

Origins and Ontogeny of Flightlessness in the Galapagos Cormorant

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The flightless Galapagos Cormorant (*Phalacrocorax harrisi*) is a remarkable bird: not only is it incredibly rare and possessed of a severely limited and specialized range, it is the only cormorant, of 27 confamilials, to have lost the ability to fly. This flightlessness, moreover, evolved within the last million years on the youngest islands of the Galapagos archipelago, from a small population of birds that used their wings to make the journey from the mainland to the rich waters of Fernandina and Isabela. But what set of conditions caused the ancestors of the Galapagos Cormorant to lose their functional wing structures? What set of adaptive pressures led to the development of the flightless character? In other words, what advantages did flightlessness and an underdeveloped pectoral apparatus confer upon the cormorant, and what benefits does it receive from its unique morphological adaptations? To begin to answer these questions, we must examine the life of the cormorant today, its diet, habits, and the circumstances of its environment, and discover, or at least attempt to identify, the use it makes of the flightlessness adaptation and of flightlessness-related adaptations. Such an analysis, conducted primarily on evidence reported in Wilson et al, 2008, reveals a slightly unorthodox explanation as to the purpose and primary benefit of the cormorant's flightless characters, centered around an increase in diving ability and overall foraging efficiency.

We must first establish and undertake to examine the physical features of *Phalacrocorax harrisi's* environment – the geological, climatological, and biotic circumstances that define the space in which the cormorant lives, mates, and forages for food. The Galapagos Cormorant's range is restricted to the two westernmost islands of the archipelago, being found only on Fernandina Island and the northern and western coasts of Isabela Island,¹ and in especially high concentrations in and around the Bolivar Channel between the two islands. The cormorant is a benthic feeder, subsisting on squid, crustaceans, and bottom-dwelling fish it searches out among rocky crevices and seafloor

¹ Wilson, et al, "What Grounds Some Birds for Life? Movement and Diving in the Sexually Dimorphic Galapagos Cormorant," *Ecological Monographs*, Vol. 78 No. 4 (2008), pp. 633-652.

substrates.² In foraging for its prey, the cormorant rarely ventures very far from its colony or nesting sites, neither ranging very great distances along the coastline nor exploiting various food sources farther out to sea. We will see, later, how the cormorant's foraging habits relate directly to its reduced pectoral characters and to the special circumstances under which flightlessness became a feasible and practicable adaptation for its ancestors. In a study conducted between August 2003 and August 2005, Wilson, et al. found that among sixteen female and fourteen male cormorants tagged and tracked, foraging trips were conducted at a mean distance of approximately 690 meters from the nest, and at a mean distance of 230 meters from the shore.³

The Galapagos Cormorant's food supply depends upon the unique geological and climatological characteristics of the western Galapagos and the islands that it inhabits. The Galapagos is situated at a confluence of major ocean currents, receiving the cold Humboldt Current sweeping up and off the coast of South America from Antarctica to the south, the warm Panama Current from the north, and the cold Cromwell Current from the west. The cold water of the Cromwell Current brings nutrients to the western islands, but the geological construction of these islands concentrates the effects of the current. The underwater slopes of the volcanoes that form Fernandina and Isabela are extremely steep, and drop off precipitously to the ocean floor at the base of the Galapagos Plateau.⁴ Where the other islands essentially slope down to the depth of the plateau upon which all of the shield volcanoes that make up the archipelago are based, Fernandina and the western side of Isabela decline directly to the Pacific seafloor. As the Cromwell current flows into the islands from the west, it encounters the steep incline of the Galapagos Plateau and wells up to the surface, bringing cold, nutrient-rich water with it and producing high phytoplankton concentrations that form the base of the rich food chain that the cormorant

² Wilson, et al. 2008.

³ Wilson, et al. 2008.

