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CAPILLARY-TUBE DEPTH GAUGES FOR DIVING ANIMALS: AN ASSESSMENT OF THEIR ACCURACY AND APPLICABILITY

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Abstract.—Gauges to measure the maximum depths attained by diving animals were constructed from plastic tubing lined with soluble indicator powder, at a cost of $0.10 each. In our tests, the differences between real and estimated depths averaged <3% with single immersions of gauges to any depth up to 140 m. With multiple immersions errors were usually <10% and always <25%. The accuracy of the gauges was not affected by depth or duration of dive, rate of descent, or underwater movements simulating a bird's swimming. Errors resulted from severe jarring of the devices underwater, plunge-diving, accumulation of moisture within the tubes, and use of excessive hydrophilic indicator. Potential errors associated with high air-sea temperature gradients were not realized in our tests. With careful construction and deployment the gauges should provide accurate depth estimates without adversely affecting free-living animals. Methods for attaching the gauges to birds are reviewed.

INDICADORES DE PROFUNDIDAD DE TUBOS CAPILARES PARA ANIMALS QUE SE SUMERGEN: UNA EVALUACIÓN DE SU EXACTITUD Y APLICABILIDAD

Resumen.—Indicadores para medir la profundidad máxima lograda por animales que se sumergen fue construida de tubería plástica revestida con un indicador soluble en polvo, a un costo de $0.10 cada una. En nuestras pruebas, las diferencias entre profundidades reales y estimadas promedió <3% despues de sumergir los indicadores una sola vez a profundidades de hasta 140 m. Con multiples inmersiones los errores eran usualmente <10% y siempre <25%. La exactitud de los indicadores no fue afectada por la profundidad o por la duración de la inmersión, razón de descenso o movimientos debajo del agua simulando los de un ave nadando. Los errores surgieron por sacudidas severas de los indicadores una vez sumergidos, clavados, acumulación de humedad dentro de los tubos, y uso excesivo del indicador hidrofílico. Los errores potenciales asociados con los gradientes de alta temperatura mar-aire no se consideraron en nuestras pruebas. Con la construcción y uso cauteloso, los indicadores deben proveer estimados de profundidad exactos sin afectar adversamente los animales de prueba. Los métodos para colocar los indicadores a las aves fueron revisados.

The underwater foraging activities of diving animals are poorly known and difficult to study, but are obviously of great importance in their lives. We report tests on a simple gauge that measures maximum diving depths and is a useful tool in ecological, behavioral, and physiological studies of these animals. Capillary-tube depth gauges have been reliably used for many years by SCUBA divers (Miller 1979). The gauge is a calibrated plastic tube with a narrow, uniform bore open to the water at one end. As the depth increases, water is forced into the tube and the depth can

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be read off the calibrations at the air-water interface. The device has been modified, by lining the lumen with water-soluble indicator dye or powder to function as a maximum depth gauge. The amount of indicator remaining in the tube upon its recovery shows the minimum volume of the air space and hence the maximum depth attained. These gauges have been used to demonstrate remarkable diving abilities of free-living penguins (Adams and Brown 1983, Montague 1985, Kooyman et al. 1971) and auks (Burger and Simpson 1986). Some features of the gauges were analyzed in these reports, but the present paper is the first rigorous assessment of their accuracy and applicability.

FUNCTIONAL PRINCIPLES, SENSITIVITY, AND POTENTIAL ERRORS

Although commonly known as capillary depth gauges, maximum depth gauges do not function by capillarity. The compression of the air space within the tube follows the general gas law:

$$\frac{P_1V_1}{T_1} = \frac{P_2V_2}{T_2} \tag{1}$$

where P, V, and T represent pressure (in atmospheres), volume (cm^3) and temperature (°K), respectively. The effects of temperature differentials are considered later in this paper and can be omitted at this stage. Since the diameter of the device remains constant, the equation can be modified to determine changes in the length (L) of the air column in the tube, as follows:

$$P_sL_s = P_dL_d \tag{2}$$

where P_s is the pressure at the water surface (1 Atm), L_s is the original length of the air column at the surface, and P_d and L_d are the pressure and length of air column at depth d, respectively. The length of air space remaining (L_d) at depth d can be determined from the length of undissolved indicator (Fig. 1).

