



Review Article

AQUATIC AND AERODYNAMIC ADAPTATIONS OF THE FLIGHTLESS CORMORANT (*PHALACROCORAX HARRISI*) FOR DEEP-SEA FORAGING: A COMPREHENSIVE REVIEW

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ABSTRACT

The Flightless Cormorant (*Phalacrocorax harrisi*) of the Galápagos Islands exhibits remarkable evolutionary modifications that enable efficient underwater foraging in deep marine environments. Unlike other cormorants, this species has lost the ability to fly and instead developed physiological, anatomical, and behavioral adaptations suited for benthic and pelagic diving. Hydrostatic pressure, oxygen storage limitations, and buoyancy changes strongly influence diving performance, while modifications in plumage, musculature, and limb structure support powerful underwater propulsion. Increased blood volume, reduced wing size, strong webbed feet, and dense body feathers enhance the bird's diving efficiency and stability in cold waters. Behavioral traits—including synchronized foot paddling, wing-drying posture, and cooperative nest-building—further illustrate the species' ecological specialization. Despite its evolutionary success, the flightless cormorant remains vulnerable due to restricted distribution, climate events, invasive predators, and human activities. This review summarizes current knowledge on the aquatic and aerodynamic adaptations of *P. harrisi*, highlighting its foraging ecology, diving physiology, reproductive behavior, and conservation concerns.

Keywords: Flightless Cormorant, *Phalacrocorax harrisi*, Aquatic adaptation, Diving physiology, Foraging behavior.

INTRODUCTION

The Flightless Cormorant (*Phalacrocorax harrisi*) of the Galápagos Islands represents one of the most remarkable examples of avian adaptation and evolutionary specialization. Found only on Fernandina and Isabela Islands, this species has undergone unique morphological and behavioral transformations that distinguish it from the 27 other cormorant species worldwide. While most cormorants are capable of sustained flight and rely on aerial mobility to forage across open waters, *P. harrisi* has abandoned flight entirely and evolved exceptional diving capabilities suited for the volcanic and nutrient-rich marine ecosystems of the archipelago. Over thousands of years, the species adapted to local ecological conditions characterized

by abundant coastal fish, squid, and benthic organisms located close to shore. The absence of terrestrial predators and the abundance of nearshore food resources reduced selective pressure for flight, ultimately resulting in the shortening of wings, reduction of keel musculature, and increased development of powerful legs and webbed feet for underwater propulsion. These adaptations enable the cormorant to dive efficiently, navigate turbulent waters, and capture prey at depths typically ranging from 5 to 20 meters. Despite the loss of aerial ability, the species retains behavioral traits seen in flying cormorants, such as the characteristic wing-drying posture, though in *P. harrisi* this behavior serves little aerodynamic purpose. Other adaptations such as dense plumage for buoyancy control,

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enhanced underwater vision, and modified foraging strategies—demonstrate the complex interplay between environmental pressures and evolutionary change. With a population estimated at only 1500–1600 individuals, the Flightless Cormorant is currently classified as “Vulnerable,” making it essential to understand its biology for effective conservation strategies. This review examines the major physiological, anatomical, ecological, and behavioral adaptations that allow *Phalacrocorax harrisi* to thrive as a deep-sea forager. It also highlights the species’ vulnerabilities, ecological significance, and the need for further research to support long-term conservation.

Research on cormorants has extensively documented their remarkable physiological, anatomical, sensory, and behavioral adaptations that facilitate efficient underwater foraging. Early foundational work by Hustler (1992) demonstrated that buoyancy plays a significant role in shaping underwater foraging strategies in *Phalacrocorax africanus*, highlighting how the balance between body density and buoyant forces constrains diving depth and duration. Building on this, Schmid *et al.* (1995) provided one of the first energetic assessments of underwater swimming in cormorants, showing that the species expends substantial metabolic energy due to their relatively low buoyancy and dense musculature. Later studies such as Ribak *et al.* (2005) revealed that great cormorants use a burst-and-glide swimming pattern to optimize energy use while submerged. Visual adaptations also play a crucial role in prey detection. Katzir and Howland (2003) showed that great cormorants possess unique corneal refractive power and efficient underwater accommodation, enabling them to focus accurately on fast-moving prey. Similarly, Strod *et al.* (2004) found that the species maintains high visual resolution even in turbid water, demonstrating strong amphibious visual acuity. Complementing these results, White *et al.* (2007) concluded that cormorants employ a heron-like foraging strategy with precise visual targeting. Strod *et al.* (2008) further expanded understanding of sensory ecology by showing that prey detection efficiency varies between clear and turbid waters, emphasizing the importance of underwater visibility. Beyond vision, recent work by Hansen *et al.* (2017) uncovered that great cormorants can detect auditory cues underwater, suggesting an underappreciated multimodal sensory integration. Larsen *et al.* (2020) confirmed amphibious hearing capabilities in *P. carbo*, demonstrating specialized ear structures that function effectively both in air and underwater.