⁴ Paul D. Stewart, *Galapagos: The Islands that Changed the World*, (New Haven: Yale University Press, 2006), 34.

and other seabirds exploit.⁵ Fig. 1 illustrates the incredible concentrations of phytoplankton present to the west of Isabela and Fernandina, in contrast to the less productive waters of the rest of the archipelago. This abundant food reserve, however, is subject to the seasonal climatic oscillation that substitutes the warm waters of the Panama Current from December to May for the colder waters of the Humboldt Current that bathe the Galapagos from June to November.⁶ The season that portends rain, abundance, reproduction and growth on land produces, in the oceans, a period of scarcity, while the “dry” season that drives such marked adjustment among, for example, Darwin’s famous ground finches or the drought-adapted Palo Santo trees, creates a wealth of food of all kinds in the seas. This annual oscillation is overshadowed in severity by the irregular El Nino cycle, which by essentially a reversal of the Pacific’s South Equatorial Countercurrent periodically throws the marine environment of the Galapagos into extreme confusion and exacerbates and prolongs this scarcity to far more deadly and dire proportions. The Galapagos Cormorant can be severely affected by El Nino events because of this reduction in its food supply, suffering extremely high mortalities and population loss. In the 1982-83 El Nino, as reported by Carlos Valle, the Galapagos Cormorant population of an estimated 650-800 pairs was cut in half.⁷ However, after the return of normal climatic conditions and the reestablishment of a steady and abundant food supply, cormorant populations have on multiple occasions made a robust and rapid recovery.⁸

The abundance of food available to the cormorant as a result of the peculiar climatological and geological features of the western Galapagos helps to explain its foraging habits, which, as discussed earlier, rarely involve the cormorant’s venturing

⁵ Julian Fitter, Daniel Fitter, David Hosking, *Wildlife of the Galapagos*, (Princeton: Princeton University Press, 2000), 36.

⁶ Stewart, 34.

⁷ Carlos A. Valle, Malcolm C. Coulter. “Present Status of the Flightless Cormorant, Galapagos Penguin, and Greater Flamingo Populations in the Galapagos Islands, Ecuador, after the 1982-1983 El Nino,” *The Condor*, Vol. 89 No. 3 (May 1987).

⁸ Valle, 1987.

beyond a kilometer from its nesting site. While all cormorants are surface divers (as opposed to blue-footed boobies or pelicans, which dive from the air), many make use of the volant character to forage at greater distances or to exploit otherwise unattainable food sources. But because of the richness of marine food sources in and around Fernandina and Isabela, and the high volume of prey available to the cormorant, the use of flight as a means of enhanced access to additional food sources is no longer necessary. By the simple fact of high prey availability in the waters of the western Galapagos, the usual benefits of flight are not as advantageous or imperative as they might be in the cormorant's confamilials. Similarly, the absence of mammalian predators on the Galapagos renders what is traditionally the primary benefit of the volant character, the ability to escape and evade terrestrial predators, no longer important. Many have interpreted this absence of imperative in the traditionally conferred benefits of flight as the cause of the Galapagos Cormorant's loss of the volant character and the reason for its reduced pectoral apparatus. Without the need for flight, either to evade predators or to locate and exploit supplementary sources of food, the wings and pectoral apparatus and their continued maintenance would become a liability to the cormorant, which over a long enough period of time might lose its fully developed wing structure in favor of the reallocation of the metabolic resources used in its construction and upkeep to other areas or efforts of importance. Because of the lack of an imperative for flight, those cormorants that chanced to possess underdeveloped or imperfect wing structures would not be affected negatively and would not suffer in terms of reproductive success; and thus these underdeveloped wing characters might be passed on to their offspring and proliferate through the population. In fact, because of the high relative metabolic costs of fully developed wings and the pectoral apparatus (cf. McNab 1994, Wilson 2008),⁹ those cormorants with underdeveloped wing structures or those that were able to allocate resources otherwise occupied with the pectoral apparatus to other efforts such as hunting

⁹ Brian K. McNab, "Energy Conservation and the Evolution of Flightlessness in Birds," *The American Naturalist*, Vol. 144 No. 4 (1994), pp. 628-642.

or reproduction, would likely be more successful than those cormorants with a fully developed pectoral apparatus still expending the energy necessary for its upkeep and construction. Put concisely, this hypothesis holds that in the case of the cormorant the energetic and developmental costs of flight are balanced by few benefits and thus selection favors individuals with reduced pectoral apparatus and, consequently, with lower metabolic and developmental requirements.