In seawater, pressure increases by 1 Atm for every 10.08 m increase in depth, in addition to the 1 Atm at the surface. The pressure at depth d is thus 1 + d/10.08. Equation 2 can be modified to predict the depth attained:

$$d = 10.08\left(\frac{L_s}{L_d} - 1\right) \tag{3}$$

Given constant temperatures, the behavior of the air and water in the tube should be highly predictable, producing a curvilinear relationship between d and L_d (Fig. 1). The gauges are clearly more sensitive to depth changes at shallow depths. For example, a 1 m increase in depth produces a 2.4 mm change in L_d in a 100 mm gauge at 10 m, but only 0.3 mm at 50 m.

The success of the gauge depends on factors affecting the air space in the tube and errors may result from temperature changes, accumulation of water droplets in the lumen, and use of excessive indicator. We read

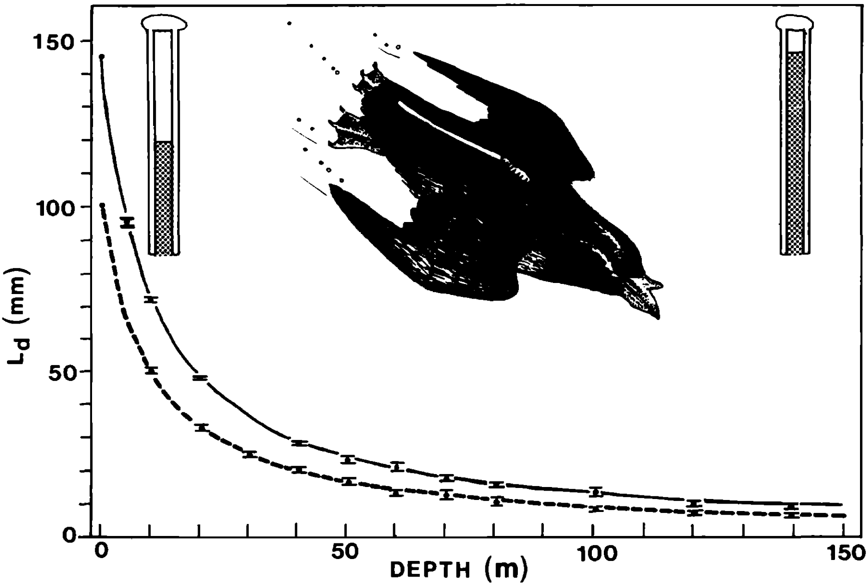

FIGURE 1. Changes in the length of undissolved indicator (L_d, see text) of maximum depth gauges at depths 0–140 m. Solid and dashed lines indicate the L_d predicted from equation 3 for gauges 145 and 100 mm long, respectively. Dots show actual means (±SD) of readings from 10 gauges of each type lowered to the depths indicated. The sketches show the penetration of water into the gauges at 10 and 140 m, and a gauge taped to the dorsal plumage of a Rhinoceros Auklet *Cerorhinca monocerata*.

our gauges with a maximum precision of 0.5 mm. The potential errors produced at this scale were acceptable within the depth range of most birds and smaller marine mammals. For example, with a 100 mm long gauge, an estimated depth of 100 m could result from real depths between 94–106 m (Fig. 2).

METHODS FOR TESTING DEPTH GAUGES

Depth gauges were made from lengths of flexible plastic Tygon (R) tubing, coated internally with a thin layer of icing sugar. The indicator was applied by blowing gently through the open tubing to moisten the lumen walls and then sucking very small amounts of dry icing sugar up the tube. The tube was knotted tightly at one end, without stretching it, and cut to size. Except where noted, the tubing had an internal diameter of 1.6 mm and the lumen length was either 100 or 145 mm. Sample gauges were lowered into seawater at Bamfield, British Columbia. The length of undissolved indicator (L_d) was read to the nearest 0.5 mm using a ruler, without stretching the tubing.

