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## Breeding Patterns of Galápagos Penguins as an Indicator of Oceanographic Conditions

Abstract. *Surface water changes associated with El Niño have been known to affect deleteriously top carnivores along coastal South America. Data on the breeding strategies of Galápagos penguins and other seabirds indicate that the biological effects of El Niño extend much farther west. The breeding biology of these seabirds is adapted to frequent changes in productivity which are associated with El Niño.*

Plants and animals living along the western coast of South America are dramatically affected by an influx of warm water called El Niño (*1*). The frequency, causes, and dimensions of El Niño are not well understood. Oceanographic conditions have been monitored during El Niño, but, despite our knowledge of the extent of physical changes, little is known about the short- and long-term impact on top carnivores. El Niño is accompanied by a large-scale decrease in the intensity of the southeast trade winds, an apparent weakening of coastal upwelling, and a rise in surface water temperatures (*2*). Offshore waters of higher temperature and salinity approach the coast as the upwelling subsides (*3*); warmwater animals appear off the Peruvian coast, and fish stocks become less available to seabirds which cease breeding and die in large numbers (*4*). It has been believed that the effects of periodic warming on seabirds and other animals were limited to the immediate coastal waters (*5*). However, the life-history patterns of the Galápagos penguin (*Spheniscus mendiculus*) show that El Niño affects seabirds far removed from coastal South America and are consistent with two hypotheses about the occurrence of warm water and its associated effects. They are (i) that El Niño occurs more frequently than every 7 years (*2, 6*) and (ii) that the circulation of the South Pacific subtropical gyre prior to El Niño is intensified as a result of strong southeast trade winds (*7*). The reproductive biology of the Galápagos penguin and other seabirds can be utilized to test these hypotheses.

A major El Niño event occurred in the Galápagos Islands in 1972. Because I was studying penguins during this same time period, I will use the 1972 El Niño event to document the normal changes in oceanographic conditions. During most of 1971, equatorial waters in the eastern tropical Pacific were colder than usual, an indication that equatorial upwelling was unusually intense. By January 1972, warm surface waters were present west of Peru but were warmest from June 1972 until January 1973. During the next 3 months, surface water temperatures decreased and normal upwelling conditions were restored (*3*).

The oceanic disturbance of El Niño extends over much of the eastern tropical Pacific, including the water surrounding the Galápagos Islands (*3, 5*). Maxwell measured fluctuations in salinity, primary productivity, and nutrient concentrations in the Galápagos Islands from September 1971 to July 1972 (*8*). These changes were synchronous with changes in the Peruvian water. Therefore, if this relationship between these two bodies of water is "normal," the effects of El Niño should be similar in the Galápagos Islands and along coastal South America.

The Peruvian Current is primarily responsible for the cool surface waters along coastal South America. However, Pak and Zaneveld (*9*) documented that the Cromwell Current flows eastward through part of the Galápagos Islands, and Maxwell (*8*) concluded that the Cromwell Current is responsible for the cool surface waters around Fernandina Island and Isabela Island. As is the case in other coastal environments, primary productivity is greatest when the surface temperature is coolest (*8*). Surface waters around Fernandina Island and western Isabela Island, which have the coolest waters of the island group, are normally between 15° and 22°C (*10, 11*). In keeping with earlier hypotheses for coastal South America, El Niño in the Galápagos Islands should occur more frequently than every 7 years. Moreover, if oceanic circulation is intensified by the trade winds preceding El Niño, the upwelling of the Cromwell Current should be magnified.

Seabirds such as the Galápagos penguin, flightless cormorant (*Nannopterum harrisi*), and brown pelican (*Pelecanus occidentalis*) should be particularly vulnerable to changes in upwelling since their diet consists primarily of small fish associated with the Cromwell Current. The distributions of Galápagos penguins and flightless cormorants are constrained by these cool surface waters (*11, 12*). Feeding frenzies, in which these seabirds repeatedly dive for fish, do not occur when surface waters are warm and schooling fish are presumably absent. Only three out of 25 feeding frenzies at Punta Espinosa, Fernandina Island, oc-


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curred when the temperature of the surface water was above 23°C.

