ASPECTS OF THE DIVING BIOLOGY OF COMMON MURRES

(*Uria aalge*)

by

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Title: ASPECTS OF THE DIVING BIOLOGY OF COMMON MURRES (Uria aalge)

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Aspects of the diving biology of Common Murres (Uria aalge) were investigated. Dive durations and corresponding rest durations were measured in free-ranging birds. Lactic acid levels were measured in blood samples taken from nondiving birds, and from diving birds upon surfacing.

Dive durations increased linearly with depth of water. Rest duration increased with dive duration, the rate of increase rising steeply after dive durations reached approximately 2 minutes. The mean blood lactic acid level of murres diving 105 seconds or less did not differ significantly from that of nondiving murres. Murres diving for 2 minutes or longer showed a mean blood lactic acid level significantly higher than that of birds diving 105 seconds or less.

The results suggest that at some point during

submergence there is a substantial increase in dependence on glycolysis. This shift in metabolism appears to occur between dive durations of 105 seconds and 2 minutes.

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INTRODUCTION

Investigations into the biology of diving birds and mammals have revealed numerous biochemical and physiological adaptations that allow these animals to endure extended periods of submergence. Since the lack of available oxygen may be the most imposing restriction on a diving bird or mammal, it is not surprising to find that these animals exhibit several physiological processes that act to forestall hypoxia and prolong the dive.

One means of extending dive duration is an increase in the capacity to store oxygen. Guthrie (1926) calculated oxygen storage capacities in domestic ducks and chickens, based on blood volume and blood oxygen capacity. Based on calculated rates of oxygen consumption per kilogram of body weight, he found that the maximal oxygen storage capacities of ducks are almost twice as high as those of chickens. More recently, Lenfant et al. (1969) found oxygen capacities of 22.4 (vol.%) for the Adelie Penguin (Pygoscelis adeliae) and 20.1 for the California Murre (Uria aalge californica), whereas Chiodi and Terman (1965) found an oxygen capacity of 14.0 (vol. %) for the domestic hen. Another comparison of blood volumes in aquatic and nonaquatic birds showed that in general aquatic birds have larger blood volumes,

larger erythrocyte volumes (per unit of body weight), and higher concentrations of hemoglobin, than do nonaquatic birds (Bond and Gilbert, 1958). California Murres were found to have a hematocrit of 50 (vol. %) and a hemoglobin concentration of 15.1 g/cm^3 (Lenfant et al., 1969), as compared to a hematocrit of 34 (vol. %) and a hemoglobin concentration of 10.4 g/cm^3 for the chicken (Chiodi and Terman, 1965). A study of oxygen storage capacities of phocid seals and otariid seals revealed that the phocid seals, which habitually dive deeper and for longer duration than do otariid seals, have total oxygen storage capacities of more than twice those of the otariid seals studied (Lenfant et al., 1970).

A second means of increasing oxygen storage is an increase in tissue concentrations of myoglobin. The presence of large amounts of myoglobin in the muscles of diving birds is indicated by the deep red color of these muscles. Scholander (1940) found that the pectoral muscles of penguins contained 4 volumes per cent of oxygen, an amount which was consumed within 5 minutes of submersion. Robinson (1939) found that a sample of harbor seal muscle contained 7,715 mg of myoglobin per 100 gm of muscle, over seven times the quantity (per gram) as did samples of beef muscle.

Although diving vertebrates generally tend to have

greater capacities for oxygen storage than do nondivers, the additional oxygen stored is not sufficient to allow for the prolonged dive durations which they commonly endure. Other physiological and biochemical processes must be operating to conserve or supplement oxygen stores.

Forced-dive experiments testing the effects of and responses to hypoxia in many vertebrates demonstrated distinct decreases in heart rates during submersion (Scholander, 1940; Butler and Taylor, 1973). Bradycardia has been found to occur in all vertebrates studied, including nondivers, although the rate and extent of cardiac slowing varies. Cook et al. (1977) found that the heart rate of the Maccoa Duck (Oxyura maccoa), a specialist diver, decreased to 24.7% of the pre-dive rate during submergence, whereas in the Cape Shoveller (Anas smithii), a duck that rarely dives, heart rate during submergence only decreased to 58.7% of the pre-dive rate. In seals the heart rate decreased to 30% of the pre-dive value immediately upon submergence (Scholander, 1940). However, recent studies indicate that while bradycardia occurs in free-ranging animals, the effect is not nearly so pronounced as it is in forced-dive experiments (Elsner et al., 1964; Elsner et al., 1966; Kooyman and Campbell, 1972).