To simulate the activities of a bird making multiple dives within a day, a sample of 10 devices (100 mm long) was lowered to 10 m in five episodes, each separated by 2–4 h. Each episode involved 30 submersions where

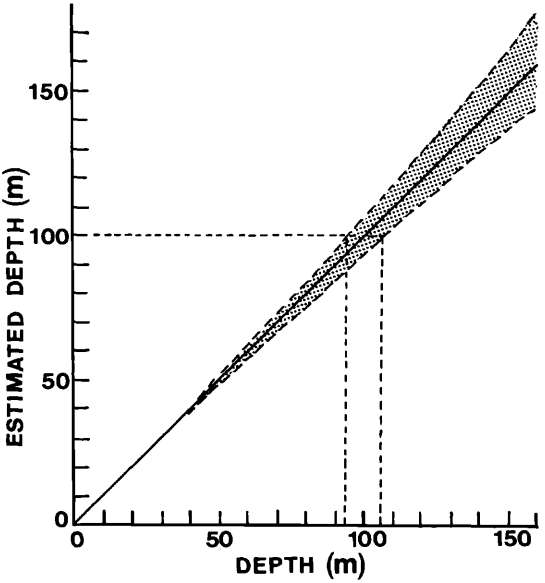

FIGURE 2. Relationship between real depth and estimated depth, showing the potential error resulting from reading precision of 0.5 mm in a 100 mm gauge (shaded portion). The dotted line shows that with this potential error, an estimated depth of 100 m could result from real depths of 94–106 m.

the devices were submerged for 45–50 s and at the surface for 10–15 s. This schedule simulated the activities of diving seabirds, such as Common Murres (*Uria aalge*), which spend about 7% of the day diving (Cairns et al. 1987) and have a dive : pause ratio of 3.6:1 (Dewar 1924).

The effects of locomotion of an animal were simulated by pulling and jarring ten 100 mm gauges for 30 s at the end of a hand line at 10 m depth. This was done both mildly, to simulate normal locomotion in smaller marine mammals or birds, and violently, to the maximum degree possible by hand, to simulate thrashing movements in a large mammal. Controls were simply held at 10 m for 30 s. To test the effects of plunge-diving by birds, we dropped samples of 10 gauges from 8–10 m to the sea surface and allowed them to submerge to 5 and 10 m deep, in separate trials. Controls were lowered from the sea surface.

To test the effects of temperature, gauges were placed on black plumage of a stuffed Common Murre in full sun for 7 h, followed by submersion in cool seawater. Controls were placed in shaded air. Temperatures in gauges were measured with a Bailey Thermalert TH-6D thermometer, using a thin wire thermistor inserted 2–3 cm down the lumen. Air and sea surface temperatures were made with the same thermistor and with a mercury thermometer.

RESULTS

Accuracy of gauges in a single test dive.—When submerged to each depth once, the gauges were highly accurate, with virtually no differences between the readings observed and those predicted from equation 3 (Fig. 1). The co-efficient of variation among groups of ten samples was always <2%. The differences between the estimated and real depths averaged 2.4% (range 0.8–5.0%) and 2.6% (0.0–7.2%) for 100 and 145 mm tubes, respectively. Gauges with internal diameters of 1.6 and 0.8 mm were equally accurate at all depths.

The effects of multiple submersions and simulated locomotion.—The differences between the real and estimated depths increased progressively with increasing frequency of dives (Fig. 3). These deviations were the result of small droplets of water remaining on the lumen wall after surfacing, progressively reducing the available air space. The errors in depth estimates appeared to reach an asymptote after 120 dives and remained within 24%. When subsequently submerged for single dives to deeper depths (20, 30, and 35 m), these errors decreased substantially and were usually <10% (Fig. 3).

