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*Igor Krupnik, Michael A. Lang,  
and Scott E. Miller  
Editors*

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# Capital Expenditure and Income (Foraging) during Pinniped Lactation: The Example of the Weddell Seal (*Leptonychotes weddellii*)

*Regina Eisert and Olav T. Oftedal*

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**ABSTRACT.** Weddell seals, like many true seals (Phocidae), store nutrients in body tissues prior to lactation and then expend these “capital reserves” in pup rearing. During lactation, 40% or more of the initial mass of a lactating Weddell seal may be expended to cover the combined costs of maternal metabolism and milk production. However, most lactating Weddell seals also begin active diving to depths of 300 m or more by three to four weeks postpartum, and dietary biomarker data indicate that at least 70% of Weddell seals forage in late lactation. Thus, Weddell seals may employ a combined capital and income (foraging) strategy. Determining the relative importance of capital expenditures and food consumption to maternal reproduction will require accurate measurement of maternal energy expenditure, the magnitude of milk production, changes of maternal nutrient stores over lactation and the success of foraging efforts. Alternative scenarios include the following: (1) prey consumption is opportunistic rather than essential because body reserves of Weddell seals are sufficient for reproduction, (2) foraging is necessary only in those females (such as small or young seals) that have limited body stores relative to lactation costs, and (3) successful foraging is critical to the lactation strategy of this species. If alternative 2 or 3 is correct, the drops in pup production observed in Erebus Bay (McMurdo Sound, Ross Sea) during years of unusually heavy ice accumulation may reflect changes in foraging opportunities due to adverse impacts of heavy ice on primary production and on prey populations. Further study is needed on the effects of annual, cyclic, or long-term changes in prey abundance on Weddell seal reproduction.

## INTRODUCTION

Mammalian reproduction is characterized by a period of lactation in which large quantities of nutrients are transferred from mother to young (Oftedal, 1984b). This process puts a great physiologic demand on the mother, who must either acquire the additional nutrients needed for milk secretion by increased food consumption, mobilize nutrients from stored reserves in the body, or employ some combination of both (Oftedal, 2000). Along the continuum from intensive foraging to sole dependence on stored reserves, mammals that rely mostly on feeding can be characterized as “income breeders,” whereas those that rely on stored reserves are “capital breeders” (Jönsson, 1997). Income breeders are highly influenced by local climatic conditions that impact immediate food supply, whereas capital breeders should be relatively independent of food resources

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during lactation by virtue of their previously stored body reserves.

Among Antarctic mammals, two groups rely heavily on stored reserves during lactation: baleen whales (suborder Mysticeti) and true seals (family Phocidae). Baleen whales, such as the blue whale (*Balaenoptera musculus*), fin whale (*Balaenoptera physalus*), humpback whale (*Megaptera novaeangliae*), and minke whale (*Balaenoptera acutorostrata*), migrate to Antarctic waters to forage on seasonal abundances of prey, such as krill, squid, and fish, and deposit large amounts of fat and other body constituents at this time (Lockyer, 1981, 1984; Oftedal, 1997). However, these baleen whales migrate back to subtropical or temperate regions to give birth and lactate. Stored energy and nutrients fuel most or all of lactation as these species feed little if at all at the calving grounds (Oftedal, 1997). Thus, baleen whales export substantial quantities of nutrients from the Southern Ocean to more temperate regions. By contrast, phocid seals, such as southern elephant seal (*Mirounga leonina*), crabeater seal (*Lobodon carcinophagus*), Ross seal (*Ommatophoca rossii*), leopard seal (*Hydrurga leptonyx*), and Weddell seal (*Leptonychotes weddellii*), both feed and lactate in Antarctic areas. Elephant seals typically remain on land and fast throughout a three to four week lactation (Arnbom et al., 1997) and are thus true capital breeders. On the basis of data from satellite-linked dive recorders, Ross seals are also capital breeders, as they haul out on pack ice for only about 13 days in mid-November to give birth and lactate (Blix and Nordøy, 2007). Unfortunately, little is known about reproduction in crabeater or leopard seals, but Weddell seals appear to employ a hybrid breeding approach: partly capital use and partly food consumption.

The ability to rely solely on stored reserves to support the energy and substrate demands of lactation is limited by body size (Oftedal, 2000). Nutrient reserves increase in direct proportion to body mass ( $BM^{1.0}$ ), but rates of energy expenditure (including lactation) increase in proportion to body mass raised to the power of  $3/4$  ( $BM^{0.75}$ ). Thus, the capacity to support metabolism and lactation from body stores alone increases with body size, and larger species can support metabolism and lactation from stored reserves for longer periods of time. The benefit of being able to store large quantities of nutrients for subsequent use was likely an important factor in the evolution of large body size in both seals and whales.

