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Summer activity pattern and Field Metabolic Rate of adult male sea otters (*Enhydra lutris*) in a soft sediment habitat in Alaska

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A B S T R A C T

Individual follows and instantaneous sampling were used to examine the behavior of adult male sea otters (*Enhydra lutris*) in Simpson Bay, Prince William Sound, Alaska, during the summer (May to August) of 2005 and 2006. Six behaviors (foraging, grooming, interacting with other otters, patrolling, resting, and swimming at the surface) were observed during four time periods (dawn, day, dusk, and night) to create 24-h activity budgets. Adult male sea otters were observed during 190 focal follows, representing 98 h of observation. Male otters allocated 27% of their time (over a 24-h period) to resting, 26% to swimming, 19% to grooming, 14% foraging, 9% to patrolling and 5% to interacting with other otters. Field Metabolic Rate (FMR) was estimated by combining the energetic costs for foraging, grooming, resting, and swimming behavior of captive otters from Yeates et al. (2007) with our activity budgets. Our study considered 'patrolling' to be energetically similar to 'swimming' and therefore the two categories were combined. This combined category accounted for the greatest percentage (43%) of energy expended each day followed by grooming (23%), resting (15%), feeding (13%) and other (5%). The estimated weight specific FMR for all activities was 686.7 kJ day^{-1} kg^{-1} and the total FMR was 19.04 MJ day^{-1}. The FMR was 6.6 times the resting metabolic rate and 2.2 times greater than the allometric prediction for terrestrial mammals of similar size but similar to other marine mammals. With a peak summer sea otter density in 5.6 otters km^{-2}, the low percentage of time spent foraging (even after correction for possible sampling biases) indicates that Simpson Bay is still below equilibrium density.

1. Introduction

One of the earliest descriptions of male sea otter behavior in Alaska was by Kenyon (1969). He described territoriality as being weakly expressed in sea otters, but later studies showed territoriality to be a prominent behavior in adult males. Studies of territorial male sea otter behavior have since been conducted in California (Vandevere, 1970; Loughlin, 1980; Jameson, 1989; Ralls and Siniff, 1990), and Alaska (Calkins and Lent, 1975; Garshelis et al., 1986; Gelatt et al., 2002; Pearson and Davis, 2005; Bodkin et al., 2007). Sea otters are sexually segregated when not breeding (Garshelis et al., 1984; Riedman and Estes, 1990). In expanding populations, male sea otters are the first to explore new, prey-rich areas (Garshelis et al., 1984). Prior to their protection under the International Fur Seal Treaty in 1911, the sea otter population in Prince William Sound (PWS), Alaska, had been reduced by commercial hunting. Currently, the population of sea otters in PWS is listed as stable or increasing under the Endangered Species Act (Fish and Wildlife Service, 2005). Male sea otters began to re-inhabit eastern PWS in the late 1970s. Simpson Bay remained a male area until the 1980s (Garshelis et al., 1984, 1986), but is now used by territorial males and females with pups (Gilkenson, 2004; Pearson et al., 2006).

In Alaska, adult males establish territories during the summer and autumn (Pearson and Davis, 2005). Males enter areas preferred by females and establish resource-based breeding territories during non-winter months (Garshelis et al., 1984; Jameson, 1989; Pearson et al., 2006). The peak of breeding occurs during the autumn in PWS, although evidence of copulations has been reported for all seasons (Garshelis et al., 1984).

Maintaining a territory can be energetically expensive for males (Kodric-Brown and Brown, 1978; Pearson et al., 2006) and may have negative consequences including: 1) decreased time available for foraging and resting, 2) increased energy expenditure due to courtship, mating and defense activities (e.g., patrolling boundaries) and 3) risk of injury or death due to agonistic encounters with conspecifics and predation (Clutton-Brock et al., 1988; Apollonio et al., 1989; Vehrencamp et al., 1989; Gosling and Petrie, 1990; Isvaran and Jhala, 2000; Pearson et al., 2006). However, territoriality increases access to females and therefore enhances reproductive success (Vehrencamp et al., 1989; Rosser, 1992; Isvaran and Jhala, 2000; Bro-Jorgensen and Durant, 2003; Pearson et al., 2006).

