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Abstract.—Depth recorders are among the most useful tools available for ornithologists interested in waterbird foraging behavior. Despite their widespread use in the literature, there is little information available about their precision and accuracy, including, for the case of TDRs, device drift. We examined the uncertainty associated with two types of depth-recorders deployed on Thick-billed Murres *Uria lomvia* in the Canadian Arctic in 2007 for up to 48 hours. The maximum depth obtained by capillary tube maximum-depth gauges (MDGs), a cheap and simple depth-recorder, was highly correlated ($R^2 = 0.87$) with maximum depth obtained by electronic time-depth recorders (TDRs) attached to the same bird (n = 29) up to depths of 100 m. Deeper than 100 m or in deployments of 144 hours, MDGs were unreliable. We suggest that the maximum depth for Thick-billed Murres in the Canadian Arctic is about 150 m, rather than the 210 meters previously reported using MDGs recorders, and that caution should be used when quoting maximal maximum depths for species diving deeper than 100 m using this method. We also attached two Lotek TDRs to the same bird (n = 18) and examined the similarity of the two recorders. The average difference increased from about 0.5 m near the surface to about 1.0 m below 60 m, with extreme differences of up to 4 m obtained. Furthermore, TDRs submerged to known depth were accurate within ± 2 m. The effect of these variations on measurements of maximum and average depth and duration was about 0.6-1.3 m (depth) or s (duration), which is similar to the manufacturer's accuracy specifications (±1%). Finally, we examined the drift (offset from zero at the surface) within the TDRs. Drift varied from -2.5 to + 2 m, with 9 out of 36 recorders showing no drift, and no change amongst years for individual recorders. Drift was lowest (most negative) at the colony, higher during flight and highest (most positive) on the water surface, despite very small differences in altitude (<50 m). We suggest that drift may be a useful tool for quantifying at-sea behavior, especially in conjunction with temperature logs. We conclude that MDGs are reliable up to 100 m and within 48 hours, and that TDRs are precise within ±2%, but that more research needs to be completed on device accuracy and precision. *Received 4 March 2008, accepted 11 September 2008.*

Key words.—Thick-billed Murre, *Uria lomvia*, Hudson Bay, depth recorders, activity patterns, device drift.

The study of seabird foraging behavior has been greatly improved by the development of miniaturized bird-borne devices, as seabird biologists can now examine and quantify many aspects of seabird foraging behavior that were formerly difficult or impossible to observe (e.g. stomach temperature probes: Wilson *et al.* 1992; Putz *et al.* 1998; Charrassin *et al.* 2001; Catry *et al.* 2004; mouth-opening recorders: Simeone and Wilson 2005; satellite tags: Jouventin and Weimerskirch 1990; Weimerskirch 2007; accelerometers: Watanuki *et al.* 2003; Ropert-Coudert *et al.* 2004; Wilson *et al.* 2006; crittercams: Takahashi *et al.* 2004; Watanuki *et al.* 2008). Nonetheless, the simplest devices are often the most useful. For example, depth-recorders continue to be widely used to answer diverse questions, at least partly because their relative affordability allows for large sample sizes and small size allows for limited impact on behavior (Elliott *et al.* 2007). Even capillary tube maximum-depth gauges (MDGs, Burger and Wilson 1988), one of the earliest inventions, continue to be used despite their limitation for recording only maximum depth, because their small cost allows them to be deployed when the likelihood of retrieval is low (Mougin and Mougin 2000; Falk *et al.* 2000b; Casaux *et al.* 2001; Bried 2005; Castillo-Guerrero and Mellink 2006; Peck and Congdon 2006).

