

## SHORT COMMUNICATION

# The high cost of reproduction in sea otters necessitates unique physiological adaptations

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## ABSTRACT

Superimposed on inherently high basal metabolic demands, the additional energetic requirements of reproduction can push female sea otters beyond physiological limits. Indeed, the resulting energy imbalance contributes to disproportionately high rates of mortality at the end of lactation in this species. To examine and quantify metabolic changes associated with reproduction, we measured the resting metabolic rate (RMR) of a female sea otter across gestation, lactation and non-reproductive periods. Concurrently, measurements were made on a non-breeding control female. Our results suggest that RMR declines during gestation. Conversely, RMR increases during lactation, reaches a peak at 3–4 months postpartum, and remains elevated until weaning. Combining these direct measurements with published data, we found the cost of pup rearing to be significantly higher than previously estimated. High baseline energy demands and limited energy reserves, combined with significant lactation and pup rearing costs, appear to necessitate metabolic and thermal lability during key reproductive stages.

**KEY WORDS:** *Enhydra lutris*, Gestation, Lactation, Resting metabolic rate, Energetics, Parental investment

## INTRODUCTION

Sea otters (*Enhydra lutris*) are extreme income breeders (Stearns, 1992; Thometz et al., 2014). High baseline energy demands and minimal energy reserves require females to forage throughout lactation to meet their own caloric needs as well as the energy demands of a dependent pup (Kenyon, 1969; Payne and Jameson, 1984; Thometz et al., 2014). Although increasing onboard fat reserves generally improve the body condition of female sea otters over the course of gestation (Chinn et al., 2016), these reserves are minimal in comparison to other marine mammals, which can utilize large energy-rich blubber stores (Costa and Williams, 1999). Consequently, female sea otters significantly deplete onboard fat reserves within the first weeks postpartum (Chinn et al., 2016) and must acquire the majority of the energy required for pup rearing during the 6 month dependency period (Riedman et al., 1994; Jameson and Johnson, 1993).

Meeting the increasing caloric demands of a pup can lead to poor body condition, and ultimately push females beyond physiological limits, leading to mortality around the time of weaning (Chinn et al., 2016; Monson et al., 2000; Tinker et al., 2006). This condition,

termed end-lactation syndrome, is the main cause in, or a major contributing factor to, over half of adult female sea otter deaths in California (Chinn et al., 2016). Thus, there appears to be a direct link between reproductive costs in this species and population-level trends. The first study to estimate pup rearing costs in sea otters suggested that female energy demands reach twice prepartum levels by the time a pup nears weaning (Thometz et al., 2014); however, this study only examined the metabolic needs of pups and could not account for the energetic cost of milk production. In general, terrestrial mammals exhibit increased resting metabolic rate (RMR) during lactation, although the extent and duration of this increase are highly variable among species (Brockway et al., 1963; Fleming et al., 1981; Garton et al., 1994; Hammond and Diamond, 1992; Harder et al., 1996; Król et al., 2003; Poppitt et al., 1994; Prentice et al., 1989; Spaaij et al., 1994; Speakman and McQueenie, 1996; Stephenson and Racey, 1993a,b; Thompson and Nicoll, 1986). In contrast, the cost of milk production in marine mammals appears minimal in the species studied to date (Antarctic and Galapagos fur seals: Costa and Trillmich, 1988; Northern elephant seals: Costa et al., 1986; California sea lions: Williams et al., 2007). Given the wide variation among species with regards to lactation energetics, it is inappropriate to predict lactation costs for sea otters.

In addition to potential metabolic changes during lactation, sea otters exhibit unique and prolonged changes in core body temperature ( $T_{\text{core}}$ ) during gestation. Declines in  $T_{\text{core}}$  in the days preceding parturition have been documented in both terrestrial (Eliason and Fewell, 1997; Fewell, 1995; Melanie et al., 1988; Williams et al., 2011) and marine (Katsumata, 2010; Katsumata et al., 2006) mammals. In contrast, data from temperature-logging time–depth recorders (TDRs) implanted in wild sea otters have revealed a characteristic decline in  $T_{\text{core}}$  by 1.5°C over the last 3 months of gestation (Esslinger et al., 2014). This prolonged change in  $T_{\text{core}}$  may indicate a decline in RMR during gestation, as has been documented for some phocids (Hedd et al., 1997; Renouf and Gales, 1994; Sparling et al., 2006).