Another physiological adjustment seen in diving vertebrates and associated with the onset of bradycardia

is a redistribution of circulating blood. Blood flow to many parts of the body, including that to most skeletal muscle, is essentially shut down, while blood flow to the heart and brain remains constant or increases (Irving, 1934; Johansen, 1964). This adjustment in circulation has been demonstrated in many vertebrates, including seals, ducks, and penguins (Scholander, 1940; Johansen, 1964), alligators (Andersen, 1961), and snakes (Murdaugh and Jackson, 1962). Johansen (1964) demonstrated that peripheral vasoconstriction may act selectively, supplying blood to organs most essential for the animal's underwater activities.

Scholander (1940) found that seals and ducks were able to remain submerged much longer than their oxygen stores would last if the metabolic rate during diving were the same as the pre-dive metabolic rate. Similarly, Andersen (1959a) foundthat oxygen consumption of domestic ducks during submergence was only 20% of the predive level. These investigators suggested that the relatively low rates of oxygen consumption were due to decreased metabolism during submergence. Further study demonstrated a reduction in heat production in seals and ducks during submergence, supporting the hypothesis of decreased metabolism (Scholander et al., 1942; Andersen, 1959a).

The physiological processes mentioned above help

to prolong the period of aerobic metabolism. However, once the oxygen supply from the blood hemoglobin and tissue myoglobin is reduced, the organism must rely to a greater extent on anaerobic glycolysis. Although glycolysis allows for rapid energy production, the energy yield per unit of fuel is only one twelfth that of aerobic metabolism (Bartholomew, 1977). Anaerobiosis results in the production and accumulation of lactic acid which, in quantity, may disrupt the pH of the blood, and thereby limit the time an animal can utilize anaerobic metabolism. In poikilotherms anaerobiosis may account for most of the ATP production during activity, while in homeotherms it is generally believed to be of primary importance during short bursts of intense activity (Bartholomew, 1977).

Few studies have been done to determine the roles of aerobic versus anaerobic metabolism in free-ranging diving vertebrates. Some investigators believe that diving vertebrates depend entirely upon aerobic metabolism during the majority of their dives, and that anaerobiosis is utilized primarily as a safety mechanism, during escape from predators, or during unusually long foraging and exploration dives (Seymour, 1979; Kooyman et al., 1980; Butler, 1982). Kooyman et al., (1980) found that post-dive arterial lactic acid concentrations in free-ranging

Weddell seals (Leptonychotes weddelli) did not differ significantly from resting levels unless the previous dive exceeded 20-25 minutes in duration. Dives exceeding 20-25 minutes presumably exhaust oxygen supplies, and force the animal to depend to a greater extent on glycolysis. Overall, less than 3% of the monitored dives of free-ranging Weddell seals exceeded this limit, requiring an increase in anaerobiosis.

Studies have shown that lactic acid accumulates in the muscles of diving vertebrates during submergence and is released into the circulating blood when breathing is resumed (Scholander et al., 1942; Andersen, 1959a; Andersen et al., 1965; Kooyman et al., 1980). Under laboratory conditions, Scholander (1940) found that the blood lactate concentration in captive diving Gentoo Penguins (Pygoscelis papua) increased gradually during submergence, followed by a steep increase in lactic acid levels upon emergence. A similar pattern was seen in blood lactic acid levels of captive diving ducks (Andersen et al., 1965). During 13 minutes of submergence the lactic acid level rose from a predive value of 2.0 mmol/l to 5.1 mmol/l. An additional increase of 8.5 mmol/l was seen upon emergence. Thus in these diving birds there is a slow leakage of lactic acid to the circulating blood during submergence. Data from these studies indicate that anaerobic glycolysis begins

to operate early during the submergence period.

Unfortunately, blood lactic acid levels have not been measured in diving birds under natural conditions. Many marine birds regularly perform extended foraging dives. However, few data are available from direct measurements of dive durations and depths attained by these birds. Dewar (1924) reported depths, based largely on fish net mortalities, and dive durations for a number of aquatic birds. He concluded that birds are probably incapable of dives exceeding three minutes in duration, and rarely dive deeper than 30 meters. Schorger (1947) reported that Common Loons (Gavia immer) and Oldsquaws (Clangula hyemalis) were often caught in fish nets in the Great Lakes at depths of 60 meters. The longest dive he observed for an Oldsquaw was 70 seconds, in 10.5 meters of water.

Seabirds such as Macaroni Penguins (Eudyptes chrysolophus) and Gentoo Penguins have endured forced submersions of 5 minutes and 7 minutes, respectively (Scholander, 1940). Under more natural conditions, Kooyman et al. (1971) recorded a maximum dive duration of over 18 minutes, and a maximum depth measured by depth recorder, of 265 meters, for the Emperor Penguin (Aptenodytes forsteri). King Penguins (Aptenodytes patagonica) have been known to attain depths of over 240 meters (Kooyman et al., 1982).