Despite the abundance of studies using depth-recorders, there is little information available on their precision and accuracy. Burger and Wilson (1988) assessed the accuracy of MDGs by simulating seabird diving and showed that error was usually below 10% and always below 25%. They attributed some

of the uncertainty to variation caused by temperature and manufacturer imperfections (Burger and Wilson 1988). For albatrosses diving shallower than 3 m, MDGs were accurate when diving depth was greater than 0.5 m, diving frequency was low and when the recorders were placed on the birds' backs; the overall relationship for 14 albatrosses had R^2 = 0.46 (Hedd *et al.* 1997; A. Hedd, pers. comm.). We know of no information on the accuracy of MDGs for free-living birds diving to deeper depths. The importance of quantifying the uncertainty of MDGs on free-ranging seabirds is shown by their continued use (Bried 2005; Castillo-Guerrero and Mellink 2006; Peck and Congdon 2006) and by their use in inter-specific studies of maximum dive depth, where values for many species are derived exclusively from MDGs (Prince *et al.* 2001; Watanuki and Burger 1999; Burger 2001).

Furthermore, to the best of our knowledge, the precision of electronic time-depth recorders (TDRs) has never been tested on free-living birds. Most reporters rely on the precision estimates provided by the companies, although these estimates are usually obtained in the laboratory and ignore effects of wear-and-tear over many years, pressure differences due to non-zero forward speed (Bernoulli principle) and pressure differences due to acceleration and turbulence (Wilson *et al.* 2002; Fedak 2004; an exception is Hays *et al.* 2006).

Even when the bird is at the surface, TDRs sometimes reported nonzero pressure. The observation of nonzero pressure at the surface represents imperfect calibration or change in passive electronic components over time, and is referred to as drift or zero-offset. In some cases, drift on a given device is maintained over long time periods ("static drift"), and in other cases drift changes over a single record ("drifting drift"). Although some TDRs come with drift corrections (e.g. "ZOC" program by Wildlife Computers; Jensen Software Systems; Igor Mori Pro.Exe), usually these corrections need to be made manually and it is often unclear how these are done (corrected once for entire record, or corrected for each dive?) or

what impact they have on the overall results (e.g., Rodary *et al.* 2000; Mills 2000, Mori *et al.* 2002). Furthermore, many authors never document whether drift corrections were applied at all (e.g., Schreer *et al.* 2001; Elliott *et al.* 2007). This is particularly important for shallow-diving species where dive depth may be less than the zero-offset correction (e.g., Nolet *et al.* 1993; Hays *et al.* 2001, 2006), but could also be important for separating minor differences in depth between dives for deep-diving species. It is currently unknown what factors affect drift. Although usually considered a nuisance, were drift to be influenced by activity (flying, resting, swimming), then drift may actually be a useful way of quantifying behavior.

In this study, we examined the accuracy of MDGs and precision of TDRs in a field setting, by attaching them simultaneously to a deep-diving seabird (140+ m in depth, Elliott *et al.* 2007, 2008). We also documented zero-offset correction ("drift") over multiple time-scales and during different activities. Thick-billed Murres are one of the most-studied seabirds, primarily because they are abundant and easily observed during the breeding season (Gaston and Hipfner 2000). Because of their large size and robust disposition (i.e. Common Murres, *Uria aalge*, sometimes abandon after handling), many studies have used depth recorders to examine diverse aspects of Thick-billed Murre ecology (Benvenuti *et al.* 1998, 2002; Falk *et al.* 2000a, 2002; Mehlum *et al.* 2001; Watanuki *et al.* 2001, 2003; Jones *et al.* 2002; Mori *et al.* 2002; Paredes *et al.* 2005, 2006). In fact, the first study using TDRs on any alcid occurred on Thick-billed Murres (Croll *et al.* 1992). Yet none of the studies examined the accuracy of the recording devices used directly.

METHODS

All observations were carried out on breeding adult Thick-billed Murres at Coats Island, Nunavut, Canada (see Elliott *et al.* 2007, 2008). We used R 2.4.1 for all statistical analyses and report values ± SE.