Because of the unique physiology of sea otters and the apparent role of reproductive energetics in driving observed patterns of mortality in California, we measured the RMR of two formerly wild female sea otters under controlled laboratory conditions to examine reproductive energetics in this species. Metabolic measurements of a reproductive female were conducted weekly across three distinct stages (gestation, lactation and non-reproductive periods); concurrent measurements were obtained monthly from a non-breeding female. This approach enabled us to track metabolic changes associated with reproduction and refine previous estimates of the cost of pup rearing in the smallest marine mammal.

## MATERIALS AND METHODS

### Animals

In August of 2014, two adult female southern sea otters [*Enhydra lutris nereis* (Merriam 1904)] from Moss Landing, CA, USA,

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deemed unfit for the wild by the US Fish and Wildlife Service because of their penchant for human interaction, were removed from the wild and brought to the Monterey Bay Aquarium, Monterey, CA, USA. Both females were in good health, with one female in the early stages of pregnancy. This provided a unique opportunity to study reproductive energetics in sea otters. Both females were transferred to the Long Marine Laboratory, at the University of California, Santa Cruz, for metabolic trials. At the time of capture, the reproductive female was estimated to be 4 years old and weighed 22 kg. She gave birth to a female pup on 26 November 2014, which she nursed and reared in captivity for 7 months before weaning occurred. The non-breeding adult female was estimated to be 3 years old at the time of capture and weighed 18 kg. All work was conducted under US Fish and Wildlife permits MA186914 to J. Packard and MA45505B to T.M.W.

### Metabolic measurements

Individuals were fasted overnight prior to metabolic trials to ensure individuals were in a post-absorptive state (Costa and Kooyman, 1984). Otters were placed individually in water beneath a clear acrylic dome attached to a PVC pipe frame (1.0 m L×0.9 m W×0.5 m H), which allowed it to float on the water surface. Trial length ranged from 20 to 120 min, during which an animal was allowed to move freely. Trials were conducted outdoors under seasonal environmental conditions (air temperature 6.8–22.7°C, water temperature 11.6–17.4°C), representative of routine conditions for wild southern sea otters. Observers monitored and recorded the behavior of each animal during metabolic trials. The rate of oxygen consumption ( $\dot{V}_{O_2}$ ) was measured continuously. Steady-state, resting conditions were defined as individuals floating near-motionless on the surface of the water for a minimum of 5 min.

An open-flow respirometry system designed for aquatic mammals was used to determine  $\dot{V}_{O_2}$  for each individual (Thometz et al., 2014; Williams et al., 2004). Air was pulled through the metabolic dome at 150 l min<sup>-1</sup> by a mass flow controller (Flow kit 500H, Sable Systems, Henderson, NV, USA). Sub-samples of dome exhaust were dried (Drierite, W. A. Hammond Drierite, Xenia, OH, USA), scrubbed of CO<sub>2</sub> (Baralyme, Chemetron Medical Division, Allied Healthcare Products, St Louis, MO, USA) and dried again, before entering an oxygen analyzer (model FC1-B, Sable Systems). The oxygen content of the dome was maintained above 20.10% to avoid hypoxic conditions. Oxygen content of dome exhaust was logged every 1.0 s on a laptop computer. Flow rates were corrected to standard temperature and pressure (STPD) and  $\dot{V}_{O_2}$  was determined using standard methods (Withers, 1977). The oxygen analysis system was calibrated with dry ambient air (20.94% O<sub>2</sub>) and the system was checked for leaks a minimum of once a month using 100% nitrogen gas (Davis et al., 1985; Fedak et al., 1981).

Individuals were weighed once a week with a platform scale (320D Vet-Bat, Arlyn Scales, Rockaway, NY, USA). The reproductive female participated in weekly metabolic trials, while the control female participated in monthly trials. The two animals were measured over the same time period, under identical environmental conditions and with the same equipment. Following parturition, metabolic trials were conducted with the mother–pup pair together, as separation would have resulted in highly agitated behaviors (e.g. swimming and vocalizing) not conducive to the collection of RMR data. Using eqn 1 ( $\dot{V}_{O_2}=25.85-0.062\times\text{age}$ ) from Thometz et al. (2014), the pup's age-specific  $\dot{V}_{O_2}$  was subtracted from the combined  $\dot{V}_{O_2}$  of the mother–pup pair to estimate the individual  $\dot{V}_{O_2}$  of the female. During a mother–pup