At 400–500 kg, the female Weddell seal is one of the largest of the phocid seals and has long been assumed to rely on stored reserves for lactation (Tedman and Green, 1987). If so, lactating Weddell seals should be relatively

immune to environmental variables that affect local food supply in the areas where they give birth and lactate. However, population censuses have indicated tremendous variation ( $>50\%$ ) in annual pup production associated with changes in ice conditions in Erebus Bay in the Ross Sea (R. Garrott, Montana State University, personal communication, 2007). It is not known whether this variation is related to ice-related changes in prey abundance and diversity or to some other consequence of sea ice accumulation, such as navigational difficulties for seals traveling under the ice. A step in addressing this issue is to evaluate the importance of stored reserves versus acquisition of food to lactation performance of the Weddell seal.

In this paper we briefly discuss breeding strategy, mass change, lactation performance, and foraging by Weddell seals, with comparisons to other phocid species. This paper is a preliminary contribution based on a project in 2006–2007 examining energy expenditure, milk production, and changes in body reserves in lactating Weddell seals in McMurdo Sound, Antarctica.

## EVOLUTION OF CAPITAL BREEDING AMONG PHOCID SEALS

Animals that employ capital breeding incur energetic costs associated with the deposition, transport, and mobilization of stores (Jönsson, 1997). The resulting energetic inefficiency is thought to favor “income breeding” except in specific circumstances such as uncertainty or inadequacy of food at the time of reproduction (Jönsson, 1997). However, among some capital breeders, such as phocid seals that fast during lactation, a major benefit appears to be abbreviation of lactation, with consequent reduction of maternal metabolic overhead and the time devoted to pup rearing. Milk production from stored reserves is also much more efficient than production based on food consumption (Agricultural Research Council, 1980), especially if foraging requires significant effort. This permits an increase in the proportion of energy available for transfer to the offspring (Fedak and Anderson, 1982; Costa et al., 1986). At the extreme, lactation is reduced to as little as four days in the hooded seal, with up to 88% of the energy transferred to pups incorporated into tissue growth (Bowen et al., 1985; Oftedal et al., 1993). Thus, it is not clear that capital breeding is always more energetically costly than income breeding. A variety of other parameters, including animal size, food availability, transport costs, neonatal developmental state, and type of maternal care, are thought to be important to the evolution of capi-

tal breeding systems (Boyd, 1998; Trillmich and Weissing, 2006; Houston et al., 2006).

There is also uncertainty whether maternal capital expenditure is limited primarily by energy or by nutrient stores, such as protein. In the fasting state, catabolized protein is lost continually from the body (Nordøy et al., 1990; Owen et al., 1998), and lactating mammals must export milk protein to support offspring growth. Yet excessive loss of body protein leads to progressive and eventually lethal loss of function (Oftedal, 1993; Liu and Barrett, 2002). Animals that fast during lactation typically produce milks that are low in both protein and carbohydrate (Oftedal, 1993). As both protein and carbohydrate in milk potentially derive from amino acids (either directly or via gluconeogenesis), this suggests that high protein demands may be selected against during the evolution of capital breeding (Oftedal, 1993). In the grey seal (*Halichoerus grypus*), daily milk production and final offspring mass were significantly correlated with initial maternal protein but not initial fat stores (Mellish et al., 1999a), despite the fact that most of maternal body energy reserves are stored as fat. Although phocid seals are often thought to be unusually efficient at conserving protein during fasting, this assumption may have to be reconsidered (Eisert, 2003). Thus, capital breeding may be limited by the size of protein stores as well as by the magnitude of energy stores.

Seals are the best-studied group of mammalian capital breeders (Oftedal et al., 1987a; Costa, 1991; Boness and Bowen, 1996; Boyd, 1998; Mellish et al., 2000; Oftedal, 2000; Schulz and Bowen, 2004). Otariid seals remain ashore for approximately one week after giving birth and transfer approximately 4% of body protein and 12% of body energy to their pups, after which they undertake regular foraging trips to sea (Oftedal et al., 1987a; Costa, 1991; Oftedal, 2000). This strategy of an initial fasting period followed by foraging cycles occurs in at least one phocid, the harbor seal *Phoca vitulina* (Boness et al., 1994), and perhaps in other species that feed during lactation [e.g., bearded seal *Erignathus barbatus*, harp seal *P. groenlandica*, and ringed seal *P. hispida* (Lydersen and Kovacs, 1996, 1999)]. However, many large phocids fast throughout the lactation period [e.g., land-breeding grey seal *H. grypus*, hooded seal *Cystophora cristata* and elephant seals *Mirounga angustirostris* and *M. leonina* (Fedak and Anderson, 1982; Costa et al., 1986; Oftedal et al., 1993; Arnbohm et al., 1997)]. As the true seals (family Phocidae) encompass a wide spectrum from mixed capital-income to extreme capital breeding, this family is an excellent model system for testing hypotheses about the evolution of capital breeding strategies. Factors thought to have favored the evolution of

extreme capital breeding in phocids include large body size (Boness and Bowen, 1996; Oftedal, 2000), limited availability of food (Boyd, 1998), the impact of unstable nursing substrates (Oftedal et al., 1987a; Lydersen and Kovacs, 1999), and reduction of maternal metabolic overhead costs (Fedak and Anderson, 1982; Costa, 1991).