During 1970, 1971, and 1972 I spent 169 days at Punta Espinosa studying Galápagos penguins (*13*). I also monitored the breeding of brown pelicans, which frequently feed on small schooling fish. The mean surface temperature during the breeding season of Galápagos penguins at Punta Espinosa was 22°C [standard deviation (S.D.) = 1°C]; no breeding occurs when mean surface temperatures rise to 25°C (S.D. = 2°C, $N = 31$; $t = 5.9$, $P < .001$) (*11*). Nesting failures during periods of warm surface waters (El Niño) further substantiated the correlation between cool, productive water and breeding (Fig. 1). Weight loss and nest desertion of adult Galápagos penguins during periods of warm seawater are also evidence that a decrease in the food supply is associated with warm water.

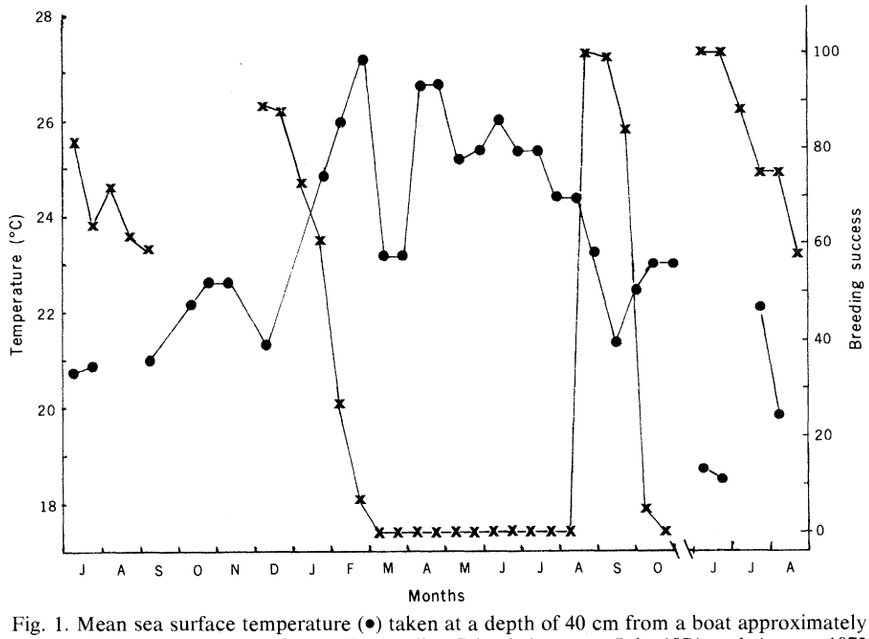


Fig. 1. Mean sea surface temperature (•) taken at a depth of 40 cm from a boat approximately 100 m offshore at Punta Espinosa, Fernandina Island, between July 1971 and August 1973 (standard error was ± 0.2°C for all months except January and February 1972 when it was 0.6°C). Sample size varied between 5 and 20. Galápagos penguin breeding success (x) is the number of active nests divided by the number of known nests. The number of known nests varied from $N = 3$, 1 to 15 December 1971, to $N = 111$, 1 to 7 September 1971 (*21*).