Marine mammals exhibit higher resting metabolic rates than terrestrial mammals (Yeates et al., 2007). However, sea otters

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represent an extreme, exhibiting resting metabolic rates that are ca. 3 times the allometric prediction for a terrestrial mammal of similar size (Davis et al., 1988; Iverson, 1972; Morrison et al., 1974; Costa, 1978; Costa and Kooyman, 1984; Yeates et al, 2007). Since they are the smallest marine mammal, sea otters also have the highest surface-to-volume ratio, which increases potential heat loss. In addition, other marine mammals depend on a subcutaneous blubber layer for insulation, whereas sea otters rely on fur to trap an air layer next to their skin for thermal insulation (Williams et al., 1992). This air layer compresses as the otter dives, thereby reducing insulation. As a result, sea otters experience elevated thermal energetic costs which are offset by an increased resting metabolic rate, increased activity, and by the heat produced during food digestion and assimilation (HIF, Heat Increment of Feeding) (Costa and Kooyman, 1984).

In previous studies, sea otter activity budgets have been made using scan sampling (Estes et al., 1986), radiotelemetry (Garshelis et al., 1986; Gelatt et al., 2002), or have been derived from time-depth recorders (Bodkin et al., 2007). The goal of this study was to assess the diel activity patterns of male sea otters in Simpson Bay, a fjord in northeastern Prince William Sound, Alaska, using individual follows (Mann, 1999) combined with instantaneous sampling (Altmann, 1974; Lehner, 1996; Mann, 1999; Pearson and Davis, 2005). These sampling techniques were conducted during 6-hourly periods corresponding to dawn, day, dusk, and night. The activity budgets were then used to estimate FMR based on previously measured energetic costs for different activities (Yeates et al., 2007).

2. Methods

2.1. Study Site

Simpson Bay (ca. 60.6°N Lat., 145.9°W Long.), located in north-eastern Prince William Sound, Alaska (Fig. 1), was used as the study site because of its reasonable size, protection from rough seas, and reliable presence of sea otters. It is composed of two arms (north-western and southeastern) and is approximately 21 km^2 in area; 7.5 km long in the northwestern arm, 5 km long in the southeastern arm, and 2.5 km across at the widest point. The average depth is about 30 m, and the maximum water depth is 125 m. The benthos is mostly glacial clay, silt, and gravel with some rocky hard reefs. There are no large-bodied kelps (e.g., *Nereocystis*) that form canopies, but large fronds of sugar kelp (*Laminaria saccharina*) cover the benthos in many areas of the bay from the subtidal to a depth of ca. 10 m (Davis, unpublished observations).

The bay was re-colonized by male sea otters in 1977, and females moved into the area between 1983 and 1985 (Garshelis 1983, Rotterman and Simon-Jackson 1988). For the past 8 years, it has been occupied during the summer by an average of 118 ± 9.9 SD sea otters, including adults and subadults (90 ± 6.9 SD) and pups (29 ± 4.4 SD) (Davis, unpublished observations). During the winter, the number of otters in the bay decreases to ca. 50, although where they disseminate is poorly understood. This research was conducted under a Letter of Confirmation No. MA-043219 from the U.S. Fish and Wildlife Service.

2.2. Focal observations

Field observations of male sea otter behavior were conducted during the summers (early May through late August) of 2005 and 2006 using individual follows (Mann, 1999) and instantaneous sampling (Altmann, 1974; Lehner, 1996; Mann, 1999; Pearson et al., 2005). The research team, composed of a driver, recorder and observer, conducted surveys from a 6-m skiff. A regular schedule was followed by dividing the bay into three sections: north bay, west bay and east bay. Each day, one of these sections was selected in rotation for making observations, and another section was selected as an alternate should logistical problems occur. Boat-based observers determined if an otter was male by the presence of a penile ridge or testicular bulge (visible through binoculars), or by observing copulatory or patrolling behavior. Patrolling is a form of locomotion whereby a male swims belly-down with its head out of the water while scanning the surface, presumably for receptive females or other territorial males. Female sea otters primarily float on their backs or swim submerged, making patrolling a conspicuous male behavior (Pearson et al., 2006).

Individual follows occurred approximately twice a day during one of four 6-hourly 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). Individual follows lasted 31 min (minute 0–minute 30) and instantaneous samples (Altmann, 1974; Lehner, 1996) were taken once per minute during which the behavioral state (foraging, grooming, interacting with another otter, resting, swimming at the surface, or patrolling) was recorded from a distance of ca. 30 m or greater so as not to alter the animals' behavior. Behaviors were identified based on descriptions by Packard and Ribic (1982). Latitude and longitude were also recorded every minute using a Global Positioning System (GPS).

