



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: I. Activity budgets of female sea otters and their pups in Simpson Bay, Alaska

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ARTICLE INFO

Article history:

Received 5 February 2015

Received in revised form 19 May 2015

Accepted 21 May 2015

Available online xxxx

Keywords:

Activity budget

Alaska

Enhydra lutris

Maternal care

Pup development

Sea otter

ABSTRACT

Parental care is necessary for the survival of most mammalian offspring. However, this is especially true for neonatal sea otters (*Enhydra lutris*), which are the most altricial of marine mammals born at sea. 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. We studied the behavior of female sea otters and their pups during the first three months postpartum in Simpson Bay, Alaska. Six behaviors for females and seven behaviors for pups were recorded to produce 24-h activity budgets. Pups were classified into three behavioral/size categories: Category 1 (C1) 0–<4 wks old; Category 2 (C2) 4–<8 wks old; Category 3 (C3) 8–12 wks. The percentage of time females spent feeding increased from 9% (C1) to 32% (C3) reflecting the increased nutritional requirements of the maturing pups. C1 females spent 21% of their time swimming in a meandering manner, possibly to protect young pups from predation, which decreased to 8% for females with C3 pups. The time spent resting by females (ca. 50%) was independent of pup category. C1 pups spent 83% of their day resting which decreased to 48% for C3 pups. Time spent nursing remained constant (ca. 8%) for all pup categories, but feeding on solid food provided mainly by the female increased to 17% (C3 pups). The percentage of time that pups spent swimming increased to 17% (C3 pups) as they developed strength and coordination. Our results provide a quantitative picture of the changes in female and pup behavior and activity patterns during the early and critical developmental stages of altricial pups at sea.

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1. Introduction

Parental care is essential for the early survival of most mammalian offspring (Clutton-Brock, 1991). However, this is especially true for neonatal sea otters (*Enhydra lutris*), which are the most altricial of marine mammals born at sea. Sea otter pups are incapable of swimming for the first four to six weeks of life unlike cetaceans (whales and dolphins) and sirenians (manatees and dugongs) that can swim immediately after birth (Hanson et al., 1993; Kenyon, 1969; Payne and Jameson, 1984). As a result, female sea otters must not only feed their pups, but also protect them from drowning, hypothermia and predation while at sea. Female mammals generally spend 80% of their reproductive lifespan caring for young (Gittleman, 1994), while male parental care occurs in fewer than 5% of all mammalian species (Clutton-Brock, 1991). Female sea otters provide continuous care, with no assistance from the male, until the pup is weaned at about six months of age, and this incurs a cost (i.e., increased foraging, reduced body condition, increased vulnerability to predation) in terms of her survival and the

ability to successfully rear future offspring (Monson et al., 2000; Trivers, 1974; Zeveloff and Boyce, 1980).

Most of the mortality of dependent sea otter pups occurs during the first 60 days after birth with an average survival rate of 60% during the first three months (Monnett and Rotterman, 2000; Riedman et al., 1994; Siniff and Ralls, 1991). Factors that affect pup mortality are unclear, but probably include maternal condition, maternal age and/or experience, quality of maternal care, local variation in food supply and/or pollutants, the behavior and density of resident males, and weather (Monnett and Rotterman, 2000). Among mammals, the amount of time and energy that a parent invests differs depending on whether the offspring are altricial or precocial. Altricial offspring are immature, helpless and require postnatal care for an extended period of time as the young develops the skills necessary for survival (Künkele and Trillmich, 1997; Langer, 2008). Most mammals, including sea otters, produce altricial neonates (Derrickson, 1992).

In contrast, most marine mammals and ungulates are precocial and have well developed locomotor and sensory abilities (Derrickson, 1992; Hennemann, 1984). The young are born with a rapid development of inter-individual recognition between the female and the young, which is especially true in gregarious species (Nowak et al.,

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2000). However, dichotomous labeling of the development of neonates is misleading. Instead, it is more realistic to consider offspring development as a continuum (Zeveloff and Boyce, 1980). For example, young may be labeled as an intermediate type whose sensory systems are functional but thermoregulatory capabilities are inefficient, such as pigs, or locomotory capabilities are limited (primates) (Nowak et al., 2000).

Until they are weaned and can survive on their own, there are four major causes of pup mortality that female sea otters must prevent or avoid: drowning, hypothermia, starvation and predation. Many of the behaviors exhibited by females during the early life of their pups are a response to these threats. Unlike most marine mammals that have a blubber layer for insulation in water, sea otters rely on fur for thermal insulation and an elevated resting metabolic rate to maintain a stable core body temperature of ca. 37°C typical of most mammals (Costa, 1982; Costa and Kooyman, 1982; Kenyon, 1969; Williams et al., 1992; Yeates et al., 2007). Grooming the fur is essential for maintaining an air layer adjacent to the skin, which provides 70% of the thermal insulation (Costa and Kooyman, 1982; Davis et al., 1988; Kenyon, 1969; Williams et al., 1992). Despite the critical importance of grooming for thermoregulation, young sea otter pups cannot groom themselves effectively and must rely on the female to groom them during the initial 8–10 weeks after birth (Payne and Jameson, 1984). The combined inabilities of neonatal sea otters to swim and groom, two critical behaviors essential for survival, make them especially vulnerable to drowning and hypothermia and require the female's attention and care until these skills are perfected.

During gestation, the offspring of eutherian marine mammals (there are no metatherian marine mammals) derive all their energy from the female through the placenta, and provisioning continues postpartum during lactation as the energy requirements of the maturing neonate rapidly increase. Weaning marks the final transition from milk to solid food, and it may be abrupt or last months to years (Langer, 2008). In species such as sea otters, the female provides both milk and solid food for the physiologically immature (in terms of diving and foraging ability) and inexperienced young. Hence, the female must forage both for herself and her young until the pup is self-supporting. With an already elevated metabolic rate (resting metabolic rate is 2–3-fold greater than terrestrial mammals of similar size (Costa, 1982; Costa and Kooyman, 1982; Kenyon, 1969; Williams, 1989), the mass specific energetic demand on females is higher than most other mammals, especially just prior to weaning as pups approach a body mass and energy requirement similar to adults (Langer, 2008; Thometz et al., 2014). The female cannot sustain this heavy energetic demand for long periods and must balance the investment in a single offspring to maximize her lifetime reproductive success (Reid et al., 1995).

