Journal of Experimental Marine Biology and Ecology 481 (2016) 81–91

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Development of an altricial mammal at sea: II. Energy budgets of female sea otters and their pups in Simpson Bay, Alaska

Michelle Cortez [a,*], Caroline E.C. Goertz [b], Verena A. Gill [c,1], Randall W. Davis [a]

[a] Department of Marine Biology, Texas A&M University, OCSB, 200 Seawolf Parkway, Galveston, TX 77553, USA
[b] Alaska SeaLife Center, Seward, AK 99664, USA
[c] U.S. Fish and Wildlife Service, 1011 East Tudor Rd., Anchorage, AK 99503, USA

ARTICLE INFO

Article history:
Received 7 August 2015
Received in revised form 26 March 2016
Accepted 28 March 2016
Available online 29 April 2016

Keywords:
Energy budget
Alaska
Enhydra lutris
Maternal care
Pup development
Sea otter

ABSTRACT

Lactation is a critical and energetically expensive period of reproduction, especially for female sea otters (*Enhydra lutris*) and their pups, both of which have resting metabolic rates that are ca. 2.5-fold higher than terrestrial mammals of similar size. The simultaneous energy budgets for female Alaskan sea otters and their pups during the first three months postpartum were calculated based on published activity budgets for wild animals and metabolic rates for specific behaviors of captive sea otters. Pups were classified into three behavioral/size categories: Category 1 (C1) 0–<4 wk. old; Category 2 (C2) 4–<8 wk. old; and Category 3 (C3) 8–12 wk. Energy for growth ($Energy_{growth}$) averaged 0.0416 MJ day^{-1} for all pups. The combined daily energy expenditure to support resting metabolism and activity ($Energy_{r+a}$) for C1 and C2 pups was 1.31 and 2.61 MJ day^{-1}, respectively, of which most (C1: 99%; C2: 84%) was associated with resting-equivalent behaviors (i.e., resting, nursing and being groomed by the female). $Energy_{r+a}$ for C3 pups was 4.62 MJ day^{-1} of which 49% was associated with resting-equivalent behaviors, while 35% was associated with active behaviors (i.e., feeding, swimming and grooming). The underlying resting metabolic rate for all behaviors represented 100% of $Energy_{ingest}$ for C1, 94% for C2 and 85% for C3 pups. $Energy_{r+a}$ for all females was similar regardless of pup age and averaged 10.88 MJ day^{-1} (range 10.79–11.03). $Energy_{r+a}$ for C1 females was associated mainly with self-grooming and pup grooming (30%) and swimming (25%), while only 10% was associated with feeding. $Energy_{r+a}$ for C3 females was mainly associated with feeding (37%) with less energy devoted to swimming (10%) and grooming (14%). Lactation energy ($Energy_{lactation}$) in C3 females was 3.5-fold greater than in C1 females. Ingested energy for C1 females was 19.55 MJ day^{-1}, which increased to 22.13 MJ day^{-1} for C2 females and 26.53 MJ day^{-1} for C3 females. As with pups, the underlying resting metabolic rate for all female behaviors represented 70% of $Energy_{ingest}$ for C1 females and 72% for C2 and C3 females. Hence, thermogenesis dominated the metabolism of female sea otters as with their pups. These results provide a quantitative picture of the energetics of Alaskan female sea otters and their pups during early pup rearing in a species that has one of the highest mass specific resting metabolic rates of any mammal and the most altricial neonate born at sea.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

Mammalian female reproductive effort can be defined as the additional energy required for supporting offspring from the moment of pregnancy until weaning (Beck et al., 2003; Gittleman and Thomson, 1988; Millar, 1977). Lactation is the most energetically demanding phase of reproduction and the most susceptible to failure (Boyd, 1998; Costa et al., 1986; Costa and Gentry, 1986; Gamel et al., 2005; Gittleman and Oftedal, 1987; Gittleman and Thompson, 1988; Jenness, 1986; Millar, 1977; Rogowitz, 1996). As a result, female mammals often face a choice of either allocating resources to existing or future offspring (Parent-Offspring Conflict), and this choice will ultimately affect lifetime reproductive success and fitness (Gonzalez-Voyer and Kolm, 2010). If resources are scarce, adults may abandon offspring to maintain body condition so that they can breed again when conditions improve. If the young are nearly self-sufficient, abandonment is part of normal weaning (Gonzalez-Voyer and Kolm, 2010). However, very young mammals will starve if abandoned. Although all mammals supply milk to their young, the duration of lactation varies across species (Balshine, 2012; Case, 1978a). Lactation duration can be as little as 4–5 days in phocid seals (Order Carnivora, Family Phocidae) or over 2.5 years in chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus*) (Lefèvre et al., 2010; Pellow, 1984). Even after weaning, the mother and young of some species, such as primates, may remain together for years enabling offspring to learn foraging skills and predator avoidance (Gijsbertus et al., 2006).

* Corresponding author.
E-mail address: michellecrtz@gmail.com (M. Cortez).
[1] Current: Bureau of Ocean Energy Management, 3801 Centerpoint Circle, Anchorage, Alaska 99503, USA.

http://dx.doi.org/10.1016/j.jembe.2016.03.018
0022-0981/© 2016 Elsevier B.V. All rights reserved.

Once a female reaches peak milk production, further energy demands by the growing offspring can no longer be provided by lactation alone. At this point, the young begin eating solid food to supplement milk to meet their daily energetic demands (Langer, 2008). This is beneficial to the female and initiates the weaning process, which may be gradual or abrupt (Langer, 2008). At full weaning, the young are capable of foraging independently, although mortality is often high during the first year (Galef, 1981). The weaning mass of young mammals influences survival and serves as an indicator of maternal effort and population stress (Boltnev et al., 1998; Lee et al., 1991).

Lactation can result in a three-fold increase in resting energy metabolism relative to a non-breeding female (Costa et al., 1986; Gittleman and Thompson, 1988; Rogowitz, 1996). Female mammals compensate for an increase in energetic demand during lactation by mobilizing energy stores (mainly fat), increasing food consumption or reducing energetically expensive activities (Bowen et al., 2001; Gittleman and Thompson, 1988; Mellish et al., 2000; Rogowitz, 1996). The particular compensatory strategy used will have an impact on the growth and development of the offspring (Burns et al., 2004). Female polar bears (*Ursus maritimus*) fast during the final phase of gestation and initial phase of lactation in the den and rely on body fat and protein for milk production. Depletion of female fat stores, if food is scarce, can result in cub starvation due to the cessation of lactation (Derocher and Stirling, 1998). Among marine mammals, phocids and baleen whales reduce activity and thermoregulatory costs (through migration to warmer waters) and rely on energy reserves (i.e., blubber) to support lactation until offspring are weaned (Beck et al., 2003; Bonnet et al., 1998; Boyd, 1998; Gittleman and Thompson, 1988; Skibiel et al., 2013). This strategy is referred to as capital breeding in which feeding and reproduction are spatially and temporarily separated and include a fasting period during offspring development.

The most common compensatory strategy for increased energetic demands due to lactation is to increase food intake, which can be 1.7 to 2.9-fold greater than that of non-lactating females (Costa et al., 1986; Gittleman and Thompson, 1988; Mellish et al., 2000; Rogowitz, 1996). Many sea lions and fur seals (Order Carnivora, Family Otariidae) use an income-based foraging strategy where they feed throughout a long lactation period (Bonness and Bowen, 1996; Burns et al., 2004; Costa et al., 1986; Gamel et al., 2005). The energetic demand on female sea otters to sustain their own metabolic requirements and those of their maturing pups is very high and ultimately may influence the time of weaning. The resting metabolism of adult sea otters is 2–3 times higher than that of similar-sized terrestrial mammals, and consequently they must consume about 25% of their body mass in food each day (Finerty et al., 2009; Kenyon, 1975; Osterrieder and Davis, 2009; Yeates et al., 2007). Young marine mammals have higher mass specific metabolic rates than adults, which is necessary to maintain a core body temperature of ca. 37° C in the marine environment (Thompson et al., 1987), although heterothermy often occurs in young marine mammals (Laws, 1953; Irving et al., 1962; Yeates et al., 2007).

The goal of this study was to construct *simultaneous* energy budgets for wild female sea otters and their pups during the first three months postpartum based on: 1) detailed simultaneous activity budgets, 2) published metabolic rates for certain behaviors in captive California sea otters and 3) growth rates of captive Alaskan sea otter pups. As a result, these are the most comprehensive estimates of field metabolic rate and food consumption yet assembled for female sea otters and their pups because they include the energetics of resting thermogenesis, activity, lactation and pup growth.

2. Materials and methods

2.1. Study site

Simpson Bay (ca. 60.6° N, 145.9° W) is a relatively shallow fjord located in northeastern Prince William Sound, Alaska, with an average water depth of 30 m (maximum depth 125 m). It is approximately 21 km^2 in area — 7.5 km long in the northern and western bays, 5 km long in the eastern bay and 2.5 km wide at the entrance of the bay. Simpson Bay is a well-studied site for sea otter ecology (Cortez et al., 2016; Finerty et al., 2009; Gilksinson et al., 2011; Osterrieder and Davis, 2009; Osterrieder and Davis, 2011; Wolt et al., 2012) because of its easy access, protection from rough seas, and continual presence of sea otters (Fig.1).

The benthos consists primarily of soft sediments (mud, mixed mud and gravel) with some rocky reefs (Gilkinson et al., 2011; Noll et al., 2009). None of the large-bodied kelps (e.g., Nereocystis) that elsewhere form canopies are present, but large fronds of sugar (*Laminaria saccharina*), split (*Laminaria bongardiana*), and sieve (*Agarum clathratum*) kelp cover the benthos in many areas of the bay from the subtidal to a depth of approximately 10 m (R.W. Davis, pers. Obs.). After near extinction from the 19th century fur trade, the bay was recolonized by male sea otters in 1977, and females moved into the area between 1983 and 85 (Garshelis, 1983; Rotterman and Jackson, 1988; VanBlaricom, 1988). Since 2002, this Alaskan bay has been used during the summer (June–August) by an average of 125 ± 15.2 sea otters, including adults and subadults (93 ± 9.0) and pups (32 ± 7.0), giving an average summer density of 6.0 otters km^{-2} (updated from Wolt et al., 2012). During the winter, the number of otters in the bay decreases to ca. 50, although where they go is poorly understood (Wolt et al. 2012). This research was conducted under a Fish and Wildlife Permit 078744.