2.3. Data analysis

Time/activity budgets were created for each behavior observed during each of the four time periods, and over a combined of 24-h period. Multivariate analysis of variance (MANOVA) was used to test differences in the relative amount of time a male otter spent performing each of the six behaviors (dependent variables) among the four time periods (independent variables). MANOVA tests were performed using *SPSS, Version 15* statistical software (SPSS, Chicago, IL). The alpha level for these tests was set at 0.05. In addition, a canonical variants analysis (similar to a discriminate functions analysis) was run to determine those behaviors (independent variables) that characterized (i.e., best distin-guished among) the variance in time spent among the four time periods (dependent variables). The canonical variants analysis was run using *CANOCO, Version 4.5* software (CANOCO, Ithaca, NY).

Field Metabolic Rate (FMR) was estimated by combining the oxygen consumption (ml O_2 min^{-1} kg^{-1}) for resting (13.3), feeding (21.6), grooming (29.4), swimming (29.6), and interacting (24.5) for captive otters (Yeates et al. 2007) with the activity budgets for the male otters in this study. Yeates et al. (2007) trained test animals to make voluntary dives and surface under a clear acrylic dome. Oxygen consumption was determined under four conditions: 1) resting on the surface, 2) grooming, 3) following serial foraging dives, and 4) following single non-foraging dives. Foraging costs were determined by measuring oxygen consumption following prey-searching dives. Test animals were trained to dive to the bottom of a 9.1-m deep, 4-m diameter seawater storage tower with the metabolic dome at the surface of the water. A rocky substrate along with 3–5 kg of live crabs (*Cancer* spp.) and live mussels (*Mytilus edulis*) were placed at the bottom of the tank to simulate foraging conditions in the wild. The test otter was allowed to forage by making repeated dives to the bottom to collect prey items. Following the collection of the prey, the otter surfaced beneath the metabolic dome while handling and consuming the prey. All measurements followed the methods of Williams et al. (2004b) using an open-flow respirometry system for aquatic mammals (Yeates et al. 2007). Behaviors in our study that did not fall into one of the classifications of Yeates et al. (2007) were categorized as 'other' (e.g., interacting with conspecifics). For purposes of comparison, our study considered 'patrolling' to be energetically similar to 'swimming' (following a description of swimming costs and behaviors for sea otters in Williams, 1989), and therefore the two categories were combined. The weight specific FMR (kJ day^{-1} kg^{-1}) was calculated as the product of the energetic cost of each activity, a conversion factor of 2.0083×10^{-2} kJ ml^{-1} O_2 (Schmidt-Nielsen, 1997), and the number of minutes per day spent