The activity budgets of lactating female sea otters indicate critical behaviors for successfully rearing pups, whereas the activity budgets of pups indicate the development and acquisition of behaviors and skills critical for survival that are acquired at different stages of maturation up to the time of weaning (Hanson et al., 1993; Monnett and Rotterman, 2000; Payne and Jameson, 1984). Although the general behavior of lactating females and young pups has been described (Hanson et al., 1993; Osterrieder and Davis, 2011; Payne and Jameson, 1984; Thometz et al., 2014), the simultaneous behavior and activity budgets of wild female sea otters and their pups during early maturation have not been thoroughly quantified using direct observation even though they have a critical influence on individual fitness.

Behavioral observations of marine mammal at sea are difficult due to limited accessibility, sea state, natural light levels or the inability to observe them once they submerge (Schofield et al., 2006). For sea otters, some researchers have used abdominally implanted archival recorders and radio transmitters to track animals at sea and record the depth and duration of dives. These devices indicate when the animals are active or inactive, but cannot distinguish the full range of normal behaviors. In contrast, direct observations, when feasible, enable detailed

descriptions of behavior and daily activity patterns which are generally not possible with telemetry (Schofield et al., 2006).

In this study, we observed the behavior of female sea otters and their pups in Alaska. Our null hypothesis was that female behavior and activity patterns did not change as neonatal pups matured. To test this hypothesis, we used direct observation to determine the simultaneous 24-h activity budgets for females and their pups during the first three months postpartum, which represents the first half of the period of pup dependency and the time of greatest mortality (Monnett and Rotterman, 2000). Our results provided new insight into pup maturation and their care and provisioning by the females during the early stages of pup development.

2. Materials and methods

2.1. Study site

Simpson Bay (ca. 60.6° N, 145.9° W), located in northeastern Prince William Sound, Alaska (Fig. 1), was used as the study site because of its protection from rough seas, reliable presence of sea otters and easy access. It is approximately 21 km² 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.

The study area has an average water depth of 30 m (maximum depth of 125 m) and a benthos 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 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 (RW Davis unpublished data). The bay was re-colonized by male sea otters in 1977, and females moved into the area between 1983–85 (Garshelis, 1983; Rotterman and Jackson, 1988; VanBlaricom, 1988). Since 2002, it 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) with 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 disperse is poorly understood (Wolt et al., 2012). This research was conducted under a Letter of Confirmation No. MA-043219 from the U.S. Fish and Wildlife Service.

2.2. Boat-based observations

The behavior of female sea otters with dependent pups was recorded from May to August of 2008–11. The high latitude location of this study made visual observations possible 24-h which were divided into four, 6-h time periods corresponding with astronomical dawn (05:00–11:00), day (11:00–17:00), dusk (17:00–23:00) and night (23:00–05:00). The research team, composed of a driver, recorder and spotter, made observations from a 7-m skiff. To maximize otter encounters, no systematic vessel track was followed. Instead, the skiff approached animals opportunistically on search paths that minimized the possibility of encountering an otter more than once during a 3–4 h session. However, the females were not tagged, so we could not be certain whether they were observed on subsequent days. 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 10–22x) without disturbing them. The behaviors of the female and pup were recorded simultaneously once per minute for 30 min (i.e., instantaneous focal follow; Altmann, 1974) before moving to another female and pup. If a female was disturbed, the observation was terminated and not included in the analysis.

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) (Fig. 2; Table 1; Osterrieder and

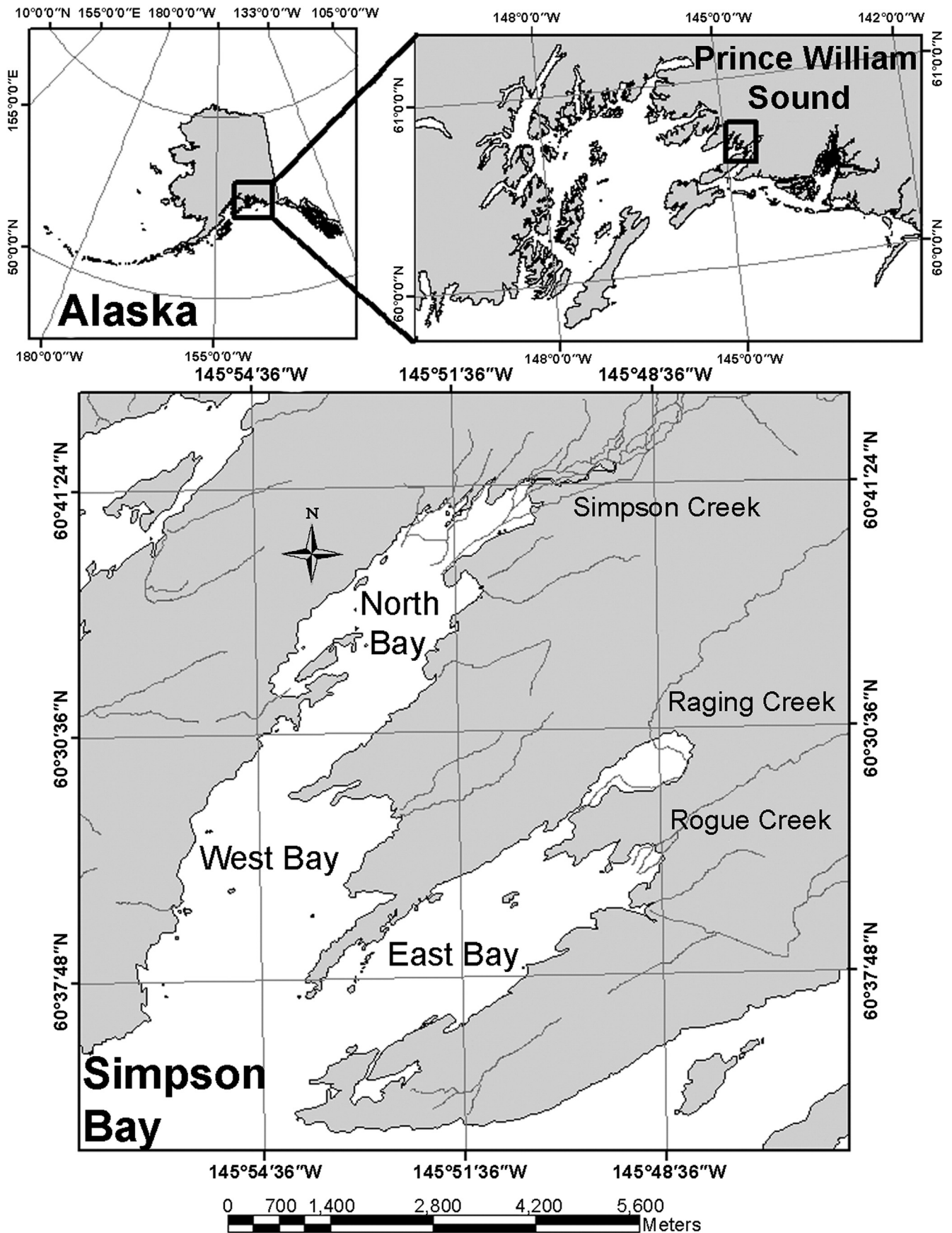


Fig. 1. Simpson Bay, Prince William Sound, Alaska (Wolt et al., 2012). X's denote shore-based observation stations.