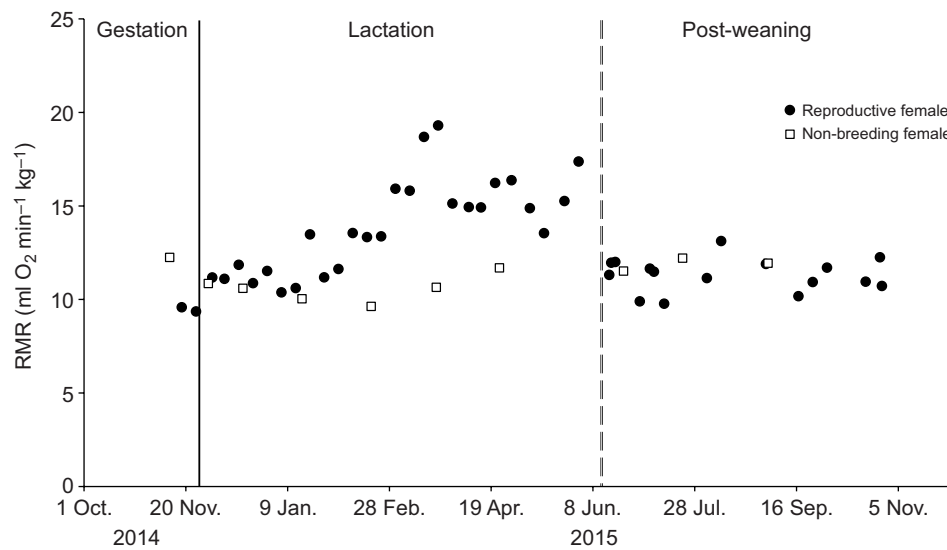
trial, both otters needed to float near-motionless at the water surface for a minimum of 5 min. Often, when the pup was lying still on its mother's chest it was nursing; this was classified as resting. Also, during a synchronized resting period, if the female occasionally passively licked the pup, this was still classified as resting. If the female began actively grooming the pup, the pair was no longer considered resting. Although we could not separate the pair for metabolic trials throughout dependency, as weaning approached we conducted representative, independent measurements to validate the use of eqn 1 (Thometz et al., 2014) in determining the female's RMR during lactation.

### Determining the longitudinal cost of reproduction

We used the energetic data collected in this study to revise the previous estimate of sea otter pup rearing costs (Thometz et al., 2014), which lacked species-specific reproductive energetics data. We compared the reproductive female's RMR during gestation and lactation periods with her post-weaning, non-reproductive RMR and determined the percentage change in RMR between those stages. We then used the percentage change values to adjust previously determined field metabolic rates of adult females across different reproductive stages (Thometz et al., 2014). Next, although quantitative data regarding pup prey retrieval are lacking, we estimated the amount of energy a pup may contribute to its own demands via foraging across dependency. The average age of first prey retrieval is 63 days [M. M. Staedler, Maternal care and provisioning in the southern sea otter (*Enhydra lutris nereis*): reproductive consequences of diet specialization in an apex predator, Masters thesis, University of California Santa Cruz, USA, 2011]; therefore, all pup energy demands prior to this point were assumed to be met solely by the mother. At 63 days postpartum, the proportion of energy demands met by a pup was modeled as a linear increase of 0.5% of pup energy demands each day. This estimation was based on the progressive increase in diving and foraging abilities documented for dependent pups (Thometz et al., 2015) and the knowledge that despite such increases, pups continue to nurse and solicit food from mothers until weaning [Payne and Jameson, 1984; M. M. Staedler, Maternal care and provisioning in the southern sea otter (*Enhydra lutris nereis*): reproductive consequences of diet specialization in an apex predator, Masters thesis, University of California Santa Cruz, USA, 2011]. We acknowledge that the true start time and progression of independent energy retrieval by pups is highly variable and that modeling this as a linear trend may overestimate prey retrieval initially and underestimate prey retrieval near weaning. We did not factor assimilation efficiency into these calculations because: (1) females provide food in both milk and solid form; (2) they feed on >30 prey types, all of which differ in this regard; and (3) pups contribute to their own energy needs during the later stages of dependency – those values would not be affected by the female's assimilation efficiency. Therefore, calculated daily metabolic demands represent the net amount of energy a female must obtain to meet her own needs and those of her pup.