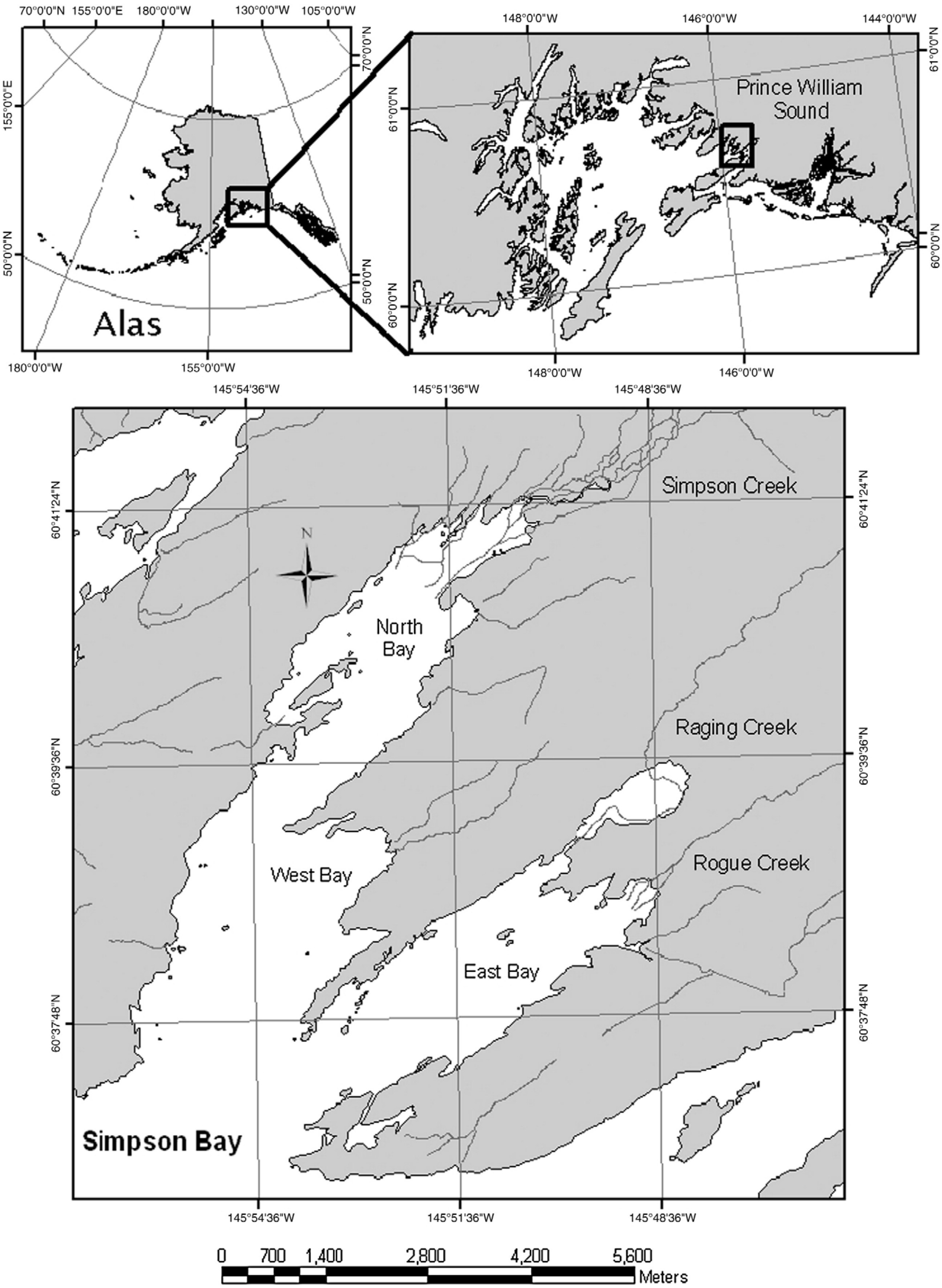

Fig. 1. Prince William Sound, Alaska.

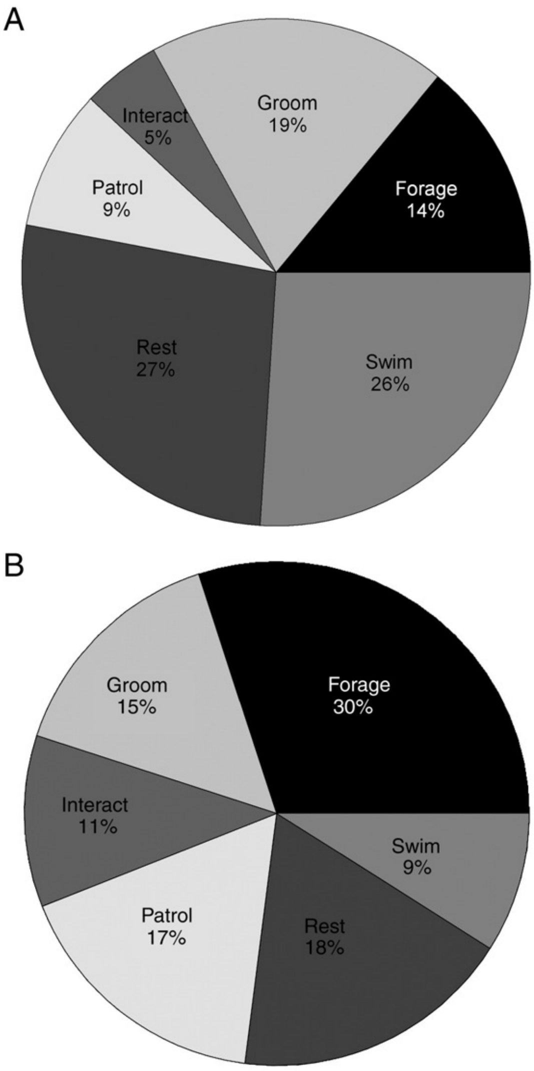

Fig. 2. A) Twenty four hour activity budget for adult male sea otters in Simpson Bay, Alaska during summers (May to August) of 2005–2006 B) Daytime only activity budget for adult male sea otters in Simpson Bay, Alaska during summer 2003 (Pearson et al., 2005).

in each activity (i.e., proportion of day in each activity times 1440 min day^{-1}). The total FMR (MJ day^{-1}) was calculated as the product of the weight specific FMR and the mean body mass (27.7 kg) of adult male sea otters (Yeates et al. 2007) divided by 1000 to convert kJ to MJ. Adult, male Alaskan sea otters can range in body mass from 18 to 45 kg. The average weight of an adult male from Amchitka Island, Alaska is 28.3 kg (Riedman and Estes, 1990). The 27.7 kg body mass reported by Yeates et al. (2007) for California otters was used in this study because of its similarity to the average body mass previously reported for adult male Alaska sea otters.