Fig. 2. Pup Categories: (A) Category 1; (B) Category 2; (C) Category 3.

Davis, 2009, 2011; Payne and Jameson, 1984). Category 1 pups (C1; ca. 0 – <4 wks in age) were incapable of swimming or grooming and had a dense natal fur (i.e., lanugo). Category 2 pups (C2; ca. 4 – <8 wks in age) exhibited coordinated swimming (but no diving or complex grooming behavior), had begun to molt their lanugo, and were about half the female's body length. Category 3 pups (C3; ca. 8–12 wks in age) exhibited coordinated swimming and grooming, made short, shallow dives, had molted into their adult pelage and were almost the same size as the female. The term C1, C2 or C3 female refers to a female with a C1, C2 or C3 pup, respectively.

Six behaviors were recorded for the female (resting, swimming, feeding, pup-grooming, self-grooming, interacting), and seven behaviors were recorded for the pup (resting, swimming, feeding, nursing, self-grooming, being groomed, interacting) (Table 2). In this study, the term swimming for the female and older pups generally meant the animal was floating supine (on its back) at the surface using alternate pelvic paddling. Swimming for the C2 pups generally meant swimming prone (belly down), which differs from subsurface swimming during

Table 2
Description of female and pup behavioral states.

Activity	Female	Pup
Foraging for the female, feeding for the pup	Foraging dives to the benthos using simultaneous pelvic paddling to acquire food, handling/ingesting prey; includes dives and interdiver intervals	Handling/ingesting captured prey or begging/stealing prey from the female
Nursing	Only recorded for pup	Pup suckling while laying on the female's abdomen or along side
Self-Grooming	Vigorous rubbing, licking, aerating own fur	Vigorous rubbing, licking, aerating own fur
Being Groomed	Only recorded for pup	Female vigorously rubbing, licking and aerating the pup's fur
Pup-Grooming	Mother vigorously rubbing, licking and aerating the pup's fur	Only recorded for female
Interacting	Interacting with any otter including the pup; Can be social or reproductive	Interacting with any otter including the female and other pups
Swimming	Generally occurs at the surface, floating belly up and using alternate pelvic paddling but sometimes submerged using simultaneous pelvic paddling	Generally occurs at the surface, paddling belly down; Older pups begin using alternate pelvic paddling; Occasionally submerged swimming using simultaneous pelvic paddling
Resting	Floating belly up motionless or with slight movement of forepaws, head or feet; hauled out; sleeping	Laying on females' abdomen; floating belly up motionless or with slight movement of forepaws, head or feet; hauled out; sleeping

foraging when simultaneous pelvic paddling is used (Fish, 1996). For pups, the term feeding generally meant eating prey that was provided by the female, but included limited foraging for shallow prey items by C3 pups. Nursing was not recorded for the females as it occurred while the female was resting, swimming or pup grooming. Being groomed was used when the female groomed a pup that was not nursing. Time, tidal state, weather, water depth, and GPS location were also recorded for each focal follow.

2.3. Shore-based observations

Because of the dense forest that surrounds Simpson Bay, shore-based observations of sea otter behavior are very difficult. In contrast, this is the preferred method for sea otter behavioral research in other areas (e.g., California) because of the high-energy (i.e., large ocean swell) coastline that makes boat-based observations logistically difficult and the accessibility to higher open vantage points (Estes et al., 1982, 1986; Ralls and Siniff, 1990). To compare results for these two observational methods, we also recorded the behavior of females and their pups from observations made at five shore locations (Fig. 1) from May to August in 2010–11. These observations were performed during dawn (05:00–11:00), day (11:00–17:00) and dusk (17:00–23:00). Because higher light levels are needed for observing from shore through a telescope, no observations were performed at night. The research

Table 1
Behavioral and size class characteristics for pup categories (Adapted from Osterrieder and Davis, 2011).

	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	50–75%	Begins molting natal fur
Category 3	8–12	Swims and makes shallow dives ^a	>75%	Molt complete with adult pelage

^a Dives longer than 30 sec.

team, composed of a spotter and recorder, made observations from alternating shore-based stations. Females and pups were observed opportunistically using a 50 – 80x telescope (Questar Corp., New Hope, Pa.). The behaviors of the female and pup were recorded simultaneously once per minute for four hours (i.e., instantaneous focal follow; Altmann, 1974) in a manner similar to the boat-based observations. Time, tidal state, weather, water depth, and GPS location were also recorded for each focal follow. If visual contact with a female was lost during the four hour period, the observations were not used in the analysis.

2.4. Data analyses

The percentage of time spent in each behavior recorded from boat-based observations was summed for each 6-h time period and for 24-h to make activity budgets for females and pups. The percentage of time spent in each behavior recorded from shore-based observations was also summed separately to compile a dawn to dusk activity budget. Multivariate analysis of covariance (MANCOVA) was used to test for correlations between female and pup behavior (the dependent variables) due to time of day and pup category (the independent variable) with year as a covariate to remove the influence of year if it was found to be significant using SPSS (Version 15 statistical software, Chicago, IL) at $\alpha = 0.05$. The mean time spent among the female and pup's behaviors for each category was tested using Tukey HSD post hoc tests. A MANCOVA was also used to test for differences between the boat and shore-based methods among dawn, day and dusk activity budgets also with year as a covariate to remove the influence of year if it was found to be significant. However due to a smaller sample size (fewer observations in only three time periods), category was excluded from the analysis to reduce the number of dependent variables, so the boat-based observations from all categories (C1–C3) were combined for this analysis. The shore-based observations were also subdivided into thirty minute samples for analysis.

