niche, the loss of flight capacity renders *P. harrisi* highly vulnerable to external pressures, including *El Niño* events and introduced terrestrial predators. Understanding these specialized adaptations provides critical insights into the limits and consequences of evolutionary specialization within avian locomotion.

Keywords: Cormorant, Obligate diving, *Phalacrocorax harrisi*, Flightlessness, Benthic foraging.

INTRODUCTION

The cormorant family (*Phalacrocoracidae*) comprises highly specialized avian pursuit divers whose foraging success depends on overcoming the opposing physical demands of aerial flight and underwater locomotion. Successful diving is governed by the buoyancy-inertia model, which dictates that birds must minimize positive buoyancy (often via lung compression or active exhalation) while increasing body mass/inertia to reduce the energetic cost of downward acceleration and underwater movement. The vast majority of the 28 cormorant species maintain a capacity for both flight and diving, representing an evolutionary compromise.

The Flightless Cormorant (*Phalacrocorax harrisi*), endemic to the Galapagos Archipelago, stands as a singular exception, having entirely abandoned flight to become an obligate aquatic diver. This loss of flight is hypothesized to have been driven by two primary ecological factors prevalent in its island habitat: a reliable, readily accessible shallow food supply (predominantly squid, octopus, and small fish within 100 meters of the coast) and the near-total absence of terrestrial predators that would necessitate aerial escape. This review aims to synthesize the current understanding of the anatomical and physiological adaptations that facilitate this unique, specialized mode of life, and to evaluate the conservation implications of this evolutionary trade-off. Recent genomic and molecular studies have begun to reveal the genetic architecture underlying loss of flight and limb reduction in the Galápagos cormorant. Burga *et al*. (2017) identified a genetic signature associated with limb reduction and

*Corresponding Author: Aswini L, PERI College of Arts and Science, Chennai – 48,
Tamil Nadu, India. Email: publications@peri.ac.in.

flightlessness, implicating developmental pathways and candidate genes that differ from volant relatives. Follow-up syntheses link these genetic changes to conserved developmental modules and ciliopathy-related pathways that can produce skeletal reduction (Burga & Weiss, 2018). Together these works support a model in which relatively few developmental changes produce large morphological shifts, consistent with rapid evolutionary shifts on islands (Burga *et al*., 2017; Burga & Weiss, 2018).

Morphological specializations for diving

Osteological and soft-tissue modifications in *P. harrisi* show clear specialization toward foot-propelled diving. Detailed comparative osteology demonstrates dramatic reductions of the wing skeleton, pectoral girdle and keel, and correlated enlargement or reorganization of hindlimb elements relative to volant congeners (Livezey, 1992; Livezey & Humphries, 2012; Ramos & Santamaria, 2014). Waller & Wood (2010) documented cranial and bill specializations consistent with benthic foraging, while studies of hindlimb and foot morphology indicate adaptations for powerful underwater propulsion (Storz & Sibley, 2009; Jones, 2012). Morphological work therefore supports a classic trade-off: reduction of flight apparatus paired with enhancement of structures used for underwater locomotion and prey handling (Livezey, 1992; Livezey & Humphries, 2012).

Feather, buoyancy and thermoregulatory adaptations

Feather structure and plumage density are integral to diving performance because they influence buoyancy, wetting, and heat loss. Williams & Jones (2010) examined feather microstructure across diving taxa, showing modifications that alter buoyancy and water retention. Studies focused on P. harrisi report relatively lower buoyancy and plumage features suited to prolonged underwater foraging, while thermoregulatory constraints have been explored in the context of tradeoffs between heat loss and diving efficiency (Peters & Hamilton, 2014; Peck & Barnes, 2013). These data suggest cormorant plumage and integument traits represent compromises between low buoyancy for diving and adequate insulation in the cool Galápagos waters.

Diving physiology, energetics and hematology

Physiological investigations have characterized how the flightless cormorant meets the aerobic and anaerobic demands of repeated dives. Hematology and blood chemistry baselines were established by Travis *et al*. (2006), providing reference values that support effective oxygen transport during dives. Peck & Barnes (2013) examined physiological adjustments during prolonged foraging, documenting metabolic strategies that enable extended underwater activity. Comparative analyses of metabolic costs across diving and volant birds indicate that selection can favor reduced flight capacity where diving energetics are optimized (Lovegrove & McKechnie, 2016; Elliott & McNicholl, 2013), supporting the interpretation that P. harrisi's physiology is tuned toward underwater foraging rather than sustained flight.