### WEDDELL SEAL: EXAMPLE OF AN INTERMEDIATE STRATEGY?

The Weddell seal represents an interesting, if not fully understood, example of a species where a continuum of capital to mixed capital-income breeding strategies may occur within the same population. Lactating Weddell females fast and remain with their offspring for at least the first week postpartum, but on the basis of a new biomarker method of detecting feeding (Eisert et al., 2005), at least 70% of females feed to some extent during the latter half of a lactation period that lasts six to eight weeks (Bertram, 1940; Kaufmann et al., 1975; Thomas and DeMaster, 1983). During late lactation, an increase in diving activity (Hindell et al., 1999; Sato et al., 2002) and a decrease in rates of maternal mass loss relative to pup mass gain have also been observed (Hill, 1987; Testa et al., 1989). However, the importance of food intake to the energy and nutrient budgets or to reproductive success of lactating Weddell seals is not known, nor has the magnitude of capital expenditure (depletion of maternal body stores) been studied. Three scenarios appear possible: (1) Females are able to complete lactation without food intake but take prey opportunistically (until recently, the prevailing belief). (2) Because of individual differences in nutrient stores and reproductive demand, some females (such as small or young females) have an obligatory need for food intake, while others do not. (3) Food intake is an essential part of the lactation strategy of this species because maternal body stores are inadequate in the face of such an extended lactation period (the longest of any phocid).

Uncertainty regarding the dependency of lactating Weddell seals on local food resources complicates efforts to interpret the influence of environmental factors on maternal condition (Hill, 1987; Hastings and Testa, 1998), pup growth and survival (Bryden et al., 1984; Tedman, 1985; Tedman and Green, 1987; Testa et al., 1989; Burns and Testa, 1997), and population dynamics (Stirling, 1967; Siniff et al., 1977; Testa, 1987; Hastings and Testa, 1998). A strong dependency, in some or all females, on local food resources for successful lactation might limit breeding colonies to areas of local prey abundance or result in

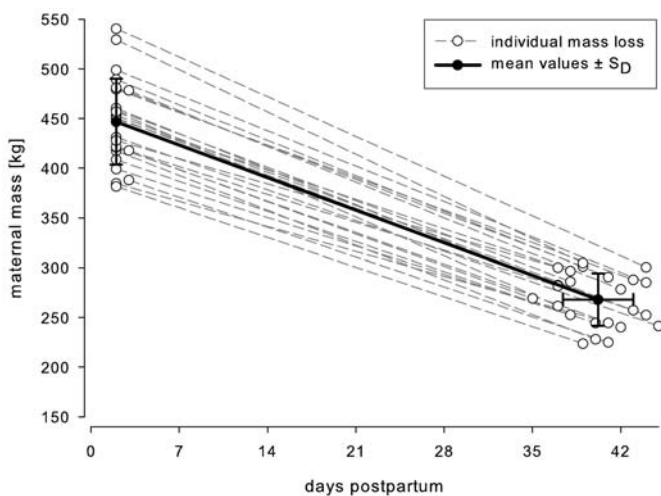
the vulnerability of populations to annual or long-term changes in prey availability, as might occur due to changes in sea ice or shifts in water currents.

