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RESEARCH ARTICLE

Energetic demands of immature sea otters from birth to weaning: implications for maternal costs, reproductive behavior and population-level trends

N. M. Thometz[1],*, M. T. Tinker[2], M. M. Staedler[3], K. A. Mayer[3] and T. M. Williams[1]

ABSTRACT

Sea otters (*Enhydra lutris*) have the highest mass-specific metabolic rate of any marine mammal, which is superimposed on the inherently high costs of reproduction and lactation in adult females. These combined energetic demands have been implicated in the poor body condition and increased mortality of female sea otters nearing the end of lactation along the central California coast. However, the cost of lactation is unknown and currently cannot be directly measured for this marine species in the wild. Here, we quantified the energetic demands of immature sea otters across five developmental stages as a means of assessing the underlying energetic challenges associated with pup rearing that may contribute to poor maternal condition. Activity-specific metabolic rates, daily activity budgets and field metabolic rates (FMR) were determined for each developmental stage. Mean FMR of pre-molt pups was 2.29±0.81 MJ day^{-1} and increased to 6.16±2.46 and 7.41±3.17 MJ day^{-1} in post-molt pups and dependent immature animals, respectively. Consequently, daily energy demands of adult females increase 17% by 3 weeks postpartum and continue increasing to 96% above pre-pregnancy levels by the average age of weaning. Our results suggest that the energetics of pup rearing superimposed on small body size, marine living and limited on-board energetic reserves conspire to make female sea otters exceptionally vulnerable to energetic shortfalls. By controlling individual fitness, maternal behavior and pup provisioning strategies, this underlying metabolic challenge appears to be a major factor influencing current population trends in southern sea otters (*Enhydra lutris nereis*).

KEY WORDS: Energetics, *Enhydra lutris*, Maternal investment, Ontogeny, Oxygen consumption.

INTRODUCTION

Across mammalian species, the most energetically taxing life-history period for females is lactation, which can require as much as three to four times the energy intake needed during non-lactating periods (Millar, 1977; Williams et al., 2007). When nursing, the metabolic demands of dependent young are inextricably linked to their mother, who must provide enough energy to support the needs of her young while managing the metabolic cost of milk production and her own energetic requirements. A variety of factors including

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duration of lactation, metabolic demands of offspring, energetic reserves of the female, and the availability of prey resources will determine the success of the female in accomplishing this task (Boness and Bowen, 1996; Bowen et al., 2001; Burns et al., 2004; Georges and Guinet, 2000; Verrier et al., 2011). Ultimately, these factors will impact daily behavioral responses, the level of energy invested in reproduction, and the overall fitness of adult females and offspring (Andersen et al., 2000; Georges and Guinet, 2000; Millar, 1975; Oftedal et al., 1987; Pontier et al., 1993).

As the smallest marine mammal species, sea otters [*Enhydra lutris* (Linnaeus 1758)] face extraordinary energetic challenges associated with aquatic living (Riedman and Estes, 1990). High surface area to volume ratios result in elevated heat loss to the environment (Dejours, 1987), which sea otters counter-balance with dense fur insulation and increased metabolism (Costa and Kooyman, 1984; Kenyon, 1969; Morrison et al., 1974; Williams, 1989; Yeates et al., 2007). Consequently, sea otters have one of the highest known mass-specific metabolic rates of any marine mammal and represent an extreme in mammalian metabolism (Costa and Williams, 1999; Morrison et al., 1974; Williams, 1989; Yeates et al., 2007). As a result of these elevated metabolic demands, adult sea otters consume 20–25% of their body mass in food per day (Costa and Kooyman, 1982; Kenyon, 1969; Morrison et al., 1974) and spend an average of 20–50% of the day foraging depending on habitat, sex, reproductive status and per-capita prey availability (Estes et al., 1986; Ralls and Siniff, 1990; Staedler, 2011; Tinker et al., 2008; Yeates et al., 2007). For adult females, energetic costs associated with reproduction must be added onto these inherently high metabolic demands.

Typically, female sea otters give birth to a single pup once a year with lactation lasting an average of 6 months (Jameson and Johnson, 1993). For other marine mammal species, lactation may be as short as 4 days, as observed in hooded seals, or last several years, as reported for some toothed whales [i.e. bottlenose dolphin (*Tursiops* sp.), sperm whale (*Physeter macrocephalus*) and beluga whale (*Delphinapterus leucas*)] (Boness et al., 2002). Provisioning strategies in marine mammals can range from strict capital breeding to strict income breeding (Jönsson, 1997). Capital breeders, such as phocid seals and mysticete whales, acquire sufficient energetic stores prior to giving birth and typically fast throughout lactation (Boness et al., 2002; Lockyer, 1984; Lockyer, 2007; Stearns, 1992; Trillmich, 1996). In contrast, income strategists, such as otariid seals and many odontocete whales, have minimal energetic reserves at parturition and must forage throughout lactation (Boness and Bowen, 1996; Huang et al., 2009; Perrin and Reilly, 1984; Stearns, 1992).

Along this continuum, sea otters represent extreme income strategists among marine mammals. High metabolic demands likely prevent female sea otters from building up large fat reserves prior to

> **List of symbols and abbreviations**
> FMR   field metabolic rate
> RMR   resting metabolic rate
> SORAC   Sea Otter Research and Conservation
> $\dot{V}_{O_2}$ rate of oxygen consumption

giving birth. This species also lacks a blubber layer that is typically utilized by many marine mammals for both insulation and energy storage (Kenyon, 1969; Williams and Worthy, 2002). Lacking this reserve, female sea otters must spend a large proportion of time foraging throughout lactation (Gelatt et al., 2002; Staedler, 2011) to continually support the increasing metabolic demands of a growing pup. The cost is likely considerable and despite foraging throughout lactation, female sea otters are reported to lose body mass over the course of pup dependency (Monson et al., 2000). However, to date, neither the energetic demands of immature sea otters nor the cost of lactation for adult females have been quantified.

The extreme metabolic demands of female sea otters provide a unique opportunity to examine mammalian limits to maternal provisioning in a wild carnivore. Because lactation occurs at sea, it is currently not feasible to measure sea otter maternal investment directly via milk transfer. Instead, we used a combination of laboratory methods and field-based observations to quantify the energetic requirements of sea otters throughout ontogeny. These data were used in combination with previously published values for adult female metabolic rates and activity budgets to assess the underlying energetic challenges associated with pup rearing that may contribute to low maternal physiological condition near the end of lactation. Specifically, we quantified activity-specific metabolic rates, daily activity budgets and field metabolic rates (FMR) of southern sea otters [*Enhydra lutris nereis* (Merriam 1904)] in five developmental stages (Table 1) from birth through weaning. From these data, we estimated both daily and cumulative energetic demands superimposed on adult females rearing dependent young, and assessed the physiological and ecological implications of age-specific energy demands on both immature and adult female sea otters.

