Aquatic Mammals 2010, *36*(3), 270-277, DOI 10.1578/AM.36.3.2010.270

Stomach Temperature Telemetry Reveals that Harbor Seal (*Phoca vitulina*) Pups Primarily Nurse in the Water

Jason F. Schreer,[1] Jennifer L. Lapierre,[2] and Michael O. Hammill[3]

[1]*Department of Biology, SUNY Potsdam, Potsdam, NY 13676, USA; schreejf@potsdam.edu*
[2]*Center for Sleep Research, Semel Institute for Neuroscience and Human Behavior, University of California–Los Angeles; and Neurobiology Research (151-A3), Veterans Affairs Greater Los Angeles Health Care System, North Hills, CA 91343, USA*
[3]*Maurice Lamontagne Institute, Department of Fisheries and Oceans, Mont-Joli, Québec, Canada G5H 3Z4*

Abstract

Research on a captive harbor seal (*Phoca vitulina*) mother-pup pair showed that ingestion of milk caused a decrease in stomach temperature (Hedd et al., 1995). Herein the feasibility of stomach temperature telemetry for measuring nursing behavior was tested in wild harbor seal pups from the St. Lawrence River Estuary. Fifteen pups were outfitted with time-depth recorders, stomach temperature transmitters (STT), and stomach temperature recorders in 2002 and 2003. Twelve pups were recaptured, and seven yielded usable stomach temperature data. Excluding a mortality that lost its transmitter the day of release, transmitter retention time ranged from at least 7 to 22 d (12.5 ± 1.45 d) based on a STT signal at recapture. Pups that gained more weight had a higher frequency of decreases in stomach temperature (DST) (R^2 = 0.954, $p < 0.001$). Depth and external temperature data showed that most DST occurred while pups were "in the water" (57%) followed by "just before or after hauling out" (19%), "just before or after entering the water" (15%), and "hauled out" (9%) ($\chi^2 = 56.376$, $p < 0.001$). The frequency DST did not change with age, and there was no diel pattern of DST, which also did not change with age. These findings indicate that transmitter retention times are sufficient to monitor most of the nursing period for harbor seals, that stomach temperature can be used to quantify nursing characteristics in the field, and that a telemetric technique is needed for harbor seals as most nursing events occur in the water.

Key Words: telemetry, stomach temperature, harbor seal, *Phoca vitulina*, nursing, pups

Introduction

Nursing is fundamental for the growth, development, and ultimate survival of phocid neonates, yet few studies have detailed the characteristics of this behavior (Bowen, 1991; Rosen & Renouf, 1993; Hedd et al., 1995). Previous studies of nursing behavior have typically relied on visual observations, which are limited by proximity to the animal, hours of daylight, access to haul-out sites, and weather (Venables & Venables, 1955; Newby, 1973; Lawson & Renouf, 1985; Eliason, 1986; Godsell, 1988; Stein, 1989; Thompson & Wheeler, 2008). Additionally, variation in methodologies and measurement criteria make comparisons between studies difficult (Bowen, 1991; Hedd et al., 1995). Estimates of total milk intake during the nursing period via labeled-water techniques (Costa, 1991) and calculations based on metabolic rates and growth during lactation (Fedak & Anderson, 1982) only provide estimates of total milk intake in between samplings but do not provide temporal or spatial information on nursing behavior. Stomach temperature telemetry provides a possible tool to overcome many of these limitations.

Archival units capable of detecting and recording changes in stomach temperature have enabled the detection of prey ingestion (Wilson et al., 1992). When used in combination with time-depth recorders, this technology has provided insight into the foraging ecology and behavior of many aquatic species (Wilson et al., 1992; Lesage et al., 1999; Austin et al., 2006). In addition to prey ingestion, results from a study on a single captive harbor seal (*Phoca vitulina*) mother-pup pair (Hedd et al., 1995) supported the use of stomach temperature telemetry for monitoring nursing behavior in captive harbor seals. The ingestion of milk was shown to cause an observable decrease in stomach temperature.

In the present study, the use of stomach temperature telemetry was applied to measuring and quantifying nursing behavior in wild harbor seal pups. This allowed several basic hypotheses to be tested. First, most nursing events for harbor seals occur in the water because observations of nursing in hauled-out harbor seals are somewhat rare

(Schreer, Lapierre, & Hammill, pers. obs.), and nursing in the water has been observed prior to this study (Venables & Venables, 1955). Second, nursing bout duration will increase with age as previously reported for a single harbor seal mother-pup pair in captivity (Hedd et al., 1995) and for harbor seals in the field (Rosen & Renouf, 1993). Lastly, there will be diel patterns in nursing behavior that will change with age as observed for a single pup in captivity (Hedd et al. 1995).