## MASS CHANGES DURING WEDDELL SEAL LACTATION

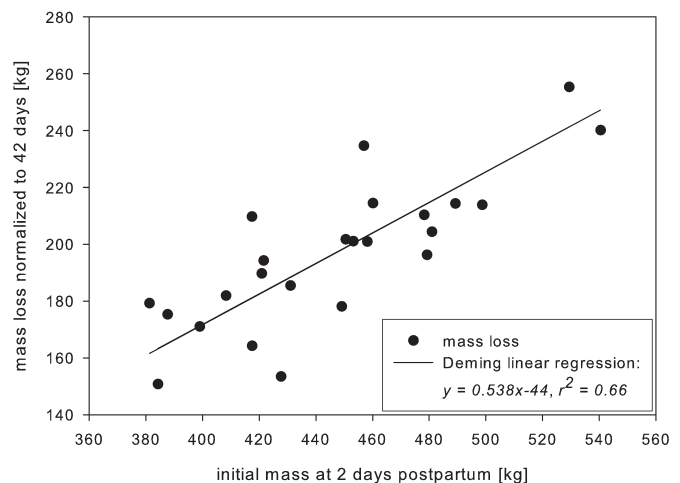
Prior work on Weddell seals has focused primarily on mass changes of mothers and their pups, under the assumption that if mothers are fasting, there should be correspondence between maternal mass loss, maternal milk output, and pup mass gain, as is the case in other true seals that fast throughout lactation. In these species, maternal body mass and age are strong determinants of total milk energy output and, consequently, of pup growth and weaning mass (Iverson et al., 1993; Fedak et al., 1996; Arnbohm et al., 1997; Mellish et al., 1999b). By contrast, females feed during a variable proportion of lactation in almost half of extant phocid species (Bonner, 1984; Oftedal et al., 1987a; Boness et al., 1994; Boness and Bowen, 1996; Lydersen and Kovacs, 1999; Eisert, 2003). Bowen et al. (2001a) found that the positive correlation of maternal body mass with pup weaning mass was much weaker in harbor seals than in species that fast during lactation, presumably because supplementary feeding results in a partial decoupling of maternal mass loss and milk transfer to the pup. Similar patterns have been found in ice-breeding

grey seals *H. grypus* and harp seals *P. groenlandica* (Baker et al., 1995; Lydersen and Kovacs, 1996, 1999).

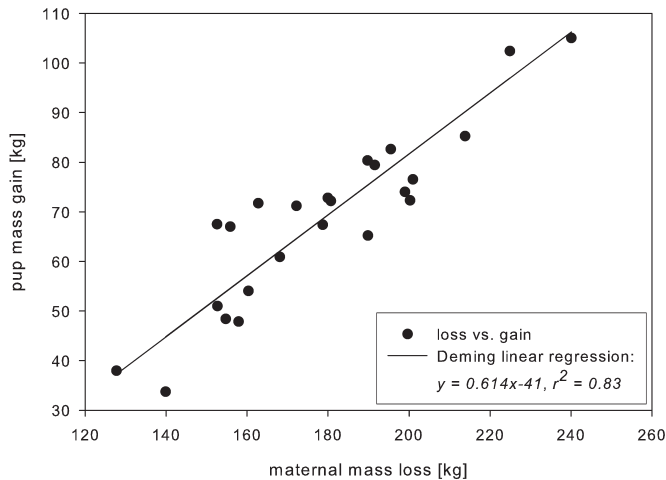
Extant data for Weddell seals are more complex. Weddell seal females certainly lose a large amount of body mass: for example, females that we studied in 2006 and 2007 lost 40% of their two-day postpartum mass during about 40 days lactation (Figure 1). The daily mass loss of 1.0% of initial mass is lower than values of 1.5%–3.4% for fasting and lactating females of the northern elephant seal, southern elephant seal, land-breeding gray seal, and hooded seal (Costa et al., 1986; Carlini et al., 1997; Mellish et al., 1999a, 1999b), but Weddell seal lactation is so prolonged that overall mass loss (42%) is equal to or greater than that in the other species (14%–39%). If mass loss is standardized to a lactation length of 42 days, initial mass predicts 66% of the variation in mass loss, indicating that large females lose more mass than small females (Figure 2). Is this because large females expend more energy (on metabolism and milk production) or because they feed less? Females that lose more mass also support more mass gain by their pups: pup mass gain was positively correlated to maternal mass loss (Figure 3). Tedman and Green (1987) found a similar strong positive correlation ( $r = 0.85$ ,  $P < 0.001$ ) between maternal mass loss and pup mass gain, whereas data from studies by Hill (1987) and Testa et al. (1989) indicate a much weaker correlation between maternal mass loss and pup mass gain ( $r = 0.16$ ,  $P = 0.005$ ,  $n = 35$ ).



**FIGURE 1.** Change in body mass of lactating Weddell seals from early (2–3 days postpartum) to late (35–45 days postpartum) lactation at Hutton Cliffs, Erebus Bay, McMurdo Sound. Data were obtained from 24 females in 2006 and 2007. Average rate of mass loss was 1.0% of initial mass per day.



**FIGURE 2.** Relationship of maternal mass loss to initial maternal mass of lactating Weddell seals. Initial mass was measured at two to three days postpartum. Mass loss was normalized to 42 days and compared to initial mass by Deming linear regression. Data are from the same 24 females at Hutton Cliffs, Erebus Bay, McMurdo Sound, as in Figure 1.



**FIGURE 3.** Pup mass gain in relation to maternal mass loss of lactating Weddell seals. Mother and pup data are paired ( $n = 24$ ) and reflect the same time periods (from 2–3 days to 35–45 days postpartum) for both. Pup gain and maternal loss were compared by Deming linear regression.