This hypothesis is supported by studies of metabolic rates of other flightless avian species and by the foraging habits of the cormorant as they relate to energy expenditure. Though there have been no studies concerning the relationship of metabolism and flightlessness in *Phalacrocorax*, we can use data from studies conducted on *Rallidae* (of which there are many flightless species) as a proxy for this relationship in the Galapagos Cormorant and other members of its genus. The basal metabolic rates of all flightless species of rails are lower than those of their flighted congeners.¹⁰ Moreover, the pectoral muscles needed to power the wing structure during flight are disproportionately metabolically expensive, requiring a huge amount of energy to maintain and operate even at base levels.¹¹ When corrected for body mass discrepancies between species, data indicate a positive correlation between basal metabolism and pectoral muscle mass. In other words, those rails with reduced pectoral muscle masses have lower basal metabolic rates. The Galapagos Cormorant, compared with its congeners, has a greatly reduced pectoral muscle mass – where, in some cormorant species, the pectoral muscle can comprise greater than 15% of total body mass, in the Galapagos Cormorant the pectoral muscle makes up only 1.3% of total body mass. It would thus follow that *P. harrisi* gains a reduction in metabolism from the loss of its fully developed pectoral characters. The foraging habits described in an earlier section of this paper also accord with the understanding that the cormorant, like many other avian species, lost its wings because the benefits of flight were exceeded by metabolic and energetic gains. In general, flight is

¹⁰ McNab, 1994.

¹¹ McNab, 1994.

a much more efficient foraging technique than swimming, producing far higher net energy returns per foraging trip.¹² But when the costs of wing construction and maintenance are factored into this net energy calculation, there is a narrow window of foraging distances over which swimming actually produces a greater energy gain than flight.¹³ This optimal foraging distance is approximately 200-800 meters per expedition (see Fig. 3), in very close accordance with the mean distance traveled by the cormorants in Wilson's 2008 study, of approximately 690 meters from the nest. The cormorant, it seems, is able to forage within that distance that allows it advantages over a flighted existence, and to thus solidify the metabolic and developmental gains it receives from an underdeveloped pectoral apparatus.

But improved energy conservation on its own is, I think, insufficient to explain the morphology of the cormorant and its loss of a functional wing apparatus. The underdevelopment of the wing affords the cormorant certain further advantages that help to explain some of the selective pressures that motivated the acquisition of flightlessness. Many of these advantages center around the cormorant's diving habits, and confer benefits related to an enhanced diving ability. Firstly, the cormorant's underdeveloped wing structure and low plumage density help it to reduce underwater drag due to the vibration of primary and secondary feathers.¹⁴ The smaller area of the alar membrane in the cormorant's underdeveloped wing reduces heat loss at depth in the relatively cold water in which the cormorant forages. More importantly, however, the cormorant's stunted wings and sparse plumage reduce the energy it has to expend fighting the buoyancy of air trapped in its feathers when foraging underwater. All diving birds have to spend energy when underwater to balance the upthrust of the air inevitably trapped between their feathers and in their plumage. Though cormorants are some of the most

¹² Wilson, et al. 2008.

¹³ Wilson, et al. 2008.

¹⁴ Bradley C. Livezey, "Evolution of Flightlessness in Rails (Gruiformes: Rallidae): Phylogenetic, Ecomorphological, and Ontogenetic Perspectives," *Ornithological Monographs*, No. 53, 2003. Wilson, et al. 2008.

efficient at preventing air accumulation in their plumage, the Galapagos Cormorant's smaller wings and underdeveloped plumage mean that it has even less air in its feathers to impede its diving ability. The pectoral muscle reductions discussed earlier in the context of basal metabolic rate efficiencies also improve the diving abilities of the cormorant, as a smaller pectoral muscle mass allows for reduced underwater drag due to reduced body girth.¹⁵ Moreover, because the pectoral muscle tissue is so energy-expensive (see discussion of pectoral muscle mass and basal metabolic rates), and uses oxygen at a disproportionate rate during diving (even though the cormorant does not use the pectoral muscles for underwater locomotion), the reduction of the pectoral muscle mass improves the cormorant's energy and oxygen efficiency and allows it to accomplish longer dive durations.