MDGs vs. TDRs

We used capillary tubes closed at one end by a tight knot (Tygon tubing, 15 cm in length, 0.125" external di-

ameter, 0.0625" internal diameter, lightly dusted inside with icing sugar; see Croll *et al.* 1992 who actually used 15 cm tubes not 65 cm tubes written therein, D. A. Croll, pers. comm.) attached by a short string to the metal band, while attaching a Lotek 1100 TDR (4.5 g) to the other leg, as described below (n = 29). We compared the maximum depths obtained by the MDG and the TDR attached simultaneously to the same animal during deployments in July 2007. To examine how this result might affect the distribution of maximum depths reported for an animal, we also compared the maximum depths obtained by capillary tubes during 1998 with those obtained by TDRs in 2004-2007 at Coats Island. We separated incubation from chick-rearing because chick-rearing birds dive deeper than incubating birds (Benvenuti *et al.* 2002, Elliott *et al.* in press). All deployments were for 48 hours. In 2008, we completed another set of deployments for 144 hours (n = 6). As the MDGs and TDRs were attached at a similar location (the leg), we used the temperature log on the TDR to determine average temperature over the entire deployment ("average temperature"), average temperature at the colony ("colony temperature") and maximum temperature ("maximum temperature") to examine whether temperature affected MDG accuracy, as has been suggested by others (Hedd *et al.* 1997, Burger and Wilson 1988). We specifically tested the hypothesis that above-average temperature increases apparent MDG depth.

Precision of TDRs

In 2007 we used duct tape to attach Lotek 1100 TDRs to spiral plastic color bands, which were attached, one on each foot (n = 18; records every 3 s; details in Elliott *et al.* 2007). The Lotek 1100 TDRs have reported accuracy (±2%) and commercial value similar to those produced by other companies (Wildlife Computers, Star Oddi). We assume that error for Lotek recorders varies in a way typical for commercially-available TDRs and that our results are largely applicable to most TDRs. We calculated the absolute value of the difference between the logs for each recording, after accounting for drift (defined as average pressure during the final previous surface interval longer than 5 mins). We only included values during diving (defined as when drift-corrected depth was below 2.1 m based on the accuracy results described below). No TDR was used more than once during these tests, so all data are independent. In 2008, we measured the accuracy of recorders by submerging them in a plastic bag to 100 m along a rope with an anchor (n = 12), holding the plastic bag still for one minute at each 25 m interval.

Instrument Drift

Even when the bird was at the colony (and the pressure should read zero), our TDRs sometimes reported nonzero pressure. The observation of nonzero pressure at the surface represents imperfect calibration or change in passive electronic components over time, and is referred to as "drift". We use drift synonymously with zero offset correction. In some cases, drift on a given device was maintained over long time periods, and in other cases drift was consistent over a single record. Thus, on a larger sample size of birds obtained 2005-2007, we compared drift across various time scales, from within a single deployment to across all three years. We obtained average drift values for when the bird was at the colony,

flying and on the water, but not diving, as determined from the temperature log (Elliott *et al.* 2007, 2008).

RESULTS

MDGs vs. TDRs

Usable data were obtained from 29 MDG deployments. MDG maximum depths were highly correlated with TDR maximum depths (Fig. 1), although error was greater beyond about 100 m. Once values greater than 100 m were excluded, the slope was not significantly different from one (Fig. 1). That accuracy deteriorated below 100 m is also reflected in our comparisons between MDG maximum depths from 1998 and TDR maximum depths over 2004-2007; the distribution of maximum depths were generally comparable, except for depths greater than about 100 m (Fig. 2). There was no relationship between maximum depths obtained by the electronic and MDGs for deployments of 144 hours; all MDGs reported depths of >200 m for this interval although no bird actually dove deeper than 100 m. The residual of MDG depth on TDR depth (from regression in Fig. 2) was independent of average (t_{12} = 0.85, P = 0.41) and maximum temperature (t_{12} = 1.91, P = 0.08), but was higher for deployments with above-average colony temperature (t_{12} = 2.68, P = 0.02). There was no
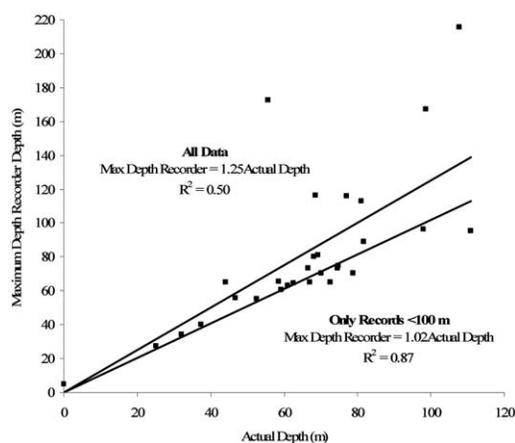