### RESULTS AND DISCUSSION

The reproductive and control females had comparable non-reproductive RMRs (Welch's *t*-test,  $t_{18,9}=-0.47$ ;  $P=0.65$ ). The control female had a consistent RMR (11.15±0.93 ml O<sub>2</sub> min<sup>-1</sup> kg<sup>-1</sup>) throughout the data collection period (Fig. 1), providing support that changes in the reproductive female's RMR were driven by intrinsic physiological processes associated with reproduction and not by extrinsic factors. During gestation, the reproductive female's



**Fig. 1. Longitudinally measured mass-specific resting metabolic rate (RMR) of a reproductive female and a non-breeding female over a 1 year period.** Birth of the reproductive female's pup (solid vertical line, 26 November 2014) and pup weaning (dashed vertical line) are indicated, and major reproductive stages (gestation, lactation and post-weaning) are shown in relation to those reproductive events.

average RMR was 16.6% lower than her own non-reproductive RMR (Table 1). Although we were only able to obtain two measurements of RMR during gestation, these data suggest that sea otters reduce metabolic rates during gestation, as has been found for gray (Sparling et al., 2006), harp (Hedd et al., 1997; Renouf and Gales, 1994) and elephant (Maresh et al., 2015) seals.

Whether RMR declines in parallel with characteristic changes in sea otter  $T_{\text{core}}$  over the second half of gestation (Esslinger et al., 2014) warrants further investigation, but such a relationship has been documented for harp seals (Hedd et al., 1997). Further, across a wide range of species, reductions in  $T_{\text{core}}$  are associated with metabolic reductions (for review, see Geiser, 2004). For individuals living in cold environments, lowering  $T_{\text{core}}$  may reduce thermoregulatory costs and allow individuals to allocate energy elsewhere (e.g. storage or fetal development). Therefore, a decline in sea otter  $T_{\text{core}}$  and RMR over the last half of gestation may be a physiological adaptation to facilitate increased fat deposition and improve body condition prior to parturition. Given the high cost of sea otter reproduction, this adaptation would be advantageous to females preparing for lactation and pup rearing. Indeed, nutritional pre-loading and improved body condition around parturition have been reported in wild sea otters (Chinn et al., 2016).

Although we could not separate the mother–pup pair for the majority of metabolic trials during lactation, as weaning approached we were able to validate the use of eqn 1 from Thometz et al. (2014)

in determining the mother's RMR from combined mother–pup  $\dot{V}_{\text{O}_2}$  measurements. We successfully conducted an independent metabolic trial with the pup (199 days old, 14.2 kg), and its measured RMR ( $13.19 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$ ) was similar to the predicted value ( $13.63 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$ ), confirming our methods were appropriate. The reproductive female's RMR during lactation was significantly higher than her non-reproductive RMR (Welch's  $t$ -test,  $t_{33,8} = -4.82$ ;  $P < 0.0001$ ); however, this increase was not consistent across lactation (Table 1). At parturition, RMR increased from low gestational levels to values comparable to her non-reproductive RMR. The reproductive female's RMR did not increase above non-reproductive levels until the second month postpartum, at which point it increased steadily (Fig. 1). The reproductive female's RMR peaked 3–4 months postpartum, and although it declined slightly following that peak, it remained elevated for the remainder of lactation (Table 1).

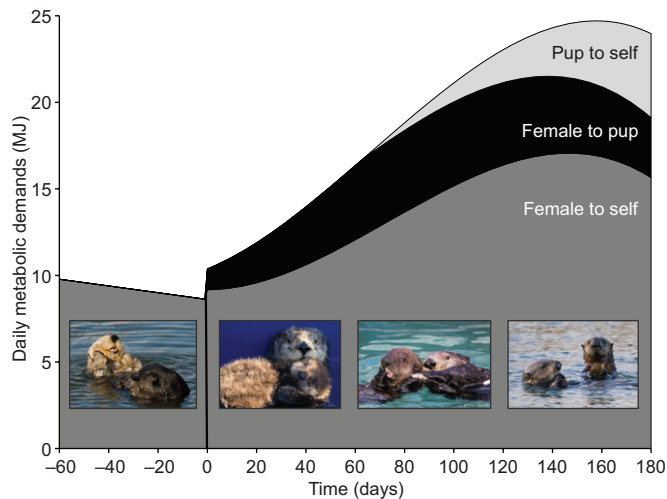
By combining reproductive energetics data from this study (Table 1) with previously published behavior-specific metabolic rates (Williams, 1989) and activity budgets [M. M. Staedler, Maternal care and provisioning in the southern sea otter (*Enhydra lutris nereis*): reproductive consequences of diet specialization in an apex predator, Masters thesis, University of California Santa Cruz, USA, 2011; Thometz et al., 2014] of female sea otters, we found the cost of pup rearing to be significantly higher than previously estimated (Thometz et al., 2014). During the final 3 months of