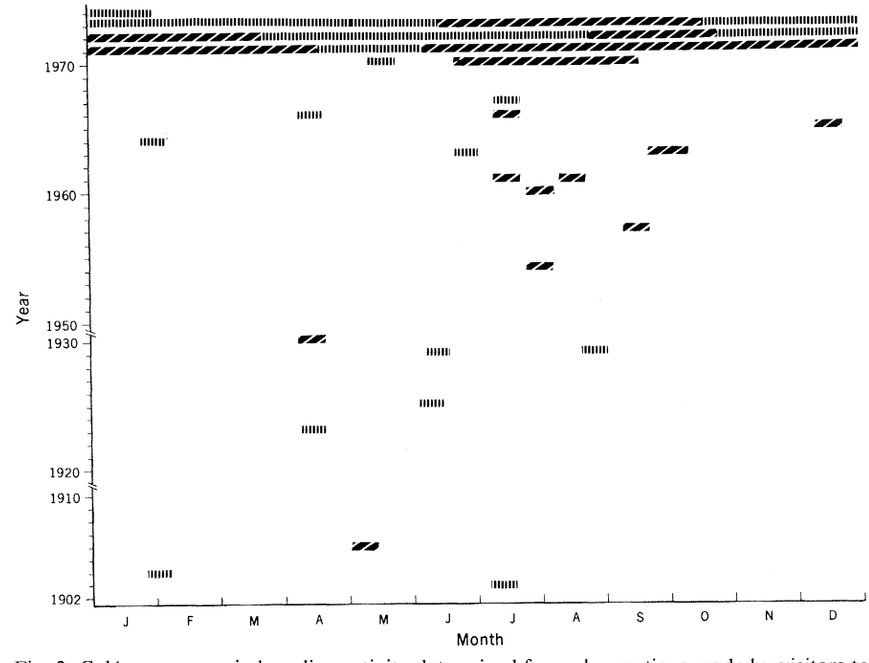


Fig. 2. Galápagos penguin breeding activity determined from observations made by visitors to Fernandina Island and Isabela Island (*7*). Continuous observations of breeding by tourist-boat guides and myself were made from mid-June 1970 until October 1972; ▮▮▮▮▮▮▮ = no breeding activity; ◪◪◪ = breeding (eggs or chicks).

The nesting failure of brown pelicans during 1972, an El Niño year, further documents the importance of cool, productive surface waters for the breeding success of these birds. Pelicans commenced egg-laying at Punta Espinosa on 29 August 1972. Out of 22 nests, only four nests (one with a single egg and the other three with a lone chick) survived 70 days. Two of the surviving nests had chicks that were emaciated. Eight other chicks found dead appeared to have starved. Thus, El Niño adversely affects several species of seabirds in the Galápagos. However, these data suggest nothing about the frequency of El Niño.

Breeding strategies of an organism are honed by natural selection over thousands of generations. Breeding biology, therefore, unlike physical measurements, is a long-term indicator of environmental conditions.

Other species of penguins, none of which are subjected to similar periodic interruptions of their food supply, molt after breeding (*14*). Reproduction and molting are perhaps the most energy-intensive activities of penguins and should occur when food is most readily available. Molting at least yearly is essential for survival. Thus, if breeding strongly reduces an individual's chance of molting successfully, molting should precede breeding or breeding should be skipped entirely. In seasonally variable environments with two plankton blooms, there should be little difference in adult survival whether molting occurs before or after breeding. Reproductive success, however, should be lower if breeding coincides with a smaller plankton bloom because less food would be available for the offspring. In environments where fluctuations in food availability are unpredictable, a penguin that breeds when food is abundant may be unassured of sufficient food after reproduction to complete the molt.

Molting as a prelude to breeding is an adaptation to unpredictable fluctuations in marine productivity associated with changes in upwelling. The fact that Galápagos penguins molt before breeding suggests that El Niño or food fluctuations are common. I found four adult penguins which had been dead less than 2 days and had just completed the molt. Their lack of fat reserves and their empty stomachs attested to death by starvation.

Most seabirds breed annually or biannually (*15*). During a 15-month period encompassing El Niño, 55 out of 75 pairs of Galápagos penguins bred twice and 18 pairs three times. This is the most frequent egg-laying cycle of any seabird of which I am aware. Energetically, egg-laying may be relatively inexpensive as compared to molting, incubation, and the rearing of young. Thus, if egg-laying is energetically inexpensive and if the frequency and duration of El Niño is unknown, selection would be expected to favor repeated breeding attempts, which should result in the highest reproductive success. The egg-laying pattern of Galápagos penguins suggests that there is no reliable proximate cue for conditions when young will be present.