This difference could stem from differences in the masses of animals studied: in our study and in that of Tedman and Green (1987) mean female mass was about 450 kg at the beginning of lactation, whereas the average in Hill's study was 406 kg. This suggests that the strength of the correlation of maternal mass loss and pup mass gain may increase with maternal size. Assuming that decoupling of maternal mass loss and pup growth in the Weddell seal can be attributed to foraging, feeding may be obligatory for small females but optional or opportunistic for large females (Testa et al., 1989).

## ISOTOPIC MEASUREMENTS OF EXPENDITURES

Change in body mass alone is, at best, an imprecise measure of energy expenditure (Blaxter, 1989) and is invalid if animals are obtaining significant energy from food. The very high costs of lactation entail both metabolic costs (such as the energy expenditure associated with maternal attendance of pups and the energetic cost of milk synthesis) and substrate costs (the energy transferred into milk as fat, protein, carbohydrate, and minor constituents). Currently, the only method of accurately assessing metabolic energy expenditure in wild animals is the doubly labeled water (DLW) technique in which differences in the kinetics of hydrogen and oxygen isotopes provide an estimate of carbon diox-

ide production (see reviews by Nagy, 1980, and Speakman, 1997). Because of the high economic cost of  $^{18}\text{O}$ -labeled water, this procedure has usually been applied to mammals of small body size (Speakman, 1997); among phocids it has been applied to pups (e.g., Kretzmann et al., 1993; Lydersen and Kovacs, 1996). However, the DLW method may provide valuable insight into maternal metabolic expenditures during lactation, as reported for sea lions and fur seals (e.g., Arnould et al., 1996; Costa and Gales, 2000, 2003). In Weddell seals it would be particularly interesting to know if metabolic energy expenditures vary in accord with diving activity, stage of lactation, and food consumption. In animals that fast, one would expect metabolic rates to decline over the course of the fast, whereas energy expenditures should increase with increases in activity and in association with digestion and metabolism of food constituents (e.g., Blaxter, 1989; Speakman, 1997). However, there remain a number of technical issues to overcome, including selection of an appropriate model of isotope behavior and estimation of average respiratory quotient (RQ, ratio of carbon dioxide production to oxygen consumption), which differs between fasting and feeding animals. Model and RQ errors can directly impact energetic estimates and thus need to be assessed (Speakman, 1997). There are also logistic problems in accurately administering water isotopes to large, unsexed animals living in very cold and windy environments, but these are not prohibitive: in 2006 and 2007, we successfully dosed about 20 lactating Weddell seals in Erebus Bay, McMurdo Sound, with doubly labeled water; sample analyses are still in progress.

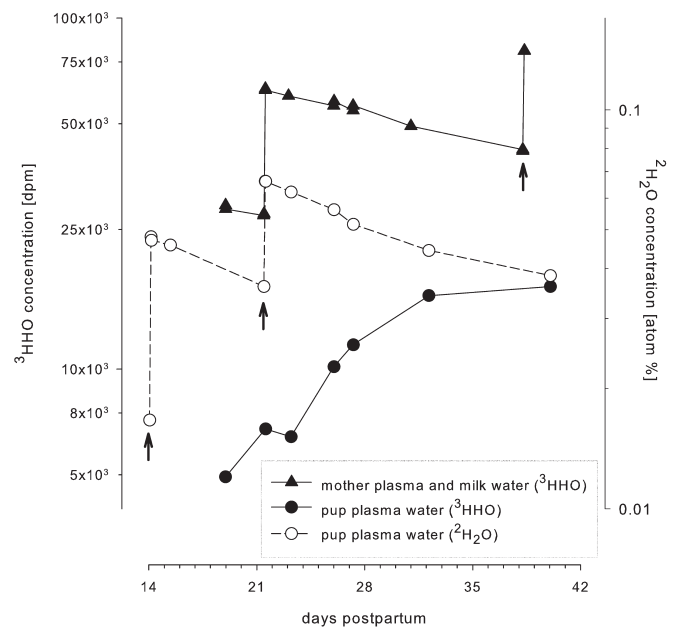
The DLW method does not, however, measure export of substrates via milk. It is therefore also necessary to measure milk yield and milk composition to estimate reproductive costs associated with the output of milk constituents (Oftedal, 1984b). The most widely used method for estimating milk production in seals relies on the dilution of hydrogen isotope-labeled water in nursing young (e.g., Costa et al., 1986; Oftedal and Iverson, 1987; Oftedal et al., 1987b; Tedman and Green, 1987; Lydersen et al., 1992; Iverson et al., 1993; Lydersen and Hammill, 1993; Oftedal et al., 1993; Lydersen and Kovacs, 1996; Oftedal et al., 1996; Lydersen et al., 1997; Mellish et al., 1999a; Arnould and Hindell, 2002). If milk is the exclusive source of water (both free and metabolic) for the offspring, then milk consumption can be estimated from water turnover and milk composition (Oftedal and Iverson, 1987). The accuracy of this method depends on the ability to correct estimates of milk intake for isotope recycling (Baverstock and Green, 1975; Oftedal, 1984a), for changes in pool size (Dove and Freer, 1979; Oftedal,