Figure 1. Maximum depth obtained by MDGs and TDRs attached to the same Thick-billed Murres. Regression lines shown are for all data (upper line) and only those data points with MDGs below 100 m (lower line).
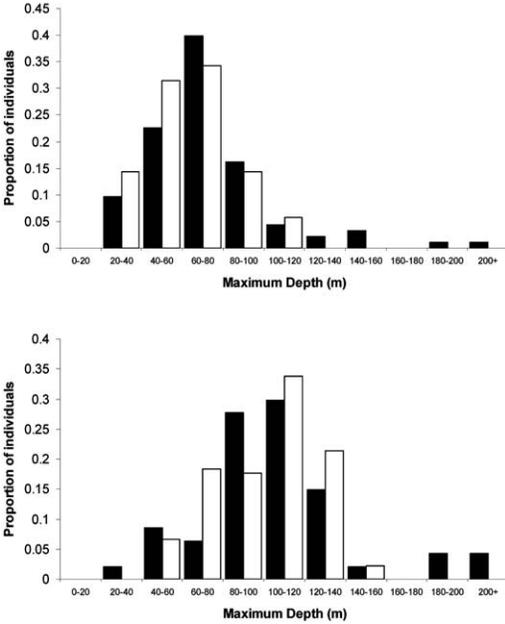
Figure 2. Proportion of Thick-billed Murres with a given maximum depth for (a) incubating and (b) chick-rearing murres. Dark bars are MDGs, light bars are TDRs.

relationship with number of dives ($R^2 = 0.01$, $P = 0.64$).

There was a significant difference between maximum depths obtained by MDGs and those obtained by TDRs during chick-rearing ($\chi^2 = 20.57$, df = 8, $P = 0.003$; Fig. 2), but not during incubation ($\chi^2 = 4.28$, df = 8, $P = 0.83$; Fig. 2). Several records from the MDGs were exceptionally deep: 181 m, 194 m, 227 m and 444 m during chick-rearing and 173 and 268 m during incubation.

Precision of TDRs

The two TDRs attached to the same individual usually differed by less than 1.0 m during dives, although two deployments differed on average by greater than 1.0 m (Table 1). Uncertainty increased with dive depth, at least up to 60 m, and there were few recordings below that depth (Fig. 3). Maximum difference was always less than about 4.0 m (Table 1). All recorders submerged to known depth read drift-corrected values within 2 m of actual depth (average difference = 1.2 ± 0.8 m).

Instrument Drift

Drift was a significant factor on most of the TDRs, varying between -2.3 and 1.5 m. Nine out of 36 TDRs had essentially no drift, apart from occasional spikes to PSI of about 1.0. Drift was not greater (t-test $P > 0.40$) during 2007, when the TDRs were three years old, compared to 2005, when the recorders were new. At the colony, drift decreased with temperature (Fig. 4). Drift was lowest (most negative) at the colony (colony vs. air average difference = 0.33 ± 0.08, paired t_{45} = -4.22, $P < 0.001$, Fig. 5), followed by during flight and was highest (most positive) on the water surface (air vs. water difference = 0.13 ± 0.03, paired t_{45} = -4.39, $P < 0.001$, Fig. 5).