Numerous studies have analyzed foraging behavior and prey interactions. Grémillet *et al.* (2006) used underwater video to show that cormorants can injure prey even without consuming them, potentially increasing fish mortality in ecosystems. Cosolo *et al.* (2010) emphasized that prey behavioral traits influence cormorant foraging success, with certain fish escape patterns prompting adaptive hunting responses. Van Eerden and Voslamber (1995) reported mass-fishing events by cormorants in turbid lakes, demonstrating behavioral flexibility and cooperative foraging strategies. Cook *et al.* (2012) used GPS and time-

depth loggers to show that Cape cormorants display plasticity in dive patterns, adjusting their foraging depth and duration according to prey availability. Several studies have examined predator–prey dynamics and fisheries conflict. Russell *et al.* (2008) explored artificial fish refuges as a management tool to reduce predation, finding promising but context-dependent outcomes. Lemmens *et al.* (2016) supported this by showing that underwater refuges can protect fish populations from cormorant predation in multi-pond systems. Ferrari *et al.* (2015) observed underwater interactions between cormorants, sea lions, and harbor seals, suggesting complex interspecies competition within marine food webs.

Environmental factors also shape cormorant behavior. Grémillet *et al.* (2012) reported that fish remain vulnerable even in highly turbid water, indicating that cormorants rely not only on visual cues. Enstipp *et al.* (2007) linked prey abundance to predatory performance, indicating that environmental variability strongly influences foraging output. In extreme conditions, Grémillet *et al.* (2005) demonstrated that cormorants can forage even during polar night, highlighting extraordinary sensory and behavioral adaptation. Modern techniques have enabled detailed analyses of underwater movements. Gómez-Laich *et al.* (2015) employed animal-borne cameras (“selfies”) to capture real-time underwater behaviors, documenting prey pursuit kinematics. Potier *et al.* (2015) emphasized strong individual repeatability in foraging behavior, suggesting personality-linked ecological strategies. Machovsky-Capuska *et al.* (2012) expanded the sensory ecology framework by revealing how plunge-diving birds such as gannets accommodate visually underwater, offering comparative insights relevant to cormorant evolution. Finally, studies such as Grémillet *et al.* (2003) have developed bioenergetic models to estimate daily food requirements, serving as valuable tools in conservation and fisheries management. Jackson (1997) provided historical and cultural context by documenting traditional fishing partnerships involving cormorants an example of coevolutionary human–bird interaction. Engineering-focused research by Xue *et al.* (2016) examined wing loading and webbed-foot biomechanics, offering quantitative biomechanical support to observations of underwater propulsion. Collectively, these studies provide a comprehensive understanding of how cormorants—particularly *Phalacrocorax harrisi* and related species combine specialized sensory systems, modified anatomy, adaptive behavior, and high energetic performance to excel as underwater predators. This body of literature forms a strong foundation for analyzing the aquatic and aerodynamic adaptations of the flightless cormorant in detail.

MATERIALS AND METHODS

This review adopted a systematic evidence-synthesis approach to examine the aquatic and aerodynamic adaptations of the flightless cormorant (*Phalacrocorax harrisi*). Peer-reviewed journal articles, conference proceedings, ecological reports, and comparative avian

physiology studies were retrieved using scientific databases including Scopus, Web of Science, PubMed, ScienceDirect, and Google Scholar. The search used keyword combinations such as “flightless cormorant,” “underwater foraging,” “adaptations,” “vision underwater,” “buoyancy regulation,” and “avian diving physiology.” A total of 25 core studies spanning the years 1992 to 2020 were selected based on their relevance to underwater locomotion, visual and sensory adaptations, prey detection, biomechanics, and ecological foraging behavior. Articles were screened for (i) empirical field observations, (ii) experimental laboratory findings, (iii) sensory physiology studies, and (iv) biomechanical or hydrodynamic analysis. Comparative studies on closely related species—such as great cormorants, Cape cormorants, imperial cormorants, and gannets—were also included to triangulate findings and provide evolutionary context. Information extracted from each study included: morphological characteristics, diving patterns, sensory mechanisms, energetic costs, locomotion modes, prey capture strategies, and environmental influences (turbidity, depth, temperature). The data were synthesized thematically to generate a comprehensive understanding of how *P. harrisi* integrates morphological, physiological, and behavioral traits for efficient deep-sea foraging.

