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# An Evolutionary Perspective On The Morphology and Ontogeny of *P. harrisi*

The Flightless Cormorant (*P. harrisi*) belongs to the long array of strikingly unusual organisms endemic to the Galapagos Archipelago. There are several remarkable morphological features of P. *harrisi* shared by no other member of the family Phalocrocoracidae. The most distinctive feature is the highly underdeveloped flight apparatus. P. harrisi has diminutive wings with a loading capacity only one third the size necessary to fly, reduced pectoral muscles and a correspondingly vestigial carina (Kricher 104) Further features that distinguish *P. harrisi* from confamilials are its enlarged body size and disproportionately large pelvic apparatus (Livezey 210) . These unique features, contribute to energy conservation, diving efficiency and diving ability. They arose due to changes in regulatory genes selected for in past period of prolonged food scarcity or in the process of intraspecific competition.

A prime advantage of the underdeveloped flight apparatus is energy conservation. In the particular environment of P. harrisi, the energetic costs of development and maintenance of the flight apparatus are not balanced by the conventional benefits of predator evasion and improved foraging energetics. In its evolutionary past the Flightless Cormorant was not subjected to mammalian predation( Kricher 105). Hence, the ability to fly conferred no advantage in escape and is not adaptive in this respect (MCall 570). When it comes to aerial piracy by frigate birds, flightlessness may even be advantageous since the frigate birds are wary to pursue a bird on the water surface for fear of becoming water logged (Roots 116). In terms of foraging energetics it is more difficult to explain P. harrisi's loss of flight.

One would expect the net energy gain, defined as energy gain from foraging minus travel cost, to be higher for volant birds for two reasons. First, energy spent per unit time traveled is lower when flying compared to swimming or diving. Second, prey encountered per unit of foraging time usually increases with distance from the nesting site due to intraspecific and interspecific competition (Wilson 643). If the energy gain from foraging is higher and the travel cost is lower, then the net energy gain must also be higher for volant birds. Although this may be the case, it does not mean the ability to fly will always be energy conserving when looking at a birds entire energy requirements and expenditures. The flight apparatus is energetically expensive because it raises basal metabolic rates and its development and maintenance require energy input (McCall 570). Although no one has studied how basal metabolic rates differ between P harrisi and confamilials, comparisons have been made between flightless and volant rails. In the family Ralidae it was found that the basal rates of metabolism for all flightless rails are lower than those of volant confamilials. It was also found that basal rates of metabolism corrected for body mass scale linearly with body mass (McNab 628, see figure 1). Regarding the flightless cormorant, we find that its pectoral body mass makes up only 1.3% of its body mass while other members of the family Phalocrocoracidae have pectoral muscle, which constitute up to 15% of body mass (Lizevey 184). This suggests that P. harrisi has a significantly lower basal metabolic rate in its flightless condition than if it had a fully developed flight apparatus.