2.2. Activity budgets

Data collection for the activity budgets of females and pups has been described (Cortez et al., 2016). Briefly, we recorded the behavior of female sea otters with dependent pups during the summer months of May–August 2008–11. The research team, composed of a driver, recorder and spotter, made observations from a 7-m skiff. When a female and pup were sighted, the skiff was maneuvered close enough (ca. 100 m) to observe their behavior with the aid of binoculars (Nikon 10–22×) without disturbing them. The behaviors of the females and pups were recorded simultaneously once per minute for 30 min (i.e., instantaneous focal follow; Altmann, 1974) before switching to another pair. If a female showed signs of disturbance (e.g., swimming away from the skiff), the behavioral observations were not included in the analysis, although this was rare.

Six behaviors were recorded for females (resting, swimming, feeding, self-grooming, pup-grooming and interacting) and seven behaviors were recorded for associated pups (resting, swimming, feeding, self-grooming, being groomed, nursing, interacting) (Supplementary Data 1). The pups were divided into three behavioral and size classes (Categories 1–3) based on relative size, swimming ability and fur (i.e., lanugo, molting, adult pelage) (Table 1). The percentage of time spent in each recorded behavior was summed to compile 24-h female and pup activity budgets.

2.3. Energy budgets

2.3.1. Energy budget for pups

The energy required for the growth in wild pups ($Energy_{growth}$; MJ day^{-1}) was based on the average rate of daily mass gain for seven captive sea otter pups from Alaska during the first three months after birth held in the Alaska SeaLife Center, Shedd Aquarium and Seattle Aquarium. Only non-releasable orphaned pups that were admitted at a very young age were included in these calculations. Captive pup age was estimated based on several factors including the umbilicus, dentition, body mass, pelage and behavior. A multilevel growth curve model was used to generate a relationship between body mass and age as a single growth curve (Independent Variable: Age [Days after birth]; Dependent Variable:

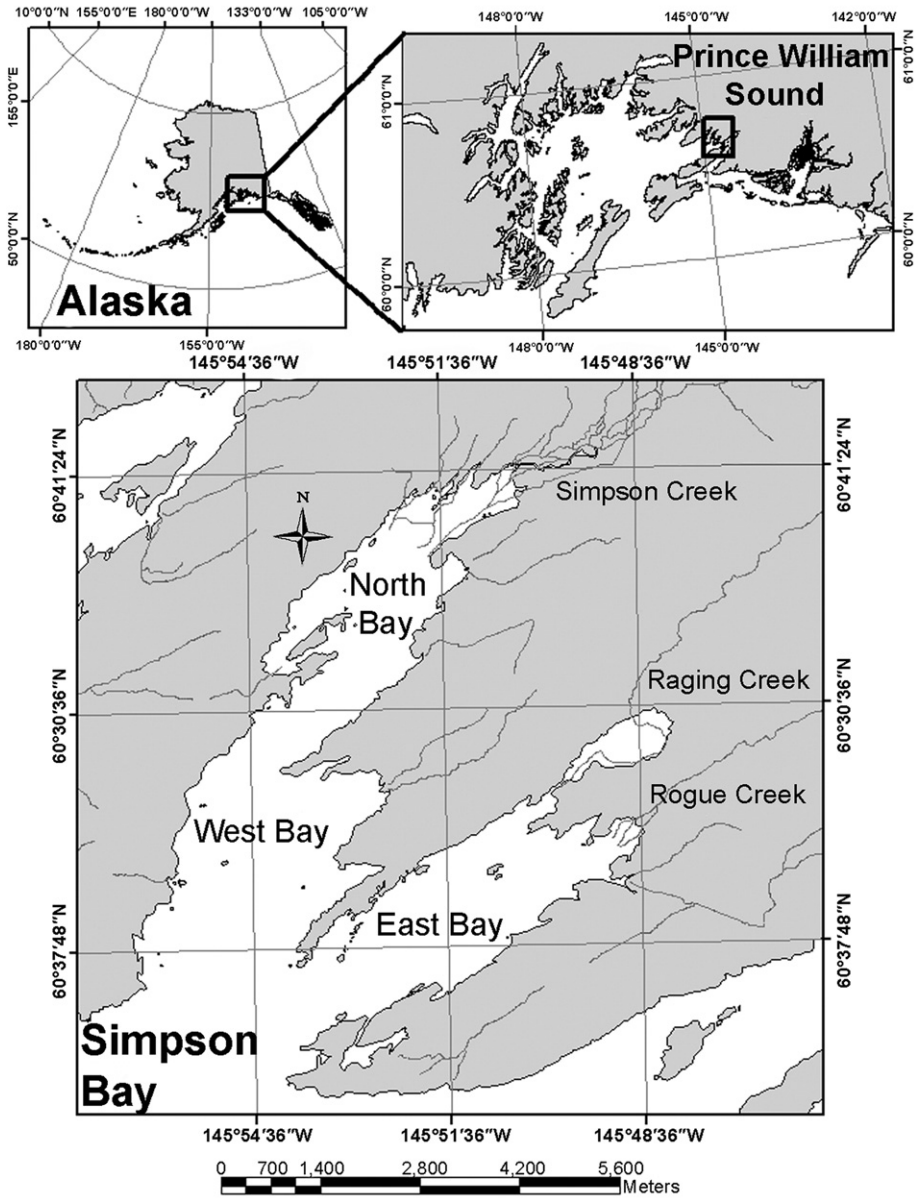

Fig. 1. Simpson Bay, Prince William Sound, Alaska.

Body mass [kg]; Nested Variable: Individual Pups). This approach was necessary because the frequency of weighing differed among pups. The result was best described by the polynomial equation:

$$\text{Body Mass(kg)} = 1.49 - 8.65 \times 10^{-3}(\text{Age}) + 1.98 \times 10^{-3}(\text{Age})^2 - 2.17 \times 10^{-5}(\text{Age})^3 + 9.28 \times 10^{-8}(\text{Age})^4$$

where age was the number of days after birth (Fig. 2). Using this equation, a mean body mass and daily mass gain (kg day^{-1}) were then calculated for each pup category (C1: Days 2–30; C2: 31–60; C3: 61–90). Growth was assumed to be lean tissue with a composition of 85% water and 15% protein (Fomon et al., 1982). Energy$_{growth}$ was calculated as the product of daily mass gain (kg day^{-1}), the fraction of lean tissue that is protein (0.15), cost of protein synthesis (4500 kJ kg^{-1} protein) and the conversion factor of 0.001 MJ kJ^{-1} (Webster, 1985).

Table 1
Criteria for estimating the three age categories for pups.
Adapted from Osterrieder and Davis (2009).

	Age estimate (Weeks)	Behavior	Length (compared to female)	Fur
Category 1	0–4	No swimming or diving	<50%	Dense natal fur
Category 2	4–8	Swimming with coordinated body movements; no diving	50–67%	Initial molting of natal fur
Category 3	8–12	Swims and makes shallow dives[a]	68–75%	Molt complete with adult pelage

[a] Dives longer than 30 s.

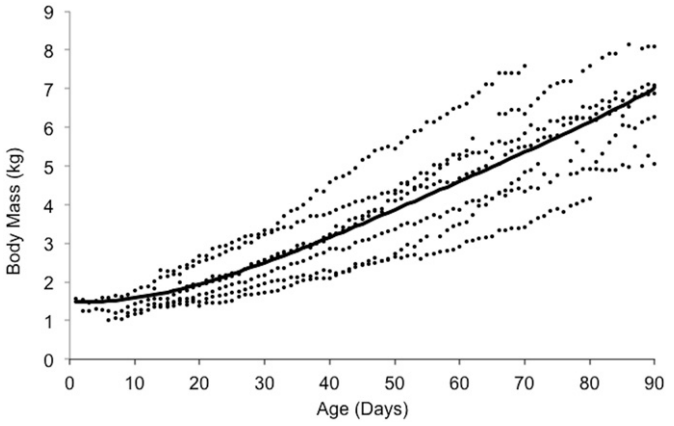

Fig. 2. Growth curve compiled from body masses of captive Alaskan sea otter pups (scatterplot) and an average growth rate (bold line; kg day^{-1}) which was best described by the equation: a. Body Mass (kg) = $1.49–8.65 \times 10^{-3}(day) + 1.98 \times 10^{-3}(day)^2–2.17 \times 10^{-5}(day)^3 + 9.28 \times 10^{-8}(day)^4$.

The combined daily energy expenditure to support resting metabolism and activity for each pup category ($Energy_{r+a}$; MJ day^{-1}) was calculated using the activity budget and the oxygen consumption (ml O_2 min^{-1} kg^{-1}) for each behavior based on measurements from captive California sea pups (Tables 2 and 3; Thometz et al., 2014; Supplementary Data 2). $Energy_{r+a}$ includes the energy expenditure for all behaviors in the daily activity budget, including resting, which is associated with thermogenesis (regulated production of heat) to offset heat loss in water. Based on the descriptions in Thometz et al. (2014), the metabolic rates for C1 pups were comparable to those for the pre-molting pups, while the metabolic rates for C3 pups were comparable to those for molting pups. The metabolic rates for the C2 pups were assumed to be an average of the pre-molting and the molting pup values. The in-air and in-water measurements were averaged since there was no significant difference between them. The nursing and being-groomed behaviors in pups were considered energetically similar to resting behavior.

The daily, mass-specific energy expenditure for each behavior (kJ day^{-1} kg^{-1}) was estimated as the product of the rate of oxygen consumption for that behavior, a conversion factor of 0.02 kJ ml^{-1} O_2 (Schmidt-Nielsen, 1997), and the total minutes spent each day devoted to that behavior (i.e., proportion of 24 h in each behavioral activity budget state multiplied by 1440 min day^{-1}) (Yeates et al., 2007; Thometz et al., 2014). Total energetic cost for each behavior (MJ day^{-1}) was calculated as the product of the mass specific energy expenditure for each activity and the mean body mass for each pup category (based on the growth rate of captive pups; see above) divided by 1000 to convert kJ to MJ (Thometz et al., 2014; Yeates et al., 2007). Finally, $Energy_{r+a}$ for each pup category was calculated as the sum of the daily energetic costs for all behaviors.

The daily net energy expenditure ($Energy_{net}$; MJ day^{-1}) for pups was estimated as the sum of $Energy_{growth}$ and $Energy_{r+a}$ (Table 4). Metabolizable energy ($Energy_{met}$) accounts for the Heat Increment of Feeding (HIF), which was assumed to be 10% of $Energy_{ingest}$, and was calculated using the $Energy_{net}$ ($Energy_{met} = Energy_{net} / 0.9$) (Costa and Kooyman, 1984). To calculate the digested energy ($Energy_{digest}$), urinary energy (i.e., energy used for the synthesis of urea) from milk consumption was assumed to be 2% of $Energy_{ingest}$ and was calculated using the $Energy_{met}$ ($Energy_{digest} = Energy_{met} / 0.98$) (Oftedal and Iverson, 1987). Finally, ingested energy ($Energy_{ingest}$) was calculated by assuming an assimilation efficiency of 97% for milk ($Energy_{ingest} = Energy_{digest} / 0.97$) (Oftedal and Iverson, 1987).