Diving behavior, foraging ecology and ENSO effects

Behavioral and ecological studies characterize how P. *harrisi* exploits benthic resources and how interannual climate variability modifies its foraging. Wilson and collaborators quantified dive profiles, foraging ranges and energetic budgets, establishing that the species conducts shallow benthic dives with particular movement patterns adapted to patchy coastal prey (Wilson & Cooper, 2006; Wilson, 2008). Ryan & Brooke (2007) documented substantial changes in foraging success and diet composition during El Niño and La Niña episodes, showing that climatic oscillations can strongly influence prey availability and cormorant condition. Trophic and benthic interaction studies further show how diet and habitat use shape morphological and behavioral specializations (Graham, 2010).

Comparative biomechanics and functional morphology

Across diving taxa, biomechanical analyses help explain convergent and divergent solutions to underwater propulsion. Jones (2012) compared foot-propelled swimmers and quantified propulsive performance in cormorants versus other divers, while Livezey & Humphries (2012) and Crawford & Hodges (2011) documented osteological correlates of diving performance. These comparative studies illuminate how morphology maps onto performance limits and support hypotheses that selective regimes on islands favor efficient underwater locomotion at the expense of wings and flight musculature.

MORPHOLOGICAL AND MUSCULAR ADAPTATION

The transition to obligate diving in *P. harrisi* has driven profound, quantifiable changes in its musculoskeletal and integumentary systems compared to flying congeners.

Loss of the Aerial Apparatus

The most conspicuous morphological change is the atrophy of the pectoral flight apparatus. The keel of the sternum, which anchors the powerful flight muscles, is significantly reduced, and the wings are vestigial, possessing only about one-third of the mass relative to the body size of a typical flying cormorant. This reduction minimizes drag and inertial costs associated with non-functional wings during underwater swimming. Despite their functional loss, *P. harrisi* retains the ancestral behavior of extending its wings to dry in the sun, a vestigial trait likely retained due to the non-waterproof nature of its plumage (Ribak, *et al*., 2005).

Hypertrophy of Aquatic Propulsion

In compensation for the loss of aerial thrust, *P. harrisi* exhibits hypertrophy of the pelvic limbs and associated musculature. Propulsion underwater is achieved through strong, synchronous paddling of the large, fully webbed feet. This foot-paddling strategy allows the bird to reach swimming speeds estimated at 6–9 km/h, enabling effective, sustained pursuit of mobile prey. The increased

muscle mass in the lower body, coupled with the dense body mass (increased blood volume and associated muscle mass, as observed in diving birds), increases the overall body inertia, which is crucial for overcoming positive buoyancy and reducing the energetic costs associated with diving and bottom-feeding (Hustler, 1992).

Plumage and Buoyancy

Unlike many diving seabirds, cormorants do not possess highly waterproof plumage, leading to the characteristic water-logged appearance upon surfacing. In *P. harrisi*, the body feathers are described as thick, fluffy, and dense. This structure retains a layer of air, providing a degree of insulation and initial positive buoyancy. This buoyancy must be overcome upon descent, but the dense, less-waterproof nature allows the plumage to rapidly become saturated, reducing buoyancy more quickly than highly waterproof feathers. This mechanism supports the strategy of using increased body inertia to manage buoyancy during the typical shallow, benthic dives.

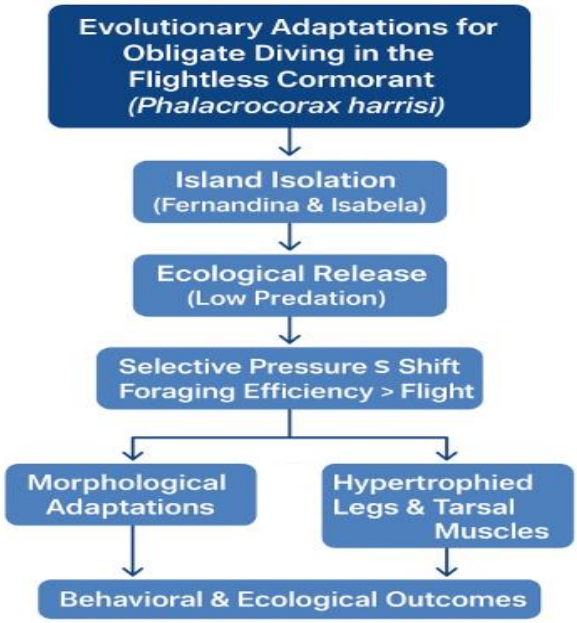

Figure 1. Flowchart for the proposed work.