Materials and Methods

This study was conducted near Bic (48º 24' N, 68º 51' W) and Métis (48º 41' N, 68º 01' W), Quebec, Canada, located on the south shore of the St. Lawrence River Estuary from May to July of 2002 and 2003. Harbor seal pups were captured in the water using an aluminum dip net (1-m diameter hoop attached to a 2-m handle) and an inflatable boat powered by a 30-hp outboard motor (Dubé et al., 2003). Once captured, pups were weighed (± 0.5 kg), sexed, and tagged with a numbered flipper tag placed in the interdigital webbing of one hind flipper (Jumbo Rototag, Dalton, England) and a numbered pyramid head tag (Jumbo Rototag, Dalton, England) glued to the fur covering the head (Loctite #422 cyanoacrylate glue and #7452 accelerator, Loctite Corp., Mississauga, ON, Canada). A cylindrical VHF radio transmitter (4.0 cm [length] × 2.0 cm [diameter], model A1-2, Holohil Systems, Carp, ON, Canada) was also glued caudal to the head tag. Pup age (d) was calculated by subtracting published mass at birth (11.1 ± 0.22 kg) from mass at first capture (kg) and dividing by published growth rates (0.544 kg d^{-1}) for pups at this site (Dubé et al., 2003).

To measure dive behavior and stomach temperature, pups were equipped with a time-depth recorder (TDR), a stomach temperature transmitter (STT), and a heart-rate/temperature recorder (HTR) that was used just as a temperature recorder. The TDRs (model LTD100, Lotek Marine Technologies Inc., St. John's, Newfoundland, Canada; or models MK3 and MK8, Wildlife Computers Inc., Redmond, WA, USA) were programmed to record pressure every second (every 5 s for the MK3) and external temperature every 60 s. The unaltered, cylindrical STTs (32 g, 58 mm [length] × 20 mm [diameter], range 8 to 44° C, accuracy ± 1° C, resolution 0.02° C; Wildlife Computers Inc., Redmond, WA, USA) were introduced into the seal's stomach by intubation using flexible tubing (25.5 mm O.D. × 19 mm I.D. clear vinyl tubing and 12.5 mm O.D. × 8.9 mm I.D. polyethylene tubing) and a wooden bite block (321 mm × 48 mm × 19 mm plywood with 29-mm hole). The tip (about 5 mm) of the STT was lodged into the leading edge of the larger tubing (note, the I.D. of the larger tubing was 1 mm smaller than the O.D. of the STT). To ease insertion, the STT and vinyl tubing were coated with K-Y® water-soluble jelly. The tubing was subsequently inserted up to a distance approximately half the standard length of the animal and the smaller, more rigid tubing was pushed through the center of the larger tubing to dislodge the STT into the stomach. The STT transmitted 10-ms duration electromagnetic pulses, modulated at 5 KHz, to the HTR (60 g, 7 × 5 × 1.4 cm, 2 MB; Wildlife Computers Inc., Redmond, WA, USA) at intervals that varied linearly with stomach temperature (i.e., the warmer the temperature, the shorter the pulse interval). In the laboratory, similar STTs have shown reaction times of 6 to 15 s (Lesage et al., 1999) with a precision of 0.2° C (Gales & Renouf, 1995; Lesage et al., 1999). The HTRs were programmed (Hyper Terminal, Hilgraeve Inc., Monroe, MI, USA) to store the time between successive pulses. The TDR was affixed dorsally between the scapulae just caudal to the VHF transmitter, while the HTR was placed near the dorsal midline above the stomach. Total equipment load (maximum mass in air of 190 g) was less than 2% of body mass at initial deployment (mean = 1.2%). Pups were released immediately following all measurements and attachments toward the direction where the mother was last observed. The entire period from capture to release was approximately 30 min.

Pups were relocated via their VHF transmitters using a portable receiver and Yagi antenna (R2000, ATS, Isanti, MN, USA) and captured as described above. To determine if the STT was still present, a polar BG750 heart rate wrist monitor (Polar Electro Oy, Kempele, Finland) was used to detect the signal. In all but one case, the STT was present at the final capture. The STT was not removed from the pup because it was expected to be regurgitated or passed within a short period of time as had been observed in adult harbor seals (Lesage et al., 1999). Additionally, it was thought more important to quickly reunite the pup with its mother than to subject them to gastric lavage.