RESULTS
Metabolic rates
Mass-specific metabolic rates of sea otters decreased as a function of age, irrespective of activity state (Fig. 1, Tables 2, 3). For resting behavior, the relationship between rate of oxygen consumption ($\dot{V}_{O_2}$) and age of pups was best described by a simple linear regression ($\hat{R}^2=0.552$; Fig. 1A):

$$\dot{V}_{O_2} = 25.85 - 0.062 \times \text{age} . \quad (1)$$

For moderately active behavior, the relationship between $\dot{V}_{O_2}$ and age was best described by a piecewise linear regression:

$$\dot{V}_{O_2} = 35.08 - 0.089 \times \text{age} , \quad (2)$$

$$\dot{V}_{O_2} = 19.06 - 0.006 \times (\text{age} - 180) , \quad (3)$$

for animals ≤180 and >180 days of age, respectively ($\hat{R}^2=0.633$; Fig. 1B). For highly active behavior, the relationship between $\dot{V}_{O_2}$ and age was best described by a piecewise linear regression:

$$\dot{V}_{O_2} = 40.51 - 0.098 \times \text{age} , \quad (4)$$

$$\dot{V}_{O_2} = 22.87 - 0.004 \times (\text{age} - 180) , \quad (5)$$

for animals ≤180 and >180 days of age, respectively ($\hat{R}^2=0.493$; Fig. 1C). The functional relationships for moderately active behavior and highly active behavior indicate that mass-specific metabolic needs of immature sea otters reach an asymptote around the time of weaning, with average values ($\dot{V}_{O_2}\sim19$ and 22 ml O_2 min^{-1} kg^{-1} for moderate and highly active behavior, respectively) that are consistent with those measured for adult sea otters (Williams, 1989; Yeates et al., 2007). It is likely that resting metabolic rate (RMR) also reaches an asymptotic value shortly after weaning, and the lack of statistical support for a breakpoint in this case probably reflects sample size limitations (only three data points were recorded for resting animals >200 days of age).

In-air metabolic rates were measured for the three youngest developmental stages and across activity levels (Table 2). Developmental stage ($F_{2,35}=19.90$, $P<0.001$) and activity level ($F_{2,35}=24.04$, $P<0.001$) both had a significant effect on mass-specific metabolic rates. The RMR of pre-molt pups was 28% higher than that of post-molt pups ($P<0.001$). Although pre-molt pups displayed higher resting and moderately active mass-specific metabolic rates than molting pups, the values were not significantly different ($P=0.33$). In-air highly active metabolic rates of molting pups were 26% higher than those of post-molt pups ($P<0.001$). Differences between in-air moderately active and highly active metabolic rates were not statistically significant ($P=1.00$). Only one pre-molt pup was observed being highly active during in-air trials, and therefore no mean value was reported (Table 2).

In-water metabolic rates were measured for all five developmental stages and across activity levels (Table 3). As with in-air measurements, developmental stage ($F_{4,137}=51.23$, $P<0.001$) and activity level ($F_{2,137}=59.18$, $P<0.001$) had significant effects on in-water mass-specific metabolic rates. Within each age class, resting, moderately active and highly active metabolic rates differed significantly from one another ($P<0.001$). The metabolic rates of pre-molt pups and molting pups were significantly different from those of all other developmental stages ($P<0.005$), but were not significantly different from one another ($P=1.00$). The RMR of pre-molt pups was 47% higher than that of dependent immature individuals ($P<0.005$), while the moderately active metabolic rate of molting pups was 42% higher than that of dependent immature sea otters ($P<0.005$). The metabolic rate of highly active molting pups was 14% higher than that of post-molt pups and 42% higher than that of juvenile individuals. Mass-specific metabolic rates of dependent immature animals differed significantly from all developmental stages ($P≤0.005$) except juveniles ($P=0.24$). Only one pre-molt pup was observed being

Table 1. Developmental stages and classifications for immature sea otters in the present study

Age class	Age (days)	Description
Pre-molt pup	1–45	Natal pelage, extremely buoyant, unable to dive
Molting pup	46–90	Shedding natal pelage, short diving attempts
Post-molt pup	91–135	Adult pelage, short diving and foraging attempts, rarely feeds on own captured prey
Dependent immature	136–180	Adult pelage, makes regular foraging dives, contributes moderately to own energetic demands
Juvenile	181–250	Adult pelage, weaned from adult female

Age classes are adapted from those previously described for immature sea otters (Payne and Jameson, 1984).
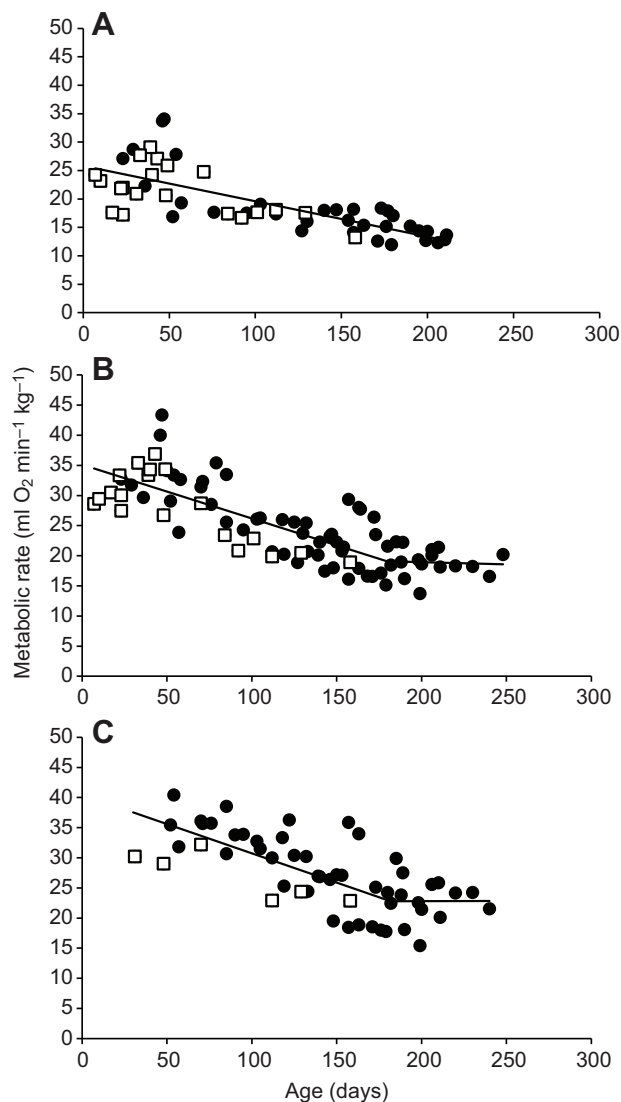
Fig. 1. Metabolic rate in relation to age for southern sea otters. Values for resting (A), moderately active (B) and highly active (C) sea otters are compared. Each point represents results from a single respirometry trial; data points for all study animals (n=7) are included, with in-air (open squares) and in-water (filled circles) measurements identified. Lines represent the results of piecewise linear regression analyses with breakpoints at the average age of weaning (~180 days) representing the point at which metabolic rates begin to plateau at approximately adult levels. Regressions and statistics are presented in the Results.