**Table 1. Resting metabolic rate of a female sea otter during three reproductive stages**

Reproductive stage	Pup age (days)	Pup mass (kg)	Pup developmental stage	Trials ( $N$ )	RMR ( $\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$ )	% Change
Gestation (late)	–30–0	–	Fetus	2	$9.47 \pm 0.16$	–16.6
Lactation	1–21	$1.94 \pm 0.49$	Neonate/pre-molt	3	$11.37 \pm 0.41$	0.2
	22–70	$4.33 \pm 0.89$	Pre-molt/molting	7	$11.38 \pm 1.03$	0.3
	71–100	$7.44 \pm 0.55$	Molting/post-molt	4	$14.04 \pm 1.26$	23.7
	101–130	$9.44 \pm 0.57$	Post-molt	4	$17.23 \pm 2.07$	51.8
	131–160	$11.00 \pm 0.70$	Dependent immature	4	$15.62 \pm 0.79$	37.55
	161–200	$12.58 \pm 1.01$	Dependent immature	4	$15.26 \pm 1.59$	34.44
Post-weaning/ non-reproductive	>200	–	Independent immature	17	$11.35 \pm 0.88$	–

Pup developmental stage was defined using classifications from Thometz et al. (2014). Pup age range and mass (mean  $\pm$  s.d.) during each developmental stage are provided. The number of successful metabolic trials used to determine the resting metabolic rate (RMR; mean  $\pm$  s.d.) for each stage is specified ( $N$ ). The percentage change in RMR for each stage was determined by comparing the RMR values determined for gestation and lactation periods with the post-weaning/non-reproductive RMR.





**Fig. 2. Average daily metabolic demands of an adult female sea otter during late gestation and across lactation in relation to the birth date of a pup.** Time in days, spanning 60 days prepartum to 180 days postpartum (average age of weaning), is displayed on the x-axis. Average daily energy demands of an adult female (dark gray) were determined using previously published values for female sea otter activity-specific metabolic rates (Williams, 1989) and adult female activity budgets as described in Thometz et al. (2014), and adjusted based on lactation costs determined in this study. During gestation, RMR was modeled to linearly decline from non-reproductive levels (at  $-90$  days) to the measured RMR during gestation from this study (at day  $-1$ ) in accordance with known changes in core body temperature ( $T_{\text{core}}$ ) (Esslinger et al., 2014). Following parturition, energy demands of a dependent pup (Thometz et al., 2014) are stacked on top of adult female energy demands and further divided into energy that must be provided to the pup by the female (black) and energy gained by a pup itself as it increases its independent foraging (light gray). Within each stacked area, the text denotes who is obtaining the required calories and who is receiving those calories. Given that the average age of first prey retrieval by a pup is 63 days [M. M. Staedler, Maternal care and provisioning in the southern sea otter (*Enhydra lutris nereis*): reproductive consequences of diet specialization in an apex predator, Masters thesis, University of California Santa Cruz, USA, 2011], all pup energy demands prior to this point must be met by the adult female in either milk or solid form. Beginning at 63 days postpartum, the proportion of pup energy demands met by the pup itself via foraging was modeled as a linear increase of 0.5% of pup demands per day. Photo credit: Joe Tomoleoni.

lactation, females must meet daily energy demands that are 85–110% higher than non-reproductive demands, despite increasing independent foraging by pups to support their own energy needs (Fig. 2). For a small marine mammal with limited energy reserves, this prolonged and sustained increase in daily metabolic demands represents an extreme energetic challenge. Despite foraging as much as 50–60% of each day (Esslinger et al., 2014; Thometz et al., 2014; Thometz et al., 2016), females are often in negative energy balance during lactation (Chinn et al., 2016). Further, any delay in independent foraging by pups can greatly increase the energetic burden on adult females during an already energetically taxing period when onboard reserves have been depleted. Not surprisingly, the incidence of end-lactation syndrome-related mortality is highest in areas where prey resources are limited (Chinn et al., 2016).

