PATTERNS OF SEA OTTER HAUL-OUT BEHAVIOR IN A CALIFORNIA TIDAL ESTUARY IN RELATION TO ENVIRONMENTAL VARIABLES

DANIELA MALDINI[1], ROBERT SCOLES, RON EBY, AND MARK COTTER
Okeanis, PO Box 583, Moss Landing, CA 95939

ROBERT W RANKIN
Pacific Whale Foundation, 300 Maalaea Road, Suite 211, Wailuku, HI 96793

ABSTRACT—This study provides the first in depth assessment of Sea Otter haul-out patterns in Elkhorn Slough, California and their relationship to environmental variables. Seasonal and daily water and air temperature fluctuations are a good predictor of Sea Otter haul-out patterns but are affected by the availability of haul-out sites at different tide levels. The cost effectiveness of this choice may be maximal at night because of lack of human disturbance. Southern Sea Otters (*Enhydra lutris nereis*) were observed during 50 bimonthly 24-h periods between August 2007 and July 2009 (n = 1187 h) from a shore-based observation site located above a non-territorial male resting area on the north side of Moss Landing Harbor. We counted the number of Sea Otters in the area (both in the water and on land) at 30-min intervals. We also recorded tide height, and air and water temperature. Thirty-minute counts averaged 42 Sea Otters using the area (land and water) during the day and 66 at night. The average number of Sea Otters hauled out in the study area during the same haul-out event was 22, and the maximum number was 93. Sea Otters were observed hauled out on 70% of the days surveyed, and the proportion of Sea Otters hauled out was significantly higher at night. Higher numbers of Sea Otters on land was significantly correlated with lower air and water temperature, and with mid-range tide-heights. We speculate that haul-out behavior could play an important role in energy conservation; however, human-related traffic patterns in the area may negatively affect this energy conservation strategy.

Key words: behavior, California, California Sea Otter, Elkhorn Slough, *Enhydra lutris nereis*, haul-out

Our study is the first rigorous quantitative analysis of the environmental factors affecting haul-out behavior in Sea Otters. Sea Otters are the only member of the family *Mustelidae* that use the marine environment exclusively to feed, breed, give birth, and raise pups (Riedman and Estes 1990). Because Sea Otters live only in regions where water temperature is usually <15°C, survival requires maintaining high metabolic rates. In fact, Sea Otters consume an average of 25% of their body weight per day depending on their age, reproductive status, and health (Morrison and others 1974; Costa and Kooyman 1982). Sea Otters also have the thickest fur known for a mammal (26,413 to 164,662 hairs/cm^2), and this insulation layer needs to be properly maintained through grooming (Davis and others 1988; Williams and others 1992). Despite these adaptations, a cold-water lifestyle incurs high metabolic costs. During studies of wild Sea Otters, Yeates and others (2007) found that a foraging Sea Otter has a daily energy expenditure (6.1 ± 1.1 MJ day^{-1}) which is twice that predicted for phocid seals. Yeates and others (2007) also found that Sea Otters are able to compensate for these high foraging costs by spending long periods of time resting, which allows Sea Otters to achieve Field Metabolic Rates (FMR) similar to those of other mammals. However, because water's heat transfer by conduction is 25 to 100 times greater than that of air, Resting Metabolic Rates (RMR) for Sea Otters are 2.4 times higher than predicted for terrestrial mammals of equivalent size (Iverson 1972; Costa and Kooyman 1984).

In the absence of other factors, such as high risk of predation, unavailability of haul-out space, and other disturbances, resting on land should present an energetic advantage for Sea

[1] Current address: Pacific Whale Foundation, 300 Maalaea Road, Suite 211, Wailuku, HI 96793

Otters by decreasing their rate of heat loss (Williams 1989). This would be particularly advantageous when environmental conditions are unfavorable. In fact, haul-out behavior is commonplace at extreme temperatures such as those found in Alaska and Russia, where large groups of otters gather on land (Barabash-Nikiforov and others 1968; Reidman and Estes 1990). In California, however, haul-out behavior has been less common and it is generally limited to a small number of animals per haul-out event (Faurot 1985).