highly active during in-water trials, and therefore no mean value was reported (Table 3).

Activity budgets

Detailed activity budgets were determined for all five developmental stages (Table 4) and used in FMR calculations (Table 5). The amount of time each day spent engaged in specific activities changed markedly with age. In general, individuals greatly reduced time resting and grooming with age and spent more time foraging (Fig. 2). Pre-molt pups spent on average 58±28% of their day resting, while post-molt pups, dependent immature animals and juvenile animals spent on average 28–29% of their day resting. Grooming time declined throughout immature age classes, reaching its lowest level for juvenile sea otters. Conversely, the percent time spent performing energetically expensive behaviors (e.g. foraging, swimming) increased with age. Dependent immature animals foraged 2.8 h more per day than molting pups, while juveniles foraged 3 h more than post-molt pups and 2.5 h more than dependent immature animals (Fig. 2). Swimming only accounted for 9–10% of the daily budgets of molting pups, post-molt pups and dependent immature animals, but comprised 16% of the activity budget of juvenile animals. Nursing was the most consistent behavior throughout dependency and accounted for 13–16% of the activity budget of all dependent sea otters.

Energetic demands and field metabolic rates

In-air (Table 2) and in-water (Table 3) activity-specific metabolic rates were combined with detailed activity budgets (Table 4) to determine daily energetic demands for each developmental stage. Total daily energetic demands increased threefold from birth to weaning (Table 5). Although resting required little energy compared with other behaviors, it accounted for 55% and 32% of the FMR of pre-molt and molting pups, respectively (Table 5). Swimming had a large impact on the energetic expenditure of juveniles, accounting for 18% of FMR. The largest contributing factor to FMR in older age classes was foraging behavior, accounting for 36% and 47% of FMR for dependent immature and juvenile animals, respectively. The FMR of dependent immature and juvenile animals were the highest of all age classes measured in this study (Table 5). On a mass-specific basis, molting pups displayed the greatest energetic demand (0.87 ± 0.24 MJ day^{-1} kg^{-1}) of all developmental stages and juveniles exhibited comparable daily mass-specific demands (0.59 ± 0.11 MJ day^{-1} kg^{-1}) to adults (Fig. 3).

DISCUSSION

Energetic demands of immature sea otters

The unique, longitudinal data set described in this study details the metabolic demands of sea otter pups and provides the first energetic profile of developmental and, thus, baseline maternal investment costs for this species. As might be expected, pre-molt pups displayed the lowest total FMR of all age classes because of a combination of inactivity and small body size (Table 3). Although molting pups displayed the second lowest FMR (Table 3), they maintained the highest mass-specific daily energetic demands of all age classes (Fig. 3), presumably as a result of shedding of their natal pelage and growing adult coats. Once past the molt stage, sea otter pups spent much of their time learning to dive and forage. The increase in energetically expensive behaviors combined with decreased time spent resting with age (Fig. 2), concomitant with increasing body mass, resulted in higher overall energetic requirements for post-molt

Table 2. Body mass and mass-specific metabolic rates (means ± s.d.) of six post-absorptive sea otters measured dry on a haul-out across three developmental stages

Age class	Mass (kg)	Resting (ml O$_2$ min^{-1} kg^{-1})	Moderately active (ml O$_2$ min^{-1} kg^{-1})	Highly active (ml O$_2$ min^{-1} kg^{-1})
Pre-molt pup	3.09±0.81	23.18±3.85	31.93±3.15	–
Molting pup	5.67±1.05	22.16±3.90	28.29±4.58	30.61±2.26
Post-molt pup	9.08±1.01	17.49±0.59	21.00±1.30	23.67±1.04

Table 3. Body mass and mass-specific metabolic rates (means ± s.d.) of seven post-absorptive sea otters measured in water across five developmental stages

Age class	Mass (kg)	Resting (ml O_2 min^{-1} kg^{-1})	Moderately active (ml O_2 min^{-1} kg^{-1})	Highly active (ml O_2 min^{-1} kg^{-1})
Pre-molt pup	3.09±0.81	26.03±3.34	31.36±1.55	–
Molting pup	5.67±1.05	24.89±7.98	32.55±5.31	35.38±3.03
Post-molt pup	9.08±1.01	16.88±1.75	23.43±2.78	30.82±3.69
Dependent immature	12.06±1.02	16.08±2.26	21.19±4.24	24.34±5.76
Juvenile	14.42±1.39	13.63±1.08	18.98±2.28	23.05±3.74

pups and dependent immature sea otters than for younger age classes (Table 5).

Juvenile sea otters had the highest overall energy requirements of all developmental stages (Table 5) and exhibited mass-specific energetic demands similar to those of adults (Fig. 3). These newly weaned sea otters no longer have the benefit of obtaining food from their mothers and are likely inefficient foragers in comparison to adult conspecifics. As a result, juvenile sea otters competing with adults for limited prey resources may face considerable energetic hurdles when trying to meet metabolic demands during the first years post-weaning (Burns, 1999). We hypothesize that of all immature age classes, high metabolic demands have the greatest impact on juvenile sea otters during their first year post-weaning.

