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BLOOD RESPIRATORY PROPERTIES IN SOME ANTARCTIC BIRDS

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INTRODUCTION

There exists a surprising shortage of information on the respiratory properties of avian blood. Although birds share homeothermy with mammals and require efficiency in O_2 transport matching or exceeding that of mammals, avian blood differs from that of mammals in important respects.

The present study compares blood respiratory properties in three species of penguins: the Adélie Penguin (*Pygoscelis adeliae*); the Gentoo Penguin (*P. papua*); and the Chinstrap Penguin (*P. antarctica*). Blood was obtained at various stages of development. The measurements and calculations included hematocrit (Hct), hemoglobin content (Hb), and mean corpuscular hemoglobin content (MCHC). The HbO_2 dissociation curves and their pH dependence (Bohr effect) were also determined. Less comprehensive information was obtained from the Giant Fulmar (*Macronectes giganteus*) and the antarctic Skua (*Catharacta skua*).

MATERIAL AND METHODS

The study was performed during the 1971 antarctic cruise of the research vessel *Alpha Helix* of the University of California. The animals were collected in the vicinity of Anvers Island near Palmer Research Station (64°45′ S–64°05′ W). The blood analysis was performed in the laboratories of *Alpha Helix*. The HbO_2 dissociation curves were determined employing the mixing method (Lenfant and Johansen 1965) and using a radiometer blood microsystem (BMS 3 and PHM 71) for measurement of blood gas tensions and blood pH. Hemoglobin content was measured spectrophotometrically after conversion to cyanmethemoglobin (Oser 1965). Hematocrit was measured in microhematocrit tubes after centrifugation for 10 min at 10,000 rpm.

The blood was collected from the brachial vein by percutaneous puncture. Heparin (1000 units per 5 ml blood) was used as an anticoagulant. Following collection, blood was stored on ice until used for analysis of respiratory properties.

RESULTS

Table 1 and figures 1 and 2 summarize the results. The three species of penguins studied are aquatic birds and practice habitual diving for feeding and migration. They all show high blood hemoglobin contents corresponding to O_2 capacities of about 22.5 vol% in Adélie and Gentoo Penguins and up to 27.5 vol% in the Chinstrap Penguin. It is of interest that the Chinstrap and to a lesser extent the Gentoo Penguin appear to practice longer periods of breath-holding between surfacings when diving, and they also dive to greater depths than the Adélie Penguin. The mean corpuscular hemoglobin concentration was closely similar in the species of penguins and averaged about 38%. The values for the nondiving petrel and Skua were lower (31–34%). The chicks of Adélie and Gentoo Penguins, 3–4 weeks old, both showed considerably lower hemoglobin concentrations than the

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TABLE 1. Blood respiratory properties of adult and young Antarctic birds.

Species	N	Hemoglobin content (g/100 ml blood ± SE)	Hematocrit (% ± SE)	MCHC (% ± SE)	P_{50} at pH 7.4 (mg Hg)	Bohr factor ($\Delta \log P_{50}/\Delta pH$)
P. adeliae[a]	8	16.49 ± 2.0	46.2 ± 2.5	37.6 ± 3.2	34.4	–0.505
P. adeliae[b]	12	11.05 ± 1.9	29.0 ± 3.8	37.6 ± 3.8		
P. papua[a]	5	16.44 ± 3.2	43.4 ± 6.7	38.0 ± 5.0	32.0	–0.562
P. papua[b]	6	11.88 ± 0.6	31.1 ± 3.0	38.5 ± 3.8		
P. antarctica[a]	6	19.57 ± 1.7	52.8 ± 3.4	37.7 ± 3.0	29.8	–0.618
Macronectes giganteus[a]	14	14.64 ± 2.6	43.4 ± 3.5	33.8 ± 3.8	42.5	–0.350
Catharacta skua[a]	2	13.97 ± 1.4	45.0 ± 2.0	31.0 ± 3.2	42.5	no data

[a] Adults.
[b] Chicks.