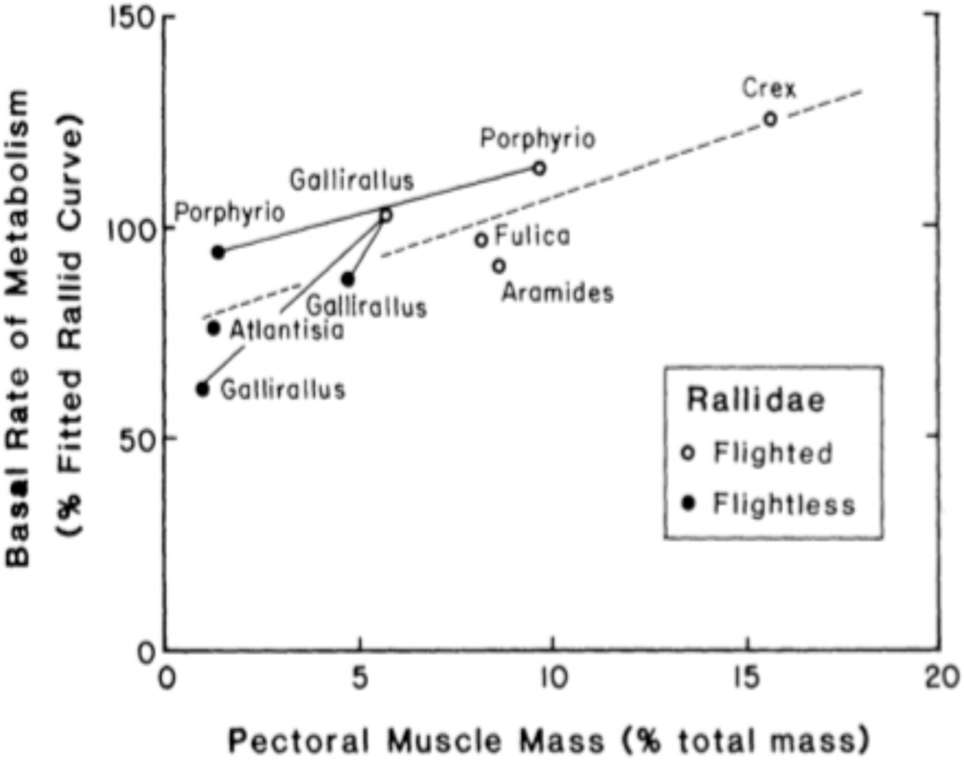

Figure 1.

A further study by Wilson demonstrates that when adding the cost of maintaining a flight apparatus into the foraging calculus, it is more energy efficient to swim when foraging within 750m of the nesting site (Wilson 644, see figure 2).

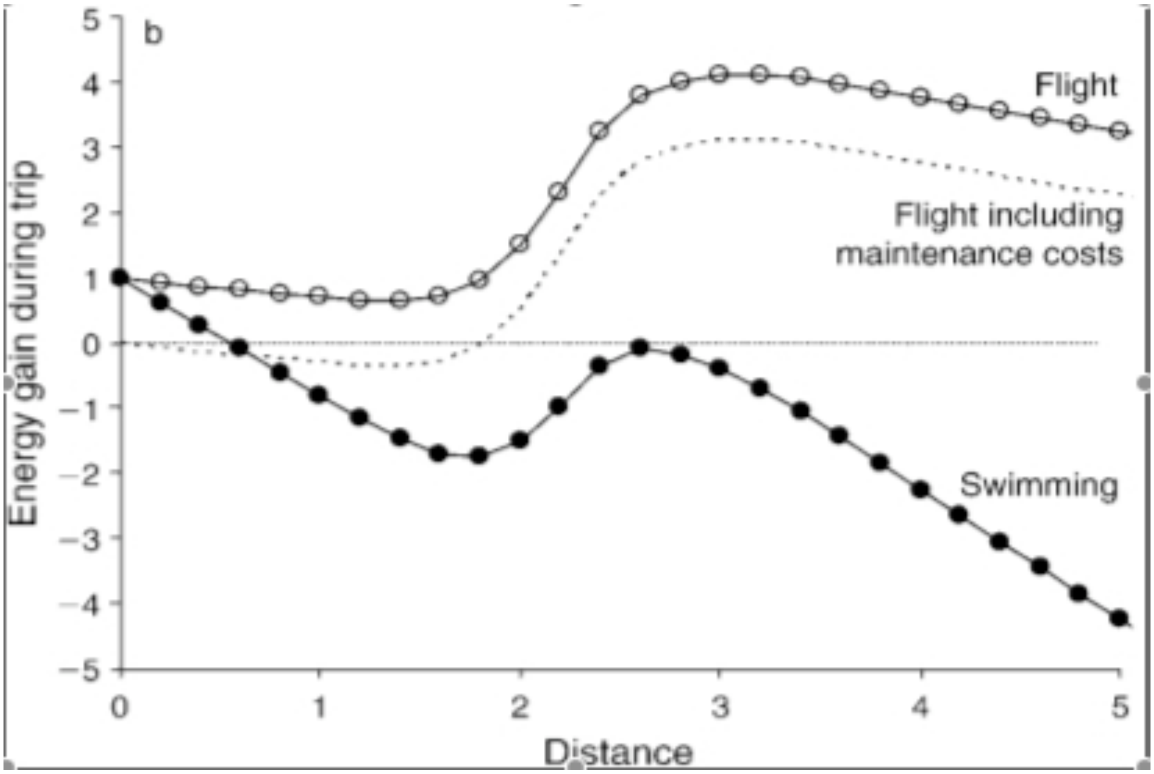

Figure 3

When studying the cormorants range we find that its mean distance from the nest is 700m while the mean distance from shore is 230m (Wilson 638).