Heretofore we have treated the loss of the volant character and the reduction in the pectoral apparatus to be the main morphological adaptation of the Galapagos Cormorant. But *P. harrisi* exhibits another primary morphological characteristic with an almost equally large adaptive value. The great body mass of the Galapagos Cormorant, along with its flightlessness, is one of the main features that distinguishes *P. harrisi* from other cormorant species. The Galapagos Cormorant is nearly two times the mass of any other cormorant, weighing up to 4 kg, compared with approximately 2.2 kg among congeners.¹⁶ This increased body mass confers numerous diving-related advantages to the cormorant. First, mass-specific metabolic rate decreases with increasing mass, while oxygen storage capacity scales linearly with increasing mass, so a larger cormorant both uses its energy more efficiently and has access to a greater store of oxygen when diving.¹⁷ Increased body mass also reduces heat loss because of a reduced surface-area to volume ratio, an advantage in the relatively cold water in which the cormorant forages for food. Although the cormorant's increased body mass does not necessarily allow it to dive

¹⁵ Wilson, et al. 2008.

¹⁶ Wilson, et al. 2008.

¹⁷ Wilson, et al. 2008.

deeper than other congeners (there is no significant correlation between body mass and dive depth among cormorants),¹⁸ it does allow it to stay underwater *longer*. The 2003-2005 study conducted by Wilson, et al, recorded a maximum dive duration of 196 seconds, having predicted a maximum dive duration for *P. harrisi* based on the data of Quintana, et al (2007), of 216 seconds.¹⁹ And though most of the dives recorded by Wilson were of durations of less than 62 seconds,²⁰ the importance of the study's being conducted during a La Nina period cannot be overstated; it may well be that the cormorant, like the finches with their tool-kit of beaks, is only called upon to make use of its diving endurance during periods when relative scarcity replaces the usual bounty of Bolivar and Espinosa. To summarize, though, the large body mass of the cormorant allows it to perform longer dives because of a more efficient use of oxygen and energy, complemented by the additional metabolic gains granted by the cormorant's reduced pectoral muscle mass. Longer dives are advantageous to the cormorant because they allow more prey to be captured for any given dive. This habit, in fact, is recorded by Wilson's study, in which 95% of cormorant dives recorded were "U-shaped" dives, or dives in which the cormorant remained at the dive's maximum depth for an extended period of time. All of the adaptations discussed above confer advantages to specifically this manner of diving – the buoyancy-related energy conservation of the cormorant's reduced wings, the metabolic and energetic efficiency gains of both a reduced pectoral muscle mass and an increased overall body mass, along with a decreased surface area to volume ratio that minimizes the cormorant's heat loss at depth – all allow it to stay underwater for a longer period of time by using its energy more efficiently. With these habits in mind, a picture begins to emerge of the cormorant as adapted for diving, as invested with a set of attributes that make it a superior diver.

¹⁸ Wilson, et al. 2008.

¹⁹ Wilson, et al. 2008.

²⁰ Wilson, et al. 2008.

It is likely that the cormorant developed these adaptations in response to several powerful selection events or periods of extreme scarcity over the last .5 to 1.0 million years.²¹ Such scarcity would favor those cormorants that foraged and dived more efficiently, allocated fewer resources to the construction and maintenance of the wing structure, and attained a balance in the food sources they exploited that allowed them to retain the greatest net energy gain. This rapid evolution could have been facilitated by changes in the genes regulating the development of the cormorant. Changes in ontogenetic timing could allow the cormorant to retain some juvenile characteristics into adulthood (paedomorphosis) and thus effect the adaptation of an underdeveloped pectoral apparatus, with all of its advantages. Likewise, peramorphic mechanisms, specifically hypermorphosis, could produce the cormorant's powerfully overdeveloped hind legs. Although the underdevelopment of the cormorant's wings could potentially be related to the allometric growth of its wings in relation to its increased body size (wing size scales at the 1/3 power to body size),²² the development of the cormorant is more likely characterized by juvenile accelerated peramorphosis of hindlimbs followed by adult alar progenesis. The Galapagos Cormorant retains juvenile characteristics in pectoral skeleton and musculature into adulthood; compared with flighted cormorants, the development of *P. harisi* is protracted, and homologous developmental stages occur progressively later.²³ The cormorant is therefore an excellent example of heterochrony, or the simultaneous development of two different characters along separate ontogenetic schedules. The cormorant's paedomorphosis, also, may have some interesting consequences. For example, it may be that the cormorant's lighter plumage, a consequence of its incomplete maturation, poses a problem with regard to the reabsorption of heat following long dives, and thus the bird has adapted a loss of iridescent plumage to aid in the absorption of heat. It is more likely, however, that both the absence of the iridescent character and the

²¹ McNab, 1994.