It is important to note that FMR values presented here were calculated from metabolic measurements taken while animals were post-absorptive. Sea otters in the wild are infrequently post-absorptive and as a consequence continually incur energetic costs associated with the digestion and absorption of prey (Costa and Kooyman, 1984; Kenyon, 1969; Payne and Jameson, 1984; Yeates et al., 2007). The relationship between activity, food digestion and thermoregulatory demands will also affect daily costs of free-ranging sea otters. In part, temporary increases in metabolic rate associated with digestion may offset thermal demands and minimize the need for activity-based heat production, potentially decreasing thermal energetic costs (Costa and Kooyman, 1984; Yeates, 2006). Thus, when taking into consideration the frequency in which sea otters feed and the energetic cost of digestion, values presented here are likely conservative estimates of daily energetic requirements for wild sea otters.

Energetic consequences for adult females

Average daily activity budgets of females with and without pups (Staedler, 2011) (Table 6) were used in combination with previously published values for behavior-specific metabolic rates of adult female sea otters (Williams, 1989) to determine daily behavior-specific energetic demands of adult female sea otters with and without pups (Table 7). Daily metabolic requirements of dependent sea otters from the present study (Table 5) were then used as a measure of additional energetic demands on females and used to determine FMRs of adult female sea otters with pups (Fig. 4). We found that by 3 weeks postpartum, a pup increases the daily energetic demands of its mother by 17% (Fig. 4). Female sea otters in both California (Table 6) (Staedler, 2011) and Alaska (Gelatt et al., 2002) have been shown to markedly reduce foraging activity during the first weeks postpartum. As a result, females must initially rely on energy stored on-board to support the additional metabolic demands of nursing and caring for a new pup. Daily energetic demands of a pup quickly increase throughout dependency and by 4 months postpartum daily costs are 78% higher for a female with a pup compared with one without. By the end of lactation, which occurs approximately 6 months postpartum, a dependent pup increases the daily energetic costs of its mother by 96% (Fig. 4). At this stage of development, the immature sea otter begins to forage and contribute in part to its own energy demands (Payne and Jameson, 1984). However, these animals also continue to nurse frequently (Fig. 2), solicit for food, and share and steal prey from their mothers (Payne and Jameson, 1984; Staedler, 2011), making them a substantial energetic burden for adult females until weaning occurs.

The total energetic impact of lactation and dependency on mothers can be quantified by summing the sequential costs for each pup developmental stage. Within the first 40 days postpartum, a female sea otter must provide 100 MJ to a new pup, and this energetic investment continues to increase substantially as development and growth of the pup continues. By 140 days, when a pup reaches the dependent immature age class, its mother has invested over 625 MJ; if a female successfully raises her pup to weaning (~180 days), she will have invested nearly 930 MJ. This energetic investment is in addition to the adult female's own elevated daily metabolic demands (Fig. 4). If at parturition an adult female is energy neutral (that is, bringing in sufficient prey to satisfy her own daily energetic needs and relying on on-board energy stores for her pup), she would lose 29 kg in body mass by the time her pup was weaned at 180 days. This value corresponds to an impossible >100% reduction in body mass and certain mortality. Obviously, female sea otters must markedly increase foraging effort during pup rearing. A study on harbor seals showed that despite significant

Table 4. Detailed activity budgets of dependent (*n*=12) and juvenile (*n*=14) sea otters

Activity	Pre-molt pup	Molting pup	Post-molt pup	Dependent immature	Juvenile
Resting on mother	29.2±21.2	5.0±8.0	1.4±4.2	1.6±7.7	0.0±0.0
Resting in water	28.9±19.2	34.7±22.7	26.9±20.8	26.7±23.2	28.9±16.6
Nursing on mother	11.6±9.3	6.5±6.5	3.2±9.4	0.9±1.6	0.0±0.0
Nursing in water	1.4±3.7	5.6±6.5	13.1±12.2	13.9±9.6	0.0±0.0
Foraging	2.2±5.3	19.3±16.3	28.7±22.3	31.1±26.1	41.4±17.3
Groomed by mother	16.8±12.8	8.4±7.4	5.4±9.6	3.5±4.0	0.0±0. 0
Passive grooming	3.1±4.6	3.1±4.0	2.9±2.7	2.7±3.6	1.6±2.6
Active grooming	2.4±4.0	7.6±7.2	6.8±5.9	6.9±5.6	7.0±5.2
Swimming	4.3±6.3	9.7±11.2	9.4±12.6	9.3±14.0	16.0±7.5
Other	0.0±0.0	0.0±0.0	2.2±3.0	3.4±3.7	5.0±5.0

Values are presented as the percent of a 24 h day spent engaged in a specific activity (means ± s.d.).

Table 5. Behavior-specific daily energetic demands and field metabolic rate (FMR) of southern sea otters across developmental stages (means ± s.d.)

Age class	Resting (MJ day⁻¹)	Nursing (MJ day⁻¹)	Foraging (MJ day⁻¹)	Grooming (MJ day⁻¹)	Swimming (MJ day⁻¹)	Other (MJ day⁻¹)	Total/FMR (MJ day⁻¹)
Pre-molt pup	1.28±0.65	0.27±0.22	0.06±0.15	0.56±0.37	0.12±0.18	0.00±0.00	2.29±0.81
Molting pup	1.60±1.11	0.47±0.38	1.12±0.95	1.24±0.78	0.52±0.61	0.00±0.00	4.94±1.84
Post-molt pup	1.26±0.95	0.73±0.70	2.32±1.84	1.14±0.80	0.58±0.78	0.14±0.19	6.16±2.46
Dependent immature	1.59±1.40	0.83±0.56	2.64±2.36	1.31±0.80	0.79±1.21	0.25±0.28	7.41±3.17
Juvenile	1.65±0.96	0.00±0.00	3.98±1.80	1.00±0.68	1.54±0.67	0.40±0.36	8.56±2.31
Adult male*	4.20	–	6.10	2.40	1.60	1.40	15.70

*Previously published values for adult male sea otters (Yeates et al., 2007) are included for comparison.

increases in both foraging effort and food intake throughout lactation, females incurred a 32% mass loss by late lactation, 97% of which was due to the depletion of fat reserves (Bowen et al., 2001). Because sea otters lack large fat reserves to draw upon during lactation (Kenyon, 1969; Williams and Worthy, 2002), increased food intake during lactation is essential for successful pup rearing.