The mean depth (10.8 ± 0.8 m [SD]) predicted by 10 gauges subjected to mild pulling and jarring, to simulate locomotion in an animal at 10 m depth, did not differ significantly, after 50 dives, from the depth predicted from controls (10.9 ± 0.7 m, $t = 0.297$, $P > 0.05$). Similar gauges (internal diameter 1.6 mm) subjected to violent pulling and jarring, however, showed significantly different depths (11.6 ± 0.5 m, n = 10) to controls (10.5 ± 0.2 m, $t = 6.46$, df = 18, $P < 0.001$) after a single dive, due to disruption of the air and water columns in the tubes. Narrow tubes (internal diameter 0.8 mm) were less affected than wider ones by this treatment (mean depth shown after jarring 10.8 ± 0.4 m; control 10.3 ± 0.2 m; $t = 3.54$, df = 18, $P < 0.01$). Gauges subjected to simulated plunge-diving showed significant deviations from controls, but errors did not increase after five plunges. On average, gauges overestimated depths by 39% and 9% in submersions to 5 and 10 m, respectively, after 10 plunges.

Effects of duration of dives and rate of descent.—Readings of L_d and resultant depth estimates did not differ significantly in gauges held at 50 m for periods of 0.5–8.0 min (Table 1), indicating that these devices were not significantly affected by the dive durations likely to occur in smaller marine vertebrates. The % error was similar to that expected from reading imprecision (see Fig. 2). Gauges were lowered to 50 and 70 m both rapidly (1.1–1.3 m s^{-1}) and slowly (0.4 m s^{-1}) with no significant differences in the resultant readings, or predicted depths (Table 2). Rates of ascent, during which water contained in the tubes is forced out, should not affect the position of the deepest miniscus recorded by the indicator.

Effects of temperature and condensation.—Changes in temperature (ΔT) within the gauges can induce errors, either by affecting the volume of air in the tube, or by causing condensation of water in the lumen. The potential effects of ΔT on the internal volume of the gauges, and hence

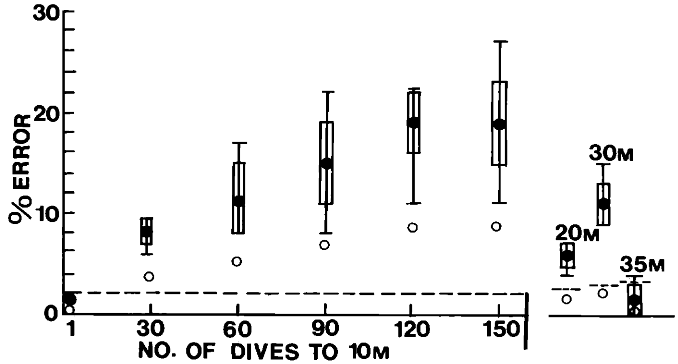

FIGURE 3. Effects of multiple submersions to 10 m on a 100 mm gauge, followed by single submersions to 20, 30, and 35 m. Open circles indicate % differences between observed and expected readings of L_d. Dots, bars and vertical lines indicate the mean, SD, and range of % differences between real and predicted depths. The horizontal dashed line shows the minimum error resulting from reading L_d with a precision of 0.5 mm.

L_d, were calculated from equation 1, and for temperatures of 0–40 C (273–313 °K):

$$\Delta L_d = 0.0034\ \Delta T \qquad (4)$$

The effects of ΔT on depth estimates depend on the depth attained, since the relationship between d and L_d is not linear. For example, a 20 C decrease in a 100 mm gauge could cause a decrease in L_d of 7% (equation 4), resulting in potential overestimations in d of 15% and 9% at 10 and 50 m depth, respectively (calculated using equation 3).

Temperature variations within a water column are generally small and unlikely to affect depth estimates, but more serious errors are possible due to large temperature gradients often found between air and water. The air within transparent tubes heats up in sunshine due to a "greenhouse" effect, and this is exacerbated by contact with plumage (Table 3). The gauges have little thermal mass and cool rapidly when placed in water. In our samples the average internal temperatures dropped from 31 C to 16 C within 30 s of submersion. Air within gauges moving from hot air to cool sea will contract, potentially producing an overestimate of the maximum depth attained. These potential errors were not realized in our tests: gauges lying on black plumage in the sun for 7 h with internal temperatures at least 25 C higher than controls in the shade, did not differ from controls when submerged in cool seawater (Table 3, *t*-tests, $P > 0.05$). Depths estimated from actual readings were much closer to the real depth than those predicted with temperature induced errors. Other factors, such as expansion and contraction of the plastic, might have negated the changes in the air space induced by temperature changes.