²² Livezey, 2003.

²³ Livezey, 2003.

cormorant's lack of mature black plumage are spandrels or un-adaptive consequences of the cormorant's aforementioned pedomorphic development program. The consequences of pedomorphosis simply invest the cormorant with certain coincidentally beneficial plumage characters.

The developmental schedules of the cormorant seem to lead us back to the same conclusion – pressures for improved diving abilities selected for adaptations that led to flightlessness in the cormorant's ancestors. The cormorant did not just limply adapt a flightless character. It is adapted for diving, for the best possible use of its available resources and for maximum efficiency of return per dive and per foraging expedition. This adaptation is effected through changes in the cormorant's ontogeny that produce an overdeveloped hindlimb, small, underdeveloped wings, and a disproportionately large body size, all of which confer advantages that improve the cormorant's diving ability. That said, the cormorant's different adaptations, and even its developmental mechanisms, are, in a sense, inextricable; those adaptations that confer diving-related advantages simultaneously confer the benefits associated with the loss of flight and the metabolic expenses associated with it, while those adaptations that have only to do with reductions in the pectoral apparatus also aid the cormorant in more efficient diving and foraging. To claim that one or the other pressure predominated is to make an arbitrary distinction; a reduced pectoral apparatus is adaptive, both for diving and as an adaptation unto itself. As always, we are restricted in our speculation about the origins of the cormorant's adaptations by the limited knowledge we possess about its past and the actual circumstances of its ancestors. We cannot hope to determine with any degree of certainty the full and complete trajectory of *P. harrisi's* adaptations or to comprehend the minute details and intricacies of the cormorant's evolution. Jonathan Weiner expressed this hopelessness quite well in *The Beak of the Finch*. He writes, "it is a fundamental difficulty of a historical science like the study of evolution that one can never establish the cause of a past event," alluding to the tied hands of the evolutionist who, though able

to analyze the adaptive advantages of a particular character in the present environment, will always remain a step behind in his ignorance of a definite history of the given biological entity, able to know the organism only in the form in which it is presented to him.