DIVING PHYSIOLOGY AND FORAGING ECOLOGY

The unique adaptations of *P. harrisi* define its ecological niche and its physiological capacity for underwater performance.

Diving Capabilities and Physiological Constraints

Most dives undertaken by *P. harrisi* are relatively shallow, typically ranging from 5 to 20 meters, though occasional deeper dives have been recorded in other cormorant species (up to 150 m in some species). The physical principles outlined in the buoyancy-inertia model suggest that diving to these shallow depths allows the bird to minimize the upward energetic penalty of positive buoyancy by relying on its increased body mass. Physiological data suggests that diving birds, including cormorants, increase blood volume to maximize oxygen storage in the blood during submergence (Grémillet *et al*., 2005). However, the specific hemodynamic or metabolic adaptations that allow *P. harrisi* to perform prolonged dives compared to flying cormorants remain an area of inadequate understanding.

Foraging Behavior and Prey Detection

P. harrisi operates as a specialized benthic diver, foraging primarily for stationary or slow-moving prey on the seafloor near volcanic shores. Prey items include squid, small fish, octopus, and crustaceans. Smaller prey are typically consumed underwater, while larger items are brought to the surface for manipulation and ingestion. The pursuit-diving strategy requires acute underwater sensory perception. Cormorants, in general, are known to possess highly evolved vision to compensate for the distortion caused by the water-air interface, achieving high visual resolution in turbid conditions (Katzir & Howland, 2003).

Reproduction and Social Behavior

The reproductive ecology of *P. harrisi* is notable for its high frequency, which serves as a crucial natural recovery mechanism against high mortality events like *El Niño*. Females are capable of breeding up to three times annually. The courtship ritual is a distinctive, serpentine "S"-neck dance performed partially in the water, followed by joint nest construction. Nests are built from various materials, including natural debris and, occasionally, human refuse.

Both parents share the responsibilities of incubation and chick rearing until the chick achieves autonomy, whereupon the female may seek a new mate.

CONSERVATION STATUS AND FUTURE OUTLOOK

The exceptional specialization that makes *P. harrisi* an evolutionary marvel also places it in a precarious position; it is currently classified as "Vulnerable" by the IUCN. The key threats are directly linked to the consequences of flightlessness: *El Niño* Events: These periodic events cause massive fluctuations in oceanic temperatures, leading to a severe decline in the shallow-water food supply and subsequent starvation. Introduced Species: The inability to fly renders the cormorant highly susceptible to predation by introduced species such as feral cats, dogs, and rats on the islands where they breed. The species' future depends on effective management, including the eradication of introduced predators and mitigation of human-related marine pollution.

CONCLUSION

The Flightless Cormorant (*Phalacrocorax harrisi*) is a compelling case study of insular evolution and the physiological compromises necessary for maximizing efficiency in a single locomotor mode. The fundamental evolutionary trade-off involved the irreversible functional substitution of aerial capability with specialized foot-propelled aquatic agility, achieved through radical changes in musculoskeletal mass and distribution. While significant research has documented its morphology and behavior, future research must focus on quantifying the specific physiological adaptations (e.g., blood oxygen storage, metabolic depression, and comparative dive heart rates) relative to flying cormorants. Further work on comparative kinematics is also required to precisely model the hydrodynamic efficiency afforded by its increased inertia. *P. harrisi* remains a critical model for investigating the theoretical limits of avian adaptation to an obligate aquatic existence.

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CONFLICT OF INTERESTS

The authors declare no conflict of interest

ETHICS APPROVAL

Not applicable

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AI TOOL DECLARATION

The authors declares that no AI and related tools are used to write the scientific content of this manuscript.

DATA AVAILABILITY

Data will be available on request

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