When compared with pinnipeds, sea otters invest considerably more energy into their young over the course of lactation than would be predicted by their body size (Fig. 5). Female sea otters invest 128% more energy per kilogram throughout pup dependency than would a similarly sized phocid seal. Likewise, the level of investment is 28% higher for a sea otter than a similarly sized otariid (Fig. 5). Given their size, limited energetic reserves and high basal metabolic demands, our data support the classification of sea otters as extreme income breeders (Stearns, 1992) among marine mammals.

Ecological implications for mother and offspring

The reproductive schedule of female sea otters is fairly rigid, with females giving birth to a pup once a year regardless of current body and environmental conditions (Riedman et al., 1994). As a result,

female sea otters are thought to utilize a 'bet-hedging' strategy, either keeping or abandoning a pup postpartum depending upon physiological and environmental factors (Monson et al., 2000; Stearns, 1992). Our results suggest that this key life-history decision has an energetic foundation: a female sea otter must balance the probability of successfully weaning a pup given her current body energy stores and her likelihood of obtaining sufficient energy to sustain both herself and pup growth, against the potential loss of future reproductive opportunities. For females in poor condition at parturition (or that are experiencing low foraging success), the optimal decision may be to 'cut losses', abandoning the current pup in favor of improving future reproductive opportunities.

Females that go through with pup rearing face a second key life-history decision in terms of the timing of weaning. Early weaning (<180 days) reduces a female's energetic investment in the current pup, thereby reducing her energetic deficit at the end of lactation and leaving her in better physical condition before giving birth to her next pup. However, early weaning exacerbates the energetic challenges faced by juveniles as a result of high mass-specific energetic demands (Fig. 1) combined with physiological and behavioral immaturity, which can reduce foraging efficiency (Burns, 1999; Noren et al., 2001; Noren et al., 2002). Conversely, delayed weaning increases the likelihood of pup survival because pups with longer dependency periods gain an energetic advantage through increased foraging experience, increased body mass and lower mass-specific metabolic demands at time of weaning (Beauplet et al., 2005; Horning and Trillmich, 1997; Trillmich and Dellinger, 1991). However, delayed weaning requires a greater energetic investment by the female (Fig. 4). If the energetic deficit accrued by a female during lactation is too large and exceeds her capacity to replenish energetic reserves before a subsequent pup is born, the female will
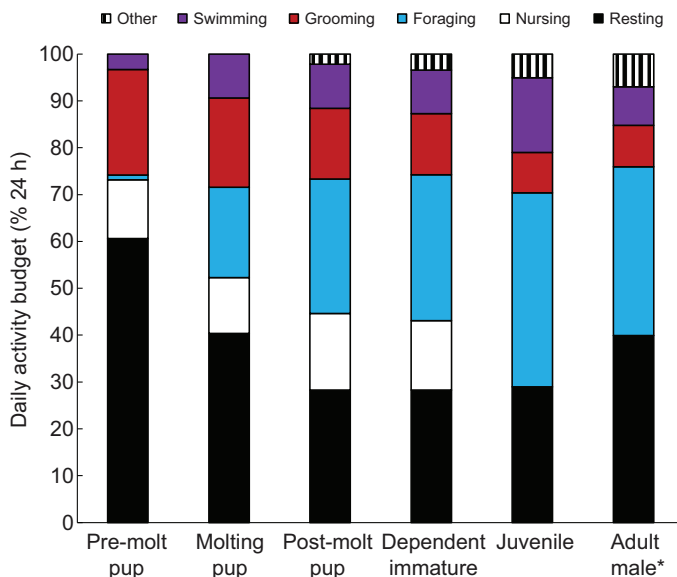

Fig. 2. Daily activity budgets for wild sea otters across developmental stages from pup to adult. Data for dependent (*n*=12) and juvenile (*n*=14) sea otters in this study are compared with data for *adult male sea otters (Yeates et al., 2007). Daily activity budgets were calculated as the proportion of all records associated with six behavioral categories: resting, nursing, foraging, grooming, swimming and other. The reported activity budgets represent proportions of 24 h periods of known activities as described in the Materials and methods.
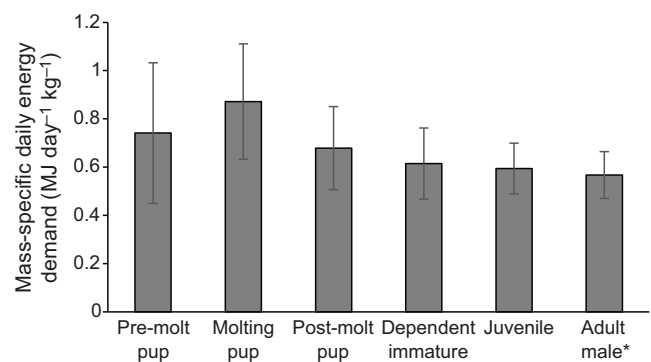

Fig. 3. Mass-specific daily energetic demands of wild sea otters across developmental stages in comparison to adult males. *Previously published value for an adult male (Yeates et al., 2007). Height of the bars and lines represent means ± 1 s.d.

Table 6. Simple activity budgets of female sea otters with and without pups adapted from Staedler (Staedler, 2011)

Activity	Female with no pup	Female with 0–3 week old pup	Female with >3–10 week old pup	Female with >10 week old pup
Resting	51.7±4.9	72.1±9.6	56.3±5.80	44.8±2.2
Active other	8.7±3.8	6.4±2.4	5.7±2.1	6.7±1.3
Foraging	39.7±6.6	21.5±9.5	38.1±5.1	48.6±1.8

Activity budgets were determined from time-depth recorders implanted in wild sea otters. Any behavior not identified as 'resting' or 'foraging' was classified as 'active other'. Values are presented as the percent of a 24 h day spent engaged in a specific activity (means ± s.d.).

have to abandon the next pup early in development (Monson et al., 2000).

The trade-offs described above imply two key decision points for an adult female: (1) whether to abandon a pup shortly after parturition and (2) at what age to wean a pup. Interestingly, the timing of these two energetically based decision points for adult females coincides with the two age classes that commonly experience the highest rates of mortality in the wild: postpartum pups and juveniles in their first year post-weaning (Estes et al., 2003; Tinker et al., 2006). A study on northern sea otters (*Enhydra lutris kenyoni*) in Prince William Sound, Alaska, concluded that female body condition was the major driver leading to postpartum mother–pup separations (Garshelis and Garshelis, 1987). In a different study conducted on northern sea otters, the authors suggested that females experiencing unfavorable environmental or physical conditions may abandon a pup early in development before a substantial energetic investment is made (Monson et al., 2000). Given the rapid increase in energetic investment for a female to raise a pup to weaning (Fig. 4), we conclude that current and future female energetic expenditures are the major drivers behind the majority of pup losses occurring shortly after birth in both northern and southern sea otters (Garshelis and Garshelis, 1987; Jameson and Johnson, 1993; Riedman et al., 1994; Tinker et al., 2006).