Upon recovery of the TDRs and HTRs, data were downloaded (using *TagTalk32*, Lotek Marine Technologies Inc., Newfoundland, Canada; and *Hyper Terminal*, Hilgraeve Inc., Monroe, MI, USA) to a portable computer and processed using programs written in *SAS* (*SAS System for Windows*, Release 8.01, 1999-2000, SAS Institute Inc., Cary, NC, USA). Pressure values were converted to depths (depth in m = pressure in psi * 0.6849315), and pulse intervals were converted to stomach temperature (temperature in °C = 20 * [4 – pulse interval]). The HTR data required correcting for missed pulses or stray pickups, and

TDR data required correcting for negative pressure values that occurred sporadically while at the surface which were subsequently converted to zero. Stomach temperature records were corrected for time drift (less than 1 min) relative to the corresponding TDR records. Simultaneous depth, temperature, and stomach temperature records were merged, and since depth was typically sampled on a per second basis, missing values for external temperature and stomach temperature were linearly interpolated (*PROC EXPAND* method = join, SAS Institute Inc., Cary, NC, USA). Triple-paned plots were generated in *SigmaPlot* (*SigmaPlot 2000 for Windows*, Version 6.00, SPSS Inc., Chicago, IL, USA) with stomach temperature, depth, and external temperature vs time of day. These plots were visually analyzed to detect and measure changes in stomach temperature. Decreases in stomach temperature (DST) were clearly evident as abrupt drops in temperature that slowly returned to baseline values (Figure 1). Once detected, the duration (± 1 min) and amplitude (± 0.1° C) of each decrease was measured. The time of day at which each event occurred was also noted. Using the diving behavior and external temperature, each event was categorized as (1) "hauled out," meaning no diving occurred for at least 30 min before and after the event (there was also an increase in external temperature); (2) "in the water," meaning the pup appeared to be performing shallow dives at the time of the event, and there was no indication of hauling out for at least 30 min before or after the event; (3) "just before or after hauling out," meaning the event occurred within 30 min before or after cessation of diving; and (4) "just before or after entering the water," meaning within 30 min before or after the resumption of diving.

Decreases in stomach temperature deemed nursing events were discriminated from mariposia (sea water drinking) by generating a histogram of the amplitudes of all DST (°C) divided by their durations (h) and visually assessing it for multimodality (Figure 2). The basis for this analysis is that ingesting relatively large volumes of warm milk, in comparison to small quantities of cold water, would yield smaller and longer DST. As it would be difficult or impossible to discriminate between mariposia and an actual or attempted feeding event, no attempt was made to do so here. However, collectively, these events are referred to as mariposia hereafter. This histogram showed a precipitous drop off at 10° C/h and, consequently, any events beyond this point (21 out of 155) were deemed mariposia and were separated out from nursing events (Figure 2). This was substantiated in that most cases of mariposia (18 out of 21) occurred in pups that lost weight (14 out of 21) or just following release (4 out of 21); the logic being that abandoned or recently released pups would be more likely to consume water or attempt to feed