Average daily milk ingestion (kg day^{-1}) was calculated as the quotient of the $Energy_{ingest}$ (MJ day^{-1}) of the pups and the energy content of sea otter milk ($Milk_{energy}$; MJ kg^{-1}) (Table 4). $Energy_{ingest}$ takes into account the energy required for activity, resting, growth, HIF, assimilation efficiency and urinary energy. $Milk_{energy}$ was based on the proximate composition of sea otter milk (63% water, 23% fat, 11% protein and 1% carbohydrate [lactose]) and the equation: $Milk_{energy}$ (kcal 100 g^{-1}) = 9.11 (% fat/100) + 5.86 (% protein/100) + 3.95 (% carbohydrate/100) (Jenness et al., 1981; Oftedal et al., 1983). Using the conversion factor of 0.04184 to convert kcal 100 g^{-1} to MJ kg^{-1}, $Milk_{energy}$ was 11.67 MJ kg^{-1}.

2.3.2. Energy budget for females

For each female category, the combined daily energy expenditure to support resting metabolism and activity ($Energy_{r+a}$; MJ day^{-1}) was calculated using the activity budget and the oxygen consumption (ml O_2 min^{-1} kg^{-1}) for each behavior based on measurements from captive adult sea otters (Table 5; Yeates et al., 2007). As with the pup energy budget, $Energy_{r+a}$ includes the energy expenditure for all behaviors in the daily activity budget, including resting which is associated with thermogenesis (regulated production of heat) to offset heat loss in water. Pup grooming behavior by females was considered energetically similar to self-grooming. When calculating the energy for swimming, the routine swimming speed for females with pups in Simpson Bay was not as energetic as that assumed by Yeates et al. (2007) and originally measured by Williams (1989). Therefore, a linear regression was calculated using the resting metabolic rate (13.3 ml O_2 kg^{-1} min^{-1}) at a speed of 0 m s^{-1} and the previously measured value of surface swimming at 0.8 m s^{-1} (29.6 ml O_2 kg^{-1} min^{-1}), which was best described by the linear regression (Surface Swimming Metabolic Rate = 13.5 + 20.1(Speed) (Williams, 1989). The normal speed of swimming for female sea otters with pups was estimated to be 50% of that observed by Williams (1989), so the energetic cost at 0.4 m s^{-1} was calculated to be 21.5 ml O_2 kg^{-1} min^{-1}.

The mass-specific energy expenditure for each behavior (kJ day^{-1} kg^{-1}) was estimated as the product of the rate of oxygen consumption for a behavior, a conversion factor of 0.02 kJ ml^{-1} O_2^{-1} (Schmidt-Nielsen, 1997), and the total minutes spent each day devoted to that behavior (i.e., proportion of 24 h in each behavioral state from the activity budget multiplied by 1440 min day^{-1}) (Yeates et al., 2007). Total energetic cost for each behavior (MJ day^{-1}) was calculated as the product of the mass specific energy expenditure for each activity and a mean body mass of 20 kg (Ballachey et al., 2003; Garshelis et al., 1986; Rotterman and Monnett, 2002; Scheffer, 1951) and divided by 1000 to convert kJ to MJ (Yeates et al., 2007). Finally, $Energy_{r+a}$ for each female category was calculated as the sum of the daily energetic costs for all behaviors.

Table 2
Behavioral metabolic rates for each pup category adapted from Thometz et al. (2014).

Behavior	Pup Metabolic Rates					
	Category 1		Category 2		Category 3	
	ml O_2 min^{-1} kg^{-1}	kJ min^{-1} kg^{-1}	ml O_2 min^{-1} kg^{-1}	kJ min^{-1} kg^{-1}	ml O_2 min^{-1} kg^{-1}	kJ min^{-1} kg^{-1}
Resting	24.6	0.49	24.1	0.48	23.5	0.47
Swimming	31.6	0.63	31	0.62	30.4	0.61
Feeding	31.6	0.63	32.3	0.65	33	0.66
Grooming	54.1	1.09	53	1.06	51.7	1.04
Interacting	31.6	0.63	31	0.62	30.4	0.61

Table 3
Activity and energy budgets for each pup category. Metabolic rates for each pup category adapted from Thometz et al. (2014). Activity budgets are from Cortez et al. (2016).

Behavior	Activity budget						Energy budget					
	Category 1		Category 2		Category 3		Category 1		Category 2		Category 3	
	Prop. of day[a]	min	Prop. of day	min	Prop. of day	min	kJ day^{-1} kg^{-1}	Total MJ day^{-1}[b]	kJ day^{-1} kg^{-1}	Total MJ day^{-1}	kJ day^{-1} kg^{-1}	Total MJ day^{-1}
Resting	0.991	1427	0.880	1268	0.569	820	705.0	1.30 (98.8)	613.5	2.18 (83.7)	386.9	2.24 (48.6)
Swimming	0.005	7	0.069	100	0.174	251	4.4	0.01 (0.6)	61.9	0.22 (8.5)	153.0	0.89 (19.2)
Feeding	0.000	0	0.017	24	0.169	244	0.0	0.00 (0.0)	15.6	0.06 (2.1)	161.4	0.94 (20.3)
Grooming	0.001	1	0.018	26	0.029	42	0.9	0.00 (0.1)	27.3	0.10 (3.7)	43.2	0.25 (5.4)
Interacting	0.004	5	0.016	23	0.059	84	3.3	0.01 (0.46)	14.5	0.10 (2.0)	51.5	0.30 (6.5)

Percentage of total energy budget shown in parentheses.
[a] Proportion of 24-h period spent in each behavioral state.
[b] C1 mass: 1.84 kg; C2 mass: 3.56 kg; C3 mass: 5.80 kg.

Since the energy ingested by the pup is supplied entirely by the female, the energetic cost of lactation ($Energy_{lactation}$) was calculated using the ingested energy intake by the pup (see $Energy_{ingest}$ for pups) and a lactation efficiency (i.e., efficiency for the conversion of food energy or body reserves into milk energy) of 0.80 ($Energy_{lactation}$ = Pup $Energy_{ingest}$ / 0.80; Prentice and Prentice, 1988) (Table 6). The net energy ($Energy_{net}$) for females was estimated as the sum of $Energy_{r+a}$ and the $Energy_{lactation}$. As with sea otter pups, metabolizable energy ($Energy_{met}$) accounted for the Heat Increment of Feeding (HIF), which was assumed to be 10% of $Energy_{ingest}$, and was calculated from the $Energy_{net}$ ($Energy_{met}$ = $Energy_{net}$ / 0.9; Costa and Kooyman, 1984). To calculate digested energy ($Energy_{digest}$) for the females, urinary energy (i.e., energy used for the synthesis of urea) was assumed to be 10% of $Energy_{ingest}$ and was calculated using $Energy_{met}$ ($Energy_{digest}$ = $Energy_{met}$ / 0.9; Costa, 1982). Lastly, ingested energy ($Energy_{ingest}$) was calculated by assuming an assimilation efficiency of 82% ($Energy_{ingest}$ = $Energy_{digest}$ / 0.82; Costa, 1982). Daily food ingestion (kg) was calculated by dividing the $Energy_{ingest}$ (MJ day^{-1}) by the average energy content of bivalves (3.42 MJ kg^{-1}) from Simpson Bay determined by bomb calorimetry (Supplementary Data 3).

2.4. Data analyses

SPSS (Version 15 statistical software, Chicago, IL) was used at $\alpha = 0.05$ to test for the correlations between female and pup energy expenditure per behavior (dependent variables) due to the pup category (independent variable) controlling for any differences within years (covariate) using multivariate analysis of covariance (MANCOVA). The differences in mean energy spent among the behaviors were tested for each category of pup using Tukey HSD post hoc tests.

3. Results

3.1. Energy budget for pups

Based on the mean growth rate of captive sea otters pups in Alaska (Fig. 2), the estimated growth rate of C1 pups (1.84 kg mean body mass) during the first 30 days after birth was 35.0 g day^{-1}, although it was non-linear and slower during the first 15 days of age (18.1 g day^{-1}) than during the second 15 days (50.8 g day^{-1}). After 30 days, the growth rate became more linear and increased. The mean growth rate of C2 pups (3.56 kg mean body mass) was estimated to be 70.2 g day^{-1}, twice the value for the less mature C1 pups. The estimated growth rate of C3 pups (5.80 kg mean body mass) increased slightly to 79.8 g day^{-1}. Based on the assumptions described above, the $Energy_{growth}$ was 0.0236 MJ day^{-1}, 0.0474 MJ day^{-1} and 0.0539 MJ day^{-1} for C1, C2 and C3 pups, respectively (Table 4).

The estimated $Energy_{r+a}$ for C1 pups was 1.31 MJ day^{-1} of which 99% was associated with resting (this included nursing and being groomed with metabolic rates that were assumed to be equivalent to resting), and 1% was associated with attempted swimming, self-grooming and interacting (Table 4; Fig. 3). The estimated $Energy_{r+a}$ for C2 pups was 2.61 MJ day^{-1} of which 84% was associated with resting equivalent behaviors (i.e., resting, being groomed and nursing as with the C1 pup), 8% with swimming, 4% with grooming and 2% with feeding on solid food (Fig. 3; Table 3). C2 pups also began interacting, which represented 2% of $Energy_{r+a}$. The estimated $Energy_{r+a}$ for C3 pups was 4.62 MJ day^{-1} of which 49% was associated with resting equivalent behaviors, which was similar to that for the adult females (Fig. 3; Table 3). C3 pups were capable of swimming, which represented 19% of $Energy_{r+a}$. Although grooming and feeding behaviors were still developing, 20% of the $Energy_{r+a}$ was associated with shallow dives and 5% with grooming. C3 pups interacted with the female and other otters, which represented 6% of the $Energy_{r+a}$.

The $Energy_{ingest}$ for a C1 pup was 1.56 MJ day^{-1}, which increased 2-fold to 3.10 MJ day^{-1} for a C2 pup and a further 1.8-fold to 5.46 MJ day^{-1} for a C3 pup (Table 4; Fig. 4). Daily milk ingestion for C1, C2 and C3 pups was 134, 266 and 468 g day^{-1}, respectively, which was 7–8% of mean body mass (Fig. 5).