Moss Landing, California is a location where Southern Sea Otters (*Enhydra lutris nereis*) haul out on land in large groups on a daily basis, and it was the ideal place to test the hypothesis that Sea Otters haul out to defray above average metabolic costs created by unfavorable environmental conditions. For this hypothesis to be supported, we expected Sea Otters to exhibit a haul-out pattern that reflected seasonal temperature changes. We also expected Sea Otters to exhibit daily haul-out patterns that reflected daily temperature fluctuations. Provided similar availability of haul-out sites, a larger proportion of Sea Otters would haul out during unfavorable environmental conditions such as when temperatures were lowest both seasonally and daily. We also predicted that availability of haul-out space, as determined by tides, would be a predictor of Sea Otter haul-out patterns.

METHODS

Study Area

Located in the middle of Monterey Bay, Elkhorn Slough is the third largest estuary in California (Caffrey and others 2002) and stretches 11 km eastward from Moss Landing Harbor (Fig. 1). Southern Sea Otters invaded Elkhorn Slough and Moss Landing Harbor in 1995 (Feinholz 1998) and their population in the slough has been fluctuating, overall maintaining high densities over the years (Kieckhefer and others 2007; Maldini and others 2010). The north side of Moss Landing Harbor has been the location of a non-territorial male resting area since 2004, while the upper reaches of the slough are currently occupied by territorial males and reproductive females (Kieckhefer and others 2007; Maldini and others 2010). Although non-territorial male Sea Otters almost exclusively use Moss Landing North Harbor, females occasionally travel through the area to feed or rest (Maldini and others 2010).

Our study site was a 0.11 km^2 area located at the north end of Moss Landing Harbor (Fig. 2). The area is adjacent to busy boat-launch ramps to the east, a small yacht harbor to the north, the mouth of Elkhorn Slough and main entrance to Moss Landing Harbor to the south, and beach access to the west (Fig. 2). North Beach is a Sea Otter haul-out site, located inside the harbor and abutted by a busy parking lot, which is used by visitors to access the ocean-facing Moss Landing Beach (Fig. 2). North Beach is 0.049 km^2, extending north to south (Fig. 2). Pedestrian access to parts of North Beach is prohibited because of the number of Harbor Seals (*Phoca vitulina*), California Sea Lions (*Zalophus californianus*), and, recently, Sea Otters using this area. The harbor has a maximum depth of 15 m and is exposed to tidal flux. Boat traffic in this part of the harbor is limited to small and medium sized yachts, small boats, and kayaks.

Our observation site (Fig. 2) was located 5 m above sea level, at the Moss Landing State Beach parking lot (UTM: Zone 10S, 608064.13 E, 4074497.87 N, WGS84). From this location, we could observe the entire extent of North Beach from above and we could easily count all Sea Otters present on the beach and in the water. The boundaries of the study area were, on the south, an imaginary line drawn from the south jetty to the restaurant dock on the opposite side (Fig. 2, A); and, on the north, another imaginary line between the boat launch ramp adjacent to Elkhorn Yacht Club and the sand spit on the opposite side (Fig. 2, B).

Sampling Methods

Sea Otters were observed during 50 bimonthly 24-h periods between August 2007 and July 2009. Land-based observers counted all Sea Otters present in the study area every 30 min. Sea Otters were categorized as being either in the water or hauled-out. Sea Otters were considered hauled-out either when completely out of the water or when their back firmly rested on the beach, even if water was partially surrounding them. Observations during daylight hours were conducted using Canon 10 × 30 Image-Stabilized binoculars. At night, observations were conducted with an ATN Scout