Common Murres (Uria aalge) are ideal animals for a

study of diving biology of birds in their natural environment. These birds are wing-propelled divers that spend virtually their entire lives at sea, and are absolutely dependent on diving for prey capture. Near the Oregon coast large numbers of swimming Common Murres can be easily observed from a boat during the breeding season (April-September). Many of these murres are adult-chick pairs. During this time the chicks cannot fly, and cannot dive effectively. The chicks are unable to capture prey items (e.g. fish and squid) for themselves, and therefore are totally dependent upon the parent birds.

There are two notable features of murre behavior that allow for the accurate measurement of dive and rest durations of adult birds accompanying chicks. First, immediately prior to diving, the adult's abdomen appears to swell and is raised slightly from the water surface, serving as a cue to the observer that the bird is about to dive. Second, the surfacing of the adult is easy to document because the adult usually emerges from a dive close to the chick and calls to the chick immediately.

Because Common Murres are readily available and easily observed, a study was designed to investigate some aspects of their diving biology under natural conditions. Specifically, the following questions were asked: How long does a foraging Common Murre prolong a dive? Is dive duration

related to depth of water? Is the rest period following a dive related to duration of the dive? Is lactic acid present in the blood, and if so, is the concentration related to dive duration? Is there a specific time during a dive at which there is a noticeable shift to greater dependence on anaerobic metabolism? Is anaerobic metabolism commonly required during diving?

MATERIALS AND METHODS

Blood samples were taken from Common Murres (Uria aalge) collected from the ocean near Coos Bay, Oregon, between 1 July 1982 and 10 September 1982. Collection sites were located between 1 and 10 km off-shore and varied in depth from 11 to 95 meters.

Birds were observed from an inflatable boat for periods between 2 and 15 minutes. During this period dive durations and successive rest durations were measured by stopwatch and recorded. Additional data on dive times, acquired during the summers of 1978 and 1980, were supplied by Dr. Daniel H. Varoujean of the Oregon Institute of Marine Biology.

Adult birds were shot upon surfacing from dives and immediately retrieved. The body cavities were opened and 1.0 ml of blood taken by heart puncture with an 18 gauge needle and 2.5 ml capacity syringe. Each blood sample was immediately injected into a refrigerated vacuum sealed test tube containing 2 ml of an 8% aqueous perchloric acid solution. The test tubes were shaken vigorously for 30 seconds and stored on ice until lactate analyses were carried out. Blood samples from nondiving chicks and adults were collected and prepared in the same manner as

outlined above. Samples were taken from 1 adult female and 17 adult males, weighing between 835 and 1140 gm (mean = 960, SD = 94). Samples were taken from 2 female chicks and 3 male chicks, weighing between 425 and 925 gm (mean = 735, SD = 206).

Blood lactic acid assays were performed within 48 hours of sample collection. Blood samples were centrifuged for ten minutes at 3000 x g in a N10B Sorvall centrifuge. Lactic acid levels were determined using Sigma Chemical Co. kit #826-UV. The analysis is based on the following reaction:

$$\text{pyruvic acid} + \underset{(\text{High } A_{340})}{\text{NADH}} \overset{\text{LDH}}{\rightleftharpoons} \text{lactic acid} + \underset{(\text{Low } A_{340})}{\text{NAD}}$$

In the presence of lactic dehydrogenase (LDH) and excess nicotinamide adenine dinucleotide (NAD), the reaction proceeds to the left. The resulting formation of NADH causes an increase in Absorbance at 340 nm, which provides a measure of the lactic acid originally present.

The procedure outlined here is for analysis of one blood sample, in replicate. The following reagents were pipetted into each of 2 vials (each containing 10 mg NAD): 2.0 ml glycine/hydrazine buffer (pH 9.2), 4.0 ml distilled water, 0.1 ml lactic dehydrogenase. Each vial was inverted several times. The contents of the two vials were combined, and 2.8 ml of the resulting mixture

was pipetted into each of 3 disposable 3 ml cuvettes. A reference was prepared by addition of 0.2 ml of 8% perchloric acid solution to one of these cuvettes. To each of the two remaining cuvettes was added 0.2 ml of sample supernatant. All cuvettes were then incubated at 25° C for one hour. The absorbance of each sample cuvette was read at 340 nm on a Zeiss PMQ II spectrophotometer and recorded. Concentrations of lactic acid were calculated directly from absorbance readings as follows:

$$\text{Blood lactic acid (mmol/l)} = \text{Absorbance}_{340} \times 7.23$$

$$\text{Blood lactic acid (mg/100 ml)} = \text{Absorbance}_{340} \times 65.1$$

Figures are given to the nearest hundredth.