Figures

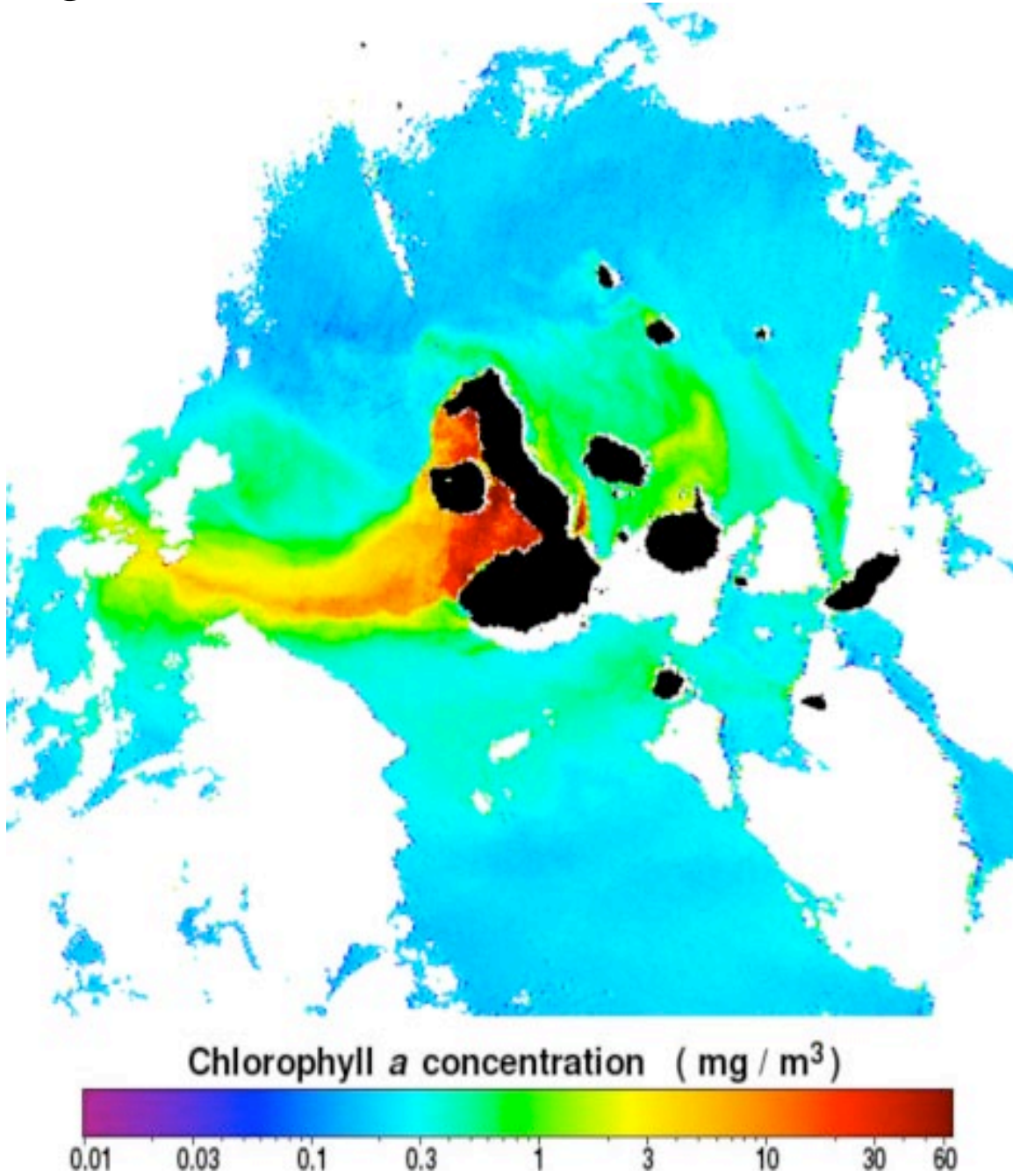


Fig. 1. Chlorophyll concentration as an indication of phytoplankton concentration.