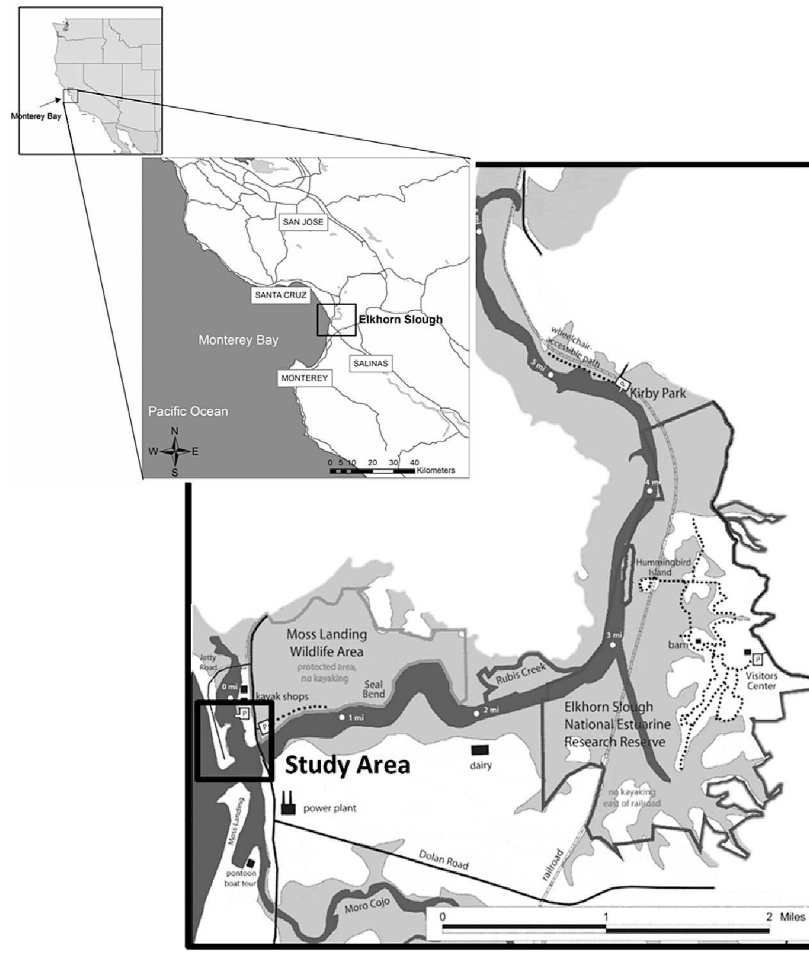

FIGURE 1. Location of Monterey Bay and map of Elkhorn Slough.

night scope. Sea Otters were counted by sweeping the binoculars from one end of the study site to the other and noting whether each Sea Otter observed was in the water or hauled-out. Air temperature, wind speed, and wind direction were recorded from a portable weather station at the beginning of each 30-min interval. Air temperature was corrected for wind chill when it was lower than 10°C and wind speed was >15 mph. Tide height and water temperature for each sampling period were downloaded from the LOBO 3 (Old Salinas River) oceanographic buoy (http://www.mbari.org/lobo/network.htm) located at UTM: Zone 10S, 607987.90 E, 4072506.30 N, WGS84 (Jannasch and others 2008).

Visibility was estimated based on distances to known landmarks and our ability to see them. When visibility dropped below the width of the study area, counting was aborted.

Data Analysis

To address the relationship between air temperature, water temperature, and other environmental covariates and Sea Otter haul-out behavior, we used Hierarchical Partitioning and Quasi-Poisson Generalized Additive Mixed Models (Chevan and Sutherland 1991) with a temporal auto-correlation structure. We analyzed data with *hier.part* (Walsh and MacNally 2008) and *mgcv* (Wood 2008) packages in the 'R' statistical computing language and environment (R Development Core Team 2010). The motivation for combining Hierarchical Partitioning with Mixed-Models was to address a