Statistical analysis of the data included Student's t-test, regression analysis, and one-way analysis of variance.

RESULTS

The maximum dive time recorded for a murre in this study was 200 seconds, in 86 meters of water, whereas the shortest dive was 20 seconds, in 23 meters of water. The mean dive time was 91.5 seconds (n = 174). Linear regression analysis of the dive data (Figure 1) shows that dive duration is a linear function of depth of water ($P < 0.5$, $r^2 = 0.4$, $n = 174$).

The relationship between duration of dive and duration of corresponding rest period is best expressed by the logarithmic regression equation $y = 5.66e^{0.02x}$ (Figure 2). The data points representing dive durations of less than about 2 minutes appear to be evenly distributed about the regression line, while most points for dives exceeding 2 minutes lie above the line. This indicates that there is a change in the relationship between dive and rest durations when dive times reach approximately 2 minutes. In general, rest periods increase with longer dives, the rate of increase rising steeply after dive durations of approximately 2 minutes.

Ratios of dive duration to the duration of the subsequent rest period were calculated and expressed as a function of dive times (Table 1; Figure 3). Dive-rest

ratios tended to decrease with increasing dive duration, when dives exceeded approximately 2 minutes.

Results of analyses of lactic acid content of murre whole blood are presented in Table 2. Blood lactic acid levels in nondiving adults ranged from 3.22 mmol/l to 4.75 mmol/l, with a mean value of 4.03 (n = 5). The maximum lactic acid level in a diving bird was 8.39 mmol/l, and the minimum was 2.36 mmol/l, with a mean value of 5.08 mmol/l (n = 12). Lactic acid levels in chicks ranged from 1.33 mmol/l to 4.82 mmol/l; the mean lactic acid value for chicks was 2.55 mmol/l (n = 5).

To determine if lactic acid levels increase, and to what degree they increase, in diving murres, the blood lactic acid data for adult murres were divided into three groups: blood lactic acid levels of nondiving birds; those of birds diving less than 2 minutes; and those of birds diving 2 minutes or longer. The lactic acid data for diving birds were separated into 2 groups on the basis that rest duration appears to increase more sharply when previous dives last approximately 2 minutes or longer. The data were divided at a dive duration of 2 minutes since no blood samples were taken from birds diving between 105 seconds and 2 minutes. Results showed a significant difference between lactic acid levels in the three groups (one-way analysis of variance, $P = .001$, $n = 17$). Student's t-test showed

that mean lactic acid levels in murres diving 2 minutes or longer differed significantly from those of nondiving birds, and from those of birds diving 105 seconds or less ($P = .05$). Mean lactic acid levels in adult murres diving for 105 seconds or less were not significantly different from mean lactic acid levels in nondiving adults ($P = .05$).

DISCUSSION

The maximum dive times of 200 seconds recorded for a Common Murre during this study is considerably longer than previously reported dive durations. Scott (1973) measured a maximum dive time of 152.2 seconds for free-ranging Common Murres. Cody (1973) calculated a mean maximum dive time for the Common Murre of 71 seconds; however this value is based on maximum dive durations during a series of forced dives. The mean dive duration of 91.5 seconds also exceeds previously reported means of 66 seconds (Dewar, 1924), 41 seconds (Cody, 1973), and 71 seconds (Scott, 1973), all calculated from birds diving in their natural environments. However, mean values of dive duration may not be useful when examined independently of the water depth at dive sites. Dewar (1924) and Scott (1973) noted a positive correlation between dive duration and depth of water in which the dives were made. The data from this study show a similar correlation. One obvious possible explanation is that murres dive deeper in deeper water in response to prey distribution. Common Murres feed primarily on mid-water fishes (Belopolski, 1957; Bedard, 1969; Scott, 1973) and have been observed surfacing with flatfishes in water up to 60 meters deep (Scott, 1973). Although no direct

measurements of actual depths the birds attained are available, Common Murres have been found entangled in fish nets set at depths of 180 meters off the coast of Newfoundland (Piatt et al., unpublished). These data indicate that murres are capable of relatively long and deep dives.