The MANCOVA showed a significant ($P < 0.0001$) difference in the energy associated with each behavior among the three pup categories. The amount of energy associated with each behavior was also significantly different among pup categories (resting: $P < 0.0001$; self-grooming: $P < 0.0001$; being groomed: $P < 0.0001$; feeding: $P < 0.0001$; being groomed: $P < 0.003$; swimming: $P < 0.0001$, nursing: $P < 0.0001$, interacting: $P < 0.0001$). A Tukey post-hoc test showed that

Table 4
Energetics calculations for the three categories of pups. Energy values are in units of MJ day^{-1} and milk consumption in units of g day^{-1}.

Category	$Energy_{r+a}$ (MJ day^{-1})	$Energy_{growth}$ (MJ day^{-1})	$Energy_{net}$[a] (MJ day^{-1})	$Energy_{met}$[b] (MJ day^{-1})	$Energy_{digest}$[c] (MJ day^{-1})	$Energy_{ingest}$[d] (MJ day^{-1})	Daily Milk Ingestion[e] (g day^{-1})
1	1.31	0.0236	1.34	1.48	1.51	1.56	134
2	2.61	0.0474	2.65	2.95	3.01	3.10	266
3	4.62	0.0539	4.67	5.19	5.30	5.46	468

[a] $Energy_{net}$ = $Energy_{r+a}$ + $Energy_{growth}$.
[b] $Energy_{met}$ = $Energy_{net}$ / 0.9 (Heat Increment of Feeding).
[c] $Energy_{digest}$ = $Energy_{met}$ / 0.98 (Urinary Energy).
[d] $Energy_{ingest}$ = $Energy_{digest}$ / 0.97 (Assimilation Efficiency of Milk).
[e] With the assumption of pups nursing exclusively.

Table 5
Activity and energy budgets for each female category. Female metabolic rates for each behavior are adapted from Yeates et al. (2007). Activity budget are from Cortez et al. (2016).

Behavior	Female Metabolic rates		Activity budget						Energy budget					
			Category 1		Category 2		Category 3		Category 1		Category 2		Category 3	
	ml O_2 min^{-1} kg^{-1}	kJ min^{-1} kg^{-1}	Prop. of day[a]	min	Prop. of day	min	Prop. of day	min	kJ day^{-1} kg^{-1}	Total MJ day^{-1}	kJ day^{-1} kg^{-1}	Total MJ day^{-1}	kJ day^{-1} kg^{-1}	Total MJ day^{-1}
Resting	13.3	0.27	0.504	725	0.525	756	0.458	659	195.9	3.92 (35.5)	204.0	4.08 (37.7)	177.9	3.56 (33.0)
Swimming	22	0.44	0.215	309	0.159	229	0.082	118	136.5	2.73 (24.8)	100.6	2.01 (18.6)	52.0	1.04 (9.6)
Feeding	21.6	0.43	0.085	122	0.132	190	0.325	467	52.6	1. 05(9.5)	81.8	1.64 (15.1)	201.0	4.02 (37.3)
Grooming	29.4	0.59	0.194	279	0.172	248	0.090	130	164.5	3.29 (29.8)	146.3	2.93 (27.0)	76.7	1.53 (14.2)
Interacting	24.5	0.49	0.003	4	0.012	17	0.045	65	2.1	0.04 (0.4)	8.5	0.17 (1.6)	32.0	0.64 (5.9)

Percentage of total energy budget shown in parentheses.
[a] Proportion of 24-h period spent in each behavioral state.

the energy expended by C1 pups in each behavior was significantly different from that for C2 and C3 pups.

3.2. Energy budget for females

The $Energy_{r+a}$ for C1, C2 and C3 females were nearly identical (only 2.2% difference), although the allocation of energy to particular behaviors differed. The estimated $Energy_{r+a}$ for a C1 female was 11.03 MJ day^{-1} of which 36% was associated with resting, 30% with self-grooming and pup grooming, 25% with swimming, 10% with feeding and <1% with interacting (Table 5; Fig. 6). The estimated $Energy_{r+a}$ for a C2 female was 10.82 MJ day^{-1} with the primary difference in energy allocation resulting from an increase associated with feeding (15%) and a decrease with swimming (19%) (Table 5; Fig. 6). Energy expenditure associated with resting (38%) and self-grooming and pup grooming (27%) was similar to that for a C1 female. The estimated $Energy_{r+a}$ for a C3 female was 10.79 MJ day^{-1} with less energy allocated to swimming (10%) and much more (37%) to feeding than C1 and C2 females (Table 5; Fig. 6). The energy expenditure associated with resting decreased slightly (33%), while that for self-grooming and pup grooming (14%) was about half that for C1 females.

$Energy_{lactation}$ for a C1 female was the lowest of all categories at 1.95 MJ day^{-1}, because C1 pups were small and could not ingest as much milk as older pups (Table 6; Fig. 7). This resulted in a slow growth rate of 35 g day^{-1}. Although the $Energy_{r+a}$ for a C2 pup was similar to that for a C1 pup, the growth rate for a C2 pups doubled (70 g day^{-1}), and the $Energy_{lactation}$ increased to 3.88 MJ day^{-1}. The growth rate for a C3 pup (80 g day^{-1}) was similar to that for a C2 pup, but the $Energy_{r+a}$ for a C3 pup increased significantly. As a result, the $Energy_{lactation}$ for a C3 female increased to 6.83 MJ day^{-1}. The $Energy_{ingest}$ for a C1 female was 19.55 MJ day^{-1}, which increased to 22.13 MJ day^{-1} for a C2 female and 26.53 MJ day^{-1} for a C3 female (Table 6; Fig. 8). The daily food ingestion for a C1 female was 5.72 kg day^{-1}, which was 29% of body mass for a 20 kg female (Fig. 8). A C2 female ingested 6.47 kg day^{-1} (32% of body mass), and a C3 female ingested 7.76 kg day^{-1} (39% of body mass).

The MANCOVA showed there was a significant difference in energy expenditure for each female category associated with grooming ($P < 0.0001$), feeding ($P < 0.0001$), swimming ($P < 0.0001$) and interacting ($P < 0.0001$). The Tukey post hoc tests showed that there was a significant decrease in the amount of energy associated with pup grooming for all female categories. The C1 and C2 females allocated similar amounts of energy for interacting and feeding, which differed significantly from that for C3 females. The energy associated with swimming differed among the three female categories.

4. Discussion

4.1. Energy budget for pups

In young mammals, energy is required for growth as well as resting metabolism and activity, so competing energetic demands exist that do not occur in mature mammals. Mature sea otters already have a resting metabolic rate that is 2.6-fold greater than the allometric prediction for terrestrial carnivores (McNab, 2008). Sea otter pups have a resting metabolic rate (0.49 kJ min^{-1} kg^{-1} or 29.4 kJ hr^{-1} kg^{-1} for a body mass of 1.84 kg; Table 2, Thometz et al., 2014) that is 1.8-fold greater than an adult otter (16.2 kJ hr^{-1} kg^{-1} for a body mass of 27.3 kg; Table 2, Yeates et al., 2007). However, if the allometric mass specific scaling factor of 0.75 for carnivores (McNab, 2008) is used, then sea otter pups have a resting metabolic rate (34.2 kJ hr^{-1} $kg^{-0.75}$) that is similar (9% less) to adult sea otters (36.7 kJ hr^{-1} $kg^{-0.75}$). Relative to other neonatal mammals, sea otter pups have an average scaled resting metabolic rate that is 2.4-fold (range 1.8–3.0) greater than neonatal dogs (*Canis lupus familiaris*) (13.4 kJ hr^{-1} $kg^{-0.75}$; Crighton and Pownall, 1974), rhesus monkeys (*Macaca mulatta*) (14.9 kJ hr^{-1} $kg^{-0.75}$; Dawes et al., 1960), sheep (*Ovis aries*) (19.4 kJ hr^{-1} $kg^{-0.75}$; Dawes and Mott, 1959) and humans (11.4 kJ $hr.^{-1}$ $kg^{-0.75}$; Hill and Rahimtulla, 1965). Hence, the 2.6-fold increase in resting metabolic rate in adult sea otters relative to adult carnivores is similar to the 2.4-fold increase in resting metabolic rate of sea otter pups relative to neonatal terrestrial mammals. However, relative to neonatal Northern fur seals (*Callorhinus ursinus*) (30.7 kJ hr^{-1} $kg^{-0.75}$; Donohue et al., 2000), harbor seals (*Phoca vitulina*) (22.4 kJ hr^{-1} $kg^{-0.75}$; Burns et al., 2005) and Northern elephant seals (*Mirounga angustirostris*)

Table 6
Energetics calculationsfor the three categories of females. Energy values are in units of MJ day^{-1}.

Category	$Energy_{r+a}$ (MJ day^{-1})	$Energy_{lactation}$[a] (MJ day^{-1})	$Energy_{net}$[b] (MJ day^{-1})	$Energy_{met}$[c] (MJ day^{-1})	$Energy_{digest}$[d] (MJ day^{-1})	$Energy_{ingest}$[e] (MJ day^{-1})
1	11.03	1.95	12.98	14.43	16.03	19.55
2	10.82	3.88	14.70	16.33	18.15	22.13
3	10.79	6.83	17.62	19.58	21.75	26.53

[a] $Energy_{Lactation} = Energy_{pup\ ingest}$ / 0.8 (Lactation Efficiency).
[b] $Energy_{net} = Energy_{r+a} + Energy_{Lactation}$.
[c] $Energy_{met} = Energy_{net}$ / 0.9 (Heat Increment of Feeding).
[d] $Energy_{digest} = Energy_{met}$ / 0.9 (Urinary Energy).
[e] $Energy_{ingest} = Energy_{digest}$ / 0.82 (Assimilation Efficiency of Clams).

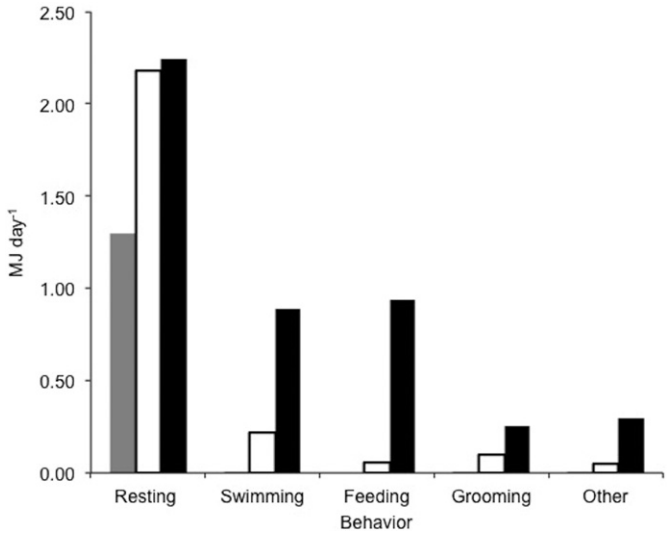

Fig. 3. Energy expenditure (MJ day^{-1}) as a function of behavior for C1, C2, C3 sea otter pups. Gray: Category 1; White: Category 2; Black: Category 3. C1 swimming, grooming and interacting accounted for <0.01 MJ day^{-1}.