MANOVA was used to test differences in the proportion of estimated energy male otters spent performing each of the six behaviors (dependent variables) among the four time periods (independent variables). A canonical variants analysis, as well as a Monte Carlo simulation, was used to determine those behavioral categories (independent variables) that characterized the variance in energy spent among the four time periods (dependent variables). The independent variables having absolute t-values>2.1 (comparable to an alpha of 0.05) were considered to be significant. The independent variables having t-values<2.1, while not strictly significant, were assessed as tendencies, and showed very strong contributions to the final explanatory model.

3. Results

3.1. Research effort

One hundred ninety focal observations (31 min each) were conducted for a total of 98 h; 25% ($n=47$) occurred during the dawn (05:00–11:00 h local time), 28% ($n=53$) occurred during the day (11:00–17:00 h local time), 26% ($n=49$) occurred during the dusk (17:00–23:00 h local time) and 21% ($n=41$) occurred during the night (23:00–05:00 h local time).

3.2. Activity budget

A combined (all four time periods) 24-h activity budget was created for male sea otters based on the 190 focal observations (Fig. 2A and Table 1). Approximately one-half of their time was spent in a combination of resting (27%) and swimming (26%), while grooming (19%) and foraging (14%) together accounted for one-third of the activity budget. Patrolling (9%) and interacting (5%) accounted for the smallest portions of the activity budget.

The MANOVA showed that the four time periods did not explain a significant difference in mean time spent among the six behaviors. The Canonical Variants Analysis showed that the behavioral categories distinguished only 4.7% of the variance in time spent among the four periods, but a Monte Carlo simulation showed this to be statistically significant (F-ratio$=9.054$; $p=0.004$). Interacting ($t=3.86$) and resting (t$=2.71$) were positively associated with dawn. Grooming ($t=1.96$), while not significant, also tended to be positively associated with dawn (Fig. 3).

3.3. Estimated Field Metabolic Rate (FMR)

Based on our activity budgets and the energetic costs for different activities of sea otters in captivity (Yeates et al., 2007), the weight specific and total FMRs for each behavior were estimated (Table 1). The combined activity of swimming and patrolling (called swimming) accounted for the greatest percentage (43.3%) of energy expended each day. This was followed by grooming (23.2%), resting (15.2%), feeding (13.1%) and other (5.1%). The weight specific FMR for all activities was 686.7 kJ day^{-1} kg^{-1} and the total FMR was 19.04 MJ day^{-1}. This represents an FMR that was 6.6 times the estimated resting metabolic rate of 2.89 MJ day^{-1} (Table 1) and 2.2 times greater than the allometric prediction ($\mathrm{FMR}=4.82\ \mathrm{Mb}^{0.734}$) , where Mb is body mass in grams and FMR is kJ day^{-1}) for mammals generally (eutherian and metatherian) based on the doubly labeled water method (Nagy, 2005).

The MANOVA showed an overall significant difference ($p=0.006$) in the relative amount of energy spent in each of the six behaviors among the four time periods. More energy was spent swimming during the day (estimated marginal mean$=0.008$) than during the dawn (estimated marginal mean$=0.004$). The Canonical Variates Analysis (Fig. 4) showed that differences in relative amount of energy

Table 1
Daily activity budget and estimated Field Metabolic Rate (FMR) for adult male sea otters.

Behavior	Proportion of day	Min per day	FMR (kJ day^{-1} kg^{-1})	FMR (MJ day^{-1})
Resting	0.27	390	104.17	2.89 (15.2)
Feeding	0.14	207	89.80	2.49 (13.1)
Grooming	0.19	270	159.42	4.42 (23.2)
Swimming [a]	0.35	502	298.42	8.27 (43.4)
Other	0.05	71	34.93	0.97 (5.1)
Total	1.0	1440	686.74	19.04 (100)

Numbers in parentheses are the percentages of the total FMR.
[a] Swimming includes the combined activities of swimming and patrolling.