DISCUSSION

MDGs deployed on free-ranging Thick-billed Murres were accurate within ±10% (cf. Burger and Wilson 1988) up to about 100 m, but were inaccurate below 100 m (Fig. 1) or for deployments of 6 days (144 hours). Below 100 m uncertainty increased substantially and there were a number of extreme records from MDGs that were not obtained using TDRs (Fig. 2). High temperatures appeared to be a major source of MDG inaccuracy, as higher temperatures likely increased moisture content in the capillary tube and consequently dissolved some of the icing sugar, inflating depth values (Burger and Wilson 1988). The threshold at which MDGs are reliable likely varies with temperature and capillary tube length; much longer tubes used on seals and large penguins are likely reliable to much deeper depths while MDGs may be less reliable for tropical species (Burger and Wilson 1988).

The maximum published depth obtained for a Thick-billed Murre (210 m using a MDG at our Coats Island study site, Croll *et al.* 1992) is likely erroneous. Apart from the evidence presented here that MDGs are unreliable below 100 m (Figs. 1 and 2), we suggest that 210 m is likely unrealistically deep for three reasons: (1) given the fixed descent and ascent rates (which change nonlinearly; see Lovvorn *et al.* 2004; Watanuki *et al.* 2003,

Table 1. Difference (absolute value) between drift-corrected TDR measurements attached to each foot of the same bird. For calculations of maximum and average differences, only values obtained at depths below 2.1 m were included.

Bird	Maximum Difference (m)	Average Difference (m) (SD)	Difference in Maximum Depth (m)	Difference in Average Depth (m)	Difference in Maximum Duration (s)	Difference in Average Duration (s)
87028	3.29	0.90 (0.63)	1.33	0.59	0.38	0.91
83064	3.07	0.78 (0.55)	1.26	0.26	0.48	1.70
81386	1.74	0.44 (0.35)	0.99	0.26	2.27	0.76
74052	1.63	0.39 (0.31)	0.04	0.04	0.56	0.12
72914	2.77	0.61 (0.49)	1.46	0.72	1.21	1.55
56976	1.56	0.33 (0.27)	0.16	0.12	0.64	0.30
69735	4.05	1.45 (1.19)	2.72	1.97	1.16	0.64
87030	2.44	0.49 (0.38)	1.43	0.31	0.37	0.43
97022	3.69	0.34 (0.40)	0.93	0.23	1.08	5.00
97023	3.21	0.62 (0.33)	0.82	0.22	0.90	1.20
63783	2.77	0.95 (0.64)	0.40	0.27	0.90	0.55
64676	2.96	0.87 (0.50)	1.40	1.13	0.92	0.56
71505	2.61	0.51 (0.43)	3.07	1.31	0.53	3.65
03887	1.30	0.29 (0.22)	1.23	0.18	0.25	0.14
03260	2.13	0.66 (0.45)	1.13	0.56	0.20	0.53
67219	4.01	1.33 (0.80)	3.84	1.57	1.65	0.21
79651	2.58	0.79 (0.56)	0.89	0.61	0.80	1.65
97012	2.00	0.41 (0.32)	0.33	0.53	1.80	1.54
Mean (SD)	2.66 (0.82)	0.68 (0.33)	1.30 (1.03)	0.61 (0.56)	0.89 (0.56)	1.19 (1.28)

2006), and using the nonlinear regressions for descent and ascent rates presented elsewhere (Elliott *et al.* 2007, 2008), a dive to 210 m would require approximately 270 s of dive time which would mean essentially no bottom time even given the maximum reported duration of 278 s (Woo *et al.* 2008); (2) a large number of studies on Thick-billed Murre dive behavior at a variety of locations support a maximum depth of 140-150 m (reviewed in Elliott *et al.* 2007); (3) over 400 deployments using TDRs at Coats Island since