Overall, sea otters appear unique in their reproductive physiology. Although many species exhibit a decline in  $T_{\text{core}}$  at the end of gestation (Eliason and Fewell, 1997; Fewell, 1995; Katsumata, 2010; Katsumata et al., 2006; Williams et al., 2011), this generally occurs in the days preceding parturition. For sea otters, this decline occurs over a 3 month period (Esslinger et al., 2014) and may be associated with metabolic changes (Table 1). A decline in RMR during gestation contrasts with

patterns observed in most terrestrial mammals (Brockway et al., 1963; Fleming et al., 1981; Garton et al., 1994; Poppitt et al., 1994; Stephenson and Racey, 1993a,b; Thompson and Nicoll, 1986), but agrees with changes observed in phocids (Hedd et al., 1997; Renouf and Gales, 1994; Sparling et al., 2006). In terms of lactation energetics, sea otters conform more to patterns observed in terrestrial rather than marine mammals, which appear to have negligible milk production costs (Costa and Trillmich, 1988; Costa et al., 1986; Williams et al., 2007). Given that the fat content of sea otter milk is within the range of other marine mammals (Jenness et al., 1981), the increased cost of lactation in this species may be a reflection of onboard reserves available for milk production and an increased need for *de novo* synthesis of fatty acids in the mammary glands (Neville and Picciano, 1997). Ultimately, reproduction is exceptionally physiologically taxing for female sea otters and appears to necessitate metabolic and thermal lability during key reproductive stages.

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#### Competing interests

The authors declare no competing or financial interests.

#### Author contributions

N.M.T. and T.M.W. conceived and designed the study. N.M.T., T.L.K. and B.P.R. conducted all experiments. N.M.T. analyzed the data. N.M.T. wrote the manuscript with editorial advice provided by all authors.

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#### References

- Brockway, J. M., McDonald, J. D. and Pullar, J. D. (1963). The energy cost of reproduction in sheep. *J. Physiol.* **167**, 318–327.
- Chinn, S. M., Miller, M. A., Tinker, M. T., Staedler, M. M., Batac, F. I., Dodd, E. and Henkel, L. A. (2016). The high cost of motherhood: end-lactation syndrome in southern sea otters (*Enhydra lutris nereis*) on the Central California Coast, USA. *J. Wildl. Dis.* **52**, 307–318.
- Costa, D. P. and Kooyman, G. L. (1984). Contribution of specific dynamic action to heat balance and thermoregulation in the sea otter *Enhydra lutris*. *Physiol. Zool.* **57**, 199–203.
- Costa, D. P. and Trillmich, F. (1988). Mass changes and metabolism during the perinatal fast: a comparison between Antarctic (*Arctocephalus gazella*) and Galápagos Fur Seals (*Arctocephalus galapagoensis*). *Physiol. Zool.* **61**, 160–169.
- Costa, D. P. and Williams, T. M. (1999). Marine mammal energetics. In *Biology of Marine Mammals* (ed. J. E. Reynolds and S. Rommel), pp. 176–217. Washington, DC: Smithsonian Institution Press.
- Costa, D. P., Boeuf, B. J. L., Huntley, A. C. and Ortiz, C. L. (1986). The energetics of lactation in the Northern elephant seal, *Mirounga angustirostris*. *J. Zool.* **209**, 21–33.
- Davis, R. W., Williams, T. M. and Kooyman, G. L. (1985). Swimming metabolism of yearling and adult harbor seals *Phoca vitulina*. *Physiol. Zool.* **58**, 590–596.
- Eliason, H. L. and Fewell, J. E. (1997). Thermoregulatory control during pregnancy and lactation in rats. *J. Appl. Physiol.* **83**, 837–844.
- Esslinger, G. G., Bodkin, J. L., Breton, A. R., Burns, J. M. and Monson, D. H. (2014). Temporal patterns in the foraging behavior of sea otters in Alaska. *J. Wildl. Manage.* **78**, 689–700.
- Fedak, M. A., Rome, L. and Seeherman, H. J. (1981). One-step N<sub>2</sub>-dilution technique for calibrating open-circuit VO<sub>2</sub> measuring systems. One-step N<sub>2</sub>-dilution technique for calibrating VO<sub>2</sub> measuring systems. *J. Appl. Physiol.* **51**, 772–776.
- Fewell, J. E. (1995). Body temperature regulation in rats near term of pregnancy. *Can. J. Physiol. Pharmacol.* **73**, 364–368.
- Fleming, M. W., Harder, J. D. and Wukie, J. J. (1981). Reproductive energetics of the virginia opossum compared with some eutherians. *Comp. Biochem. Physiol. B Comp. Biochem.* **70**, 645–648.