3. Results

3.1. Boat-based observations

In total, the behavior of 685 female-pup pairs (30 min periods) was recorded totaling 20,550 min. The percentages of observation time were similar (25–27%) among dawn, day and dusk, but slightly lower (21%) at night (Table 3). There were similar percentages of observation time for C1 and C3 pups (24% and 28%, respectively), but nearly twice as much (48%) for C2 pups. Sea otter pup births peak in the late spring and summer, which coincides with our field season. However, the amount of time pups spent in the C1 category is shorter than for C2 and C3. Our field season also ended before pups born later in mid-summer could reach the C3 category. Therefore, the pups were predominantly C2, which explains the distribution of the three categories.

3.1.1. Females

A one-way MANCOVA revealed a significant multivariate main effect for pup category (Wilks' $\lambda = 0.645$, $F(26, 1316) = 12.384$, $P < 0.0001$). Over a 24-h period, the percentages of time devoted to swimming ($F(2,671) = 12.986$, $P < 0.0001$), feeding ($F(2,671) =$

Table 4

Activity budgets for female sea otters with different pup categories in Simpson Bay, Alaska.

Behavior	Percentage of 24-hr Period		
	Category 1	Category 2	Category 3
Resting ^a	50 ^b	52 ^b	46 ^b
Swimming ^a	21 ^b	16 ^c	8 ^d
Feeding ^a	9 ^b	13 ^b	32 ^c
Pup Grooming ^a	13 ^b	10 ^b	4 ^c
Self-Grooming	6 ^b	7 ^b	5 ^b
Interacting ^a	0 ^b	1 ^b	5 ^c

Each asterisk indicates a significant difference at the $\alpha = 0.05$ level.

^a Standard Deviations: Resting: 0.376; Swimming: 0.21; Feeding: 0.331; Pup Grooming: 0.149; Self-Grooming: 0.112; Interacting: 0.062.

^{b, c, d} Categories with differing letters were statistically significant ($\alpha = 0.05$) for each behavior.

24.894, $P < 0.0001$), pup grooming ($F(2,671) = 15.851$, $P < 0.0001$) and interacting ($F(2,671) = 28.749$, $P < 0.0001$) were all significantly different among females with different category pups (Table 4). Females with C1 pups spent most of the day resting (50%; 12.29 h), which occurred in similar amounts throughout the day (Fig. 3; Fig. 4A). Swimming (21%; 4.94 h) occurred primarily during day, dusk and night (92%). Grooming their pup (13%; 3.15 h) occurred primarily during the dawn and dusk (59%), and self-grooming (6%; 1.57 h) occurred primarily during dawn (37%). Remarkably, the percentage of time devoted to feeding was only 9% (1.98 h) and occurred primarily during the day, dusk and night (85%).

Females with C2 pups also spent most of the day resting (52%; 12.57 h). Swimming decreased (16%; 3.82 h) and occurred primarily during day, dusk and night (86%). Pup grooming also decreased (10%; 2.46 h), while self-grooming slightly increased (7%; 1.67 h). However, the amount of time spent feeding increased 1.6-fold (13%; 3.19 h) and now occurred during dawn, day and dusk (78%) (Fig. 4B). The time spent interacting slightly increased (1%; 0.29 h).

In contrast, females with C3 pups spent less time resting (46%; 11.11 h) (Fig. 4C). Swimming continued to decrease (8%; 2.19 h) and occurred primarily during day and night (67%). Pup grooming continued to decrease (4%; 1.08 h) and occurred primarily during dusk and night (76%). The amount of time spent feeding increased 2.3-fold (32%; 7.24 h) and was now heavily concentrated during the day (40%) with the remainder primarily during dawn and dusk (49%). The remainder of the day spent self-grooming (5%; 1.31 h), and interacting increased 3.7-fold (5%; 1.08 h) and was concentrated during the day (33%) with the remainder primarily during dusk and night (51%).

The C1 and C2 females groomed their pups significantly more and foraged less than the C3 females. C1 and C2 females also interacted significantly less with other otters than the C3 females.

3.1.2. Pups

Over a 24-h period, the percentage of time resting ($F(2,671) = 52.035$, $P < 0.0001$), feeding ($F(2,671) = 51.420$, $P < 0.0001$), swimming ($F(2, 671) = 29.284$, $P < 0.0001$), self-grooming ($F(2,671) = 9.538$, $P < 0.0001$), being groomed ($F(2,671) = 14.220$, $P < 0.0001$) and interacting ($F(2,671) = 21.742$, $P < 0.0001$) were all significantly different among categories (Table 5; Fig. 5). C1 pups spent most of the day resting (83%; 19.74 h) (Fig. 6A). Nursing (7%; 1.80 h) occurred primarily during dusk and night (58%), and being groomed (9%; 2.24 h) occurred mainly during dawn and dusk (66%). Older C1 pups spent little time attempting to swim (<1%).

C2 pups also spent most of the 24-h period resting (73%; 17.45 h), being groomed (7%; 1.67 h) and nursing (8%; 1.99 h) (Fig. 6B). However, these pups spent part of the 24-h period in new behaviors, such as swimming, which increased from <1% to 7% (1.67 h) and attempted self-grooming (2%; 0.43 h). C2 pups began feeding on solid food provided by the female (2%; 0.40 h), which occurred primarily during the day

Table 3

Total females with pups observed from June–August of 2008–2011 in Simpson Bay, Alaska subdivided into 6-h time periods and pup categories.

Pup Category	Dawn	Diel Period Day	Dusk	Night	Total
1	33	52	44	38	167
2	83	78	87	78	324
3	57	55	54	26	192
Total	173	185	185	142	685