Croll *et al.* (1992) show a maximum depth of 148 m (Woo *et al.* 2008). A reduction in maximum dive depth for murres reduces the slope of the equation for alcid maximum depth in Watanuki and Burger (1999), making it more in line with penguins. Caution needs to be used when quoting animal species-wide maximum depths below 100 m using MDGs (Ropert-Coudert *et al.* 2006).
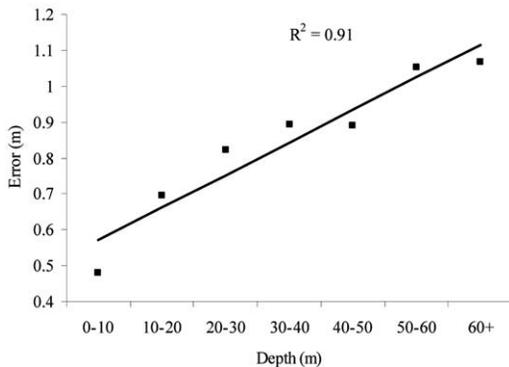

Figure 3. Precision for TDRs increased with dive depth. Values are averaged across all deployments.
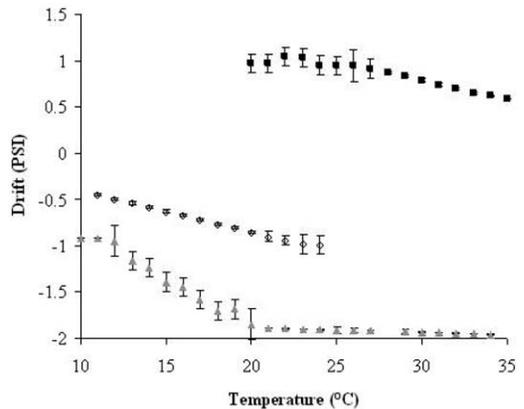

Figure 4. Average drift decreased with temperature at the colony for three representative electronic depth-recorders attached to Thick-billed Murres.
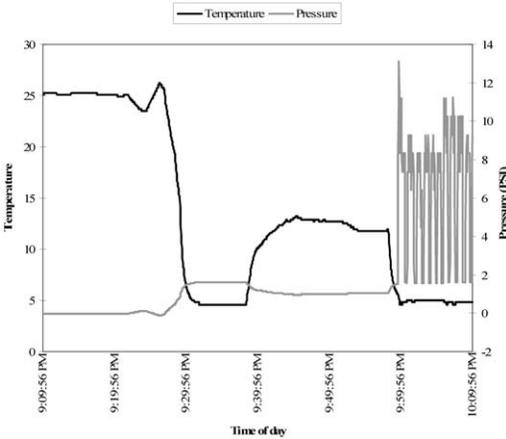
Figure 5. A typical activity record for a Thick-billed Murre. At the colony, temperature is high and pressure (drift) is low. On the water, temperature is low and pressure (drift) is high. In the air, temperature and pressure (drift) are intermediate.

Lotek TDRs were precise within about 0.5 m (near the surface) to 1 m (at 60 m) and accurate within 2 m, which is similar to the accuracy reported by the manufacturer (±1%). Regularly reported parameters, such as maximum or average depth or duration, were similarly precise to about ±2% (Table 1—typical values for these parameters are reported in Elliott *et al.* 2007, 2008). Deviations in precision could be due to differences in swim speed or acceleration between the legs (Bernoulli effect—a bird moving at 1 m/s would appear to be 0.05 m deeper, and a bird moving 2 m/s would appear to be 0.2 m deeper), differences between the position of the feet relative to the body (up to 0.1 m different), drifting drift (beyond what is already accounted for—see below), changes in depth between logging times (which were lined up within 1 s) and actual inaccuracy within the device. Notably, the small differences at shallow depths are likely more biologically meaningful than the large differences at deep depths (i.e. an error of 0.5 is more important at 5 m than an error of 1 m at 50 m). Nonetheless, we suggest that researchers examine actual precision or, if possible, accuracy of the devices rather than relying on manufacturers' specifications or device resolution, which is currently virtually the universal procedure.