RESULTS AND DISCUSSION

The flightless cormorant exhibits a unique suite of morphological modifications that optimize underwater locomotion. Reduced wing length and increased wing loading significantly minimize drag, enabling efficient propulsion through flipper-like strokes similar to penguins. Studies of great cormorants and related species show that submerged swimming is based on a burst-and-glide gait (Ribak *et al.*, 2005), which minimizes energy expenditure during deep dives. The thick, muscular legs and large webbed feet generate powerful thrust, a feature further supported by biomechanical analyses of limb loading (Xue *et al.*, 2016). These traits collectively enhance maneuverability in strong underwater currents around the Galápagos Islands. Low plumage air content and dense bones reduce buoyancy, allowing *P. harrisi* to descend rapidly with minimal energetic cost. Early energetic assessments in related species (Schmid *et al.*, 1995) showed high metabolic demands during submerged swimming; however, the flightless cormorant’s reduced plumage and hydrophobic feather properties counteract this cost. Hustler (1992) demonstrated that cormorant buoyancy strongly influences diving behavior; *P. harrisi* has evolved an optimal balance that permits long bottom times for pursuing benthic prey. Bioenergetic models (Grémillet *et al.*, 2003) indicate that such adaptations are essential for meeting daily caloric requirements within the nutrient-rich but challenging marine ecosystem. Vision is the primary sensory mechanism facilitating prey detection underwater. The species benefits from strong corneal focusing ability, similar to that documented in great cormorants (Katzir & Howland, 2003). High visual acuity even in low-visibility or turbid waters (Strod *et al.*, 2004, 2008) improves prey-

tracking success during pursuit. Studies on amphibious hearing (Hansen *et al.*, 2017; Larsen *et al.*, 2020) suggest that underwater auditory cues may also assist in detecting prey movement or avoiding predators. Multisensory capability likely plays a role in the flightless cormorant’s success in the energetically demanding benthic zone. Underwater camera studies (Gómez-Laich *et al.*, 2015; Grémillet *et al.*, 2006) show that cormorants actively chase, pursue, and capture fish via rapid neck extension and precise jaw movements. Behavioral plasticity is observed in depth, timing, and trajectory of dives, consistent with findings in Cape cormorants (Cook *et al.*, 2012). Prey ecology strongly shapes hunting strategy, as demonstrated by Cosolo *et al.* (2010), and mass-foraging events in other cormorant species highlight cooperative or opportunistic feeding strategies (Van Eerden & Voslamber, 1995). Persistent success even in turbid water (Grémillet *et al.*, 2012) indicates strong adaptability to dynamic underwater environments. Predator-prey dynamics involving cormorants have implications for fisheries, as fish injury without consumption has been documented (Grémillet *et al.*, 2006). Management studies using fish refuges (Russell *et al.*, 2008; Lemmens *et al.*, 2016) illustrate the ecological impacts of cormorant predation in freshwater systems, offering comparative insights for marine environments. Additionally, the capability to forage during extreme conditions, such as the polar night (Grémillet *et al.*, 2005), suggests that the flightless cormorant’s relatives possess remarkable sensory compensation, likely shared through evolutionary pathways. Overall, results across studies indicate that *Phalacrocorax harrisi* represents one of the most specialized seabirds for benthic and near-shore underwater foraging. Its integrated system of morphological reduction, enhanced hydrodynamics, sensory refinement, and behavioral flexibility reflects a highly advanced adaptation to the unique ecology of the Galápagos coastal habitats.

CONCLUSION

The flightless cormorant (*Phalacrocorax harrisi*) possesses a sophisticated combination of aquatic and aerodynamic adaptations that enable it to thrive as an efficient deep-sea forager. Evolutionary reduction of wing size, enhancement of leg musculature, hydrodynamic body form, and strong webbed-foot propulsion provide substantial underwater locomotion advantages. Complementary sensory adaptations—including amphibious visual accommodation and underwater auditory detection—enhance prey capture efficiency in varied water conditions. Behavioral flexibility and optimized energy management further support successful foraging in the challenging Galápagos marine environment. Together, these interlinked adaptations position *P. harrisi* as an exceptional example of evolutionary specialization following the loss of flight.

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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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