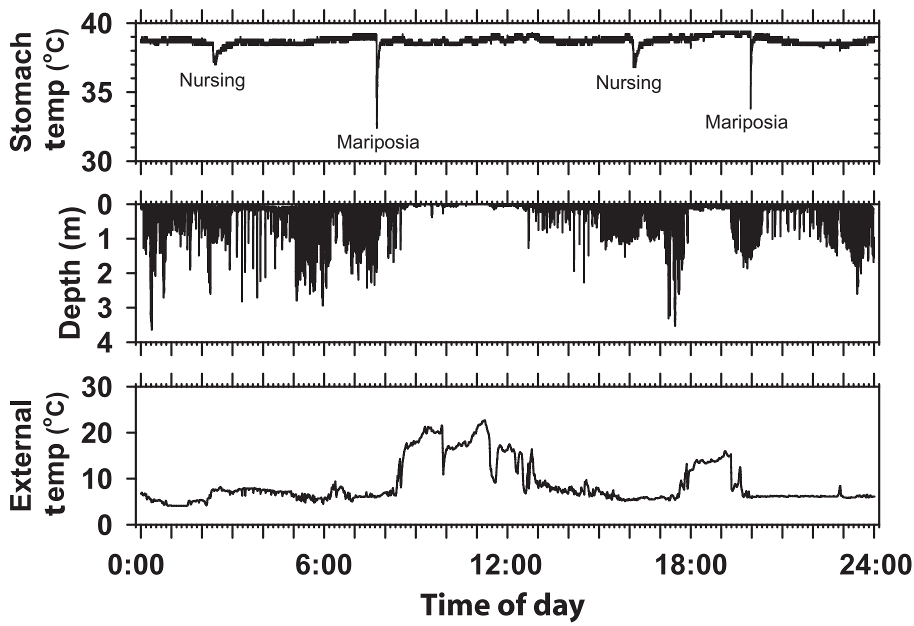

Figure 1. An example of a 1 d plot of stomach temperature, depth, and external temperature for a harbor seal pup during the nursing period

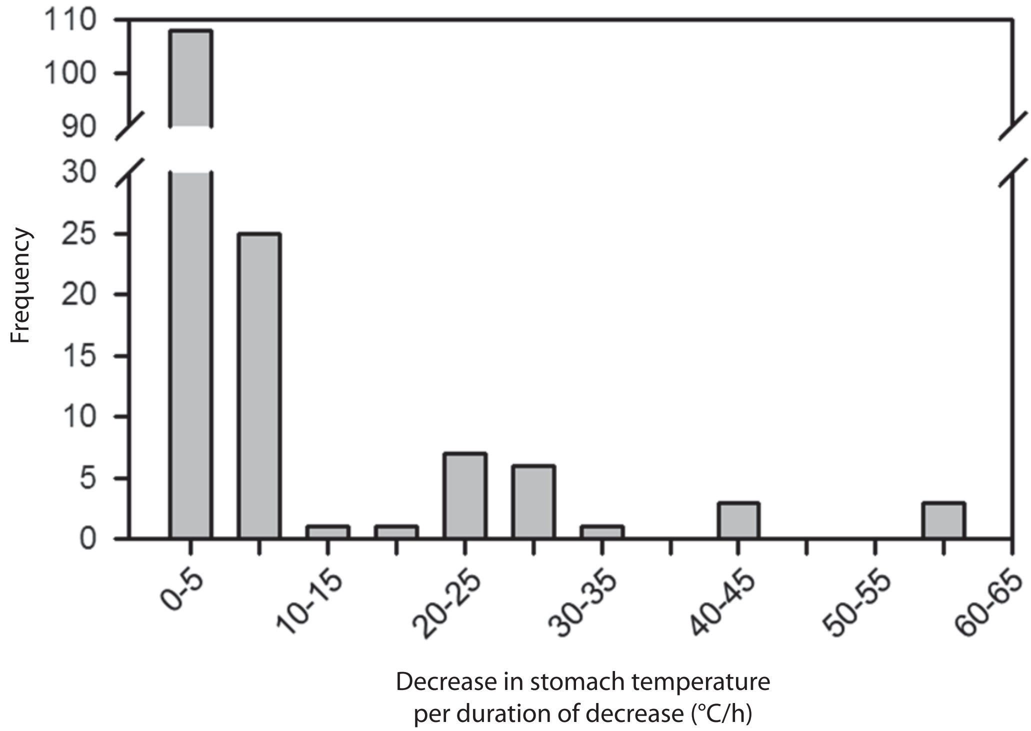

Figure 2. Histogram for the amplitude of the decrease in stomach temperature divided by the duration of the decrease for seven harbor seal pups during the nursing period; multimodality was used to discriminate decreases in stomach temperature deemed nursing events (< 10° C/h) from mariposia (sea water drinking) (> 10° C/h).

than actively nursing pups. Several studies have suggested that water ingestion increases with the length of time since the last meal (Renouf et al., 1990; Lydersen et al., 1992; Hedd et al., 1995).

To determine if DST corresponded to actual nursing events, traditional visual observations were collected at the Métis site in 2003. Over a period of 75 h, 30 nursing events were observed, all of which were for hauled-out mother-pup pairs. Unfortunately, it was not possible to observe nursing in any of the pups for which data on stomach temperature were successfully collected.