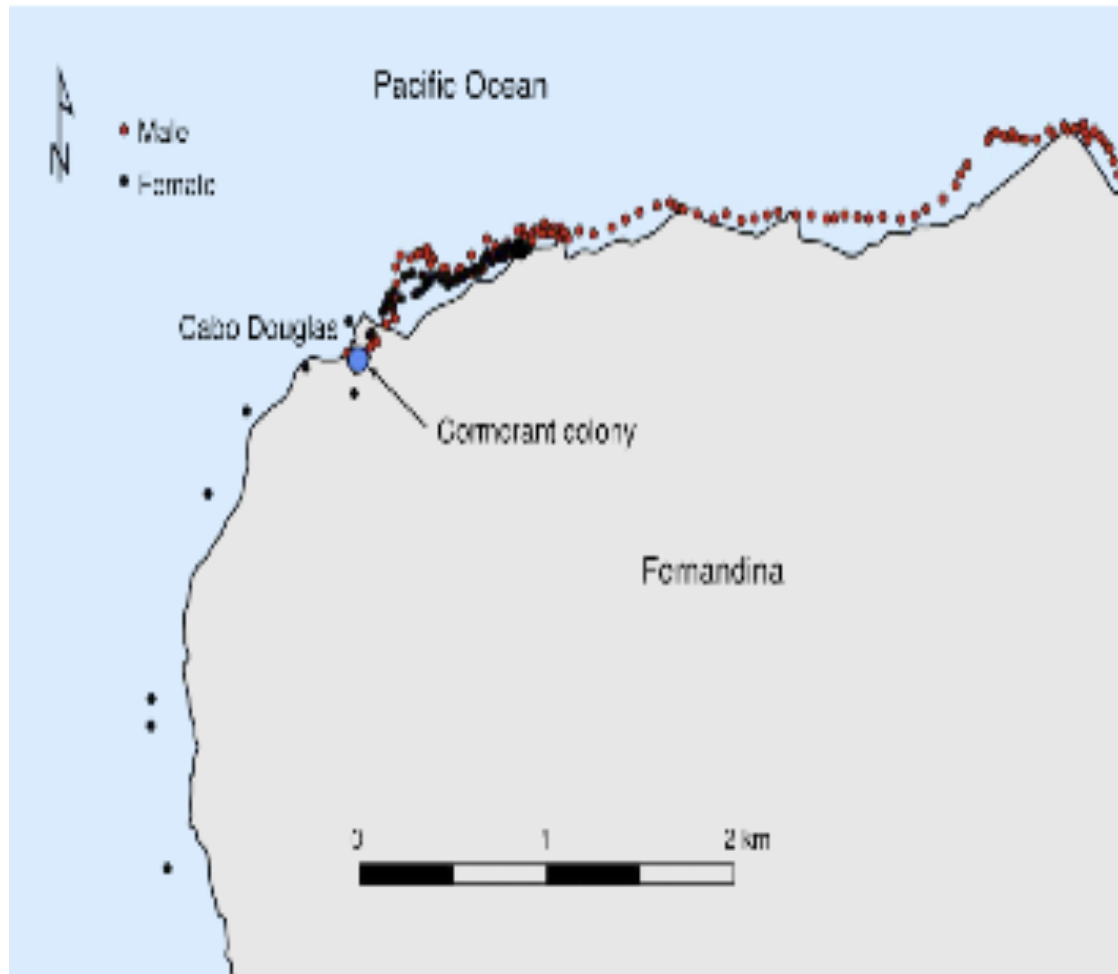


Fig. 2. GPS traces of 14 male and 16 female cormorants on foraging expeditions. From Wilson, et al, 2008.