1984a), and for any water obtained by offspring from sources other than milk (Holleman et al., 1975; Dove, 1988), such as consumption of prey, snow, or seawater and metabolic water production. Isotope studies have demonstrated that milk energy output in seals is inversely proportional to lactation length: seals with very short lactations, such as species that breed on unstable pack ice, have much higher daily energy outputs than species that breed on stable substrates, such as land and fast ice (Ofstedal et al., 1987a).

The sole published attempt at measuring milk production in Weddell seals employed two isotopes ( $^2\text{H}$  and  $^{22}\text{Na}$ ) to determine if pups were ingesting water from sources other than milk (Tedman and Green, 1987). Tedman and Green argued that if pups were obtaining all or most of their water from milk, the sodium intake predicted from milk consumption (calculated milk intake from  $^2\text{H}$  turnover multiplied by milk sodium content) would be similar to that estimated from turnover of  $^{22}\text{Na}$ . As the observed discrepancy was not large, they concluded that intake of seawater or sodium-containing prey must have been minor (Tedman and Green, 1987). However, large (20%) underestimation of sodium intake occurs in  $^{22}\text{Na}$  turnover measurements on suckling young (Green and Newgrain, 1979), and Tedman and Green (1987) do not state whether this error was corrected for in their study. The potential importance of nonmilk water as a confounding effect in isotope studies warrants further study, especially as Weddell pups have been observed to grab snow in their mouths and may consume it. At present, the Tedman and Green (1987) data are the only published data on Weddell seal lactation, and the estimated milk yield of about 3.5 kg/d or 160 kg milk over the lactation period has been cited repeatedly in comparative studies (e.g., Ofstedal et al., 1987a, 1996; Costa, 1991; Boness and Bowen, 1996; Ofstedal, 2000) but is in need of reevaluation.

In order to avoid possible errors caused by consumption of food or water by nursing Weddell seal pups, we recommend use of a two-hydrogen isotope method originally developed for terrestrial herbivores in which the suckling young begin to feed on solid foods during lactation (e.g., Holleman et al., 1975, 1988; Wright and Wolff, 1976; Ofstedal, 1981; Dove, 1988; Carl and Robbins, 1988; Reese and Robbins, 1994). Water containing tritium ( $^3\text{HHO}$ ) is given to the mother and water containing deuterium ( $^2\text{H}_2\text{O}$ ) is given to offspring so that their body water pools are separately labeled. Thus, water turnover in mother and offspring can be measured independently.

In the pup, tritium concentrations rise so long as tritium intake (via milk water) exceeds tritium loss (via excretion), reaching a plateau when intake and loss are equal. In a Weddell seal pup this occurs after about two weeks (Figure 4). As tritium loss can be estimated from the rate of water turnover of the pup (measured from deuterium kinetics) and tritium intake equals milk tritium concentration multiplied by milk water intake, modeling of isotope fluxes allows calculation of mean water intake from milk. Unlike single isotope methods, this procedure allows milk water intake by the pup to be distinguished from influx of water from all other sources, such as drinking, feeding, and metabolic water production. Once milk water intake is known, milk production can be calculated from milk composition. We applied this dual-isotope method on about 20 Weddell pups in Erebus Bay, McMurdo Sound, in 2006 and 2007.



**FIGURE 4.** Illustration of the dual-isotope procedure for a Weddell seal mother and her pup. The mother was administered tritium-labeled ( $^3\text{HHO}$ ) water and the pup was given deuterium-labeled water ( $^2\text{H}_2\text{O}$ ) by intravenous infusion at the times indicated by vertical arrows. While deuterium levels ( $^2\text{H}_2\text{O}$ ) declined following administration, tritium levels ( $^3\text{HHO}$ ) in the pup rose towards a plateau level, indicating that tritium intake via milk water exceeded tritium losses of the pup over this time period. Deuterium was measured by isotope ratio mass spectrometry, and tritium was measured by scintillation counting. Mathematical modeling of isotope behavior indicated that milk intake was about 2.5 kg over this period.