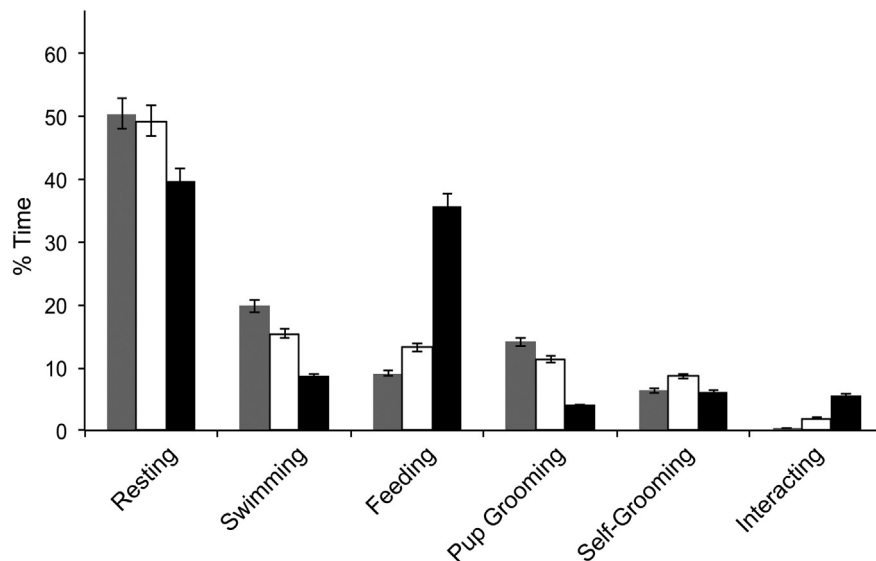


Fig. 3. Comparison of female 24-h activity budgets in Simpson Bay, Alaska from 2008–2011 subdivided by pup category. Gray: Category 1; White: Category 2; Black: Category 3. The error bars represent 0.05% error.

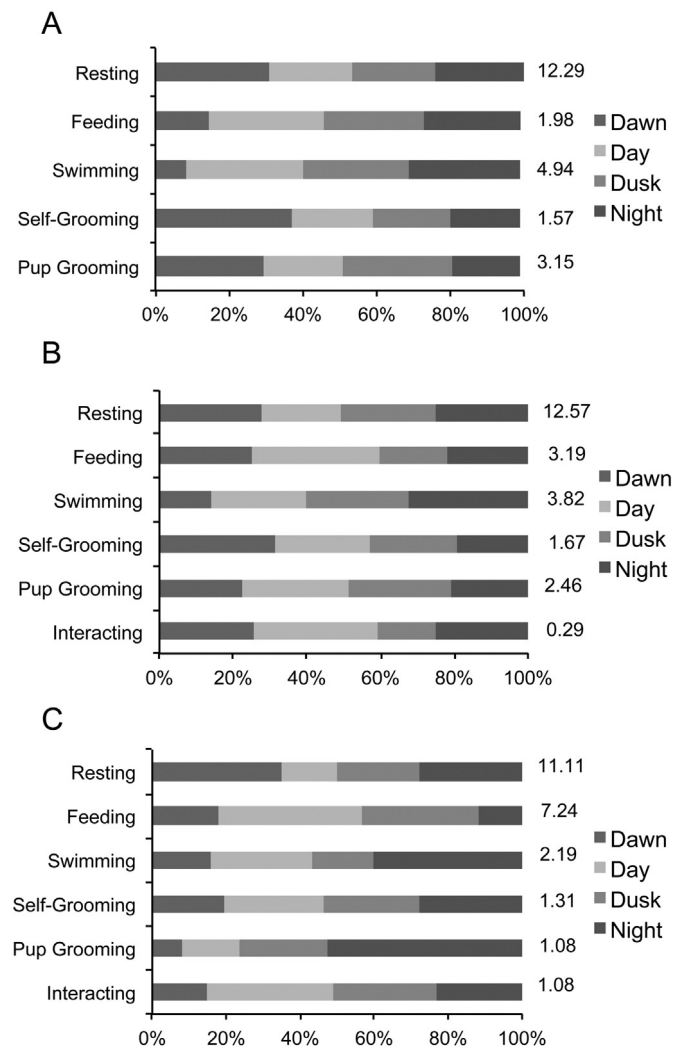


Fig. 4. Female behavior as a function of time period: (A) Category 1 Female; (B) Category 2 Female; (C) Category 3 Female. The number of hours spent in each behavior is shown at the end of each bar.

(60%). C2 pups also began to interact with other otters including the female (2%; 0.39 h), which occurred primarily during dawn and day (69%).

C3 pups spent only 48% of the 24-h period resting (11.85 h), which was comparable to the female (Fig. 6C). Feeding on solid food increased 9.6-fold (17%; 3.83 h) and occurred primarily during the day and dusk (77%) similar to the female. The percentage of time swimming increased (17%; 3.92 h) and occurred primarily during dawn and day (63%). Nursing (7%; 1.65 h) also decreased and occurred primarily during dusk and night (59%), but was still similar to the other pups. Being groomed showed little change (2%; 0.69 h) and occurred primarily at dusk and night (76%). Self-grooming also increased 1.7-fold (3%; 0.73 h), which occurred primarily during the day and night (69%). Interacting increased 3.4-fold (1.32 h) to 6% of their day.

3.2. Shore-based observations

The behavior of 22 females with pups was recorded totaling 5,280 min using the shore-based method. There were no significant differences in the percentages of time that females spent feeding ($F(1,713) = 0.008$, $P = 0.929$) and interacting ($F(1,713) = 0.368$, $P = 0.545$) between the boat-based and shore-based methods (Table 6). There were small increases in the percentages of time that females spent swimming (14% to 20%) that were statistically significant ($F(1,713) = 5.628$, $P = 0.018$). The amount of time the females spent

Table 5

Activity budgets for different pup categories in Simpson Bay, Alaska.

Behavior	Percentage of 24-h Period		
	Category 1	Category 2	Category 3
Resting ^a *	83 ^b	73 ^b	48 ^c
Swimming *	0 ^b	7 ^b	17 ^c
Feeding *	0 ^b	2 ^b	17 ^c
Nursing	7 ^b	8 ^b	7 ^b
Self-Grooming *	0 ^b	2 ^b	3 ^c
Being Groomed *	9 ^b	7 ^b	2 ^c
Interacting *	0 ^b	2 ^b	6 ^c

Each asterisk indicates a significant difference at the $\alpha = 0.05$ level.

^a Standard Deviations: Resting: 0.336; Swimming: 0.199; Feeding: 0.195; Nursing: 0.129; Self-Grooming: 0.047; Being Groomed: 0.126; Interacting: 0.083.

^{b, c} Categories with differing letters were statistically significant ($\alpha = 0.05$) for each behavior.