Current implications for southern sea otters

Population recovery of the southern sea otter has been slow and marked by occasional periods of decline since near extirpation during the fur trade of the 18th and 19th centuries (Kenyon, 1969; Tinker et al., 2006). Numerous studies have attributed the sluggish recovery of southern sea otters to elevated mortality, with the highest mortality rates occurring in postpartum pups and juveniles in their first year post-weaning, but with a disproportionately high mortality rate also observed in prime-age females (Estes et al., 2003; Tinker et al., 2006). Because adult female mortality in particular has a profound influence on the population trajectory of the southern sea otter (Gerber et al., 2004; Tinker et al., 2006), it is of concern for overall population stability and growth.

Linked to these trends is the density-dependent reduction in prey resource availability for southern sea otters in areas of high population density (Tinker et al., 2008), which contributes to poor female body

condition at the end of lactation. Often adult female deaths occur immediately before or after pup weaning (Tinker et al., 2006; USGS, unpublished), when nutritional deficiencies and poor body condition leave females particularly vulnerable to mating trauma, infection and disease. Termed 'end-lactation syndrome', this condition has been observed more frequently over the past 20 years, especially in areas of high sea otter abundance (USGS, unpublished). Our study identifies the underlying energetic mechanism driving the reduction in female body condition as lactation progresses. We hypothesize that the extremely high energetic cost of pup rearing for this species, in combination with localized prey limitations occurring along the California coast (Tinker et al., 2008), results in a physiological tipping point, manifested as an increase in end-lactation female mortality.

Conclusions

Meeting the remarkably high energetic demands of immature sea otters throughout dependency is physiologically challenging for lactating females and often results in a substantial reduction in maternal body mass by pup weaning (Monson et al., 2000). The consequences of increased energetic demands during pup rearing appear to be exacerbated in areas of limited prey availability, where such demands may result in extremely poor body condition or mortality for females at the end of lactation. Although this study focused on southern sea otters in California, these data are broadly applicable to northern sea otters in Alaska, British Columbia and Washington; particularly in areas of high sea otter abundance where resources are likely limited. We propose that the extreme energetic demands described here have cascading implications for parental provisioning strategies, life-history decisions, population dynamics and current trends in mortality in wild sea otters.

MATERIALS AND METHODS
Experimental design

Resting and active metabolic rates were determined for southern sea otters at the Monterey Bay Aquarium (Monterey, CA, USA) through the Sea Otter Research and Conservation (SORAC) program from February 2009 to March 2011. Five developmental stages, defined in relation to molting period and foraging proficiency (Payne and Jameson, 1984), were examined (Table 1). Observations of routine daily behaviors of wild pup and juvenile sea otters were collected off the coast of central California using radio

Table 7. Mean behavior-specific daily energetic demands of female southern sea otters with and without pups, not including costs associated with lactation

Female offspring status	Resting (MJ day^{-1})	Active other (MJ day^{-1})	Foraging (MJ day^{-1})	Total (MJ day^{-1})
Female with no pup	4.01	0.97	5.38	10.37
Female with 0–3 week old pup	5.60	0.91	2.92	9.42
Female with >3–10 week old pup	4.37	0.80	5.17	10.34
Female with >10 week old pup	3.48	0.95	6.58	11.01

Values were calculated utilizing adult female activity budgets (Staedler, 2011) (see Table 6) in combination with previously published behavior-specific metabolic rates of female sea otters (Williams, 1989). An average adult female body mass of 19.89 kg (Williams, 1989) was assumed for adult female energetic demand calculations. Behavior-specific metabolic rates used in the above calculations (Williams, 1989) were: 'resting'=13.5 ml O_2 min^{-1} kg^{-1}, 'active other'=24.74 ml O_2 min^{-1} kg^{-1} (average of grooming, swimming and diving behaviors) and 'foraging'=23.58 ml O_2 min^{-1} kg^{-1} (average of swimming and diving behaviors).
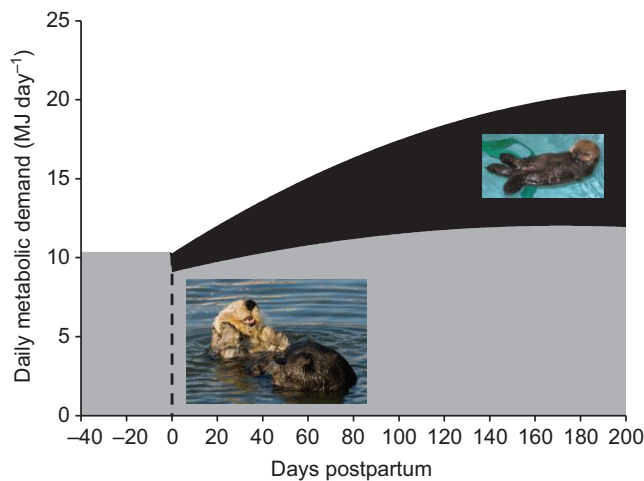
Fig. 4. Daily metabolic demands of an adult female sea otter in relation to days postpartum. Time in days, spanning 40 days before birth to 200 days postpartum, is displayed on the *x*-axis. Average daily energetic demands of an adult female (gray, Table 7) are distinguished from the additional energetic demands of a dependent pup (black, Table 5). The daily metabolic demand (equivalent to FMR) of a postpartum female is represented by the combination of female (gray) and pup (black) energetic demands on a given day. Dashed line denotes pup birth. Note that average age of weaning is 180 days. Photo credits: J. Tomoleoni (adult) and N. M. Thometz (pup).

Fig. 5. Total maternal energetic investment over the course of pup dependency in relation to average adult female body mass for marine mammals. Sea otters from the present study (circle) are compared with otariids (triangles) and phocid seals (squares). Pinniped data are adapted from previously published data (Boness and Bowen, 1996). Points represent cumulative energetic investment in a pup by an adult female by the average age of weaning. Least squares linear regression equations are $y=0.136x+70.889$ ($r^2=0.41$) and $y=0.0289x+20.615$ ($r^2=0.43$) for otariids and phocids, respectively. The dashed line is an extension of the otariid regression and is provided for comparison with the sea otter.

telemetry and high powered spotting scopes (Questar Inc., New Hope, PA, USA) between January 2000 and October 2008 for independent juvenile animals, and March 2007 and December 2008 for dependent animals. Combining activity-specific metabolic rates measured in captivity with empirically derived activity budgets of wild sea otters, we calculated FMR for each of the five developmental stages.