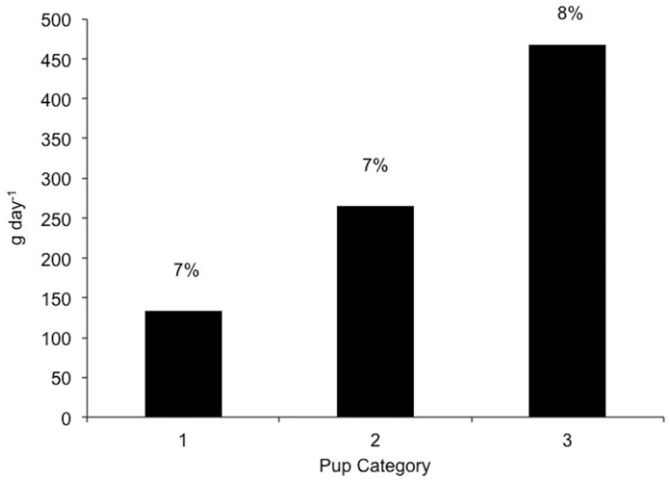

Fig. 5. Daily milk ingestion (g day^{-1}) and as a percentage of body mass for the three pup categories.

(31.1 kJ hr^{-1} kg$^{-0.75}$; Rea and Costa, 1992), the resting metabolism of neonatal sea otters is only slightly (20%) higher.

The elevated resting metabolic rate in neonatal sea otters results primarily from thermogenesis (regulated production of heat) necessary for the thermoregulation in the marine environment. Basal metabolism is so high that it represents a large percentage of the average energetic cost of other behaviors for all age categories of pups: 77% of swimming, 74% of feeding, 45% of grooming and 77% of interacting. With regards to the daily Field Metabolic Rate (FMR; MJ day^{-1}), the underlying resting metabolic rate for all behaviors represented 100% of $Energy_{ingest}$ for C1, 94% for C2 and 85% for C3 pups. Hence, thermogenesis dominates the metabolism of sea otter pups, which indicates the vital role it plays in the survival of the smallest endothermic neonate born at sea.

Compared to $Energy_{r\ +\ a}$, the $Energy_{growth}$ was only 1–1.5% of $Energy_{ingest}$ in C1 (0.024 MJ day^{-1}), C2 (0.047 MJ day^{-1}) and C3 pups (0.054 MJ day^{-1}) (Table 4). Sea otter pup growth is similar to that in fur seals and sea lions. These neonatal otariids grow slowly over a period of 4–12 months and mainly acquire lean tissue as opposed to fat (Bowen et al., 1992; Georges et al., 2001; Oftedal et al., 1987). Otariid pups usually grow at 60–380 g day^{-1}, which is significantly less than the growth rate of phocid pups (800–7000 g day^{-1}) (Boness and Bowen, 1996). Compared to the elevated growth rates in pinnipeds, growth rates of chimpanzees (*Pan troglodytes*) (12–13 g day^{-1}), gorillas (*Gorilla* sp.) (16 g day^{-1}), and humans (7.7 g day^{-1}) are minor (Case, 1978b). Growth rates from birth to weaning of wild sea otter pups in Prince William Sound averaged 83 g day^{-1} and 95 g day^{-1} for female and male pups, respectively (Monnett et al., 1991). The captive C1 pups in this study grew at 35 g day^{-1}, which increased to 70.2–79.8 g day^{-1} in the C2 and C3 pups, respectively. Hence, pup growth rates reported by Monnett et al. (1991) are probably from older (i.e., >C2) pups. Similar to C1 pups, Northern fur seal pups have a very slow growth rate during the perinatal period (1–10 days). Since fur seals are born with minimum body fat and a neonatal pelage with poor insulating qualities, most of the young pups' metabolism is associated with thermogenesis instead of growth (Boltnev et al., 1998). The highest growth rates recorded in fur seals occurred in preweaning pups after molting as they acquired body fat (Boltnev et al., 1998). Like the preweaning Northern fur seal pups, C3 pups that have molted their natal pelt also have a higher growth rate.

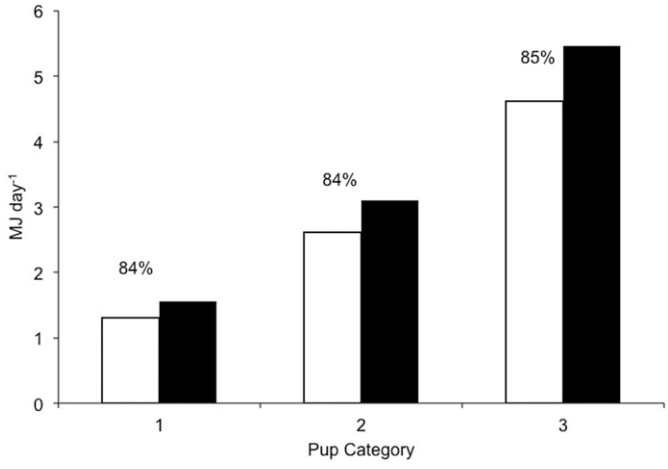

Fig. 4. Comparison of pup $Energy_{r\ +\ a}$ (white bars) and the $Energy_{ingest}$ (black bars) in MJ day^{-1}. The percentage of $Energy_{ingest}$ that is represented by $Energy_{r\ +\ a}$ is shown above the bars. The remaining $Energy_{ingest}$ was allocated to $Energy_{growth}$ and due to the Heat Increment of Feeding (HIF), urinary energy and the assimilation efficiency.

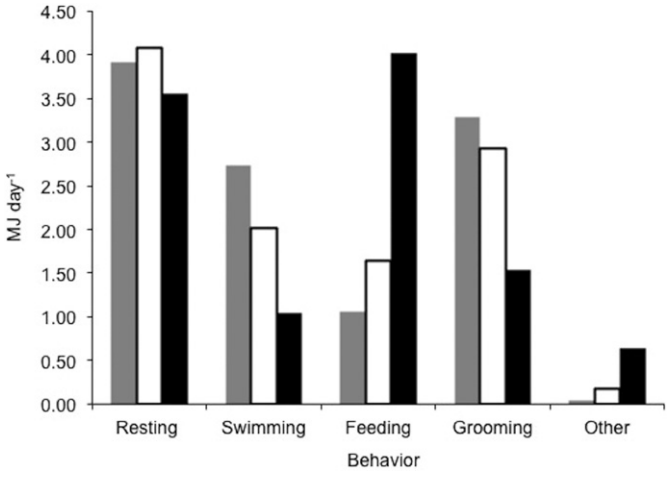

Fig. 6. Energy expenditure as a function of behavior for the three categories of females. Grooming behavior includes self-grooming and pup grooming. Gray: Category 1; White: Category 2; Black: Category 3.

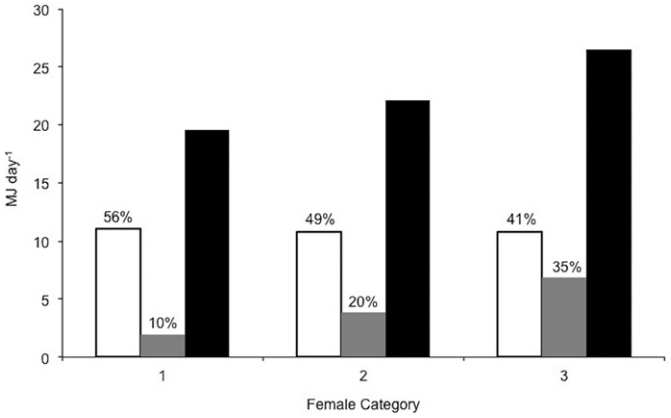

Fig. 7. Female $Energy_{r+a}$ (white bars), $Energy_{lactation}$ (gray bars) and the $Energy_{ingest}$ (black bars) in MJ day^{-1}. The percentages of $Energy_{ingest}$ that are represented by $Energy_{r+a}$ or $Energy_{lactation}$ are shown above the bars. The remaining $Energy_{ingest}$ is due to the Heat Increment of Feeding (HIF), urinary energy and the assimilation efficiency.

4.2. Sea otter pup behavioral development

As the most altricial mammal born at sea, C1 sea otter pups are totally dependent on the females for survival. These very small pups spend most of their time in resting equivalent behaviors, including resting, nursing or being groomed, and lack the strength or coordination for swimming, feeding or self-grooming. The absence of highly energetic behaviors resulted in a relatively low $Energy_{r+a}$ (1.31 MJ day^{-1}) compared with C2 and C3 pups. The $Energy_{ingest}$ for C1 pups (1.56 MJ day^{-1}) was provided entirely by milk (134 g milk day^{-1}), and nursing was considered a resting equivalent behavior (Payne and Jameson, 1984). By minimizing $Energy_{r+a}$, these pups can allocate more energy to thermogenesis and growth (Gaillard et al., 1997; Koteja, 2000).

Lactose and fat in sea otter milk provide energy, while the protein is essential for growth (Jenness, 1986). For the first 90 days, the pups consumed 7–8% of their body mass in milk. Sea otter milk is 62% water, and its dry mass is composed of about 61% fat, 29% protein and 0.03% lactose (Jenness et al., 1981; Oftedal, 1984). Pinniped milk is 49–59% water and has little or no lactose, while the dry mass of fat is higher (~74–82%) and protein mass is lower (11–22%) (Oftedal, 1984). Terrestrial carnivore milk, which is 18–34% dry mass, usually contains 7–25% lactose, 32–55% fat (the highest being from the brown bear) and 25–38% protein (Oftedal, 1984). Hence, the composition of sea otter milk is similar to that of pinnipeds with a slightly lower fat content. However, the amount of protein in sea otter milk is similar to that of terrestrial carnivores. Since sea otter pups use fur for thermo-insulation, fat does not accumulate as a blubber layer, and the elevated protein levels can be used for growth.