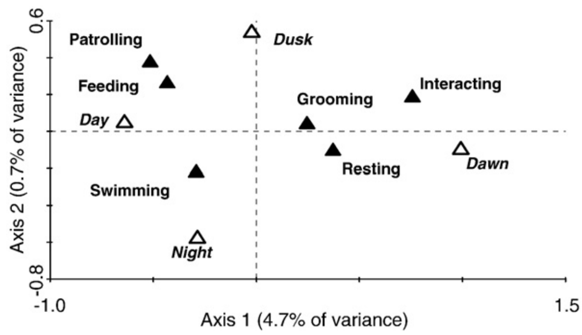

Fig. 3. Results of the Canonical Variants Analysis showing associations on the first two canonical axes for behavioral categories and time spent among the time periods.

spent in the four time periods were not explained by the five behavioral categories (F-ratio = 3.432, p = 0.272). However, energy expenditure for feeding and swimming showed a more positive association with day, whereas energy expenditure for grooming and resting showed a more positive association with dawn. The location of other behaviors near the center of the plot for the two strongest canonical axes (Fig. 4), indicated that intermediate amounts of energy were spent in those behaviors among all time periods.

4. Discussion

4.1. Previous studies of male sea otter activity patterns

Studies of sea otter activity patterns have been conducted in Alaska and California using different methods, and considerable variability has been reported for time budgets (Table 2). Sea otters have large energy requirements due to an elevated metabolic rate (Costa and Kooyman, 1984), and Kenyon (1969) estimated that they consume up to 25% of their body mass in food each day. Because of this, many of these previous studies focused on foraging behavior.

4.1.1. Radio telemetry

Garshelis et al. (1986) and Gelatt et al. (2002) used radio telemetry to determine the activity budget of sea otters. Garshelis et al. (1986) conducted their study in the region around Green Island, in south-central Prince William Sound, Alaska, where very high frequency (VHF) radio transmitters were attached to the rear flippers of 65 adult male otters. Radio signals were not detectable when the external whip antenna was submerged. This enabled activities to be categorized as foraging, resting or swimming on a 24-h basis. Signals from resting otters were uninterrupted because it was assumed that otters rest

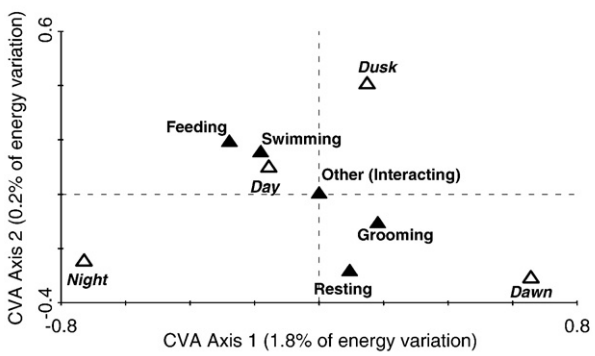

Fig. 4. Results of the Canonical Variants Analysis showing associations on the first two canonical axes for behavioral categories and energy spent among the time periods. Note that in this analysis, patrolling and swimming have been combined into a single energetics category called swimming.

Table 2
Comparison of sea otter activity budgets in Alaska and California.

Study location (source)	% time spent[a]		
	Foraging	Resting	Swimming
Prince William Sound, Alaska (this study)[b,c]	14	27	26
Olympic Peninsula, Washington (Walker et al., 2008)	8	62	8
Cross Sound, Alaska (Bodkin et al., 2007)[b,c]	28	54	N/A
San Simeon, California (Yeates et al., 2007)[d,c]	36	40	8.5
Prince William Sound, Alaska (Pearson et al., 2005)[d,c]	30	18	9
Amchitka, Alaska (Gelatt et al., 2002)[b,c]	38	45	N/A
Monterey to Piedras Blancas, California (Estes et al., 1986)[d,e]	24	59	N/A
Prince William Sound, Alaska (Garshelis et al., 1986)[b,c]	47	50	3

[a] Row totals do not all equal 100% due to different categories of activity presented by each study.
[b] Behavior throughout the 24-h cycle.
[c] Adult male sea otters.
[d] Daytime behavior.
[e] Adult sea otters, male and femaletics category called swimming.

with their rear flippers exposed. Swimming was characterized by frequent, short interruptions as the radio-tags dipped below the water surface. Feeding dives and subsequent food consumption at the surface were characterized by long breaks in the signal, followed by periods that were uninterrupted. Based on these assumptions, this study concluded that males allocated 47% of their time to foraging, 50% to resting and 3% to swimming.

Gelatt et al. (2002) conducted their study around Amchitka Island, Alaska, where VHF radio transmitters were surgically implanted in 21 adult male otters that were monitored every 10 min for 24-h twice per week. Activities were categorized as foraging, resting and other. Using similar assumptions about signal patterns, the time budget from this study was similar to that of Garshelis et al. (1986) with adult male sea otters allocating 38% of their time to foraging, 45% to resting and 17% to other activities.