TABLE 2. Movements of 16 female and 14 male Galápagos Cormorants equipped with GPS devices between 2003 and 2005.

| | | | Foraging distance (km) | | | |
|---|---|---|---|---|---|---|
| Distance category | Sex | No. GPS fixes | Mean | SE | SD | Maximum |
| From the nest | females | 54 166 | 0.659 | 0.003 | 0.731 | 5.453 |
| | males | 7370 | 0.892 | 0.014 | 1.202 | 6.356 |
| | both sexes | 61 536 | 0.687 | 0.003 | 0.806 | 6.356 |
| From the coastline | females | 9838 | 0.252 | 0.002 | 0.174 | 0.745 |
| | males | 2285 | 0.146 | 0.002 | 0.092 | 0.492 |
| | both sexes | 12 347 | 0.231 | 0.001 | 0.166 | 0.745 |

In effect, the cormorant stays within the foraging range where the cost of functional wings exceeds the energetic gains from flight. However, the following question arises: Is P. harrisi foraging within 700m form the nest because that is the only range where it can forage efficiently without flight or is this the region it would forage in even if it could fly and so the loss of flight is an added advantage? Two facts point towards the latter scenario. The waters around Fernandina and Isabella are rich in benthic fish, squid and crustaceans. This is due to the deep Cromwell current, which sweeps up the steep underwater cliffs of the Galapagos. As the Cromwell current upwells, it brings cold, nutrient rich waters to the surface (Kricher 25). The cold nutrient rich promotes high rates of phytoplankton growth (see Figure 3), which lead to high prey density and correspondingly low need for long foraging expeditions. Furthermore, since P. harrisi lost flight after it came to Galapagos it could only have lost flight ability if foraging in a 750m range.

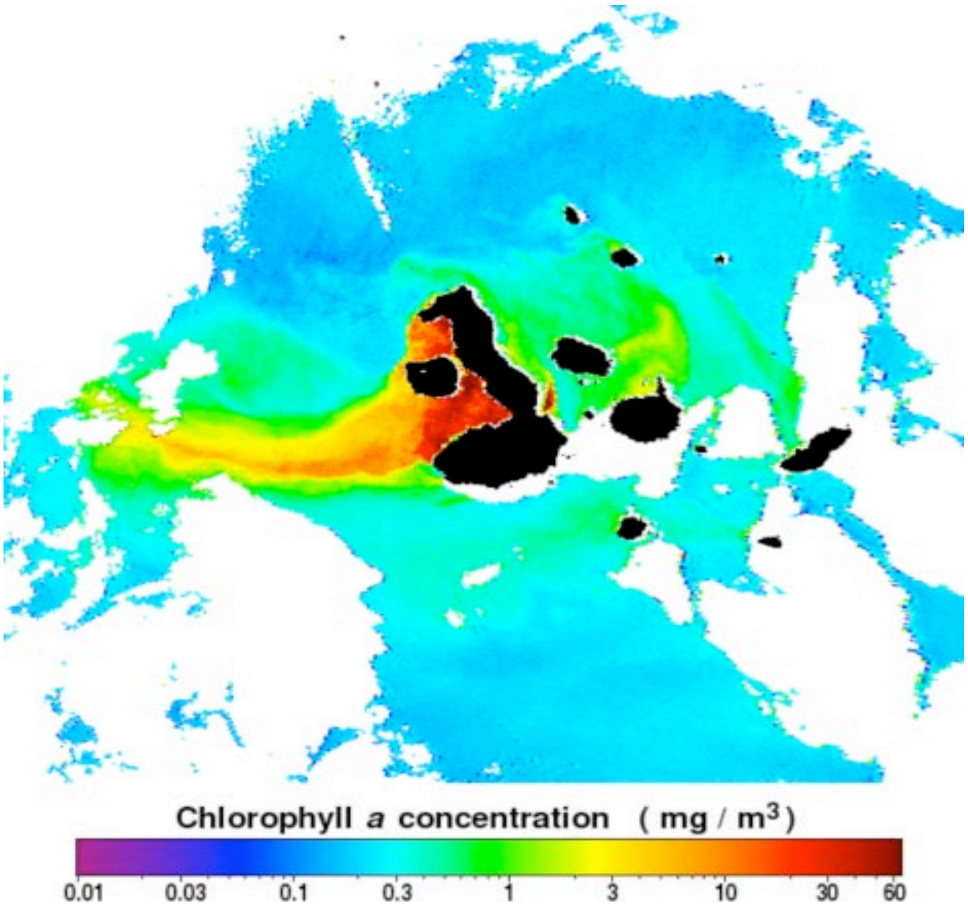

Figure 3 Courtesy of NASA Goddard's Ocean Color Team

Foraging within a greater radius requires flight ability to remain energetically profitable ands so the loss of flight would never be possible.