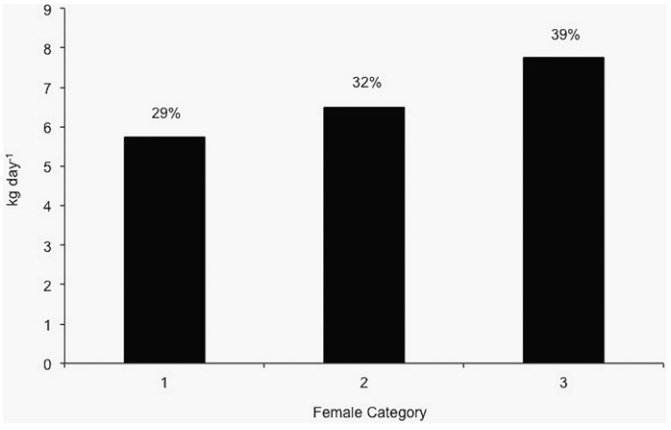

Fig. 8. Daily food consumption (kg day^{-1}) and as a percentage of body mass for a 20 kg female.

As young mammals grow, their energy requirements increase, and the energetic cost of milk production by the female increases (Kunz and Orrell, 2004). C2 pups consumed 266 g milk day^{-1} with an $Energy_{ingest}$ of 3.1 MJ day^{-1}, which was largely associated with the increase in $Energy_{r+a}$ (2.61 MJ day^{-1}). Even though 84% of their energy expenditure was allocated to resting equivalent behaviors, there was an additional expenditure of energy due to swimming (~8%). Feeding and self-grooming behaviors also begin to develop in C2 pups, although only 2% and 4% of the energy expenditure was used for these behaviors, respectively. In addition, these pups begin to molt their natal pelage (Payne and Jameson, 1984) and swim alongside the females making short, shallow dives while the females are foraging (Cortez et al., 2016). C2 pups begin to solicit food from the female, and this behavior continues until weaning (Payne and Jameson, 1984). Solid food provided by the female for C2 and C3 pups supplements milk energy, and this transition usually coincides with the peak lactation period (Langer, 2008).

The $Energy_{r+a}$ for C3 pups was 4.62 MJ day^{-1} with 49% associated with resting behavior similar to the females. By 8–10 weeks, the pups are strong swimmers in both the prone and supine position and begin diving with the foraging females (Payne and Jameson, 1984). About 19% of their energy was allocated to swimming, while 20% was allocated to foraging with the female or feeding on items obtained from the female. The development of these active behaviors corresponded to the increase in $Energy_{r+a}$. C3 pups had an $Energy_{ingest}$ of 5.46 MJ day^{-1}. If all their energy came from nursing, then these pups would have consumed 468 g milk day^{-1}. However, there was a minor contribution of solid food to the C2 and C3 pup's diet. An estimated 17% of prey captured by C2 females was shared with their pups, which increased to 25% for C3 females (M. Cortez, unpub. obs.). Regardless of the increasing contribution of solid food to the diets of C2 and C3 pups, most of the $Energy_{ingest}$ still came from milk. Since, 7% of the day was spent nursing, similar to C1 and C2 pups, C3 pups may become more efficient at consuming milk in a nursing bout, which has been seen in other mammals (i.e., Steller sea lion pups (*Eumetopias jubatus*), Northern fur seals, human infants, and horse foals) (Blaxter, 1989; Cameron, 1998; Costa and Gentry, 1986; Higgins et al., 1988).

4.3. Energy budget for females

With pup mortality occurring predominantly during the first 60 days after birth (Monnett and Rotterman, 2000; Riedman et al., 1994; Siniff and Ralls, 1991), neonatal care is critical and reflected in the females' activity budget. The female not only feeds the pup but also protects it from environmental and predatory threats while maintaining the insulating properties of its fur for thermoregulation (Cortez et al., 2016). The provisioning of any offspring during lactation is an energetically and nutritionally expensive process and is also correlated with some of the highest daily energetic expenditures (Langer, 2008; Mellish et al., 2000).

As mentioned previously, mature sea otters have a resting metabolic rate that is 2.6-fold greater than the allometric prediction for terrestrial carnivores (McNab, 2008), and this increase results primarily from thermogenesis (regulated production of heat) necessary for thermoregulation in the marine environment. As with pups, the resting metabolism of adult females is so high that it represents a large percentage of the average energetic cost of other behaviors: 61% of swimming, 63% of feeding, 46% of grooming and 55% of interacting. With regards to the daily Field Metabolic Rate (FMR; MJ day^{-1}), the underlying resting metabolic rate for all behaviors represented 70% of $Energy_{ingest}$ for C1 females and 72% for C2 and C3 females. Hence, thermogenesis dominates the metabolism of female sea otters as with their pups.

Overall, there was little difference in the $Energy_{r+a}$ (range 10.79–11.03 MJ day^{-1}) among the three categories of females, although their activity budgets were very different. There was little difference

in the daily energy expenditure associated with resting, while the energy expenditures associated with swimming and grooming (self-grooming and pup grooming together) decreased as the pups matured. The daily energy expenditure for feeding increased as the demands from the pup increased. C1 females expended 2.73 MJ day^{-1} (25% of $Energy_{r+a}$) in swimming around the study area carrying their pups, often making long, meandering loops that brought them back to the same location without any apparent reason. The purpose of this behavior remains uncertain. It may be related to heightened vigilance and predator avoidance by reducing the time that newborn pups are left unattended at the surface (i.e., bald eagles; Cortez et al., 2016; Gelatt et al., 2002; Reed, unpub. obs.) or to remain active for thermoregulation. The energy expended in meandering swimming decreased to 2.01 MJ day^{-1} (19% of $Energy_{r+a}$) for C2 females and 1.04 MJ day^{-1} (10% of $Energy_{r+a}$) for C3 females as the pups grew and the potential threat of bald eagle predation diminished.

The mass-specific metabolic rate of small mammals is much higher than that of larger mammals, and the former are unable to store enough energy as fat to compensate for long periods of fasting (Oftedal, 2000). Lactation is the most expensive stage of reproduction and is associated with an increase in foraging effort by up to 30% in larger species (Gittleman and Thompson, 1988). California sea lions (*Zalophus californianus*) increase their energy intake by nearly 4-fold over maintenance levels during peak lactation and sustain these levels for six months to support growing pups (Williams et al., 2007). Lactating Northern fur seal females consume 80% more food than a non-lactating female (Costa and Gentry, 1996). Even though elephant seals are capital breeders, females need to increase their foraging effort by 10% to store sufficient energy prior to the female's fasting period during lactation (Costa et al., 1986). In terrestrial mammals, increases in energy intake during lactation can be as high as 48% in pine voles (*Microtus pinetorum*) or 160% in red deer (*Cervus elaphus*) (Costa et al., 1986).

As the sea otter pups matured, their energy needs increased. With this elevated energy requirement from the pups, the females' foraging effort also increased, and the energy allocated to other activities, such as swimming at the surface, decreased. The energy expended in feeding increased 3.8-fold from 1.05 MJ day^{-1} (10% of $Energy_{r+a}$) for C1 females to 4.02 MJ day^{-1} (37% of $Energy_{r+a}$) for C3 females. This increase was associated with an elevated $Energy_{lactation}$, which increased 4.5-fold from 1.95 MJ day^{-1} (10% of $Energy_{ingest}$) in C1 females to 8.83 MJ day^{-1} (26% of $Energy_{ingest}$) in C3 females. Since the lactation efficiency is 80%, most of the cost to the female is in the energetic content of the milk, which comes from the diet (i.e., $Energy_{ingest}$). The $Energy_{ingest}$ for C1 females increased to 22.13 and 26.53 MJ day^{-1} for C2 and C3 females, respectively. C1 females consumed 5.72 kg prey day^{-1} (29% of body mass or ca. 560 clams day^{-1}), while C2 females consumed 6.47 kg (32% of body mass or ca. 634 clams day^{-1}). C3 females, which had to support the energetic needs of a larger and more active pup, consumed 7.76 kg prey day^{-1} (39% of body mass or ca. 760 clams day^{-1}). However, the actual number of clams consumed will depend on their mean mass, which we can only estimate.

Water conducts heat 25-fold faster than air, which makes sea otters susceptible to hypothermia in the cool waters of the North Pacific. Most marine mammals rely on blubber for thermal insulation. In contrast, sea otters rely entirely on fur that traps an air layer next to the skin and provides 70% of the thermal insulation to maintain a stable core body temperature (Costa and Kooyman, 1982; Davis et al., 1988; Kenyon, 1975; Williams et al., 1992). The marine otter (*Lontra felina*) also has no body fat, but it offsets heat loss by reducing the time spent in at sea (Estes, 1986; Valqui, 2012; Vianna et al., 2010). More than 80% of their time is spent in the dens, and they only go to the water to feed (Valqui, 2012; Vianna et al., 2010). Sea otter pups do not acquire the coordination to efficiently groom themselves until about eight weeks of age (Payne and Jameson, 1984). Therefore, they depend on the female for most of the fur maintenance during the first few months of life (Hanson et al., 1993; Kenyon, 1975). The energy expended by females to groom themselves and their pups decreased from 3.29 MJ day^{-1} (30% of $Energy_{r+a}$) for C1 females to 1.53 MJ day^{-1} (14% of $Energy_{r+a}$) for C3 females as the C3 pups developed the ability to self-groom and molted into their adult fur.

4.3.1. Catabolism of body tissue

The reliance on energy stored as fat is evident across different taxa of mammals. Black and brown bears fast for periods of 4–5 months (from 1 mo prior to parturition to 2–3 mo postpartum), while lactating polar bears fast for as long as 8 months (Oftedal, 2000). Pregnant blue whales (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*) acquire a large blubber layer that can represent 38% and 25% of their body mass, respectively, during the foraging season (Oftedal, 2000). However, even these large body energy reserves may not even be sufficient for the entire course of lactation. Larger phocids can support their daily energy requirements for lactation entirely through fat, while smaller phocids (e.g., harbor seals) must feed during the latter part of lactation (Oftedal, 2000). Otariid females are income-breeders, and they only rely on body fat for about 5–9 days after parturition and then make regular foraging trips throughout lactation (Oftedal, 2000).