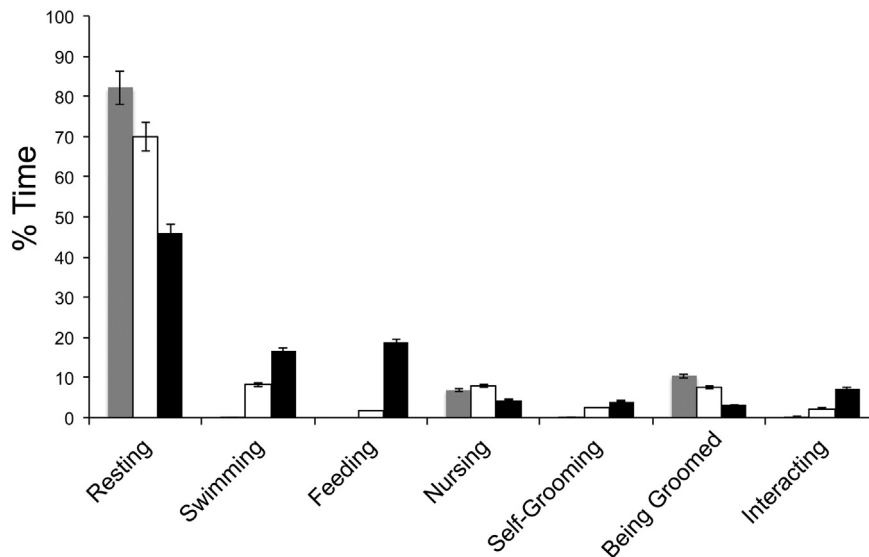


Fig. 5. Comparison of pup 24-h activity budgets in Simpson Bay, Alaska subdivided into categories. Gray: Category 1 Pup; White: Category 2 Pup; Black: Category 3 Pup. The error bars represent 0.05% error.

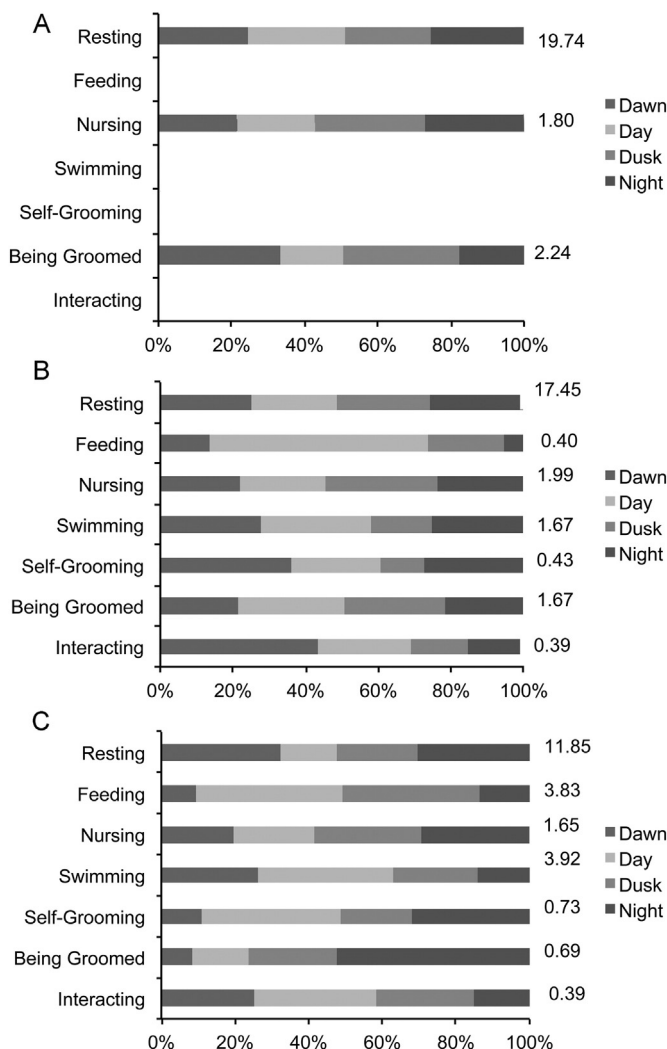


Fig. 6. Pup behavior as a function of time period: (A) C1 Pup; (B) C2 Pup; (C) C3 Pup. The number of hours spent in each behavior is shown at the end of each bar.

self-grooming was similar, yet these percentages of time were statistically significant ($F(1,713) = 10.43, P = 0.002$). Pup grooming increased slightly (9% to 12%) ($F(1,713) = 6.321, P = 0.012$) and resting also slightly decreased (50 to 42%) ($F(1,713) = 6.664, P = 0.012$) using the shore-based method as compared to the boat-based method.

There were no significant differences in the percentages of time that pups spent resting ($F(1,713) = 1.048, P = 0.306$), swimming ($F(1,713) = 0.688, P = 0.407$), feeding ($F(1,713) = 0.533, P = .466$), being groomed ($F(1,713) = 2.374, P = 0.124$), and interacting ($F(1,713) = 1.369, P = 0.242$) between the boat-based and shore-based methods (Table 7). There was a slight decrease in the time spent nursing (8% to 5%) ($F(1,713) = 7.177, P = 0.0008$) using the shore-based method and an increase in the amount of time the pup spent self-grooming (2% to 7%) ($F(1,713) = 9.424, P = 0.002$). Overall, none of the differences in female and pup activity budgets was indicative of behavioral disturbance associated with using the boat-based method.

4. Discussion

4.1. Behaviors and activities critical for pup survival

After birth, the neonate must readjust to extrauterine life (e.g., nursing), which is crucial for survival (Jørgensen et al., 2001). The female cares for her young through this adjustment until weaning. Weaning periods in mammals vary dramatically from the 3–5 day

Table 6
Comparison of female 24-h activity budgets for boat-based and shore-based methods.

Behavior	Percentage of 24-hr Period	
	Boat-Based Methods	Shore-Based Methods
Resting	50	42 ^a
Swimming	14	20 [*]
Feeding	19	19
Pup Grooming	9	12 [*]
Self-Grooming	7	7 [*]
Interacting	2	0

Each asterisk indicates a significant difference at the $\alpha = 0.05$ level.

^a Standard Deviations: Resting: 0.368; Swimming: 0.313; Feeding: 0.339; Self-Grooming: 0.131; Pup Grooming: 0.172; Interacting: 0.013.

Table 7
Comparison of pup 24-h activity budgets for boat and shore-based methods.

Behavior	Percentage of 24-hr Period	
	Boat-Based Methods	Shore-Based Methods
Resting	66	64 ^a
Swimming	9	9
Feeding	6	12
Nursing	8	5*
Self-Grooming	2	7*
Being Groomed	6	0
Interacting	3	2

Each asterisk indicates a significant difference at the $\alpha = 0.05$ level.