Interestingly, although loss of the pectoral apparatus limits the Flightless Cormorants foraging range, it makes it the means of foraging itself more efficient by improving diving efficiency and duration. The drag the flightless cormorant faces while diving is a function of body density, body girth and speed. The reduction in girth due to small pectoral muscles reduces underwater drag. In addition, drag is substantially dependant on vibration of primary and secondary feathers, which are underdeveloped in P. harrisi (Wilson 645). Diving birds must also expend energy to counteract upthrust underwater. Buoyancy due to air trapped within wings, however, is also reduced in the flightless cormorant due to diminutive, sparsely feathered wings (Roots 121). Thus the underdeveloped pectoral apparatus increases diving efficiency. In volant diving birds, pectoral muscles use body oxygen stores during diving at a disproportionately high rate, which compromises dive durations. This means that P. harrisi is able to increases its dive duration because of it underdeveloped pectoral muscle (Wilson 643).

In summary, the conditions that traditionally make flight advantageous (i.e predation, rare food resources) are not present in the Galapagos. This allowed it to lose its flight apparatus, which conserves energy when looking at a birds entire energy requirements including development, maintenance and diving.

The other striking morphological characteristics that distinguish P. harrisi from other cormorants, namely increased body mass and pelvic apparatus confer better diving ability. While the metabolic rate per unit of body mass decreases as body mass increases, oxygen storage capacity scales linearly with body mass (Wilson 640). As a result, the increased body mass of the flightless cormorant should allow it to store more oxygen but use less per unit time leading to longer maximum dive duration. In fact, when comparing average dive duration at different depths, P. harrisi consistently is able to stay underwater longer than most of its confamilials (Wilson 642, see figure 3). Longer dives allow for more prey caught in a given foraging expedition.

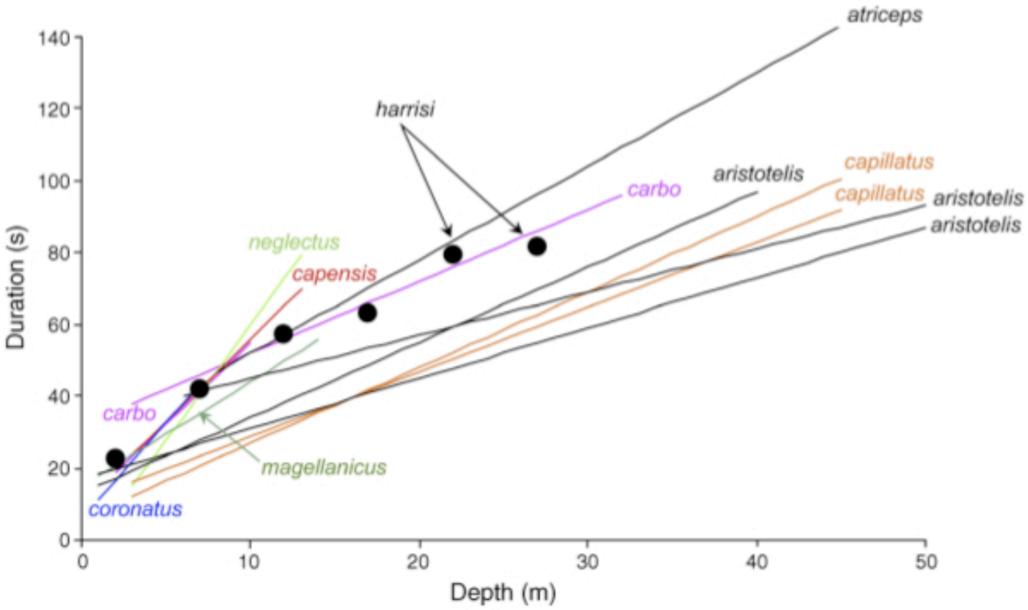

Figure 3.