## MONITORING FOOD CONSUMPTION DURING THE LACTATION PERIOD

If Weddell seals did not enter the water during lactation, it would be obvious that they must be fasting, but this is not the case. Weddell seal mothers usually remain on the ice with their pups for the first one to two weeks of lactation, but then most mothers begin diving bouts that typically increase in frequency and length as lactation proceeds. The diving behavior of Weddell seals, including lactating females as well as nursing, weaned, and yearling animals, has been extensively investigated with time-depth recorders, or TDRs, including satellite-uplinked instruments (e.g., Kooyman, 1967; Testa et al., 1989; Burns et al., 1997, 1999; Castellini et al., 1992; Sato et al., 2002, 2003; Williams et al., 2004; Fuiman et al., 2007). The recent development of instrumentation that records directional information (Harcourt et al., 2000; Davis et al., 2001; Hindell et al., 2002; Mitani et al., 2003) allows examination of dive behavior in three-dimensional space. Although food intake requires diving, even deep diving need not entail food consumption. In other words, one cannot equate dive records to actual food intake unless food intake can be independently confirmed (Testa et al., 1989).

This has led to development of a number of different methods to monitor food intake. Classically, the diet of the Weddell seal has been examined by stomach content analysis (Bertram, 1940; Dearborn, 1965; Plötz, 1986; Plötz et al., 1991), but lethal methods are no longer employed, and gastric lavage of adults requires extensive restraint or chemical immobilization. Scat analysis can provide information on those prey that have identifiable indigestible parts (Burns et al., 1998; Lake et al., 2003) or even residual prey DNA (Casper et al., 2007) in the scats. However, the relative proportions of prey are difficult to quantify without extensive feeding trials to develop correction factors for the differential rates of digestion of prey. This is not feasible in free-ranging Weddell seals. In addition, the identity of the animal producing the scat and the time it was produced are often unknown. Occasionally, Weddell seals are observed to bring large prey, such as Antarctic toothfish (*Dissostichus mawsoni*) to holes in the ice (e.g., Caelhaem and Christoffel, 1969). Such observations can be extended by deploying animal-borne underwater cameras (Marshall, 1998; Davis et al., 1999; Bowen et al., 2002; Fuiman et al., 2002; Sato et al., 2002, 2003; Fuiman et al., 2007). Although dives in which potential prey are visible have been termed “foraging dives” (Fuiman et al. 2007), it is difficult to determine the success

of prey capture attempts from the images obtained. Of course, the images provide valuable information on hunting methods of seals at depth.

Another approach is to attach instruments in the mouth or digestive tract of seals to record feeding events. Sensors have been glued to the jaw of the seal that detect opening of the mouth (Bornemann et al., 1992; Plötz et al., 2001), but prey capture may be difficult to distinguish from other jaw movements during social behavior (e.g., threats and bites). Temperature-transmitting thermistors have been introduced into the stomach to monitor changes in the temperature of stomach contents associated with ingestion of cold items, such as ectothermic fish (Bornemann, 1994; Hedd et al., 1996; Austin et al., 2006a, 2006b; Kuhn and Costa, 2006). However, stomach temperature is also affected by other factors such as water ingestion, gastric blood flow, thermal mass of gastric contents and thermistor location, so that validation studies are essential to interpretation (Ponganis, 2007). Instruments may also require considerable intervention to attach (e.g., prolonged anesthesia), may alter animal behavior, or may require recaptures for data acquisition. Thus, there is still a need for a simple method of determining when food is actually consumed by free-living seals.

As an alternative approach, food energy intake of seals has been estimated from changes in whole-body water flux using isotope-labeled water (Costa, 1987; Bowen et al., 2001b). This method relies on the assumption that uptake of water from sources other than food (e.g., drinking) is minimal (Costa, 1987; Bowen et al., 2001b), yet seals are known to voluntarily consume both freshwater and seawater (Skalstad and Nordøy, 2000; Lea et al., 2002). Lactating Weddell seals have been observed to eat snow (Eisert and Oftedal, unpublished observations). This may lead to errors of unknown magnitude in both the detection and quantitation of food intake.

As a result of the difficulties in detecting and quantifying food intake, the energetics of lactation in the Weddell seal and in other species that feed during lactation are not well described (Schulz and Bowen, 2004). However, this may be improved by combining isotope methodology with new techniques for detecting feeding using biomarkers (Eisert et al., 2005). This approach allows food intake to be confirmed at a specific point in time from the presence in body fluids of dietary *biomarkers*, i.e., specific compounds that are absorbed intact from prey but are not generated by normal metabolic processes in the predator. On the basis of studies in Weddell seals, we have identified two suitable compounds, arsenobetaine (AsB) and trimethylamine

N-oxide (TMAO) (Eisert, 2003; Eisert et al., 2005). Both are specific to, and apparently ubiquitous in, marine prey yet are neither stored nor synthesized by higher vertebrates and in mammals are eliminated rapidly from the circulation following ingestion (Edmonds and Francesconi, 1977, 1987, 1988; Yancey et al., 1982; Vahter et al., 1983; Al-Waiz et al., 1987, 1992; Van Waarde, 1988; Cullen and Reimer, 1989; Brown et al., 1990; Shibata et al., 1992; Smith et al., 1994; Svensson et al., 1994; Zhang et al., 1999; Lehmann et al., 2001). The biomarker method provides information on recent food intake within a timescale of hours to days, in contrast to fatty acid signatures or stable isotopes in fluids or tissue samples, which integrate food intake over a period of months (Iverson et al., 1997a, 1997b; Brown et al., 1999).