In an attempt to further quantify nursing behavior, simulations and models presented by Hedd et al. (1995) were considered to estimate milk volume and suckling duration from the DST. However, as outlined in their study, several sources of variation (fat content of the milk—they used cow's milk; the rate milk was added in the simulations—milk was added all at once as opposed to slowly as would be the case for nursing; metabolic rate of the mother; and ambient temperature) bring into question the accuracy of these simulated models. Additionally, other studies have also brought up concerns with estimates of the mass of the ingested meal due to factors such as the location of the STT within the stomach, the size of the meal, and the amount of previously ingested material (Wilson et al., 1995; Hedd et al., 1996; Austin et al., 2006). However, these studies found that the timing of the ingestion event could be determined accurately. Therefore, as the main goal of this study was to test the validity of using stomach temperature telemetry in the field, no attempt to estimate milk volume was made and, instead, the timing and duration of the DST were the focus.

All statistical analyses were performed in *Systat 11 for Windows* (Richmond, CA, USA). All data were tested for normality and log transformed where necessary. The effect of the number of nursing events/d on weight change was tested with linear regression. A comparison of where nursing events occurred (e.g., in the water or hauled out) was performed using a Chi-square test. The effect of age on the number of nursing events and the proportion of nursing events that took place during the day (0600 to 1800 h) was determined with linear regression for each individual and for all data pooled. The statistical significance level for all tests was set at 0.05, and all values are presented as mean ± standard error.

Results

A total of 15 pups were outfitted with recorders (5 at Bic in 2002 and 10 at Métis in 2003). Twelve of these pups were recaptured. Due to equipment failure and one mortality, seven yielded usable data (Table 1). One pup that yielded usable data was also a mortality, but it died on the ninth day of a 10-d recording period and, therefore, the data could be analyzed until the time of death. The three pups that were not recaptured were all observed with their mothers, appeared in good physical condition, and two were observed nursing from their mothers.

Transmitter retention time (all pups still had the STT when recaptured) ranged from at least 7 to 22 d (12.545 ± 1.455 d, N = 11), excluding the mortality that lost its transmitter the first day after release.

Eight of the pups (four with usable data) gained weight during the observation period, while three (all with usable data) lost weight. One of the pups that lost weight and had usable data was a mortality. Average weight gain for the eight seals that gained weight during the observation period was 0.546 ± 0.049 kg/d (range 0.346 to 0.783 kg/d).

A total of 155 DST were identified with 134 of these being categorized as nursing and 21 categorized as mariposia. The mean amplitude of the DST for events deemed nursing was 1.65 ± 0.05° C (range 0.7 to 3.8° C) and 5.39 ± 0.32° C (range 3.1 to 7.2° C) for mariposia. The mean duration of the DST was 30.10 ± 0.98 min (range 15 to 70 min) for events deemed nursing and 10.81 ± 0.64 min (range 7 to 15 min) for events deemed mariposia.

The amount of weight a pup gained was significantly affected by nursing frequency (N = 7, $R^2 = 0.954$, $p < 0.001$, weight change (g) = 264 * events/d - 332). The number of DST and their durations did not change with age for individual pups and for all pups pooled. There was also no diel pattern in the occurrence of the nursing events (48% diurnal), and no change was observed with age.

Of the 114 DST that had corresponding depth and external temperature data (the rest of the DST were from pups for which the TDR failed), most occurred while pups were "in the water" (57%) followed by "just before or after hauling out" (19%), "just before or after entering the water" (15%), and "hauled out" (9%) ($\chi^2 = 56.376$, df = 3, $p < 0.001$).

Discussion

In this study, the use of stomach temperature telemetry was tested for measuring and quantifying nursing behavior in wild harbor seal pups.

Table 1. Life history data and stomach temperature results for harbor seal pups recaptured in the St. Lawrence River Estuary in 2002 and 2003

Pup ID	Sex	Age range (dpp)[2]	Length of recording (d)[3]	Start weight (kg)	End weight (kg)	Weight change (kg)	Weight change per day (kg/d)	Nursing events[4]	Mariposia events[5]	Nursing events/day
71[1]	M	3-13	10.0	13.0	8.5	-4.5	-0.45	0	3	0.00
73	M	11-24	13.0	17.0	14.5	-2.5	-0.19	8	5	0.62
61	F	6-15	9.0	14.5	14.0	-0.5	-0.06	6	7	0.67
12	F	15-28	13.0	19.5	24.0	4.5	0.35	30	0	2.31
59	F	16-22	7.0	20.0	22.5	2.5	0.36	16	0	2.29
1	M	14-22	9.0	18.5	23.5	5.0	0.56	33	6	3.67
49	M	3-14	11.5	13.0	19.5	6.5	0.57	41	0	3.57
24	M	1-22	21.0	12.0	23.5	11.5	0.55	Equipment failure		
20	M	4-26	22.0	13.5	26.0	12.5	0.57	Equipment failure		
67	M	9-21	12.0	16.0	23.5	7.5	0.63	Equipment failure		
84	M	11-22	11.5	17.0	26.0	9.0	0.78	Equipment failure		
15	M	6-11	5.0	14.5	NA	NA	NA	Mortality		

[1]Pup 71 was found dead and, according to its stomach temperature, had died within 12 h of recapture.