- Garton, D. W., Hsu, M. J. and Harder, J. D.** (1994). Environmental temperature and metabolic rates during gestation and lactation in golden hamsters (*Mesocricetus auratus*). *Physiol. Zool.* **67**, 497–514.
- Geiser, F.** (2004). Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annu. Rev. Physiol.* **66**, 239–274.
- Hammond, K. A. and Diamond, J.** (1992). An experimental test for a ceiling on sustained metabolic rate in lactating mice. *Physiol. Zool.* **65**, 952–977.
- Harder, J. D., Hsu, M. J. and Garton, D. W.** (1996). Metabolic rates and body temperature of the gray short-tailed opossum (*Monodelphis domestica*) during gestation and lactation. *Physiol. Zool.* **69**, 317–339.
- Hedda, A., Gales, R. and Renouf, D.** (1997). Inter-annual consistency in the fluctuating energy requirements of captive harp seals *Phoca groenlandica*. *Polar Biol.* **18**, 311–318.
- Jameson, J. and Johnson, A. M.** (1993). Reproductive characteristics of female sea otters. *Mar. Mam. Sci.* **9**, 156–167.
- Jenness, R., Williams, T. D. and Mullin, R. J.** (1981). Composition of milk of the sea otter (*Enhydra lutris*). *Comp. Biochem. Physiol. A Physiol.* **70**, 375–379.
- Katsumata, E.** (2010). Study on reproduction of captive marine mammals. *J. Reprod. Dev.* **56**, 1–8.
- Katsumata, E., Jaroenporn, S., Katsumata, H., Konno, S., Maeda, Y., Watanabe, G. and Taya, K.** (2006). Body temperature and circulating progesterone levels before and after parturition in killer whales (*Orcinus orca*). *J. Reprod. Dev.* **52**, 65–71.
- Kenyon, K. W.** (1969). The sea otter in the Eastern Pacific Ocean. *North Am. Fauna* **68**, 1–352.
- Król, E., Johnson, M. S. and Speakman, J. R.** (2003). Limits to sustained energy intake. VIII. Resting metabolic rate and organ morphology of laboratory mice lactating at thermoneutrality. *J. Exp. Biol.* **206**, 4283–4291.
- Maresh, J., Adachi, T., Takahashi, A., Naito, Y., Crocker, D. E., Horning, M., Williams, T. M. and Costa, D. P.** (2015). Summing the strokes: energy economy in northern elephant seals during large-scale foraging migrations. *Mov. Ecol.* **3**, 22.
- Melanie, E., Kittrell, W. and Satinoff, E.** (1988). Diurnal rhythms of body temperature, drinking and activity over reproductive cycles. *Physiol. Behav.* **42**, 477–484.
- Monson, D. H., Estes, J. A., Bodkin, J. L. and Siniff, D. B.** (2000). Life history plasticity and population regulation in sea otters. *Oikos* **90**, 457–468.
- Neville, M. C. and Picciano, M. F.** (1997). Regulation of milk lipid secretion and composition. *Annu. Rev. Nutr.* **17**, 159–184.
- Payne, S. F. and Jameson, R. J.** (1984). Early behavioral development of the sea otter, *Enhydra lutris*. *J. Mammal.* **65**, 527–531.
- Poppitt, S. D., Speakman, J. R. and Racey, P. A.** (1994). Energetics of reproduction in the lesser Hedgehog tenrec, *Echinops telfairi* (Martin). *Physiol. Zool.* **67**, 976–994.
- Prentice, A. M., Goldberg, G. R., Davies, H. L., Murgatroyd, P. R. and Scott, W.** (1989). Energy-sparing adaptations in human pregnancy assessed by whole-body calorimetry. *Br. J. Nutr.* **62**, 5–22.
- Renouf, D. and Gales, R.** (1994). Seasonal variation in the metabolic rate of harp seals: unexpected energetic economy in the cold ocean. *Can. J. Zool.* **72**, 1625–1632.
- Riedman, M. L., Estes, J. A., Staedler, M. M., Giles, A. A. and Carlson, D. R.** (1994). Breeding patterns and reproductive success of California sea otters. *J. Wildl. Manage.* **58**, 391–399.
