Physiology of Diving and Breath-holding in Small Birds and Mammals

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The dipper (Cinclus mexicanus) and the water shrew (Sorex palustris) are the smallest true divers in their classes. These species are being studied with regard to the questions:

1) What is the relationship of diving endurance to body size?
2) Are the physiological responses to diving by the small homeotherms similar to those which have been well-described for the larger divers?

I. The dipper (body weight 40.0 to 59.9 g)

Most dives by wild, free dippers observed in the field lasted 6 sec. or less (range 1 to 9.8 sec.), although I have previously timed a dive of 12.0 sec. Natural history descriptions include claims of 1/2 and 2-3 min., but these were probably estimates, not actually timed. Caged birds (47.5-51.7 g) were force-submerged in this study for 14.8, 15.0, and 15.5 sec. without adverse effects. During these periods, the exertion of swimming was continuous. When this activity waned and the birds seemed exhausted, the cage was removed from the water.

Heart rates were recorded from ten dippers and two spotted sandpipers (Actitis macularia) during hand-held submergences of the head for 5-10 sec. duration. A Sage "Electrocardiophone" (model 157) and leads terminating with surgical staples (Clay-Adams 9 mm "Autoclips") were used for detecting the heart beats. The audio output of the "Electrocardiophone" was recorded on a portable tape recorder at 7 1/2 ips and played back at 1 7/8 ips for counting. In addition, a few recordings were obtained with a Cambridge Transcribe EKG, but this proved more temperamental. Similar rates were obtained by both methods. The results follow in Table 1.

Table 1. Heart rates during cessation of breathing.

	Nostrils Plugged			Head Under Water		
Dipper (10)	Before		After	Before		After
Mean:	520		576	551		655
Range:	442-589	309-581	481-696	484-607	295-461	586-719
Spotted sandpiper (2)						
Mean:	537	441	591	546	270	596
Range:	528-545	406-476	569-612	523-569	231-309	580-612

These heart rates are elevated by the unnatural experience of being held, but will serve as the basis for comparison with recording to be obtained in the same way from non-diving birds of similar weights, in a continuation of this study. The purpose of the comparison is to see if the extent of "diving" bradycardia and "post-dive" tachycardia are more pronounced in diving or aquatic birds than in non-divers. In preliminary equipment checks, two hand-held starlings of near fledging-age did not exhibit as pronounced heart slowing when their heads had been immersed for comparable periods.

One dipper was submerged while free to move within a 45x45x23 cm cage. The heart rates were similar to the hand-held data: 534, 387 and 651/min., before, during, and after submergence, respectively. The resting heart rate predicted for a 50 g bird is 312/min. (Calder, MS). An immature bird weighing 40 g was kept in a cage the last week of this study. Its resting heart rate was 368-372/min., compared to the prediction for 40 g of 330/min. During a brief voluntary dive for a minnow, EKG signals were lost in myogenic noise, but a post-dive tachycardia of 470/min. was recorded. These miscellaneous observations give some indications of the relationship to the hand-held submergences to the natural situation.

Fifteen dippers were banded. Nests or fledged broods being fed indicate the numbers of territories as follows:

Cascade Canyon, Jenny Lake to Fords (4.5 mi.): 5
North Fork of Cascade Canyon: 1
Paintbrush Canyon: 1
Mouth of Leigh Canyon: 1
Upper Black Rock Creek: 2
Crystal Creek: 2

II. The northern water shrew (body weight 8.5 to 17.3 g)

Small size and intense metabolism make this shrew especially interesting as a diver. Limited success in trapping was delayed until late July when drying of the land had apparently localized the shrews along the main streams.

Observations of shrews caged over aquaria included dives of only 1 to 6.3 sec., while Svilha (Murrelet 35:44, 1934) reported dives of up to one quarter min. Based upon this, I made forced submergences of a 9.7 g shrew of 15.0, and after drying, feeding, and resting, 30.0 sec. This diving was within a 12x14x17 cm cage. No adverse effects followed warming and drying. A series of four water shrews survived forced dives listed in Table 2.

Table 2. Forced Submergence of Water Shrews

Body wt. (g)	8.7	9.6	10.1	17.3
Resting respiratory rate (/min.)	-	211	214	210
Submergence time (sec.)	31.1	35.4	47.7	39.2
Water temperature (°C)	14	18	18	13
Minimum missed breaths	-	125	170	137

These dives involved continuous exertion of swimming and were terminated without losses at the appearance of exhaustion. In comparison, a Sorex cinereus of 8.0 g body weight seemed to have reached the same state of exhaustion when forced under for 14.9 sec. This species is trapped at the streamside, but does not dive, supposedly. A Microtus richardsoni, also a diving species, tolerated similar caged, forced submergences of 25.0 and 37.2 sec. while swimming continuously (67 g body wt.) A second M. richardsoni (76 g) ceased struggling at 60 sec. and drowned. The determination of maximum endurance in all but the last case is admittedly subjective, but upon removal, each animal lay exhausted on the cage floor where

artificial drying with rags was accomplished without the animals attempting to escape. It was felt that the drying may have even stimulated resumption of respiration in the 10.1 g water shrew, which appeared lifeless after removal from the water, but was released in apparent good health the following day.

Conditions under which the limited data on diving endurance times have been acquired vary considerably: field observations, forced dives, or time to final struggle in drowning. The extent of exercising during the dives is another variable. A very tentative relationship between the maximum endurance for the shrew in this study and published data from Irving and Scholander on muskrat, beaver, and seal suggest an exponential relationship of:

$$\text{diving endurance (sec.)} = 20\ (\text{weight, g})^{0.4}$$

If related to metabolic intensity alone, the anticipated exponent would be 0.25. However, the apparent excessive loss of body heat from a very small diver might be a significant factor in addition to the exhaustion of oxygen stores, and this may not be a simple relationship between endurance and metabolic intensity.

Preliminary examination of heart and lung weights showed no species differences between the water shrew and the more terrestrial S. cinereus when weights of excised, blotted organs were expressed as per cent of body weights. However, the data are limited to six water shrews and three masked shrews which died in traps or captivity.

Studies of divirg physiology in the water shrew will be continued at the Virginia Polytechnic Institute.

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