[2]Pup age (dpp) = (mass at first capture (kg) - 11.1 ± 0.22 kg)/0.544 kg d^{-1} (Dubé et al., 2003).

[3]0.5 d was added or subtracted to the length of recording when initial capture and recapture were approximately 12 h apart within their respective days.

[4]Nursing events = Events during which the amplitude of the decrease in stomach divided by the duration of the decrease was less than 10° C/h.

[5]Mariposia events = Events during which the amplitude of the decrease in stomach divided by the duration of the decrease was greater than 10° C/h. These observations may also represent feeding or attempts at feeding.

Transmitter retention time was sufficiently long to cover most of the nursing period. Considering that the STT was not altered in any way to enhance retention, as done in other studies (e.g., Austin et al., 2006), these lengthy durations are likely due to the size of the STT relative to the animal and their liquid diet.

The strongly significant effect of nursing frequency on weight change indicated that the DST observed were representative of nursing events. Average weight gain for the eight seals that gained weight during the observation period was 0.546 ± 0.049 kg/d (range 0.346 to 0.783 kg/d), which was not significantly different (one-sample *t*-test) from the mean and range from a previous study of pups from this site (0.544 ± 0.141 kg/d, range 0.118 to 0.875, N = 110; Dubé et al., 2003). Additionally, even when including the three pups that lost weight (0.334 ± 0.119 kg/d), there was no significant difference from the Dubé et al. study.

The amplitudes of the DST also indicated that they were representative of nursing events. Although not specifically quantified by Hedd et al. (1995), the amplitudes of the DST for nursing and mariposia appear to be similar to the values observed in the present study. The durations of the DST for nursing events in the present study were similar to the value reported for a single pup at 1 wk of age (26.6 min) in the Hedd et al. study but were lower than values reported when the pup was 2 to 4 wks old (48.9 to 56.9 min). This may simply demonstrate individual variation or differences between captive and natural conditions.

Application of this technique supports the hypothesis that most nursing events for harbor seals occur in the water. This indicates that most nursing events would be missed by visual observations alone and supports the need for a telemetric means of monitoring nursing behavior. This finding is supported by the rarity of nursing events observed for hauled-out harbor seals (Schreer, Lapierre, & Hammill, pers. obs.) and previous observations of in-water nursing behavior in the field (Venables & Venables, 1955) and in captivity (Hedd et al., 1995). In fact, 9 of the 26 visually observed nursing attempts in the Hedd et al. captive study occurred in the water. Interestingly, none of these in-water nursing events coincided with DST. This may demonstrate a difference between captive and field situations, at least for one captive pup, in that in-water nursing is a common practice but more successful in the field.

Applying stomach temperature to ontogenetic changes was less conclusive. There were no significant changes in nursing bout duration with increasing age. This is in contrast to other studies (Rosen & Renouf, 1993; Hedd et al., 1995) that have shown an increase in the duration of the nursing events with age. Assuming the results from these studies represent typical trends, the lack of a similar finding here was likely due to no single pup being observed for the entire nursing period (max record length = 13 d) and the small sample size. However, similar to findings in this study, Oftedal et al. (1991) found no change in milk intake rate throughout the nursing period. There was also no diel pattern for when nursing occurred, and this did not change with age. This is contrary to the findings of Hedd et al. (1995) in which a single captive pup primarily nursed nocturnally during early lactation and then diurnally later in the nursing period. The contrasting results from the present study and previous studies may simply demonstrate individual variation or differences between captive and natural conditions.