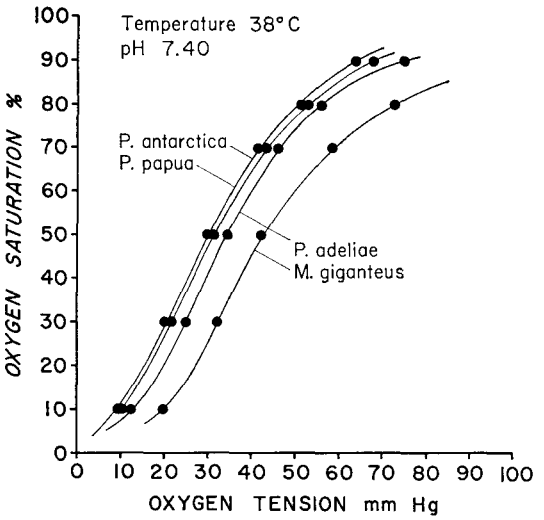

FIGURE 1. HbO_2 dissociation curves of selected antarctic birds.

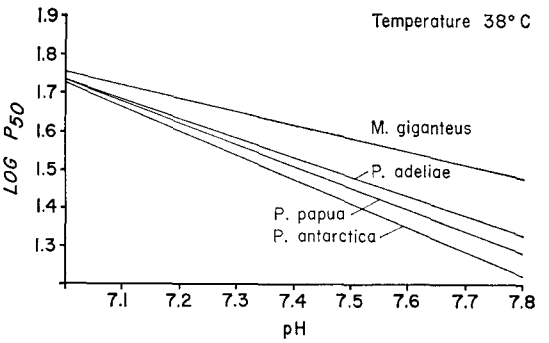

FIGURE 2. Bohr shifts ($\triangle$log P_{50}/$\triangle$log pH) of selected antarctic birds.

adults. The MCHC was, however, similar, showing that the larger O_2 carrying capacity of the adults is related to a higher hematocrit. The Giant Fulmar and the antarctic Skua show much lower hemoglobin concentration than the penguins.

The HbO_2 dissociation curves (fig. 1) show interesting features, such as the higher O_2 affinities in the diving forms. Similarly, among the divers, the Chinstrap and Gentoo Penguins practice longer periods of submersion than the Adélie Penguin and show the highest affinities. The Bohr shifts (fig. 2) show a similar correlation with diving habits, being lowest in the Giant Fulmar and highest in the Chinstrap (0.618) (fig. 2).

DISCUSSION

The hemoglobin values of the Giant Fulmar and antarctic Skua fall in the range typical of terrestrial mammals and nondiving birds. The Fulmar (*Fulmarus glacialis*) and Herring Gull (*Larus argentatus*) have 14.1 and 12.9 g Hb/100 ml blood, respectively (Clausen et al. 1971). Pigeons are distinguished by high hematocrits, 50% or more, with hemoglobin values in the range of 16–20 g/100 ml blood (Bond and Gilbert 1958). Whether the high values in pigeons are related to their superb ability for flight must remain conjectural since values from other excellent fliers are not available. Hb values in typical sedate birds such as chickens range from 9.5 to 13.5 g/100 ml blood (Holmes et al. 1933).

Habitual diving in birds, as in mammals, is associated with increased hematocrits and Hb levels (Rostorfer and Rigdon 1947). Diving ducks have reported values as high as 18 g/100 ml blood (Bond and Gilbert 1958). An earlier study on penguins (Lenfant et al. 1969) reports 16.3 g/100 ml blood for the Adélie Penguin and 16.5–17.2 g/100 ml blood for two specimens of the Emperor Penguin (*Aptenoides fosteri*). The mean corpuscular hemoglobin concentration in birds ranges from 30–45% (Bell et al. 1964; Usami et al. 1970). These values tend to be higher than those for mammals, and the values for diving forms tend to exceed those of terrestrial ones.

The limited data on HbO_2 dissociation published for birds show that flying birds have curves displaced to the right of typical mammalian curves. It has been suggested that the reduced affinity of bird blood for O_2 can be referred to their higher deep-body temperature which would displace the HbO_2 equilibrium to the right. This has been countered by Danzer and Cohn (1967) who compared human and goose blood at 37.5° and showed that the goose retained a significantly lower affinity for O_2. It has also been suggested recently that this lower affinity measured in bird blood is an artifact related to methodical deficiencies for determination of HbO_2 dissociation curves (Lutz, et al. 1973). The nucleated red cells of birds have such a high metabolic rate that all methods employed will show lower PO_2 values than suggested by the gases used for tonometry.