Rest duration was found to increase logarithmically with increasing dive duration for dive times up to approximately 2 minutes. The rest duration is assumed to be dependent on the amount of time required to replace oxygen stores and eliminate carbon dioxide. Another way of looking at dive-rest data is the dive-rest ratio. A decrease in this value indicates that with an increase in dive duration, there is an even larger increase in rest duration. Dive-rest ratios may indicate whether or not the observed birds were approaching their physiological limits of endurance. The data show a decrease in mean dive-rest ratios when dive times reach approximately 2 minutes, indicating that the birds may reach their limits of aerobic diving at about this time. After about 2 minutes, the birds begin to rely to a greater extent on glycolysis, as suggested below. Scott (1973) noted a similar decrease in dive-rest ratios for free-ranging Common Murres at a dive period of 120 - 129.9 seconds.

Blood lactic acid levels measured in this study are comparable to those measured by Andersen et al. (1965)

in domestic ducks (2.0 to 5.1 mmol/l during diving). However, due to the method of sample collection, blood lactic acid levels reported here may not represent absolute levels in the blood. Although birds were shot immediately upon surfacing, some lactic acid may have been oxidized before samples were taken, thus lowering the concentrations of lactic acid measured. The physiological response to being shot may also influence blood lactic acid levels. The data should be interpreted with these precautions in mind.

The mean post-dive blood lactic acid level of Common Murres diving 105 seconds or less did not differ significantly from the mean lactic acid level of nondiving birds, indicating that there was no increase in dependence on glycolysis during these dives. The presence of blood lactic acid in nondiving birds may mean that some tissues function anaerobically when the bird is not diving. However, the significant increase in concentration of lactic acid in the blood when previous dives were 2 minutes or longer suggests that there is a shift toward greater dependence on anaerobic metabolism when dive durations reach a time between 105 seconds and 2 minutes.

Kooyman et al. (1980) found that arterial lactic acid concentration is seals increased exponentially with increasing dive durations after the maximum aerobic dive

limit of 20 - 30 minutes had been reached. Blood lactic acid values measured for murres in the present study indicate the possibility of a similar exponential increase in lactic acid for dives of approximately 2 minutes and longer, but there are not enough data to verify this.

Results of this study indicate an increase in dependence on anaerobic metabolism during sustained dives of Common Murres. It appears that a shift toward dependence on glycolysis occurs after submersion of about 2 minutes, although data are insufficient to determine if this is an abrupt shift or if it occurs gradually.

Scott (1973) noted that the longest dive times he recorded were made by adult murres accompanied by chicks. These adults must supply all of the chicks' required food and may therefore frequently rely on the ability to make longer dives in search of prey. It is not uncommon for the adults to dive for periods of 2 minutes and longer. Thus it appears that glycolysis is frequently employed by adult murres accompanying chicks, not merely as a safety mechanism, but as a common strategy when diving. The adult in an adult-chick pair is functioning under pressures of limited mobility and the necessity of foraging for the chick as well as for itself. Therefore one might expect these birds to be operating closer to their physiological limits of submergence duration than murres without chicks, or

murres at other times of year.

Additional data are necessary for determinations of the maximum diving capabilities of Common Murres. Controlled experiments, as well as more direct field measurements, would help clarify the roles of aerobic and anaerobic metabolism in these birds during diving.

TABLE 1. Dive durations, rest durations, dive-rest ratios, and depth of water at dive sites for diving Common Murres.

Dive Duration (seconds)	Rest Duration (seconds)	Rest Duration/ Dive Duration	Depth (meters)
35	14	2.5	18
40	15	2.7	18
40	9	4.4	18
45	13	3.5	18
45	22	2.0	18
46	20	2.3	18
48	9	5.3	18
50	20	2.5	18
50	14	3.6	54
50	14	3.6	18
53	17	3.1	18
53	16	3.3	18
55	25	2.2	18
59	12	4.9	27
60	25	2.4	25
63	27	2.3	23
63	15	4.2	18
65	23	2.8	27
65	15	4.3	18
65	11	5.9	18
67	23	2.9	27
67	27	2.5	27
68	22	3.1	27
68	36	1.9	23
70	17	4.1	27
70	20	3.5	18
71	30	2.4	27
72	17	4.2	25
72	24	3.0	20
72	35	2.1	25
73	23	3.2	20
74	18	4.1	20
75	23	3.3	25
75	20	3.7	25
75	40	1.9	27
75	15	5.0	25
75	15	5.0	25
75	10	7.5	45