While the findings of this study show potential for the use of stomach temperature telemetry to measure nursing behavior, the three pups that lost weight (one also being a mortality) and the one additional mortality for which a recapture weight could not be determined, raise some concerns. That four of 15 pups either lost weight or died during the monitoring period indicates that abandonment rates may be higher in pups outfitted with stomach temperature equipment or that the transmitter itself might have impacted the pup's ability to nurse. The two mortalities demonstrate how potential abandonment can lead to death. Pup #15 was found dead 5 d after being released. It appeared to be fresh but had been partially consumed by gulls and, therefore, a usable weight could not be determined. The STT was not present, and the HTR record indicated it had been lost within the first day following release. A necropsy was performed, but aside from tissues being removed by the gulls, no obvious injuries were apparent. Pup #71 was found dead 10 d after release and appeared to have survived for the first 9 d as indicated by a severe and persistent drop in stomach temperature early on the 10th day. Considering that this pup lost 4.5 kg since the initial capture, as well as the lack of DST in its stomach temperature profile, indicated that it was likely abandoned. A necropsy of the emaciated pup showed no signs of injury, so it was assumed that it had succumbed to starvation. Although unfortunate, this study's presumed abandonment rate of 27% (4 out of 15) was similar to another study on harbor seals in Maine that only attached TDRs and found 13% abandonment, 8% missing, and 13% not recaptured out of 38 deployments (Skinner, 2006). Furthermore, assuming all abandoned pups would die soon after the nursing period, these results fall within the range of mortality rates (16 to 31%) for harbor seal pups in Washington State (Stieger et al., 1989), although slightly higher than those found for harbor seal pups at Sable Island (13 to 16%; Bowen, 1991).

While not available at the time of this study, recent work on inter-mandibular angle sensors (IMASEN) (Wilson et al., 2002; Liebsch et al., 2007) could provide a less invasive method for monitoring nursing behavior. This technique monitors the angle of the jaw by measuring the magnetic field produced by a magnet attached to the lower jaw with a sensor attached behind the nose. However, similar to stomach temperature telemetry, capture and extended handling are still required, and the sensor and magnet themselves may interfere with nursing.

In conclusion, using changes in stomach temperature to monitor nursing events has considerable potential to collect information from harbor seals that would be difficult or impossible to otherwise observe. This type of methodology is needed to explore and compare rearing strategies, lactation energetics, maternal investments, and estimates of weaning dates for phocid seals. However, concerns regarding the effects of the equipment and handling on abandonment and mortality must be considered. A strong correlation between weight change and the frequency of decreases in stomach temperature indicated that these events did represent nursing behavior. Transmitter retention times were not limiting and indicated that most of the nursing period could be monitored with this technique. An important finding was that most presumed nursing events appeared to have occurred in the water, which further indicates the need for such a monitoring technique.

Acknowledgments

All procedures were conducted in accordance with the guidelines set out by the Canadian Council on Animal Care as implemented by the University of Waterloo, Waterloo, Ontario, Canada. We thank Pierre Carter, Erin Copeland, Jean-Francois Gosselin, James Greig, and Geoff Yunker for help in the field and Meghan Ellis for compiling the graphical output. We also thank several reviewers and editors for providing comments to improve this manuscript. This work was supported by SUNY Potsdam, the University of Waterloo, the Department of Fisheries and Oceans, and the Natural Sciences and Engineering Research Council of Canada. JFS thanks XOQ.

Literature Cited

Austin, D., Bowen, W. D., McMillan, J. I., & Boness, D. J. (2006). Stomach temperature telemetry reveals temporal patterns of foraging success in a free-ranging marine mammal. *Journal of Animal Ecology*, *75*, 408-420.

Bowen, W. D. (1991). Behavioural ecology of pinniped neonates. In D. Renouf (Ed.), *Behaviour of pinnipeds* (pp. 66-117). London: Chapman and Hall.

Costa, D. P. (1991). Physiology of behaviour in pinnipeds. In D. Renouf (Ed.), *Behaviour of pinnipeds* (pp. 236-286). London: Chapman and Hall.

Dubé, Y., Hammill, M. O., & Barrette, C. (2003). Pup development and timing of pupping in harbour seals (*Phoca vitulina*) in the St. Lawrence River estuary, Canada. *Canadian Journal of Zoology*, *81*, 188-194.

Eliason, J. J. (1986). *Mother-pup behavior in the harbor seal,* Phoca vitulina richardsi. M.A. thesis, Department of Biological Sciences, Humboldt State University, Arcata, CA. 115 pp.

Fedak, M. A., & Anderson, S. S. (1982). The energetics of lactation: Accurate measurements from a large wild mammal, the grey seal (*Halichoerus grypus*). *Journal of Zoology, London*, *198*, 473-479.