C1 females forage, on average, only 2 h each day (Cortez et al., 2016), which represents only 9% of the daily activity budget during the first month postpartum. This is an extraordinarily low foraging effort for an animal with a newborn pup that needs to ingest 19.55 MJ day^{-1}, which was assumed to come entirely from the female's diet. This decrease in foraging behavior has been observed in females with young pups in other parts of Alaska and California (Gelatt et al., 2002; Thometz et al., 2014). The ability of the C1 female to obtain around 5.72 kg of food (ca. 560 clams or 8 clams $dive^{-1}$) in only 2 h time (average female dive duration: 1.69 min; Wolt et al., 2012) is difficult to reconcile with normal feeding behavior of sea otters without pups. However, pregnant females may develop some subcutaneous fat in the dorsal caudal area (R.W. Davis, unpub. obs.). In addition, otherwise healthy lactating or pregnant females that have died from boat strikes in Kachemak Bay, Alaska had abundant mesenteric fat in the omental bursa, around the kidneys and in the inguinal area that is not otherwise seen in males or non-breeding females that have been forensically examined (V.A. Gill unpublished data; Supplementary Data 4). As with otariids, these body fat deposits may allow females to reduce foraging without entering a state of starvation and devote more time to caring for their pups during the critical first two weeks when the neonate is very vulnerable to hypothermia and predation. If 50% of the $Energy_{ingest}$ comes from body fat stores instead of the diet during the first 14 days postpartum, then C1 females would use 0.13 kg fat day^{-1} (energy equivalent of fat: 39 MJ kg^{-1}; Prentice and Prentice, 1988) or a total of 1.8 kg (ca. 9% of body mass assuming a 20 kg female). This may explain the paradoxically low foraging effort observed in C1 females with vulnerable, newborn pups.

5. Conclusion

Neonatal C1 pups had a slow growth rate, which doubled in C2 and C3 pups although the $Energy_{growth}$ represented only 1–1.5% of $Energy_{ingested}$ for all age classes. The remainder was associated with $Energy_{r+a}$. For the first four weeks of life, the pup's activity was associated primarily with resting equivalent behaviors (i.e., resting, being groomed, nursing). As they matured, the C2 and C3 pups exhibited more active behaviors such as feeding, swimming and self-grooming. The increase in $Energy_{r+a}$ required an increase in the $Energy_{ingest}$. Throughout the first three months after birth, pups consumed 7–8% of their body mass in milk, but this was supplemented increasingly with solid food in C2 and C3 pups.

Sea otter females used several strategies to compensate for the increase in energetic demands of the developing pups. $Energy_{ingest}$ was 36% greater in females with C3 pups relative to those with C1 pups, which represented a 1.3-fold increase in food consumption from 29%

of body mass in C1 females to 39% of body mass in C3 females. Although the $Energy_{r+a}$ was similar for all three females, C1 females devoted more energy to swimming while C3 females expended more energy in feeding. The increase in feeding effort in C3 females was needed to support the 3.5-fold increase in milk production and provide, to a lesser extent, solid food for their pups. In contrast, C1 females fed only 9% of the day, and it is likely that they relied, at least in part, on stored body fat for metabolism and milk production during the first few weeks postpartum.

This study reveals the energetic strategies that female Alaskan sea otters use to support one of the highest metabolic rates in any adult and neonatal carnivore and the extreme effort of the female to raise an altricial pup at sea. This effort will increase as growing pups approach weaning during the autumn and early winter when air and surface water temperatures drop to freezing. How female Alaskan sea otters cope with the increasing energetic demands of feeding themselves and the pup remains uncertain and a topic for future research.

Conflict of interest

The authors declare that they have no conflict of interest.

Funding

This study was funded by Texas A&M University. The funding source had no involvement in the study design, collection, analysis of data, writing of manuscript or decision where/if to publish.

Acknowledgments

We thank the Alaska SeaLife Center rehabilitation team who cared for the pups, the volunteers who digitized paper records for analysis and L. Triggs and D. Fusco who helped obtain data for captive sea otter pups. We also thank I. Davis, K. McGovern, S. Osterrieder, L. Timm, R. Wolt and the undergraduate students who helped collect data. We thank F. Weltz and G. Davis for their logistical support and Texas A&M University for financial support. **[SS]**

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jembe.2016.03.018.

References

Altmann, J., 1974. Observational study of behavior: sampling methods. Behaviour 49, 227–267.
Ballachey, B.E., Bodkin, J.L., Howlin, S., Dorohoff, A.M., Rebar, A.H., 2003. Correlates to survival of juvenile sea otters in Prince William Sound, Alaska, 1992-1993. Can. J. Zool. 81, 1494–1510.
Balshine, S., 2012. Patterns of parental care in vertebrates. In: Royle, N.J., Smiseth, P.T., Kölliker, M. (Eds.), The Evolution of Parental Care. Oxford University Press, Oxford, United Kingdom, pp. 62–80.
Beck, C.A., Bowen, W.D., Iverson, S.A., 2003. Sex differences in the seasonal patterns of energy storage and expenditure in a phocid seal. J. Anim. Ecol. 72, 280–291.
Blaxter, K., 1989. Energy Metabolism in Animals and Man. Cambridge University Press, Cambridge.
Boltnev, A.I., York, A.E., Antonelis, G.A., 1998. Northern fur seal young: interrelationships among birth size, growth, and survival. Can. J. Zool. 76, 843–854.
Boness, D.J., Bowen, W.D., 1996. The evolution of maternal care in pinnipeds. Bioscience 46, 645–654.
Bonnet, X., Bradshaw, D., Shine, R., 1998. Capital versus income breeding: an ectothermic perspective. Oikos 83, 333–342.
Bowen, W.D., Iverson, S.J., Boness, D.J., Oftedal, O.T., 2001. Foraging effort, food intake and lactation performance depend on maternal mass in a small phocid seal. Funct. Ecol. 15, 325–334.
Bowen, W.D., Oftedal, O.T., Boness, D.J., 1992. Mass and energy transfer during lactation in a small phocid, the harbor seal (*Phoca vitulina*). Physiol. Zool. 65, 844–866.
Boyd, I.L., 1998. Time and energy constraints in pinniped lactation. Am. Nat. 152, 717–728.
Burns, J.M., Clark, C.A., Richmond, J.P., 2004. The impact of lactation strategy on physiological development of juvenile marine mammals: implications for the transition to independent foraging. Int. Congr. Ser. 1275, 341–350.
Burns, J.M., Costa, D.P., Frost, K., Harvey, J.T., 2005. Development of body oxygen stores in harbor seals: effects of age, mass, and body composition. Physiol. Biochem. Zool. 78, 1057–1068.
Cameron, E.Z., 1998. Is suckling behaviour a useful predictor of milk intake? A review. Anim. Behav. 56, 521–532.
Case, T.J., 1978a. Endothermy and parental care in the terrestrial vertebrates. Am. Nat. 112, 861–874.
Case, T.J., 1978b. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. Q. Rev. Biol. 53, 243–282.
Cortez, M., Wolt, R., Gelwick, F., Osterrieder, S., Davis, R.W., 2016. Development of an altricial mammal at sea: I. Activity budgets of female sea otters and their pups in Simpson Bay, Alaska. J. Exp. Mar. Biol. Ecol. 481, 71–80.
Costa, D.P., 1982. Energy, nitrogen, and electrolyte flux and sea water drinking in the sea otter *Enhydra lutris*. Physiol. Zool. 55, 35–44.
Costa, D.P., Gentry, R.L., 1986. Free-ranging energetics of northern fur seals. Fur Seals: Maternal Strategies on Land and at Sea. Princeton University Press, Princeton, NJ, pp. 79–101.
Costa, D.P., Gentry, R.L., 1996. The evolution of maternal care in pinnipeds. Bioscience 46, 645–654.
Costa, D.P., Kooyman, G.L., 1982. Oxygen consumption, thermoregulation, and the effect of fur oiling and washing on the sea otter, *Enhydra lutris*. Can. J. Zool. 60, 2761–2767.
Costa, D.P., 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., Le Boeuf, B.J., Huntley, A.C., Ortiz, C.L., 1986. The energetics of lactation in the Northern elephant seal, *Mirounga angustirostris*. J. Zool. 209, 21–33.
Crighton, G.W., Pownall, R., 1974. The homeothermic status of the neonatal dog. Nature 251, 142–144.
Davis, R.W., Williams, T.M., Thomas, J.A., Kastelein, R.A., Cornell, L.H., 1988. The effects of oil contamination and cleaning on sea otters (*Enhadra lutris*). II. Metabolism, thermoregulation, and behavior. Can. J. Zool. 66, 2782–2790.
Dawes, G.S., Jacobson, H.N., Mott, J.C., Shelley, H.J., 1960. Some observations on foetal and newborn rhesus monkeys. J. Physiol. 152, 271–298.
Dawes, G.S., Mott, J.C., 1959. The increase in oxygen consumption of the lamb after birth. J. Physiol. 146, 295–315.
Derocher, A.E., Stirling, I., 1998. Maternal investment and factors affecting offspring size in polar bears (*Ursus maritimes*). J. Zool. Lond. 245, 253–260.
Donohue, M.J., Costa, D.P., Goebel, M.E., Baker, J.D., 2000. The ontogeny of metabolic rate and thermoregulatory capabilities of Northern fur seal, *Callorhinus ursinus*, pups in air and water. J. Exp. Biol. 203, 1003–1016.
Estes, J.A., 1986. Marine otters and their environment. Ambio 15, 181–183.
Finerty, S.E., Wolt, R.C., Davis, R.W., 2009. Summer activity pattern and field metabolic rate of adult male sea otters (*Enhydra lutris*) in a soft sediment habitat in Alaska. J. Exp. Mar. Biol. Ecol. 377, 36–42.
Fomon, S.J., Haschke, F., Ziegler, E.E., Nelson, S.E., 1982. Body composition of reference children from birth to age 10 years. Am. J. Clin. Nutr. 35, 1169–1175.
Gaillard, J., Pontier, D., Allaine, D., Loison, A., Harve, J., Heizmann, A., 1997. Variation in growth form and precocity at birth in eutherian mammals. Proc. R. Soc. Lond. B. Biol. 264, 859–868.
Galef, B.G., 1981. The ecology of weaning: Parasitism and the achievement of independence by altricial mammals. In: Gubernick, D.J., Klopfer, P.H. (Eds.), Parental Care in Mammals. Springer, US, pp. 211–240.
Gamel, C.M., Davis, R.W., David, J.H.M., Meer, M.A., Brandon, E., 2005. Reproductive energetics and female attendance patterns of Cape fur seals (*Arctocephalus pusillus pusillus*) during early lactation. Am. Midl. Nat. 153, 152–170.
Garshelis, D.L., 1983. Ecology of sea otters in Prince William Sound, Alaska. Ph.D. Dissertation. University of Minnesota, Minneapolis, United States of America.
Garshelis, D.L., Garshelis, J.A., Kimker, A.T., 1986. Sea otter time budgets and prey relationships in Alaska. J. Wildl. Manag. 50, 637–647.
Gelatt, T.S., Siniff, D.B., Estes, J.A., 2002. Activity patterns and time budgets of the declining sea otter population at Amchitka Island, Alaska. J. Wildl. Manag. 66, 29–39.
Georges, J.Y., Groscolas, R., Guinet, C., Robin, J.P., 2001. Milking strategy in Subantarctic fur seals *Arctocephalus tropicalis* breeding on Amsterdam Island: evidence from changes in milk composition. Physiol. Biochem. Zool. 74, 548–559.
Gijsbertus, G.J., van Adrichem, Utami, S.S., Wich, S.A., van Hooff, J.A.R.A.M., Sterck, E.H.M, 2006. The development of wild immature Sumatran orangutans (*Pongo abelii*) at Ketambe. Primates 47, 300–309.
Gilkinson, A.K., Finerty, S.E., Weltz, F., Dellapenna, T.M., Davis, R.W., 2011. Habitat associations of sea otters (*Enhydra lutris*) in a soft- and mixed-sediment benthos in Alaska. J. Mammal. 92, 1278–1286.
Gittleman, J.L., Oftedal, O.T., 1987. Comparative growth and lactation energetics in carnivores. Symp. Zool. Soc. Lond. 57, 41–77.
Gittleman, J.L., Thompson, S.D., 1988. Energy allocation in mammalian reproduction. Am. Zool. 28, 863–875.
Gonzalez-Voyer, A., Kolm, N., 2010. Parental care and investment. eLS.
Hanson, M.B., Biedsoe, L.J., Kirkevoid, B.C., Casson, C.J., Nightingale, J.W., 1993. Behavioral budgets of captive sea otter mother-pup pairs during development. Zoo Biol. 12, 459–477.
Higgins, L.V., Costa, D.P., Huntley, A.C., Le Boeuf, B.J., 1988. Behavioral and physiological measurements of maternal investment in the Steller Sea lion, *Eumetopias jubatus*. Mar. Mamm. Sci. 4, 44–58.