^a Standard Deviations: Resting: 0.357; Swimming: 0.209; Feeding: 0.195; Nursing: 0.200; Self-Grooming: 0.083; Being Groomed: 0.119; Interacting: 0.021.

lactation period in hooded seals (*Cystophora cristata*) to over 900 days in chimpanzees and orangutans (Hayssen, 1993). In our study area, the average duration of pup dependency is 5.7 months (Monnett and Rotterman, 2000). As pups mature and develop their own survival behaviors or abilities, the activity budgets of females also change. Hence, the behavior of the females and young pups are complementary (i.e., combining in such a way as to enhance pup survival) but constantly changing as pups mature towards weaning and independence.

4.1.1. Drowning

Despite all the adaptations that marine mammals exhibit for living at sea, they never reacquired the ability to breathe water and are therefore susceptible to drowning. Most pinniped pups are precocial at birth and have the advantage of being terrestrial (or on ice) after birth until weaning (Ellis et al., 2000; Horning and Trillmich, 1997). However, neonatal sea otters are born on the surface of the ocean and cannot swim making them highly susceptible to drowning. In captivity, observations of sea otter pups have demonstrated that newborns sink shortly after death (Sherrod et al., 1975). Adult sea otters are excellent swimmers that use alternate or simultaneous strokes of the hind-paws (alternate and simultaneous pelvic paddling) for propulsion at the surface in a supine position and simultaneous strokes underwater or at the surface in a prone position (Fish, 1996; Williams, 1989). In addition, they also have a lung volume that is substantially larger than a terrestrial mammal of similar size, which makes them positively buoyant and enables them to rest and sleep effortlessly at the surface (Lenfant et al., 1970). As a result, the female carries the neonatal pup on her abdomen as she swims or rests at the surface, in essence serving as a moving island in the ocean.

While the female is making feeding dives, she leaves the pup floating at the surface. The pup's lanugo (i.e., neonatal fur) traps a layer of air next to the skin and makes the pup positively buoyant so that it can rest effortlessly at the surface. In our study, C1 pups, which were incapable of swimming, were the most susceptible to drowning even with their lanugo, so the females spent most (91%) of their time at the surface caring for the pups and only 9% of their time making feeding dives. More mature C2 and C3 pups developed coordination and muscular strength for swimming (about 4 weeks for surface swimming and about 6 weeks for diving) (Kenyon, 1969; Payne and Jameson, 1984), and this enabled females to spend less time carrying their pups and devote more time to other behaviors such as feeding.

4.1.2. Hypothermia

Water conducts heat 25-fold faster than air, which makes sea otters susceptible to hypothermia in the cool waters of the North Pacific. Sea otters rely on fur that traps an air layer next to the skin and provides 70% of the thermal insulation (Costa and Kooyman, 1982; Davis et al., 1988; Kenyon, 1969; Williams et al., 1992). In contrast, most marine mammals rely on blubber for thermal insulation, so grooming is not required. When a sea otter is born on the surface of the water, its fur is wet and provides little thermal insulation. Since neonatal sea otters

are unable to groom their fur, the female grooms the pup to establish this thermal insulating air layer.

As with sea otter pups, Northern fur seal pups (*Callorhinus ursinus*) are born with a natal fur that allows water to penetrate to the skin thereby providing littler thermal insulation when wetted. However, they rarely enter the ocean and spend most of their time on land until they molt into their adult pelage which traps air next to the skin and enables them to thermoregulate in water (Donohue et al., 2000). Likewise, altricial neonatal polar bears also have a fine hair coat and no subcutaneous fat for thermoregulation in water until they molt into their adult pelage, which improves thermoregulation in air and water (Kenny and Bickel, 2005).

Female sea otters rarely leave their pups on land, so neonatal pups must have waterproof fur for thermal insulation at birth. As pups develop the gradual ability to self-groom, pup grooming by the female decreased. Hence, the total time devoted to pup grooming (provided by the female and the pup) dropped from 13 to 7% as the pup matured. The decrease in total time devoted to grooming in C3 pups coincided with the molt of their lanugo and its replacement with adult fur. It appears that neonatal lanugo, which is longer than adult fur, may require additional grooming for it to retain an insulating air layer, and this grooming requirement decreases to about 7% of the activity budget for adults and pups that have molted into their adult fur.

4.1.3. Starvation

Without a thick blubber layer as an energy reserve, sea otters must forage daily throughout the year and are susceptible to rapid starvation (i.e., loss of muscle mass as the body breaks down these tissues for energy) if feeding is interrupted (Costa and Kooyman, 1982; Davis et al., 1988). Since young pups cannot forage for themselves, they depend on the female for milk and, as they mature, on solid food provided by the female (Payne and Jameson, 1984). Starvation is the greatest cause of pup mortality in pinnipeds (Mattlin, 1978). Female phocid seals typically have a shorter period of pup dependency because they fast (or greatly reduce food intake) throughout lactation (Boness and Bowen, 1996). They rely on energy stored as blubber for milk production and to satisfy their own metabolic requirements. In contrast, female otariids fast for the first week postpartum, but then make repeated foraging trips to obtain sufficient energy for themselves and lactation costs (Boness and Bowen, 1996; Bowen, 1991). As the pups grow, otariid females lengthen their foraging trips to obtain additional energy until the pups are finally weaned (Boness and Bowen, 1996).

Sea otter females are comparable to the otariid females, because they feed throughout the period of pup dependency. C1 pups obtained all of their nourishment from nursing. It is unclear how females with C1 pups were able to support both their own metabolic requirements and those of the pup when they spent only 9% of their time foraging during the first two weeks postpartum. Pregnant females may develop some subcutaneous fat in the dorsal caudal area (R.W. Davis unpublished data), mesenteric and renal fat around the small intestines and kidneys, respectively, or in the inguinal area (V.A. Gill unpublished data). This may allow females to reduce foraging without entering a state of starvation and devote more time to caring for their pup during the critical first two weeks when the neonate is very vulnerable to hypothermia and predation. However, additional research is needed to understand how the females balance their energy requirements and those of the pup during this period of complete neonatal dependency.