Investigations of the incidence of foraging in lactating Weddell seals using the biomarker method (Eisert et al., 2005) revealed that (1) ~70% of females studied in late lactation (>27 days postpartum) had concentrations of AsB and TMAO indicative of recent food intake, (2) most females appear to fast for the first three to four weeks of lactation, in agreement with observed dive activity (Hindell et al., 2002), and (3) feeding may commence as early as eight to nine days postpartum in some females. These results suggest that the onset of feeding may vary substantially among lactating seals, and the possibility remains that some females fast throughout lactation. To clarify the dose-response and kinetic characteristics of AsB and TMAO in seals, we conducted validation trials in which varying doses of biomarkers were fed to juvenile hooded seals (*Cystophora cristata*) in captivity at the University of Tromsø in collaboration with E. S. Nordøy and A. S. Blix. Plasma TMAO peaked in about six to eight hours after intake and returned to low levels within 30 hours. Thus, biomarker methods may clarify whether a dive bout within a 24-hour period is associated with food capture, a considerable improvement over arbitrary assignment of dive shapes to foraging or nonforaging categories based on untested assumptions about prey hunting behavior.

### ONTOGENY OF FORAGING IN WEDDELL SEAL PUPS

A disconnect between maternal mass loss and pup mass gain could also arise because (1) pups begin to forage independently during the lactation period, leading to mass gain without corresponding maternal loss, or (2) variation in the pattern of energy deposition (e.g., fat versus protein)

alters the pattern of pup mass gain independent of maternal expenditures.

A prolonged period of dependence is characteristic of mammals in which development of social relationships appears to be important, such as in elephants, many primates, and some odontocete whales (West et al., 2007). However, phocid seals typically wean their pups abruptly, with departure of the mother from the breeding colony. Foraging by suckling pups has so far been described for only two phocid species, the ringed seal *Phoca hispida* and the bearded seal *Erignathus barbatus* (Lydersen and Kovacs, 1999). Nursing Weddell seal pups commence diving at about two weeks of age and, on average, perform in excess of 20 dives per day (Burns and Testa, 1997). Although mothers and pups may at times dive together (Sato et al., 2002, 2003), it is unclear whether this entails any “teaching” of the pup with regards to location, type, or capture of prey. There is a single published observation of the presence of milk and crustacean prey in the stomach of a Weddell seal pup (Lindsey, 1937), and pups have occasionally been observed bringing captured fish to the surface (K. Wheatley, University of Tasmania, personal communication, May 2004). It is possible that feeding by nursing pups could reflect an inadequate rate of maternal energy transfer during lactation (e.g., Hayssen, 1993), but it is not known if feeding by pups is common or exceptional in this species.

### UNCERTAINTIES ABOUT THE WEDDELL SEAL STRATEGY

Much remains to be learned about the relative importance of foraging (income) versus stored reserves (capital) in the lactation strategies of Weddell seals at both individual and population levels. Weddell seals clearly rely extensively on stored reserves, but whether these are sufficient to support the demands of lactation in some or all females is uncertain. Foraging is much more prevalent during the lactation period than previously thought, but the magnitudes of energy and nutrient intakes are not known.

It seems likely that access to food resources is important to reproductive success at least during the second half of lactation, when most females forage. In years when heavy multiyear ice has failed to break out of McMurdo Sound due to giant icebergs that have blocked egress to the north, the numbers of Weddell pups born has been reduced by up to 50%–65% (R. Garrott, personal communication, 2007). By blocking light penetration the ice undoubtedly reduced

primary productivity in McMurdo Sound, and this could result in a reduction in prey resources for Weddell seals. This may have led mothers to seek out alternative breeding sites in closer proximity to food resources, although the mechanism by which such choice is made is not known.

It would be especially valuable to examine the variation in foraging success and reproductive performance in different areas in the Antarctic where availability of food resources varies in time and space. How flexible are the reproductive strategies of Weddell seals? Does the relative importance of income versus capital breeding vary among populations or among years? How could the reproductive success of the Weddell seal be impacted by changes in ice or currents associated with global warming? In a world of change, we need sufficient background information on the resource needs of species to be able to predict future population trends.

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