An additional advantage of increased body mass is improved thermoregulation. As body mass increases, body size increases but the ratio between body volume surface area decreases. Having a relatively small surface area in turn decreases heat loss in the cold waters of the Cromwell current in which P. harrisi forages (Roots 120). Again, this may allow the cormorant to stay in the cold water longer and improves muscle performance. The overdeveloped pelvic apparatus and in particular the enlarged feet aid in foot propelled underwater locomotion leading to better foraging outcomes (Livezey 210, Roots 121).

The discussion of P harrisi's unique morphological traits and their adaptive value raises the question of how they originated. On a genetic level these traits arise due to changes in regulatory genes, which govern ontogentic timing. Changes in these genes lead to changes in development schedules and can be responsible for rapid evolution of novel phenotypes. Within an organism different regulatory genes can be responsible for the development of different loci. As a result separate characters can develop at different times and according to different rates (Livezey 349). The two major types changes in ontogetetic timing are paedomorphosis (underdelopment) and peramorphosis (underdevelopment). The flightless cormorant is an example of ontogenetic dissacociation wherein the pectoral apparatus is paedamorphic while the pelvic apparatus is peramorphic. The underdeveloped flight apparatus in particular is neotenic, meaning it develops at a reduced rate (Mlikovsky 701). As a result, when the organism as a whole ceases to develop, the wings, carina and pectoral musculature have not developed to completion and juvenile characteristics of the pectoral apparatus are retained in adulthood. The precise peramorphic mechanism for P. harrisi's hind limb is not known, although Lizevey believes hypermorphosis i.e prolonged growth is responsible. Although genetic mechanisms underlying P. harrisi's unique morphology are relatively well understood, evolutionary pressures responsible for the changes in ontogentic timing are less well known.

One hypothesis is that the reduced pectoral apparatus and the enlarged body mass were selected for during a time of prolonged severe food shortage. In this time of dearth, individuals who were able to forage efficiently dive longer and conserve energy survived. These advantages are conferred by a reduced pectoral apparatus and increased body mass and hence these traits were selected for. The there are however two difficulties with this theory.

If the basal metabolic rate scales with pectoral muscle mass as shown by McNab one would assume that it also scales with total body mass. It is hard to explain how in a time of food shortage, high body mass and the correspondingly high metabolic rates would be selected for. There are two possible explanations. If the advantage of more prey caught due to longer more efficient diving outweighs the disadvantage of higher total basal metabolic rate, high body mass would be selected for. But this doesn't necessarily have to be the case if the conditions weren't uniformly dire but were interspersed by periods of higher food ability at a frequency significantly higher than a Flightless Cormorant's life expectancy. Under this scenario we can assume that under food shortage, a low mass individual would still be better off than a high mass individual. Although the high mass bird can catch more prey it also has greater metabolic requirements, which put it at a net disadvantage. In the intermittent periods of abundance, however one would assume that the high mass bird can easily meet or even surpass its metabolic requirements. In other words, a large mass bird may be able to make better use of the abundant times and hence be better prepared for the times of dearth, giving it an overall advantage. The second difficulty is concerns the reduction of the pectoral apparatus.

In a period of food shortage we would expect prey densities to drop dramatically. This would require a successful individual to forage in unexploited areas. If swimming is less efficient than flying for foraging radii under 750m as Wilson demonstrates, being limited to swimming by a reduced pectoral apparatus and hence to the 750m radius would be a disadvantage and selected against. It is possible, however, that due to the steep western edge of the Galapagos plateau the water becomes to deep to quickly for the surface diving flightless cormorant to effectively reach its bottom dwelling prey. Foraging close to shore may be the best strategy regardless of flight ability. Thus, flight ability would be lost because of the advantages that the loss of the functional flight apparatus confers given the restricted foraging radius.

Alternatively one could hypothesize that the conditions today resemble those in the cormorants evolutionary past and that the morphological distinctions arose simply due to intraspecific competition.  In the discussion of the pectoral muscle and body mass of P. harrisi, it was shown how each of these traits confers advantages. Given Malthusian constraints, individuals with these traits would be at a competitive advantage in the struggle for existence. If this advantage is accompanied by greater reproductive success, the entire population of volant cormorants that originally populated the archipelago could secondarily become flightless.

Which if any of the two hypotheses is correct remains not only unknown but also indeterminable. The reason is that it impossible to determine the causation of a past, unobserved event, in this case the morphological change in the Flightless Cormorant. Although we can attempt to reconstruct the past using paleontological methods, the necessary data is not available in the case of P. harrisi.

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