TABLE 1. continued

Dive Duration (seconds)	Rest Duration (seconds)	Rest Duration/ Dive Duration	Depth (meters)
76	28	2.7	20
77	25	3.1	25
77	23	3.3	25
77	21	3.7	23
78	29	2.7	20
79	75	1.1	25
80	25	3.2	20
82	24	3.4	20
82	23	3.6	23
83	24	3.5	23
85	20	4.3	25
85	50	1.7	38
85	26	3.3	18
85	37	2.3	27
86	40	2.2	22
86	27	3.2	20
86	35	2.5	27
87	28	3.1	20
87	28	3.1	20
87	25	3.5	27
87	40	2.2	25
88	19	4.6	23
88	91	.9	54
89	23	3.9	20
89	26	3.4	20
90	40	2.3	38
90	29	3.1	20
90	22	4.1	63
90	60	1.5	22
90	45	2.0	45
92	45	2.0	38
92	30	3.1	27
92	35	2.6	18
92	24	3.8	23
95	10	9.5	27
95	35	2.7	20
95	42	2.3	49
97	37	2.6	20
97	24	4.0	20
97	41	2.4	20
97	27	3.6	63
101	27	3.7	23

TABLE 1. continued

Dive Duration (seconds)	Rest Duration (seconds)	Rest Duration/ Dive Duration	Depth (meters)
101	32	3.1	23
101	30	3.4	20
103	47	2.2	54
103	42	2.5	54
104	32	3.3	23
105	55	1.9	56
110	23	4.8	20
110	63	1.7	22
115	30	3.8	22
120	30	4.0	43
120	55	2.2	22
120	35	3.4	22
120	65	1.8	90
123	49	2.5	49
125	100	1.3	67
125	80	1.6	56
127	133	.9	49
129	30	4.3	43
130	76	1.7	74
131	166	.8	67
132	85	1.5	74
133	80	1.7	74
135	70	1.9	22
140	100	1.4	58
141	148	.9	58
143	180	.8	58
145	100	1.5	85
147	107	1.4	58
152	45	3.4	43
163	157	1.0	58

TABLE 2. Dive durations and blood lactic acid levels in Common Murres.

	Dive Duration (seconds)	Blood Lactate (mmol/l)	Blood Lactate (mg/100 ml)
Chicks		1.33	11.98
		1.71	15.36
		1.72	15.49
		3.15	28.32
		4.82	43.36
Nondiving Adults		4.63	41.66
		3.36	30.27
		4.19	37.76
		4.75	42.84
		3.22	28.97
Diving Adults	67	2.69	24.22
	80	3.64	32.75
	89	2.36	21.29
	95	2.53	22.79
	100	4.69	42.18
	105	3.08	27.80
	120	8.39	75.52
	131	4.45	40.04
	140	6.38	57.38
	147	7.66	69.01
	150	7.52	67.70
	161	7.66	69.01