A low affinity for O_2 coupled with efficient ventilation and perfusion systems in birds will promote O_2 delivery to tissues by steepening the diffusion gradients between the capillaries and metabolizing cells. It is reasonable that diving birds benefit from a relatively high HbO_2 affinity that aids in a quick reoxygenation of blood during the often very brief periods between dives. A high affinity will also allow continued use of the pulmonary gas stores as they become depleted during a dive. The reduced unloading potential of blood with a high HbO_2 affinity can be partially offset by an increased Bohr shift which, from the present comparison of species, appears to be an adjunct to the diving habit (fig. 2). A more extensive examination of aquatic and terrestrial birds (Johansen, unpubl. data) has substantiated the trend for the diving forms to show higher HbO_2 affinities and higher Bohr factors. Lenfant et al. (1969) presented dissociation curves for the Adélie Penguin with a P_{50} value (35 mmHg) and a Bohr factor (−0.49) closely similar to the presently obtained values. These authors interpret the high affinity to accrue the same advantage as suggested above but feel that the Bohr factor is lower than typical for nondiving forms.

A comparison of potential adaptive values of blood respiratory characteristics in birds must often remain conjectural because behavioral traits such as ability for long continuous exercise (flying or swimming) can be present together with tolerance to O_2 deficiency from diving or in some cases from flying at high altitude.

Among the species presently compared the penguins seem, however, to show adaptive features of the blood to their diving and swimming habits.

SUMMARY

Blood respiratory properties have been compared in antarctic birds. Blood hemoglobin content, hematocrit, and mean corpuscular hemoglobin concentration (MCHC) are higher in three species of penguins than in the Giant Fulmar and the antarctic Skua. Penguin chicks show lower hemoglobin values than adults. HbO_2 dissociation curves show higher affinity in diving than nondiving birds. Among penguins, the Chinstrap Penguin, practicing longer and deeper dives, has blood with higher O_2 affinity than the other species. The Bohr effect is similarly higher in diving than nondiving birds. The adaptive value of the blood respiratory properties is discussed in the context of behavior and mode of life of the species studied.

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OBSERVATIONS ON NEW OR UNUSUAL BIRDS FROM TRINIDAD, WEST INDIES, AND COMMENTS ON THE GENUS *PLEGADIS* IN VENEZUELA

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Since the days of Leotaud (1866) and later Chapman (1894), the avifauna of the island of Trinidad, West Indies, has received considerable study. Major faunal reports by Belcher and Smooker (1934, 1935, 1937) and by Junge and Mees (1958) were substantially updated by the work of Richard and Margaret ffrench (1966) who published an account of new distributional records, and whose continued residence on the island since 1958 has led to the accumulation of much new information (ffrench 1973a). Herklots (1961) published a popular guide to Trinidadian birds, which proved to be only moderately reliable, and it has been properly reviewed by Collins (1962). A variety of biological studies of the birds themselves have been implemented by Williams (1922), by ffrench (1967), and by several workers at the New York Zoological Society field station in the Arima Valley, particularly David and Barbara Snow (e.g., Snow and Snow 1964).

Much of the field work has involved primarily the forest birds of Trinidad, and by comparison, the marsh avifauna has received relatively little attention. Belcher and Smooker (1934, 1935, 1937) collected a considerable number of birds and eggs in marshes on the periphery of the Caroni Swamp. A. Rasool collected birds on Trinidad in 1950 and 1951, apparently spending considerable time in marsh habitats. His specimens are deposited in the Peabody Museum at Yale University. C. B. Worth (1963) studied bird populations in the Nariva Swamp in connection with research in ecology of viral diseases. ffrench (ffrench and Haverschmidt 1970) conducted a detailed study of the Scarlet Ibis (*Eudocimus ruber*) in the Caroni Swamp. In view of the incomplete information available on the marsh-dwelling birds, the accompanying records are offered.

In 1965 I spent several months in Trinidad, and during my field work I observed several species previously considered rare or unknown on Trinidad. This report clarifies the status of some of these species. Only sight records are included here since the collecting of specimens was not part of my project. Details of the observations are provided for those species where identification in the field may be difficult. I deal here only with the marsh-dwelling species encountered during my field work. Several groups of ornithology students have visited the marsh subsequently; Guy Tudor and Robert Ridgely have made available to me a considerable amount of observational data.

STUDY AREA

From February to May 1965, I studied the avian ecology of a marsh along the Caroni River in northwestern St. George Co., Trinidad. The study area included a series of fresh and slightly brackish impoundments in the Laventille Swamp near Lapaille