Gales, R., & Renouf, D. (1993). Detecting and measuring food and water intake in captive seals using temperature telemetry. *Journal of Wildlife Management*, *57*, 514-519.

Godsell, J. (1988). Herd formation and haul-out behavior in harbour seals (*Phoca vitulina*). *Journal of Zoology, London*, *215*, 83-99.

Hedd, A., Gales, R., & Renouf, D. (1995). Use of temperature telemetry to monitor ingestion by a harbour seal mother and her pup throughout lactation. *Polar Biology*, *15*, 155-160.

Hedd, A., Gales, R., & Renouf, D. (1996). Can stomach temperature telemetry be used to quantify prey consumption by seals? A re-examination. *Polar Biology*, *16*, 261-270.

Lawson, J. W., & Renouf, D. (1985). Parturition in the Atlantic harbor seal, *Phoca vitulina concolor*. *Journal of Mammalogy*, *66*, 395-398.

Lesage, V., Hammill, M. O., & Kovacs, K. M. (1999). Functional classification of harbor seal (*Phoca vitulina*) dives using depth profiles, swimming velocity, and an index of foraging success. *Canadian Journal of Zoology*, *77*, 74-87.

Liebsch, N., Wilson, R. P., Bornemann, H., Adelung, D., & Plötz, J. (2007). Mouthing off about fish capture: Jaw movement in pinnipeds reveals the real secrets of ingestion. *Deep Sea Research Part II: Topical Studies in Oceanography*, *54*, 256-269.

Lyderson, C., Hammill, M. O., & Ryg, M. S. (1992). Water flux and mass gain during lactation in free-living ringed seal (*Phoca hispida*) pups. *Journal of Zoology, London*, *228*, 361-369.

Newby, T. C. (1973). Observations on the breeding behavior of the harbor seal in the state of Washington. *Journal of Mammalogy*, *54*, 540-543.

Oftedal, O. J., Bowen, W. D., & Boness, D. J. (1991). Lactation performance is unaffected by lactation stage in harbor seals (*Phoca vitulina*) on Sable Island (Abstract). *Ninth Biennial Conference on the Biology of Marine Mammals*, Chicago, Illinois.

Renouf, D., Noseworthy, E., & Scott, M. (1990). Daily fresh water consumption by captive harp seals (*Phoca groenlandica*). *Marine Mammal Science*, *6*, 253-257.

Rosen, D. A. S., & Renouf, D. (1993). Sex differences in the nursing relationship between mothers and pups in the Atlantic harbour seal, *Phoca vitulina concolor*. *Journal of Zoology, London*, *231*, 291-299.

Skinner, J. (2006). *Physical and behavior development of nursing harbor seal (*Phoca vitulina*) pups in Maine*. M.S. thesis, University of Maine at Orono. 129 pp.

Steiger, G. H., Calambokidis, J., Cubbage, J. C., Skilling, D. E., Smith, A. W., & Gribble, D. H. (1989). Mortality of harbor seal pups at different sites in the inland water of Washington. *Journal of Wildlife Disease*, *25*(3), 319-328.

Stein, J. L. (1989). *Reproductive parameters and behavior of mother and pup harbor seals*, Phoca vitulina richardsi, *in Grays Harbor, Washington*. M.A. thesis, San Francisco State University, San Francisco, CA. 110 pp.

Thompson, P. M., & Wheeler, H. (2008). Photo-ID-based estimates of reproductive patterns in female harbor seals. *Marine Mammal Science*, *24*(1), 138-146.

Venables, U. M., & Venables, L. S. V. (1955). Observations on a breeding colony of the seal *Phoca vitulina* in Shetland. *Proceedings of the Zoological Society of London*, *125*, 521-532.

Wilson, R. P., Cooper, J., & Plötz, J. (1992). Can we determine when marine endotherm feed? A case study with seabirds. *Journal of Experimental Biology*, *167*, 267-275.

Wilson, R. P., Steinfurth, A., Ropert-Coudert, Y., Kato, A., & Kurita, M. (2002). Lip-reading in remote subjects: An attempt to quantify and separate ingestion, breathing and vocalization in free-living animals using penguins as a model. *Marine Biology*, *140*, 17-27.

Wilson, R. P., Putz, K., Gremillet, D., Culik, B. M., Kierspel, M., Regel, J., et al. (1995). Reliability of stomach temperature changes in determining feeding characteristics of seabirds. *Journal of Experimental Biology*, *198*, 1115-1135.