Internal condensation caused by rapid cooling of hot air, with a high relative humidity due to proximity of the sea, is another problem likely

TABLE 1. The effect of dive duration at 50 m depth with maximum depth gauges of length 100 mm and 145 mm.

Time at depth (min)	100 mm gauges		145 mm gauges	
	Depth predicted (m)	Error[1] (%)	Depth predicted (m)	Error (%)
0.5	51.0 ± 3.1	2.0	51.2 ± 1.9	2.4
1.0	51.4 ± 4.0	2.8	51.6 ± 2.0	3.2
2.0	51.4 ± 4.7	2.8	52.5 ± 2.4	5.0
4.0	50.6 ± 3.2	1.2	53.2 ± 3.1	6.4
8.0	50.2 ± 3.8	0.4	53.5 ± 3.4	7.0
ANOVA	$F = 0.188, P > 0.05$		$F = 1.426, P > 0.05$	

[1] Deviation between the real depth and the depth predicted from the indicator reading using eq. 3.

to occur in hot areas. For example, air at 100% relative humidity contains up to 168 g/m^3 of water at 60 C, but only 9 g/m^3 at 10 C (Jorgensen 1979). Thus, a 100 mm long gauge, with an internal diameter of 1.6 mm (volume ca. 200 mm^3), at 60 C and 100% R.H. contains 3.4×10^{-5} g of water vapor. When immersed in water at 10 C, 95% of the water vapor will condense (i.e., 3.2×10^{-5} g). If all the condensed water remains in the tube, approximately 1 mm^3 of water (causing a 0.5 mm error in L_d) will condense in the lumen after 30 dives. Under extreme conditions the droplets may coalesce and run down the tube dissolving the indicator; this was experienced when deploying gauges mounted on dark-plumaged cormorants in southern Africa (Wilson, pers. obs.). Condensation problems can be reduced by minimizing the period of deployment and by attaching gauges on the undersides of the birds to reduce insolation.

DISCUSSION

Our tests revealed several real or potential sources of error associated with maximum depth gauges. Accumulation of water droplets within the lumen, through condensation, prolonged deployment, or use of excessive hydrophilic indicator, can lead to significant errors. These, and errors resulting from imprecision in reading L_d, will have progressively larger effects as depth increases. The probability of such errors can be reduced through minimizing the amount of hydrophilic indicator used; minimizing deployment times; reducing condensation by mounting devices where they will be shaded by the animal's body; using longer tubes for deep diving animals; and maximizing reading precision. Inspection of recovered gauges will usually reveal evidence of moisture accumulation and affected gauges can be discarded.

The mixing of the air and water columns within the gauge, resulting from severe jarring, caused significant errors and might preclude the use of the technique on large seals or whales. The use of narrow tubes reduced such errors. Underwater locomotion of birds should not affect the accuracy

TABLE 2. The effect of the rate of descent on depths estimated by maximum depth gauges of length 100 and 145 mm ($n = 10$ for each treatment).

Gauge length (mm)	Depth (m)	Rate of descent ($m \cdot s^{-1}$)	Mean (±SD) predicted depth (m)	Paired *t*-test (*t*)
100	50	1.3	52.9 ± 5.5	1.500,
100	50	0.4	50.4 ± 3.4	NS
100	70	1.1	69.6 ± 4.3	0.318,
100	70	0.4	69.2 ± 6.4	NS
145	50	1.1	49.7 ± 1.2	0.658,
145	50	0.4	49.4 ± 0.8	NS
145	70	1.2	73.3 ± 4.2	0.286,
145	70	0.4	73.9 ± 3.1	NS

NS = No significant difference ($P > 0.05$).

of maximum depth gauges, but gauges used on plunge-diving birds should be tested thoroughly for potential errors.

