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 O2 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 hematoctit (Hct), hemoglobin content (Hb), and mean corpuscular hemoglobin content (MCHC). The Hbo2 dissociation curves and their pH dependence (Bohr effect) were also determined. Less comprehensive information was obtained from the Giant Petrel (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 Hbo2 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 O2 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 3%. 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 adults and Bonaire. Stud. Fauna Curacao, Caribb. Islands 7:1-200.


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

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>Hemoglobin content (g/100 ml blood ± SE)</th>
<th>Hematoctit (% ± SE)</th>
<th>MCHC (% ± SE)</th>
<th>P50 at pH 7.4 (mg Hg)</th>
<th>Bohr factor (Δlog P50/ΔpH)</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. adeliae*</td>
<td>8</td>
<td>16.49 ± 2.0</td>
<td>46.2 ± 2.5</td>
<td>37.6 ± 3.2</td>
<td>34.4</td>
<td>-0.505</td>
</tr>
<tr>
<td>P. adeliae*</td>
<td>12</td>
<td>11.65 ± 1.9</td>
<td>29.0 ± 3.8</td>
<td>37.6 ± 3.8</td>
<td>32.0</td>
<td>-0.562</td>
</tr>
<tr>
<td>P. papua*</td>
<td>5</td>
<td>16.44 ± 3.2</td>
<td>43.4 ± 6.7</td>
<td>38.0 ± 5.0</td>
<td>42.5</td>
<td>-0.350</td>
</tr>
<tr>
<td>P. papua*</td>
<td>6</td>
<td>11.88 ± 0.6</td>
<td>31.1 ± 3.0</td>
<td>38.5 ± 3.8</td>
<td>29.8</td>
<td>-0.618</td>
</tr>
<tr>
<td>P. antarctica*</td>
<td>6</td>
<td>19.57 ± 1.7</td>
<td>52.8 ± 3.4</td>
<td>37.7 ± 3.0</td>
<td>32.0</td>
<td>-0.350</td>
</tr>
<tr>
<td>Macronectes giganteus*</td>
<td>14</td>
<td>14.64 ± 2.6</td>
<td>43.4 ± 3.5</td>
<td>33.8 ± 3.8</td>
<td>42.5</td>
<td>no data</td>
</tr>
<tr>
<td>Catharacta skua*</td>
<td>2</td>
<td>13.97 ± 1.4</td>
<td>45.0 ± 2.0</td>
<td>31.0 ± 3.2</td>
<td>42.5</td>
<td>no data</td>
</tr>
</tbody>
</table>

* Adults.

* Chicks.
FIGURE 1. HbO₂ dissociation curves of selected antarctic birds.

adults. The MCHC was, however, similar, showing that the larger O₂ 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 HbO₂ dissociation curves (fig. 1) show interesting features, such as the higher O₂ 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.

FIGURE 2. Bohr shifts (Δlog P₅₀/Δlog pH) of selected antarctic birds.

The limited data on HbO₂ 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 O₂ can be referred to their higher deep-body temperature which would displace the HbO₂ 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 O₂. It has also been suggested recently that this lower affinity measured in bird blood is an artifact related to methodological deficiencies for determination of HbO₂ 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 PO₂ values than suggested by the gases used for tonometry.

A low affinity for O₂ coupled with efficient ventilation and perfusion systems in birds will promote O₂ 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 HbO₂ 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 HbO₂ 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 HbO₂ affinities and higher Bohr factors. Lenfant et al. (1969) presented dissociation curves for the Adélie Penguin with a P₅₀ 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 O₂ 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, hemato-
crit, 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. HbO₂ dissociation curves show higher affinity
in diving than nondiving birds. Among penguins,
the Chinstrap Penguin, practicing longer and deeper
dives, has blood with higher O₂ 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.

ACKNOWLEDGMENT

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LITERATURE CITED

BELL, D. J., T. P. BIRD, AND W. M. McINDO00. 1964.
Changes in erythrocyte levels and mean corpus-
cular haemoglobin concentrations in hens during
the laying cycle. Comp. Biochem. Physiol. 14:
83.
BOND, C. F., AND P. W. GILBERT. 1958. Comparative
study of blood volume in representative aquatic and non-aquatic birds. Amer. J. Physiol.
194-519.

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 ffrrench
(1966) who published an account of new distribu-
tional records, and whose continued residence on the
island since 1958 has led to the accumulation of much
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 Zo-
ological 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, appar-
tently 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. ffrrench (ffrench
and Haverschmidt 1970) conducted a detailed study
of the Scarlet Ibis (Eudocimus ruber) in the Caroni
Swamp. In view of the incomplete information avail-
able 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 spe-
cies. Only sight records are included here since the
collecting of specimens was not part of my project.
Details of the observations are provided for these spe-
cies where identification in the field may be difficult.
I deal here only with the marsh-dwelling species en-
countered during my field work. Several groups of
ornithology students have visited the marsh subse-
quently; 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 north-
western St. George Co., Trinidad. The study area
included a series of fresh and slightly brackish im-
ponds in the Laventille Swamp near Lapaille

Clausen, G., B. Sanson, and A. Storefjord. 1971.
The HbO₂ dissociation curve of the fulmar and the herring gull. Respir. Physiol. 19:66-70.
Danzer, L. A., and J. E. Cohn. 1967. The dis-
Holmes, A. D., M. G. Piggot, and P. A. Campbell.
Lenfant, C., and K. Johansen. 1965. Gas trans-
port by the hemocyanin containing blood of the cephalopod, Octopus dofleini. Amer. J. Physiol.
209:991-998.
Lenfant, C., G. L. Kooymans, R. Elsner, and C. M.
J. Physiol. 216:1598-1600.
Lutz, P. L., I. S. Longmuir, J. V. Tuttle, and K.
Schmidt-Nielsen. 1973. Dissociation curve of bird blood and effect of red cell oxygen consump-
Oser, B. L. [Ed.]. 1965. Hawk's physiological chem-
Rostorfer, H. H., and R. H. Rigdon. 1947. The
relation of blood oxygen transport to resistance to
Usami, S., V. Magazinovic, S. Chien, and M. I.
Res. 2:489.

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