Hill, J.R., Rahimtulla, K.A., 1965. Heat balance and the metabolic rate of new-born babies in relation to environmental temperature; and the effect of age and weight on basal metabolic rate. J. Physiol. 180, 239–265.
Irving, L., Peyton, L.J., Bahn, C.H., Peterson, R.S., 1962. Regulation of temperature in fur seals. Physiol. Zool. 35, 275–284.
Jenness, R., 1986. Symposium: species variation in mammary gland function Lactational performance of various mammalian species. J. Dairy Sci. 69, 869–885.
Jenness, R., Williams, T.D., Mullin, R.J., 1981. Composition of milk of the sea otter (*Enhydra lutris*). Comp. Biochem. Physiol. 70A, 375–379.
Kenyon, K.W., 1975. The Sea Otter in the Eastern Pacific Ocean. Dover Publications, New York, United States of America.
Koteja, P., 2000. Energy assimilation, parental care and the evolution of endothermy. Proc. R. Soc. Lond. B 267, 479–484.
Kunz, T.H., Orrell, K.S., 2004. Energy costs of reproduction. Encycl. Energy 5, 423–442.
Langer, P., 2008. The phases of maternal investment in eutherian mammals. Zoology 111, 148–162.
Laws, R.M., 1953. The elephant seal (*Mirounga leonina* Linn.): I. Growth and age. Falkland Islands Dependencies Survey Science Reports, London.
Lee, P.C., Majluf, P., Gordon, I.J., 1991. Growth, weaning and maternal investment from a comparative perspective. J. Zool. 225, 99–114.
Lefèvre, C.M., Sharp, J.A., Nicholas, K.R., 2010. Evolution of lactation: Ancient origin and extreme adaptations of the lactation system. Annu. Rev. Genomics Hum. Genet. 11, 219–238.
McNab, B.K., 2008. An analysis of the factors that influence the level and scaling of mammalian BMR. Comp. Biochem. Physiol. A 151, 5–28.
Mellish, J.E., Iverson, S.J., Bowen, W.D., 2000. Metabolic compensation during high energy output in fasting, lactating grey seals (*Halichoerus grypus*): Metabolic ceilings revisited. Proc. R. Soc. Lond. B Bio. 267, 1245–1251.
Millar, J., 1977. Adaptive features of mammalian reproduction. Evolution 31, 370–386.
Monnett, C., Rotterman, L.M., 2000. Survival rates of sea otter pups in Alaska and California. Mar. Mamm. Sci. 16, 794–810.
Monnett, C., Rotterman, L.M., Siniff, D.B., 1991. Sex-related patterns of postnatal development of sea otters in Prince William Sound, Alaska. J. Mammal. 72, 37–41.
Noll, C.J., Dellapenna, T.M., Gilkinson, A., Davis, R.W., 2009. A high-resolution geophysical investigation of sediment distribution controlled by catchment size and tides in a multi-basin turbid outwash fjord: Simpson Bay, Prince William Sound, Alaska. Geo-Mar. Lett. 29, 1–16.
Oftedal, O.T., 1984. Milk composition, milk yield and energy output at peak lactation: a comparative review. Physiological strategies in lactation: the proceedings of a symposium. Zool. Soc. London (November 11 and 12, 1982).
Oftedal, O.T., 2000. Use of maternal reserves as a lactation strategy in large mammals. Proc. Nutr. Soc. 59, 99–106.
Oftedal, O.T., Hintz, H.F., Schryver, H.F., 1983. Lactation in the horse: milk composition and intake by foals. J. Nutr. 113, 2096–2106.
Oftedal, O.T., Iverson, S.J., 1987. Hydrogen isotope methodology for measurement of milk intake and energetics of growth in suckling young. In: Huntley, C., Costa, D.P., Worthy, G.A.J., Castellini, M.A. (Eds.), Marine Mammal Energetics. Society for Marine Mammalogy, Lawrence, KS, pp. 67–96.
Oftedal, O.T., Iverson, S.J., Boness, D.J., 1987. Milk and energy intakes of suckling California Sea lion (*Zalophus californianus*) pups in relation to sex, growth, and predicted maintenance requirements. Physiol. Zool. 60, 560–575.
Osterrieder, S.K., Davis, R.W., 2009. Summer foraging behaviour of female sea otters (*Enhydra lutris*) with pups in a soft sediment habitat in Alaska. Aquat. Mamm. 35, 481–489.
Payne, S.F., Jameson, R.J., 1984. Early behavioral development of the sea otter, *Enhydra lutris*. J. Mammal. 65, 527–531.
Pellow, R.A., 1984. Food consumption and energy budgets of the giraffe. J. Appl. Ecol. 21, 141–159.
Prentice, A.M., Prentice, A., 1988. Energy costs of lactation. Annu. Rev. Nutr. 8, 63–79.
Rea, L.D., Costa, D.P., 1992. Changes in standard metabolism during long-term fasting in Northern elephant seal pups (*Mirounga angustirostris*). Physiol. Zool. 65, 97–111.
Riedman, M.L., Estes, J.A., Staedler, M.M., Giles, A.A., Carlson, D.R., 1994. Breeding patterns and reproductive success of California sea otters. J. Wildl. Manag. 58, 391–399.
Rogowitz, G.L., 1996. Trade-offs in energy allocation during lactation. Am. Zool. 36, 197–204.
Rotterman, L.M., Jackson, T.S., 1988. Sea otter. In: Lentfer, J.W. (Ed.), Selected Marine Mammals of Alaska: Species Account with Research and Management Recommendations. Marine Mammal Commission, Washington, D.C., United States of America, pp. 237–271.
Rotterman, L.M., Monnett, C., 2002. Length-mass and total body length of adult female sea otters in Prince William Sound before and after the Exxon Valdez oil spill. Mar. Mamm. Sci. 18, 977–993.
Scheffer, V.B., 1951. Measurements of sea otters from Western Alaska. J. Mamm. 32, 10–14.
Schmidt-Nielsen, K., 1997. Animal Physiology: Adaptation and Environment. Cambridge University Press, New York.
Siniff, D.B., Ralls, K., 1991. Reproduction, survival, and tag loss in California sea otters. Mar. Mamm. Sci. 7, 211–299.
Skibiel, A.L., Downing, L.M., Orr, T.J., Hood, W.R., 2013. The evolution of the nutrient composition of mammalian milks. J. Anim. Ecol. 82, 1254–1264.
Thometz, N.M., Tinker, M.T., Staedler, M.M., Mayer, K.A., 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.
Thompson, S.D., Ono, K.A., Oftedal, O.T., Boness, D.J., 1987. Thermoregulation and resting metabolic rate of California sea lion (*Zalophus californianus*) pups. Physiol. Zool. 60, 730–736.
Valqui, J., 2012. The marine otter *Lontra felina*. A Review of its Present Status and Implications for Future Conservation. Vol. 77, pp. 75–83.
VanBlaricom, G.R., 1988. Effects of foraging by sea otters on mussel-dominated intertidal communities. In: VanBlaricom, G.R., Estes, J.A. (Eds.), The Community Ecology of Sea Otters. Springer, Berlin, pp. 48–91.
Vianna, J.A., Ayerdi, P., Medina-Vogel, G., Mangel, J.C., Zeballos, H., Apaza, M., Faugeron, S., 2010. Phylogeography of the marine otter (*Lontra felina*): historical and contemporary factors determining its distribution. J. Hered. 101, 676–689.
Webster, A.J.F., 1985. Differences in the energetic efficiency of animal growth. J. Anim. Sci. 61, 92–103.
Williams, T.M., 1989. Swimming by sea otters: adaptations for low energetic cost locomotion. J. Comp. Physiol. A. 164, 815–824.
Williams, T.D., Allen, D.D., Groff, J.M., Glass, R.L., 1992. An analysis of California sea otter (*Enhydra lutris*) pelage and integument. Mar. Mamm. Sci. 8, 1–18.
Williams, T.M., Rutishauser, M., Long, B., Fink, T., Gafney, J., Mostman-Liwang, H., Casper, D., 2007. Seasonal variability in otariid energetics: implications for the effects of predators on localized prey resources. Physiol. Biochem. Zool. 80, 433–443.
Wolt, R.C., Gelwick, F.P., Weltz, F., Davis, R.W., 2012. Foraging behavior and prey of sea otters in a soft-and mixed-sediment benthos in Alaska. Mamm. Biol. 77, 271–280.
Yeates, L.C., Williams, T.M., Fink, T.L., 2007. Diving and foraging energetics of the smallest marine mammal, the sea otter (*Enhydra lutris*). J. Exp. Biol. 210, 1960–1970.