As the pups matured and their energy needs increased, females increased foraging effort to feed themselves and their pups, which is similar to otariid females (Boness and Bowen, 1996). Even with an increase in solid food provided by the female, the percentage of the time that the pups spent nursing remained constant (7–8%). Milk yield in mammals rises until peak lactation is reached, after which there is a decline in yield until weaning (Blaxter, 1989). Even with similar nursing percentages, the amount of milk consumed by C2 and C3 pups was probably greater due to their larger stomachs and their

increase in efficiency at ingesting more milk (Blaxter, 1989). At peak lactation, part of the additional energy requirements of the growing pups comes from the ingestion of solid food provided primarily by the female. Even though the percentage of time that sea otters spend foraging can be as high as 50% (Finerty et al., 2009; Gelatt et al., 2002; Thometz et al., 2014), the heavy energetic demand placed on the female by her own elevated metabolic rate and that of the pup, especially as pups approach a body mass and energy requirement similar to adults, cannot be sustained indefinitely and is probably ameliorated as the pup begins to forage on its own.

4.1.4. Predation

Sea otters are susceptible to predation by killer whales and sharks (Estes et al., 1998; Kreuder et al., 2003). Bald eagles, which are common around Simpson Bay, are also known to prey on very young sea otter pups left alone on the surface while females forage (Anthony et al., 2008; Sherrod et al., 1975). In Amchitka, Alaska females with pups less than three weeks of age decrease their foraging time from ca. 43% to 21% and forage more at night due to potential risk of bald eagle predation (Gelatt et al., 2002). C1 females in Simpson Bay spent about 21% of their time 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. We can only speculate on the reason for this behavior, but it may be related to predator avoidance. By reducing the time that newborn pups are left unattended at the surface and by moving around the study area, females may be engaging in predator avoidance. Vigilance, which is the awareness by females for any threat to the survival of their offspring, has been documented in other marine mammals including bottlenose dolphins (Hill et al., 2008). Meandering swimming decreased for C2 and C3 females as the pups grew and the potential threat of bald eagle predation diminished.

4.2. Other behaviors and activities

4.2.1. Interacting

Interacting is a behavioral category that includes different types of social behavior. For adult females, it often means mating attempts by males. These interactions are short in duration and devoid of any copulatory behavior at the surface, which makes impregnation unlikely. For pups, this category includes female-neonate interactions and eventually interactions with other sea otters. Females with C1 pups completely avoided interactions with other otters, but females with more mature pups spent more time interacting with their pups and other otters. C1 pups were incapable of interactive behavior that we could discern. However, C2 and C3 pups were noticeably more social and interacted at the surface with other otters while the female was foraging (M. Cortez unpublished data). Females with C3 pups often allowed more separation between themselves and their pups than C1 females. The pup would often approach other rafts and disturb resting sea otters.

Play behavior is important in different species because it promotes physical conditioning, socialization, sensorimotor/cognitive skills and development of foraging skills (Bekoff, 1989; Carss, 1995). In addition, early play behavior may strengthen and maintain social bonds formed between the young and adults (Bekoff, 1989). Play behavior is commonly seen in other otter species. About 30% of the daily activity of the juvenile giant river otter (*Pteronura brasiliensis*) is associated with play and is even seen 7 to 12% of the time in the adult's activity budget as well (Londoño and Muñoz, 2006). In immature river otters, play accounted for 6% of their daily activity, which was associated with wrestling and chasing other river otters along with playing with prey (Melquist and Hornocker, 1983). Play behavior is common among other marine mammal neonates, such as chasing, displaying and object carrying (Mann and Smuts, 1999). In Galápagos fur seal pups, play behavior includes mock fighting, chasing, exhaling in water, chewing on

inanimate objects, and wiggling (Arnold and Trillmich, 1985). It is difficult to interpret the importance or significance of play behavior, but it is common to many young mammals including sea otter pups.

4.3. Differences between boat-based and shore-based activity budgets

Simpson Bay is surrounded by a temperate rainforest with only a few vantage points for making shore-based observations of sea otters. In addition, this method is very light limited because of the greater distance between the observer and the otter. In this regard, boat-based observations have the advantage in being more flexible in locating and following otters and making observations under lower light conditions. However, the question arises as to whether boat-based observations alter the behavior of sea otters, most probably as a function of the proximity between the boat and the animal. In this study, we maintained a distance of at least 100 m while observing sea otters from a skiff. Since otters could be seen from a distance of many hundreds of meters, we could determine their behavior before we approached them in the skiff. Based on behavior before and after the skiff was positioned 100 m from the otter, we are convinced that this method does not alter the animal's behavior. We tested this assertion by conducting shore-based observations using methods and a telescope that were identical to those used in similar studies of sea otters in California (Estes et al., 1982, 1986; Ralls and Siniff, 1990) and found only minor differences that were statistically significant. Furthermore, the boat-based method provided more detailed behavior observations and could be used under lower light levels that enabled 24-hr activity budgets.

Direct observations contribute important information for understanding the development of pup behavior that cannot be obtained by telemetry. Information about behavioral interactions between the pups and females or other otters is essential to understanding how the surrounding community is affected (Schofield et al., 2006). Using these recorded observations, a wider range of behaviors can be analyzed (Schofield et al., 2006). Direct behavioral studies are essential for examining ontogenetic patterns and how they influence neonatal survival (Bekoff, 1989).

5. Conclusion

Many of the behaviors exhibited by females during the early life of their pups are a response to threats to survival. As pups mature and develop their own survival behaviors or abilities, the activity budget of females also changes. C1 pups, being the most susceptible to drowning, were only left unattended 9% of their time. Females also had to maintain the thermoregulatory properties of the pup's fur. This declined in C2 and C3 pups as they began to develop the coordination to self-groom. Although pups with lanugo may require additional grooming, adult sea otters and pups that have molted into their adult fur groom about 7% of the day. The percentage of the time that all pups spent nursing remained constant at 7–8%. Although C1 pups obtained all of their nourishment from nursing, the additional energy requirement of older pups came from feeding on solid food provided primarily by the female. Overall, there were only minor differences in recorded behavior of females and pups between boat-based observations from a distance of 100 m and shore-based observations with a telescope. How females with C1 pups could support both their own metabolic requirements and those of the pup when they spent only 9% of their time foraging and why they spent 21% of their time meandering swimming are questions for further consideration. Further research is also needed on the activity budgets of females and pups during the autumn and winter, which is the most energetically demanding time for females as pups approach weaning and weather conditions become much colder.

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.

Conflict of Interest

The authors declare that they have no conflict of interest.

Acknowledgments

We thank I. Davis, K. McGovern, L. Timm and the TAMUG students for help in collecting data. Thank you to F. Weltz and G. Davis for their logistical support, and Texas A&M University for financial support. This work was supported by Texas A&M University. This research was conducted under a Letter of Confirmation No. MA-043219 from the U.S. Fish and Wildlife Service. [SS]

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