Captive animal work was conducted under US Fish and Wildlife permit MA045447 to T.M.W.; wild animal work was conducted under US Fish and Wildlife permit MA672624 to M.T.T. All animal care use protocols were evaluated and approved by Institutional Animal Care and Use Committees at both the University of California Santa Cruz and the Monterey Bay Aquarium.

Laboratory studies
Animals
Seven wild-born sea otter pups (1 male, 6 females) were measured during metabolic trials. These individuals stranded in central California as pups and were brought to the Monterey Bay Aquarium to be reared in captivity within the SORAC program and released back into the wild upon maturity. Therefore, individuals were measured during the time they were housed at the Monterey Bay Aquarium and no individuals were specifically captured for use in this study. Longitudinal measurements were made for individuals ranging in age from 7 to 248 days. Subjects were weighed before each trial (Hygeia EBSL-20, Guang-Dong, China, or SR Scales SRV945, Tonawanda, NY, USA). Individuals were housed in saltwater pools (800 gallons) at the Monterey Bay Aquarium, which were maintained with seasonal, ambient saltwater ($T_{water}=10–14°C$). Nursing pups were fed a formula consisting of Esibilac powder (PetAg Inc., Hampshire, IL, USA), water and surf clam (*Spisula solidissima*). Pups received solid food at 4 weeks and formula was completely deleted from the diet by 8 weeks. Solid diets consisted of whole or partial prey items, including white shrimp (*Litopenaeus setiferus*), surf clam, squid (*Loligo opalescens*), manila clams (*Venerupis philippinarum*), mussels (*Mytilus edulis*) and crabs (*Cancer productus* and *Cancer antennarius*).

Respirometry and metabolic demand
Age-specific energetic demands associated with various behaviors were determined by measuring oxygen consumption of pups throughout development following previously described methods for marine mammals
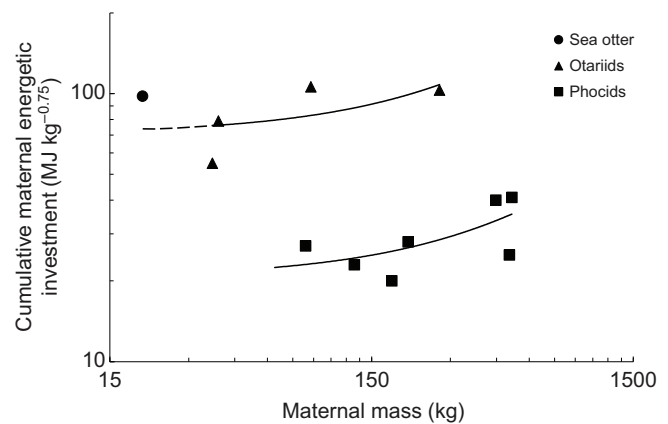
(Williams et al., 2004; Yeates et al., 2007). Pups were fasted an average of 7 h prior to metabolic trials to ensure individuals were in a post-absorptive state (Costa and Kooyman, 1984). Individuals were placed beneath one of two clear acrylic domes to accommodate metabolic measurements in air and in water. A haul-out dome (0.8×0.6×0.3 m, length × width × height) was secured onto a solid wooden base for in-air trials, while a separate dome was attached to a PVC piping frame (1.1×0.8×0.3 m, length × width × height), which allowed it to float on the water surface for in-water trials. Metabolic trials were conducted indoors under seasonal environmental conditions ($T_{air}=14–22°C$; $T_{water}=10–14°C$) that were representative of conditions wild sea otters experience along the central coast of California. Observers monitored trials by a closed circuit video camera and recorded the behavior of animals. Oxygen consumption was determined for three different activity levels: (1) resting, (2) moderately active and (3) highly active. An animal was considered highly active when rapidly moving around the dome during in-air trials or when diving, swimming submerged or rapidly swimming at the surface during in-water trials. Trial length ranged from 30 to 120 min, during which the animal was allowed to rest or move freely. Oxygen consumption was measured continuously. Specific behaviors and associated oxygen consumption rates were considered at a steady state if maintained for a minimum of 5 min.

The rate of oxygen consumption was determined using an open flow respirometry system designed for aquatic mammals (Williams et al., 2004). Air was pulled through the metabolic dome at 30–80 l min^{-1} by a mass flow controller (Flow Kit 500H, Sable Systems, Henderson, NV, USA). The exact flow of air through the dome was dependent on animal mass and was recorded continuously during each trial. Sub-samples of dome exhaust were dried (Drierite, W. A. Hammond Drierite, Xenia, OH, USA), scrubbed of CO_2 (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% by modifying the flow rate to avoid hypoxic conditions. Oxygen content of the dome exhaust was logged every 1.0 s on a laptop computer. Flow rates were corrected to standard temperature and pressure and $\dot{V}_{O_2}$ determined using standard methods (Withers, 1977). $\dot{V}_{O_2}$ for specific behaviors was calculated by dividing the amount of oxygen used while performing a given behavior by its respective duration (DATACAN V Software, Sable Systems). Before each trial the oxygen analysis system was calibrated with dry ambient air (20.94% O_2). The system was calibrated once a week with nitrogen gas (Fedak et al., 1981).

Field studies

Animals

Twenty-six free-ranging sea otters, including dependent young (1–180 days old; n=12) and juvenile individuals (6 months–2.5 years old; n=14), were observed to determine daily activity budgets. Adult females and juvenile sea otters were captured, tagged and implanted with intra-abdominal VHF radio transmitters (7.6×10.2×2.5 cm, 120 g; Advanced Telemetry Systems Inc., Isanti, MN, USA) along the Monterey Peninsula and San Simeon, CA. Dependent young were not implanted with radio transmitters and instead were located using the VHF signal of their mother. Individuals were captured and surgically implanted following standardized procedures (Ames et al., 1986; Monson et al., 2001; Williams and Siniff, 1983). Two colored plastic flipper tags (Temple Tags, Temple, TX, USA) were attached in the webbing of each hind flipper for visual identification in the field (Ames et al., 1986). Dependent and juvenile sea otters were observed along the central coast of California and behavioral data were collected by direct observation utilizing a 50×80 field spotting scope (Questar Inc., New Hope, PA, USA) from shore. By relocating tagged females at frequent intervals, pup date of birth could be determined ±1 day and behavioral data from immature animals could be obtained throughout dependency.