- Spaaij, C. J. K., van Raaij, J. M. A., de Groot, L. C. P. G. M., van der Heijden, L. J. M., Boekholt, H. A. and Hautvast, J. G. A. J.** (1994). Effect of lactation on resting metabolic rate and on diet- and work-induced thermogenesis. *Am. J. Clin. Nutr.* **59**, 42–47.
- Sparling, C. E., Speakman, J. R. and Fedak, M. A.** (2006). Seasonal variation in the metabolic rate and body composition of female grey seals: fat conservation prior to high-cost reproduction in a capital breeder? *J. Comp. Physiol. B* **176**, 505–512.
- Speakman, J. R. and McQueenie, J.** (1996). Limits to Sustained Metabolic Rate: The Link between Food Intake, Basal Metabolic Rate, and Morphology in Reproducing Mice, *Mus musculus*. *Physiol. Zool.* **69**, 746–769.
- Stearns, S. C.** (1992). *The Evolution of Life Histories*. New York: Oxford University Press.
- Stephenson, P. J. and Racey, P. A.** (1993a). Reproductive energetics of the tenrecidae (Mammalia: Insectivora). I. The large-eared tenrec, *Geogale aurita*. *Physiol. Zool.* **66**, 643–663.
- Stephenson, P. J. and Racey, P. A.** (1993b). Reproductive Energetics of the Tenrecidae (Mammalia: Insectivora). II. The Shrew-Tenrecs, *Microgale* spp. *Physiol. Zool.* **66**, 664–685.
- Thometz, N. M., Tinker, M. T., Staedler, M. M., Mayer, K. A. and Williams, T. M.** (2014). Energetic demands of immature sea otters from birth to weaning: implications for maternal costs, reproductive behavior and population-level trends. *J. Exp. Biol.* **217**, 2053–2061.
- Thometz, N. M., Murray, M. J. and Williams, T. M.** (2015). Ontogeny of oxygen storage capacity and diving ability in the southern sea otter (*Enhydra lutris nereis*): costs and benefits of large lungs. *Physiol. Biochem. Zool.* **88**, 311–327.
- Thometz, N. M., Staedler, M. M., Tomoleoni, J. A., Bodkin, J. L., Bentall, G. B. and Tinker, M. T.** (2016). Trade-offs between energy maximization and parental care in a central place forager, the sea otter. *Behav. Ecol.* doi:10.1093/behecol/aw089.
- Thompson, S. D. and Nicoll, M. E.** (1986). Basal metabolic rate and energetics of reproduction in therian mammals. *Nature* **321**, 690–693.
- Tinker, M. T., Doak, D. F., Estes, J. A., Hatfield, B. B., Staedler, M. M. and Bodkin, J. L.** (2006). Incorporating diverse data and realistic complexity into demographic estimation procedures for sea otters. *Ecol. Appl.* **16**, 2293–2312.
- Williams, T. M.** (1989). Swimming by sea otters: adaptations for low energetic cost locomotion. *J. Comp. Physiol. A* **164**, 815–824.
- Williams, T. M., Fuiman, L. A., Horning, M. and Davis, R. W.** (2004). The cost of foraging by a marine predator, the Weddell seal *Leptonychotes weddellii*: pricing by the stroke. *J. Exp. Biol.* **207**, 973–982.
- Williams, T. M., Rutishauser, M., Long, B., Fink, T., Gafney, J., Mostman-Liwanag, H. and Casper, D.** (2007). Seasonal variability in otariid energetics: implications for the effects of predators on localized prey resources. *Physiol. Biochem. Zool.* **80**, 433–443.
- Williams, C. T., Sheriff, M. J., Schmutz, J. A., Kohl, F., Tøien, Ø., Buck, C. L. and Barnes, B. M.** (2011). Data logging of body temperatures provides precise information on phenology of reproductive events in a free-living arctic hibernator. *J. Comp. Physiol. B* **181**, 1101–1109.
- Withers, P. C.** (1977). Measurement of VO<sub>2</sub>, VCO<sub>2</sub>, and evaporative water loss with a flow-through mask. *J. Appl. Physiol.* **42**, 120–123.