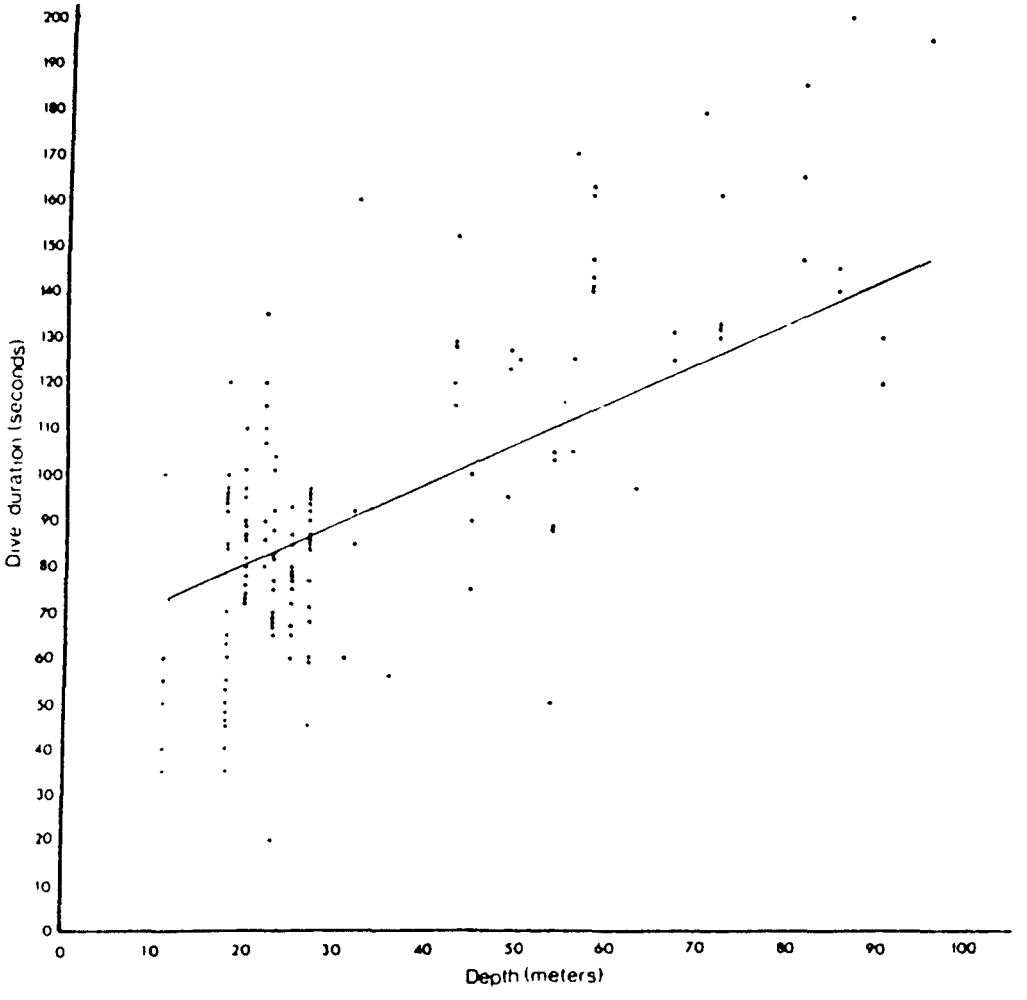

Figure 1. Dive durations of Common Murres versus depth of water at dive sites. The equation for the regression line is $y = .9X + 62.5$, ($r^2 = .4$, $n = 174$).