Activity budgets

Daily activity budgets of dependent sea otters were collected from birth until weaning in congruence with an associated study (Staedler, 2011). Instantaneous behaviors (Altmann, 1974) of pups were recorded during daylight hours, twice weekly for 6 h intervals when pups were 0–10 weeks of age and once weekly thereafter until weaning. Six-hour observation intervals took place equally throughout different times of day to cover all daylight hours. Behavior was recorded at 10 min intervals with instantaneous behaviors classified into one of 10 categories: resting on mother or in water, nursing on mother or in water (in which any part of the pup was in water), foraging, being groomed by mother, passive grooming self (slowly rubbing fur while on back), active grooming self (vigorously rubbing fur and somersaulting), swimming, and other (e.g. interacting with conspecifics). Behavior at night could not be directly observed for dependent pups and instead the proportion of behaviors during nighttime hours was assumed to be similar to activity observed during the day. This was a valid assumption because sea otters are cathemeral organisms and rest, forage, groom and perform various other behaviors at regular intervals throughout a 24 h period (Ralls and Siniff, 1990).

For juvenile animals, radio-tagged otters were located opportunistically over the study period for collection of 24 h activity sessions, with one to five sessions recorded for each individual. Behavior was measured using a combination of direct observation and radio telemetry. The temporal pattern of the VHF signal was used to determine behavior following standardized methods (Loughlin, 1980). For example, while an otter was resting at the surface the VHF signal was a constant pulse, while foraging the signal disappeared when the otter was submerged, and during behaviors such as active grooming and swimming the signal became more variable. The instantaneous behavior of a focal animal was recorded at 10 min intervals over the 24 h recording session.

Daily activity budgets for dependent pups and juvenile sea otters were then calculated as the proportion of all records associated with each behavior. Any period when behavior was recorded as 'unidentified' because of poor transmitter signal quality were removed prior to analysis. Thus, the reported activity budgets represent proportions of known activities. To reduce the potential for bias, we limit our analyses to activity sessions where <10% of the intervals were unidentified.

Analysis

Field metabolic rates

FMR values for all five developmental stages were calculated by combining empirically derived age- and behavior-specific metabolic costs with activity budgets of wild sea otters. Each behavior observed in the wild was associated with an activity level (resting, moderately active and highly active) for which $\dot{V}_{O_2}$ had been measured in either air or water. For example, foraging or swimming attempts by pre-molt pups were considered moderately active behaviors, whereas in older age groups, foraging and swimming behaviors were classified as highly active. Passive grooming was considered a

moderately active behavior for all age groups and nursing was associated with RMR. For the majority of behaviors, in-water $\dot{V}_{O_2}$ values were used. However, for any behavior during which a pup would be completely onboard an adult female (e.g. resting on mother), an in-air metabolic value was used. Active grooming could not be empirically measured during respirometry trials; therefore, a $\dot{V}_{O_2}$ value that is 2.2 times the RMR in water was assigned for active grooming behaviors for all age classes based on previously published values for sea otters (Williams, 1989; Yeates et al., 2007). $\dot{V}_{O_2}$ (ml O_2 kg^{-1} min^{-1}) values for each age class and behavior were converted to energetic demand (MJ day^{-1}) using a factor of 20.08 kJ lO_2^{-1} (Schmidt-Nielsen, 1997). The amount of energy required for each behavior was multiplied by the percentage of time an individual in a specific age group spent performing that behavior each day. FMR values were determined by summing the energetic costs of each behavior over a 24 h period. The means, variance and standard deviations of these estimates were determined using standard procedures for calculating point estimates of independent variables (Quinn and Keough, 2003). Daily energetic costs calculated from detailed activity budgets were collapsed into general behavioral categories (resting, nursing, foraging, grooming, swimming and other) for final FMR calculations. Average daily energetic demands of adult female sea otters with and without young were calculated as described above, utilizing previously published activity budgets (Staedler, 2011) and behavior-specific metabolic rates (Williams, 1989) of adult female southern sea otters and assuming an average female body mass of 19.89 kg (Williams, 1989).

Statistical analyses

We evaluated the functional relationship between age- and mass-specific metabolic rates by fitting linear and non-linear functions using maximum likelihood methods. We created separate plots of mass-specific O_2 consumption ($\dot{V}_{O_2}$) versus pup age (in days) for each activity level (resting, moderately active and highly active behavior). We then evaluated three alternative fitted trend lines for each data set: (1) a simple linear regression model, $\dot{V}_{O_2}=a+b\times$age; (2) an exponential model, $\dot{V}_{O_2}=a\times e^{b\times \mathrm{age}}$; and (3) a piecewise linear regression (Toms and Lesperance, 2003), $\dot{V}_{O_2}=a+b\times$age+c×f(age−K), where $f(x)=x$ for $x\geq0$ and $f(x)=0$ for $x<0$, and K is a functional breakpoint or 'knot value' (note that the piecewise regression model can be re-expressed as two simple polynomial functions, one for ages $\leq K$ and another for ages $>K$). We set K equal to 180 days, as this is the average age of weaning when dependent pups transition to the independent juvenile stage (Riedman et al., 1994). We present results for the model having the highest coefficient of determination (R^2) after adjusting for the number of fitted parameters, as measured by the degrees-of-freedom-adjusted R^2, or $\bar{R}^2$ (Ronchetti, 1985). Because of sample size limitations, for this analysis we combined data from both sexes and from in-air and in-water measurements.

Linear mixed-effects models were used to compare mass-specific metabolic rates among developmental stages and activity level, while accounting for non-independence of longitudinal data, random effects because of differences between individual animals, and unequal sample sizes. In-air and in-water metabolic data were analyzed separately owing to differences in the number of developmental stages sampled. For this analysis, developmental stage and activity level were treated as fixed effects and individual differences were treated as random effects. Bonferroni *post hoc* tests were used to identify pairwise differences within fixed effects. The effect of sex could not be tested because of limited sample sizes, and thus data for both sexes were pooled. Linear mixed-effects models were performed using SYSTAT 13 (Systat Software Inc., Richmond, CA, USA). Results are presented as means ± 1 s.d. and were considered significant at $P\leq0.05$.

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