4.1.2. Time-depth recorders (TDR)

Bodkin et al. (2007) conducted their study near Cross Sound, located in southeastern Alaska. VHF radio transmitters and archival time-depth recorders were surgically implanted into 21 adult sea otters (5 males). Each TDR was programmed to record depth, with 0.25 m accuracy, at 2 s intervals for 46 days. Color-coded tags were attached to the hind flippers of each individual to allow for visual recognition. Instrumented animals were observed daily from both shore and boats. Activities were categorized as foraging, resting, and other (swimming, grooming, and interacting). The males allocated 28% of their time to foraging, 54% to resting, and 18% to other diving behaviors (swimming, grooming, and interacting).

4.1.3. Scan sampling

Estes et al. (1986) used the scan-sampling method to determine the activity budget of sea otters in a rocky reef and kelp forest habitat in central California. Behavior was categorized as foraging, resting or other by sampling a group of otters in an area at 30 min intervals with 10× binoculars. Due to low luminance and poor visibility, they could not use this method at night, so the time period for the study was considered to be from dawn to dusk. The study concluded that the otters allocated 24% of their time to foraging, 59% to resting and 17% to other behaviors.

Walker et al. (2008) based their study design on the methods used by Estes et al. (1986). Scan sampling was used to determine the activity budget of translocated sea otters in rocky coastal and subtidal substrate habitats on the Olympic Peninsula in Washington State, an area known to be below equilibrium density. Sampling occurred at 30 min intervals using 10× binoculars and a high powered spotting scope. The study concluded that sea otters allocated 62% of their time to resting, 20% to grooming, 8% to foraging, 8% to swimming and 2% to other behaviors.

4.1.4. Individual follows and instantaneous sampling

Pearson et al. (2005) conducted their study in Simpson Bay, Alaska during daytime hours only (0900–1830 h local time). Activities were categorized as foraging, grooming, interacting with other otters, swimming, patrolling, and resting. Pearson et al. (2005) concluded that male otters allocated 30% of their time to foraging, 15% to grooming, 11% to interacting with other otters, 17% to patrolling, 18% to resting, and 9% to swimming (Fig. 2B).

4.2. Results from this study

4.2.1. Activity budget

We used the same individual follow and instantaneous sampling protocol as Pearson et al. (2005), but extended the observations to include the night period. These are two specific forms of focal animal sampling (Altman, 1974; Lehner, 1996) and should not be confused with group-follows or scan sampling. In our study, we conducted "individual follows" whereby observers monitored a single individual regardless of whether it was solitary or in a group, which differs from a "group-follow" where an entire group of animals is monitored (Mann, 1999). In addition, we conducted "instantaneous sampling" whereby an observer recorded an individual's behavior at preselected moments in time (i.e., every minute for 31 min). In contrast, "scan sampling" involves taking an instantaneous sample of an individual's behavior at regular intervals before moving on to the next animal, often in a group (Altmann, 1974; Mann, 1999). As a result, the behavior of a specific animal does not occur during consecutive scans. Scan sampling is valuable for sampling behavior when individual follow observations are not possible, or if the researcher wishes to keep track of group activities. Individual follows and the instantaneous sampling technique is better for determining time budgets, as well as tracking transitional changes in behavior (Altmann, 1974; Mann, 1999). While this sampling protocol may still slightly underestimate foraging behavior, we think the bias is less than that of the scan-sampling method.

Our study showed no difference in the mean time spent among the six behaviors in each of the four time periods, although foraging was associated with day and dusk (Fig. 3). These results agree with Estes et al. (1986) who reported an afternoon foraging peak that began at approximately 13:00 h, reached a maximum at approximately 16:00–18:00 h and continued until dusk. Male otters in our study allocated 27% of their time (over a 24-h period) to resting, 26% to swimming, 19% to grooming, 14% foraging, 9% to patrolling and 5% to interacting with other otters (Fig. 2A). Except for Pearson et al. (2005), previous studies have not attempted or been able to obtain the same level of detailed behavior in male activity budgets over a 24-h period (Table 2).