Repeated submersions to the same depth led to overestimates of maximum depths, and this might affect results obtained from animals diving regularly to fixed depths, such as obligate bottom feeders. The size of error depends on the frequency of diving and the depth attained. Maximum depth estimates will be more accurate with epipelagic and mid-water foragers, which tend to make infrequent forays into deeper depths.

Errors in depth estimates averaged <3% with single immersions to any depth, and with multiple immersions were usually <10% and almost always <25%. The accuracy of the gauges was not affected by depths per se, the rate of descent or the duration of submersion, within the ranges likely to be encountered in birds or smaller marine mammals. Errors related to large air-water temperature gradients, although potentially serious, were not significant in our tests. In general we feel confident that, with proper attention to construction and deployment, maximum depth gauges are reliable and accurate. Most of our findings probably apply to gauges of different diameters and lengths, but we urge researchers to do their own tests, ideally with the same air and sea temperatures likely to be encountered by the animal being studied.

Maximum depth gauges have been deployed using harnesses (Adams and Brown 1983), by suturing the devices to the skin (Kooyman et al. 1971), and attached to flipper bands (Montague 1985) and leg bands (Burger and Simpson 1986). We found waterproof adhesive tape (Superstik brand) ideal for attaching gauges to the contour feathers of alcids (Fig. 1). Gauges not recovered fall off as the tape gradually loses its adhesiveness or the bird molts. Other devices have been attached to the feathers of penguins and the fur of seals using small hose clamps or glue. Harnesses and other bulky attachments are unsuitable for aquatic birds, since they affect the birds' hydrodynamic streamlining and foraging efficiency (Wilson et al. 1986). Very long gauges needed for deep diving

TABLE 3. The effects of solar radiation on internal temperatures and subsequent accuracy of maximum depth gauges after submersion to 50 m in seawater at 12 C. The means ± SD are shown, and $n = 5$ gauges in each case.

Gauge length (mm)	100	100	145	145
Treatment prior to submersion:	On black plumage in sun	Shaded in air	On black plumage in sun	Shaded in air
Internal temperatures (°C)	56 ± 6	23 ± 1	54 ± 3	25 ± 1
ΔT gauge-sea (°C)	44	11	42	13
Following dive:				
Depth predicted if ΔT had full effect (m)[1]	60.5	52.4	59.7	52.4
Depth predicted from actual L_d reading (m)	49.2 ± 0.8	49.5 ± 1.0	51.6 ± 4.0	49.8 ± 2.7

[1] Using eq. 4 to calculate effect of ΔT on L_d and eq. 2 to calculate this effect on estimate of d (without any temperature effect, L_d is 16.7 and 24.2 mm, for 100 and 145 mm gauges, respectively, at 50 m).

species could be coiled and mounted on a small disc, and taped or glued flush with the body contour.

CONCLUSIONS

Maximum depth gauges are useful tools for the study of underwater foraging of birds and marine mammals. They are unbreakable, very small and light (our 100 mm gauges had a mass <1 g), inexpensive and easily constructed. Their flexibility and small size ensure that the hindrance associated with larger devices (Wilson et al. 1986) will be avoided. Even if the probability of recovery from free-living animals is very low, the low cost and neglible impact on the animals makes this a very viable technique. Attaching or detaching a gauge to a captured animal should be as quick as conventional banding or tagging procedures, and no more stressful to the animal.

These gauges provide only a single point estimate of the deepest dive. Among epipelagic and mid-water foragers these might represent rare exploratory dives beyond the animals' normal foraging depths. More elaborate depth gauges, using pressure transducers (Kooyman et al. 1983), autoradiography (Wilson and Bain 1984) or light-emitting diodes (R. P. Wilson et al., unpubl.), provide more comprehensive data by estimating the time spent at each depth. These gauges are, however, far more expensive, heavier and bulkier than maximum depth gauges and demand more time to deploy and interpret the data. Maximum depth gauges effectively give an initial insight into an animal's underwater capabilities and could enhance studies of diving physiology, habitat use and foraging ecology. Where very low recovery rates preclude the use of more expensive devices, or where the birds are too small to carry more elaborate devices, maximum depth gauges may represent the only viable technique to measure diving depths.

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