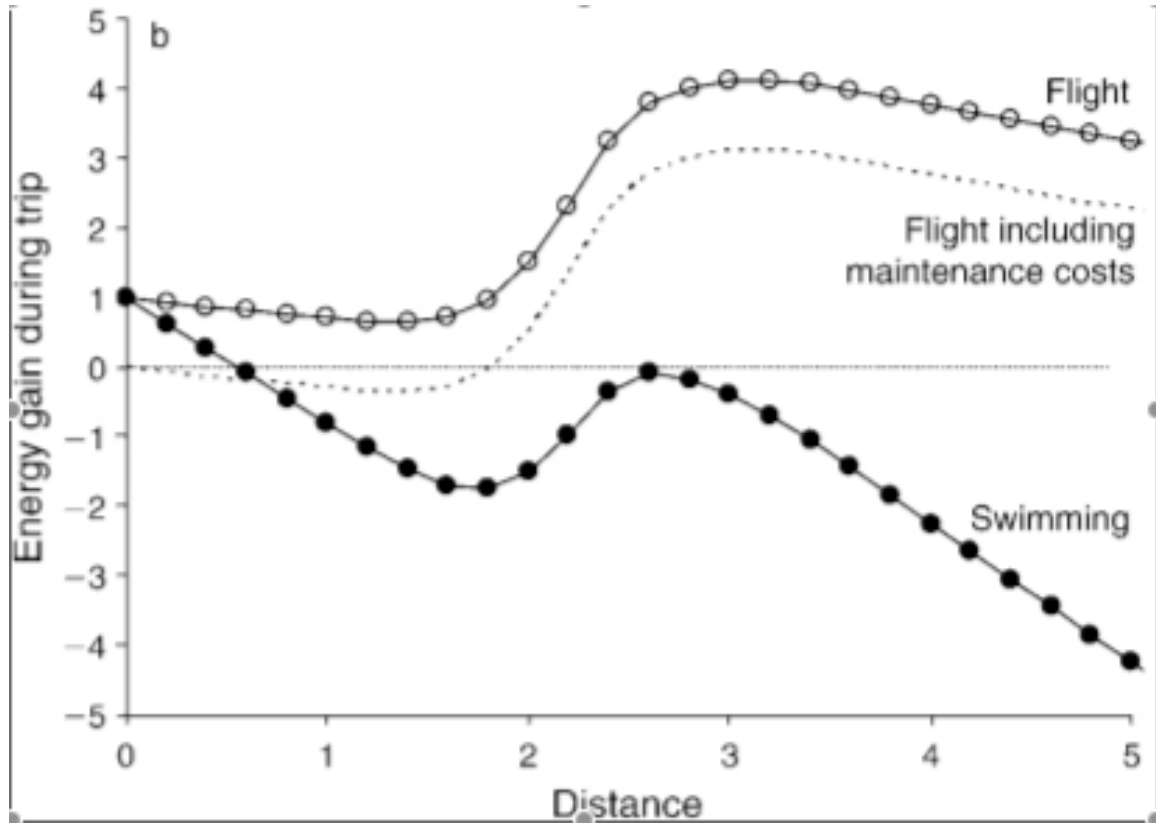


Fig. 3. Graph of energy costs and modeled net energy gain in flight foraging versus swimming foraging. From Wilson, et al, 2008.

Images



The Galapagos Cormorant dries out its stunted, adaptively underdeveloped wings as the sun sets.



A male Galapagos Cormorant brings a gift of seaweed to his mate to aid her in building the nest.



Here the pair put the seaweed, ceremoniously offered and accepted, into the nest, where the female will eventually lay her eggs.



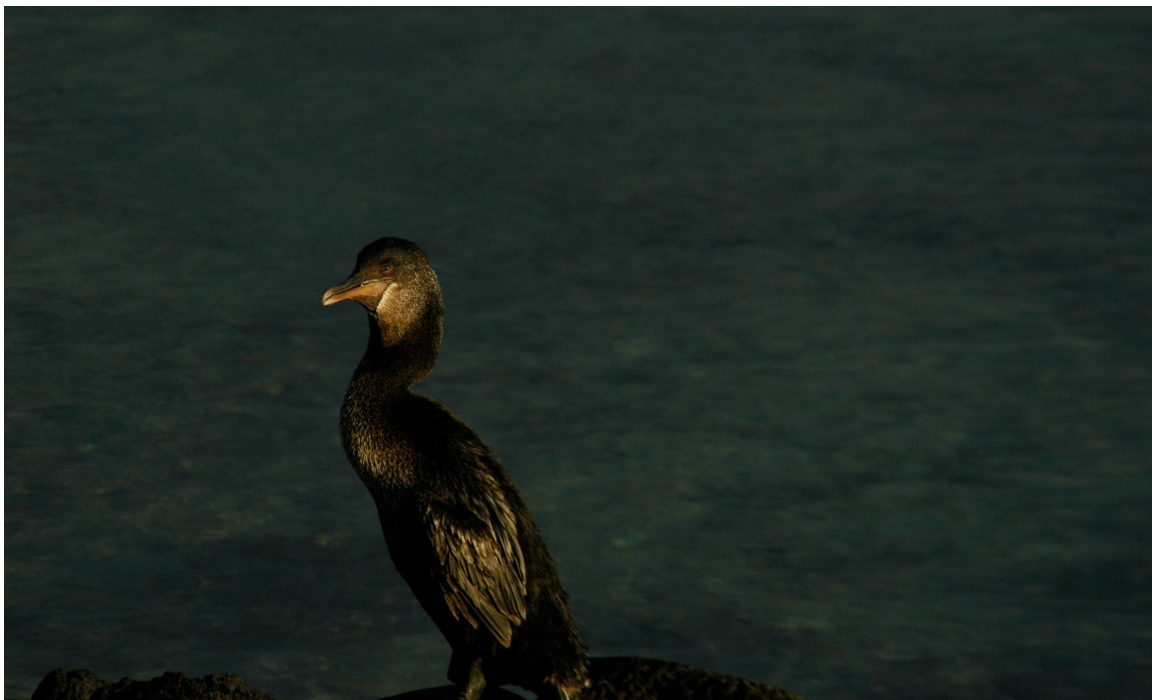
An unpaired cormorant grooms his underdeveloped wings at the edge of the water.



Looking up, he will perhaps soon go out to forage for food.



Two cormorants engage in a courtship ritual in the fading afternoon light at Punta Espinosa, on Fernandina.



The large body size and paedomorphic characteristics of the cormorant are especially evident here. It's no wonder so many researchers immediately assume neoteny in the cormorant's development, when it looks so much like an overgrown chick.



A cormorant on Isla Isabela preens on lava boulders in front of a mangrove thicket.

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