El Niño should also affect broad areas of the life history of other seabirds subjected to the same selective pressures. I observed that brown pelicans and flightless cormorants bred at least twice in 1972. Individuals of these two species were not marked, but most of the same nests were occupied both times. If the duration and timing of upwelling is unpredictable, selection should likewise favor individuals which lay eggs when conditions are favorable since eventually upwelling will persist long enough to allow the young to be reared. The life-history strategies of the Galápagos penguin and other seabirds are adapted to surviving repeated and frequent El Niño events.

Weaker evidence in support of the idea that El Niño occurs frequently may be found in the historical record of Galápagos penguin breeding activity. Figure 2, constructed from casual observations of eggs and chicks in the literature as well as my own studies, indicates that oceanographic perturbations appear to be common.

Breeding has been reported in every month of the year but I found that it is most frequent in the cool, dry season (May through December) when 13 out of 16 observations of breeding were made (*16, 17*). Some observers have failed to find breeding activity during this period; this result suggests that the timing of breeding is not rigid. The timing of breeding coincides with the presence of a band of cool water which normally extends from the Galápagos to 140°W during the Southern Hemisphere winter (*3, 18*). During June through December the presence of a cold tongue of water is especially evident (*19*).

In the last 50 years, El Niño is known to have occurred along coastal South America in 1925, 1930, 1939, 1941, 1943, 1951, 1957, 1965, and 1972 (*5*). Reports of Galápagos penguin breeding exist for only 1930, 1957, 1965, and 1972. Even these records tend to support the abnormality of these years for penguin breeding (*17*). Two downy chicks were found in April 1930 but breeding in April is unusual (Fig. 2). A segment of Bowman's (*20*) 1957 research effort (he was there for 3 months) was devoted to finding breeding penguins. Therefore, it is surprising that only two nests with chicks and one copulation were seen. In December 1965, Harris (*10*), on the basis of an examination of numerous nesting sites, found only one nest with small chicks. Breeding was a total failure in 1972; that is, no chicks fledged. The paucity of breeding reports in El Niño years despite extraordinary effort to search out evidence of breeding activity is consistent with major known water anomalies. Furthermore, since cool water precedes egg-laying (Fig. 1), the irregular breeding record indicates that fluctuations in the surface water temperature are not uncommon. Although collecting and observing Galápagos penguins have been objectives of most expeditions, the dearth of breeding reports suggests that there have been frequent influxes of warm surface water. This record suggests the irregularity of cool surface water and concomitantly the presence of warm surface waters such as those occurring during El Niño.

Wyrtki (*7*) concluded that upwelling is greatest prior to an El Niño. If growth rates can be correlated with the productivity of the water, then Galápagos penguin chicks should grow faster in months prior to El Niño. In accord with this hypothesis, young grew faster in 1971 than in 1972 (*11*). The increase in marine productivity caused by stronger trade winds and consequent increased upwelling is documented by both chick growth and breeding success. In 1971, 63 out of 82 nests fledged one or two chicks each. Only one chick survived from 92 nests active in December 1972 through March 1973; all 108 nests failed to fledge chicks in the breeding period from August through October 1973. Galápagos penguin chick growth and breeding success are consistent with increased upwelling prior to El Niño.

Oceanographic parameters are intimately related to the distribution, growth, reproductive timing, and reproductive success of Galápagos penguins. El Niño affects the breeding history and reproductive success of the Galápagos penguin. Other seabirds far removed from coastal South America, such as the brown pelican, are subject to breeding failures associated with warm surface waters. Since minor El Niño events are presumably as frequent along the Peruvian coast as they are in the Galápagos, other seabirds that are dependent on upwellings could be used to monitor minor productivity changes. The breeding biology of seabirds may be useful reflections of long-term environmental conditions. The wide impact of El Niño on surface waters must have repercussions on seabird recruitment and mortality throughout at least coastal South America and the Galápagos Archipelago.

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