The allocation of 14% of time to foraging by the male otters in this study was less than most previous studies but considerably higher than Walker et al., 2008 (Table 2). Time budgets of sea otters can be affected by food availability. The low percentage of time allocated to foraging in this study may indicate that food is more abundant in Simpson Bay than other areas in which otters have been studied or that the otter population in Simpson Bay is still below equilibrium density. Where food is relatively abundant, less time is required for feeding, and more time is available for resting or swimming (Garshelis et al., 1986; Bodkin et al., 2007). Previous studies have found that foraging intensity is negatively correlated with sea otter abundance. Otter populations below equilibrium density allocate 15–20% of their time to foraging, whereas those at equilibrium density forage 50–55% of the time (Estes et al., 1986). Simpson Bay was recolonized by otters over 25 years ago, and the number of otters using it during the summer (June–August) has been stable with ca. 90 adults and subadults and 29 pups (Davis, unpublished observations). Simpson Bay may still be below equilibrium density with 5.6 otters km^{-2} during the peak summer population. This is comparable to a California study (Estes et al., 1986) where the otter population was thought to be at or slightly below equilibrium density with approximately 7.8 otters km^{-2}.

In comparison with male otters in Simpson Bay, female otters with pups invested 21% of their time foraging (Wolt, unpublished data). Although this is 7% higher than the males, it is still at the low end of reported values from other areas, and this leads us to conclude that Simpson Bay may be below equilibrium density. It is reasonable that female otters may forage more than males in order to support their pups. Therefore, the 7% difference in foraging time between males and females can be attributed to provisioning the pup. As a result, the low percentage of time spent foraging by males may have less to do with sampling biases and may indicate that the population is below equilibrium density.

4.2.2. Estimated Field Metabolic Rate (FMR)

The weight specific FMR for all activities was 686.7 kJ day^{-1} kg^{-1} and the total FMR was 19.04 MJ day^{-1}(Table 1). This level of energy expenditure for sea otters is very similar to predicted values based on allometric regression for FMR of other marine mammals including otariids and phocids (Williams et al., 2004a, 2004b). Yeates et al. (2007) reported an FMR for adult male otters along the California coast to be 15.71 MJ day^{-1}. The difference (21%) in FMR between these two studies resulted from Simpson Bay otters spending more time performing higher energy activities such as swimming and patrolling. The "swimming" category for our energy budget is a combination of both the "patrolling" and "swimming" behaviors from our activity budget. Swimming is usually performed belly up, and can occur at speeds ranging from 0.1 to 0.5 m s^{-1}. Patrolling is performed belly-down with head raised and can occur at slightly faster speeds ranging from 0.6 to 0.8 m s^{-1} (Williams, 1989). In our calculation of FMR, both categories were considered to be surface swimming behaviors and therefore energetically similar. This combined category accounted for 35% of the Simpson Bay activity budget, whereas surface swimming accounted for only 8.5% of the activity budget in Yeates et al. (2007). In addition, grooming accounted for 19% of our activity budget verses 9% of the activity budget described by Yeates et al. (2007) Both grooming and swimming are energetically high-cost behaviors and represent over half of the Simpson Bay male sea otter activity budget. Conversely, foraging and resting are energetically mid-to-low cost behaviors. These activities account for three quarters of the Yeates et al. (2007) budget, while accounting for only 41% of the Simpson Bay sea otter budget.

Foraging accounted for only 14% of the adult male budget, which is low compared to other studies (Table 2). If we revise the male activity budget to reflect the 7% difference in foraging time from the female activity budget (i.e. increase foraging time from 14% to 21%), then the male foraging time would increase to 21% and resting time would decrease to 20%. This would increase the estimated FMR by only 2.5% to 19.50 MJ day^{1}. This low percentage increase in the FMR indicates that: 1) any potential bias in the opportunistic focal animal sampling results in relatively minor effects (2.5%) on FMR, and 2) the daily percent time allocated to foraging for male sea otters in Simpson Bay likely ranges between 14 and 21%.

5. Conclusions

We used opportunistic individual follows and instantaneous sampling to determine the daily activity budgets and to estimate the FMR of adult male sea otters in Simpson Bay. Data were collected during the summer months, and throughout the 24-h cycle. Adult males allocated 35% of their time to swimming and patrolling, 27% to resting, 19% to grooming, 14% to foraging and 5% to interacting with other otters. Although individual follows and instantaneous sampling may underestimate the percentage of time spent foraging, the estimated FMR (19.04 MJ day^{-1}) was relatively insensitive (2.5%

difference) to changes in the percentage of time spent foraging which likely ranged from 14 to 21%. Even if male sea otters allocated 21% of their time foraging, this is less than the observed in most previous studies and, in conjunction with a stable summer density of 5.6 otters km^{-2}, indicates that Simpson Bay may be at or slightly below equilibrium density.

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