There were two types of drift, static drift and drifting drift. Static drift remained constant over the course of the TDR record and across years; the baseline drift was generally a characteristic of the depth-recorder, and did not change over the recorders' lifetime; by 2007, these recorders had exceeded Lotek's quoted lifetime, but showed no change in drift. Drifting drift changed over the course of the TDR record. Thus, the difference between colony, air and water drift values, and the relationship between temperature and drift, were most obvious over short time-scales (several hours); over longer time scales they were obscured by drifting drift. Drift could be up to ±2.5 m. Thus, drift provides a limit on the threshold for defining a "dive" and, if uncorrected, could present significant problems for distinguishing shallow dives (which are common in Thick-billed Murres during the night, Croll *et al.* 1992), potentially inflating both dive duration and the number of dives. Furthermore, even for deep dives, drift could be a potential problem. For example, males dive about 5 m deeper than females during U-dives and 7 m deeper during W-shaped dives while birds capturing squid dive about 9 m deeper than birds capturing benthic shannies (Elliott *et al.* 2008; Paredes *et al.* 2008). These differences were statistically significant and were presented as biologically meaningful, yet if the same recorders had been deployed repeatedly on males vs. females or on squid specialists vs. shanny specialists, and had the authors not accounted for drift, drift alone could have accounted for a large proportion of these differences. Thus, our results show that correcting for drift is an important part of any study using TDRs.

Pressure (drift) was lowest at the colony, which might be expected given that the breeding sites were up to 50 m above sea level (Fig. 5). Nonetheless, a change of 50 m, assuming air is approximately 1000 times less dense than water, should convert to only a 0.05 m water-equivalent difference in perceived depth; our measurements were somewhat higher (0.33). Also, although murres almost always fly directly over water, there was a distinguishable difference in the drift

between flying and sitting on the water, possibly due to negative pressure created during fast flight or due to the slight increase in pressure when the foot is in the water (Fig. 5). Interestingly, at the colony temperature and pressure were negatively correlated (Fig. 4), suggesting that when the bird is brooding on the depth-recorder (high temperature) a micro-environment with negative pressure occurs. The presence of a difference in drift values between sitting on the water, flying and sitting at the colony means that minor differences in drift may be useful at obtaining at-sea activity records (flying vs. resting), especially if considered in conjunction with temperature. Temperature records are sometimes difficult to interpret by themselves, especially if water temperature is close to air temperature or if the birds do not brood tightly on the recorder. In either case, drift coupled with temperature is likely a much cheaper (a few hundred dollars for a TDR) and less-invasive method to record flight time over long periods than other proposed alternatives which cost a few thousand dollars (e.g., heart rate loggers, Pelletier *et al.* 2007; GPS loggers Weimerskirch 2007; accelerometers, Watanuki *et al.* 2003, 2006). Nonetheless, this difference was not exhibited by all depth-recorders, especially those that showed essentially no drift, suggesting that this method would need to be validated on each depth-recorder prior to use.

Our results suggest several useful recommendations for deploying depth-recorders. First, MDGs should only be used to about 100 m and for deployments of 48 hours or less. High temperatures should be considered carefully when deploying MDGs. Second, TDRs are relatively accurate, with relative accuracy increasing with depth. Third, device drift needs to be considered or accounted for, especially for shallow dives (<10 m) or for questions depending on separating small depths (<10 m). As drift changes within TDR deployments and across deployments, and varies with activity, it is important that drift corrections be standardized and occur close to the dive record. We suggest that using a surface interval relatively soon after the dive would be an appropriate peri-od to determine a drift correction. Further information on the accuracy of MDGs and TDRs would be very useful, especially for MDGs that are shorter or longer than 15 cm and for TDRs from other manufacturers.

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