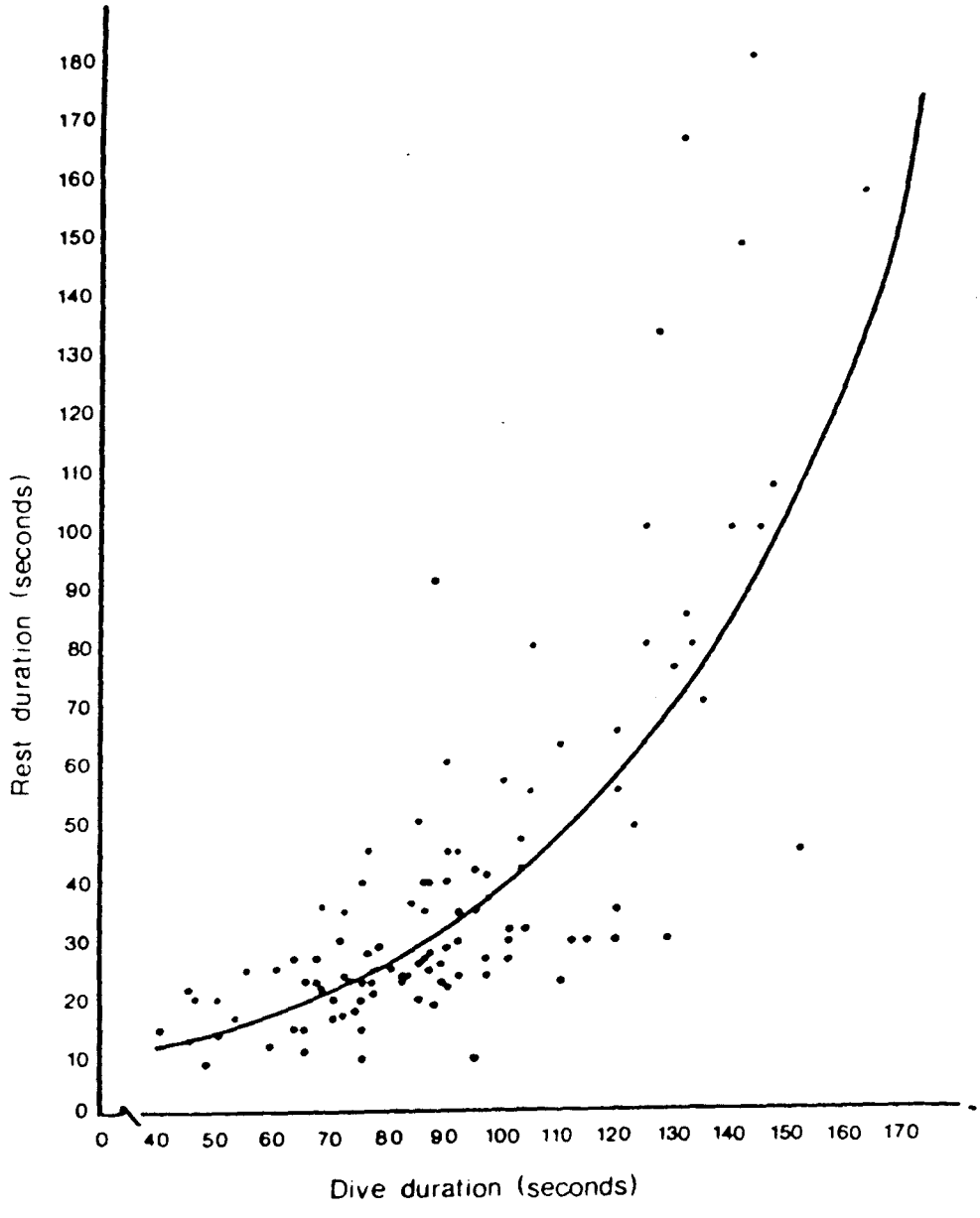

Figure 2. The relationship between duration of dives and duration of corresponding rest periods of diving Common Murres. ($y = 5.66e^{0.02x}$, $r^2 = 0.63$, $n = 110$).

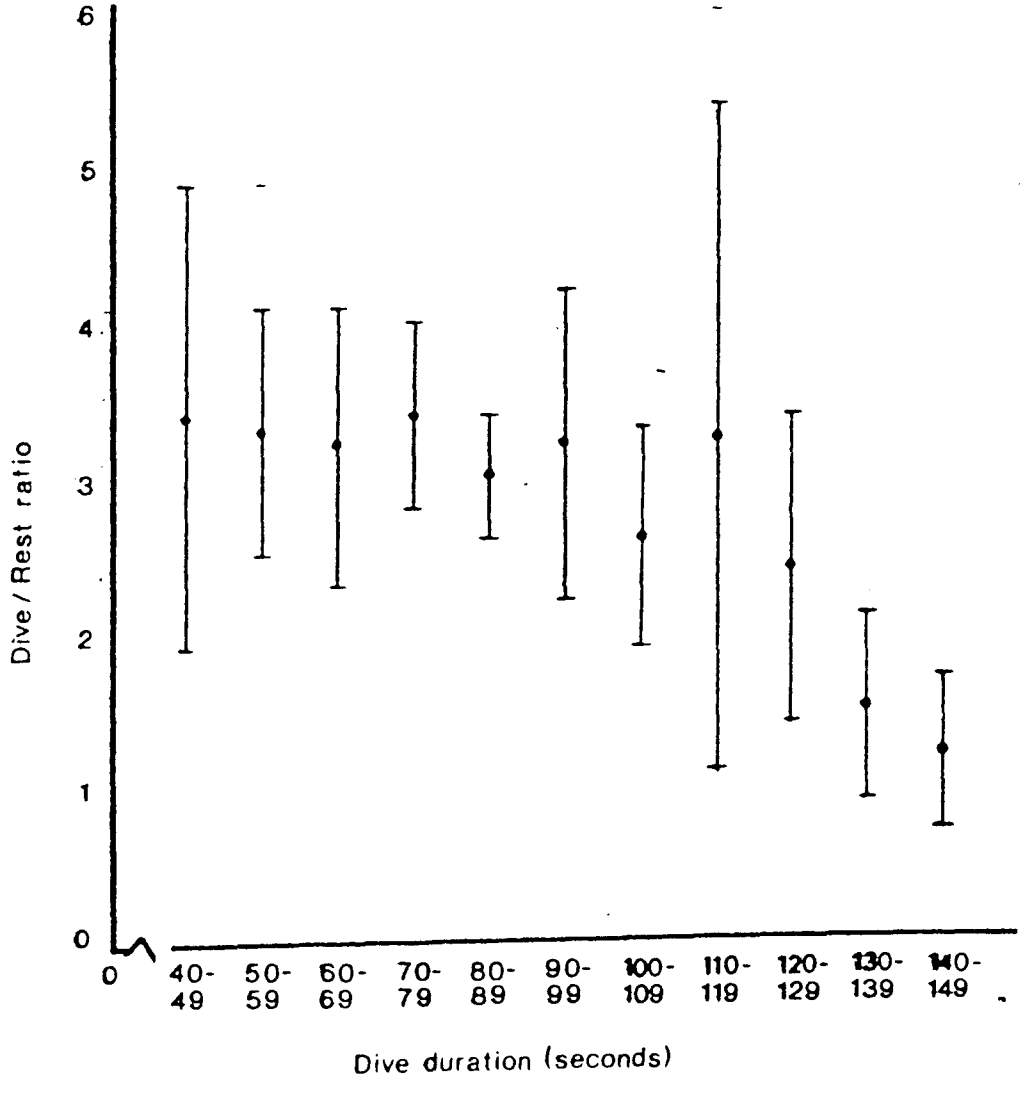

Figure 3. Dive-rest ratios expressed as a function of dive duration in diving Common Murres. Mean values of dive-rest ratios are shown for dive times in 10 second intervals. Vertical lines represent 2 standard errors from the mean.

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