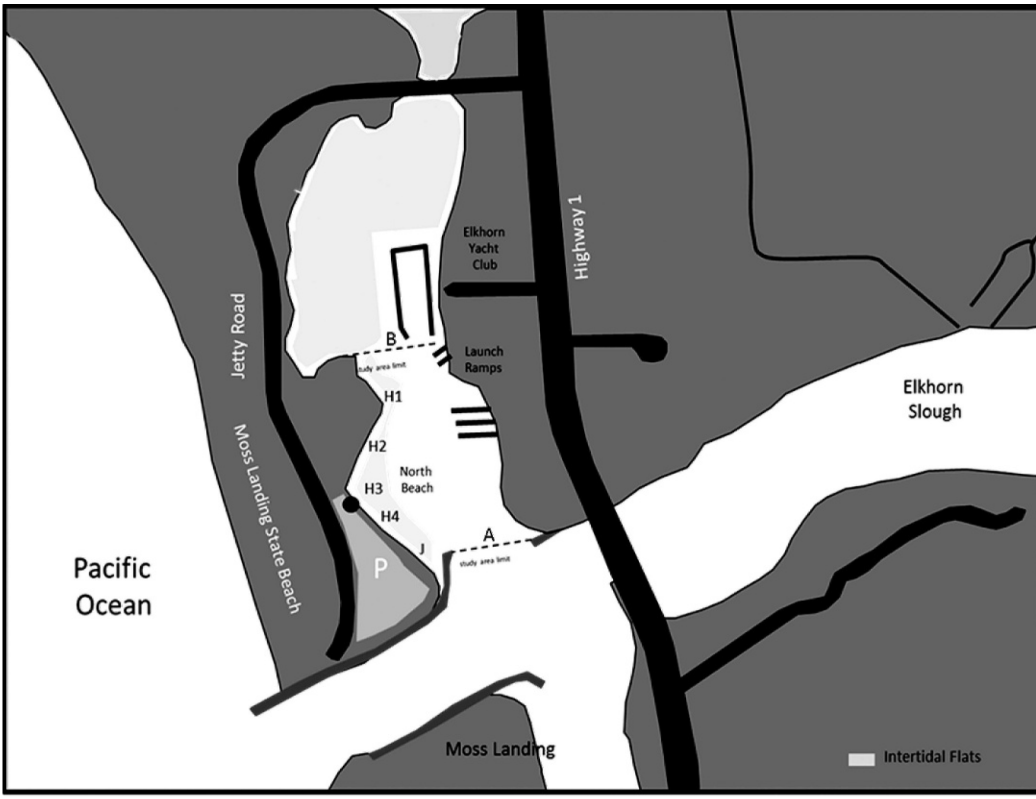

FIGURE 2. Map of the study area showing the land-based observation site (black dot) and the Sea Otter rafting area (between dotted lines A and B). The beach where Sea Otters regularly haul out is indicated by the codes H1, H2, H3, H4, and J which are the specific haul-out sites.

number of challenging attributes of the study design. For example, the relationship between marine and weather systems manifested as high correlations between certain explanatory variables (for example: air temperature and water temperature, water temperature and tide-height). Such correlations may result in inexact parameter coefficients and inflated confidence intervals for variables in a multivariate regression (MacNally 2000), making such regressions inappropriate for inferences about the importance of explanatory variables to our response variable (the number of Sea Otters that were hauled-out).

Chevan and Sutherland (1991) proposed Hierarchical Partitioning as a means of describing the independent and joint contributions of collinear variables to a full-model's goodness-of-fit, by partitioning the goodness-of-fit statistic over all possible variable combinations. We used the root mean-squared prediction error statistic as a goodness-of-fit statistic in lieu of a likelihood estimate because of model over-dispersion and our subsequent use of the Quasi-likelihood Poisson family to model counts.

Typical Hierarchical Partitioning uses Generalized Linear Models. Because repeated observations in close time-proximity (our 30-min counts) may violate the assumption of measurement independence, we included a continuous autoregressive correlation structure for model residuals within each day, which resulted in exponentially decreasing correlation estimates for pairs of observations taken on the same day, but further away in time. For this analysis, we used the *CorClasses* functions in the *nlme* 'R'package (Pinheiro and others 2010) as part of the *mgcv* package for Generalized Additive Mixed Models.

We evaluated 2 models that we will refer to as the 'base-model' and the 'full-model'. In both models, the response variable was the count of

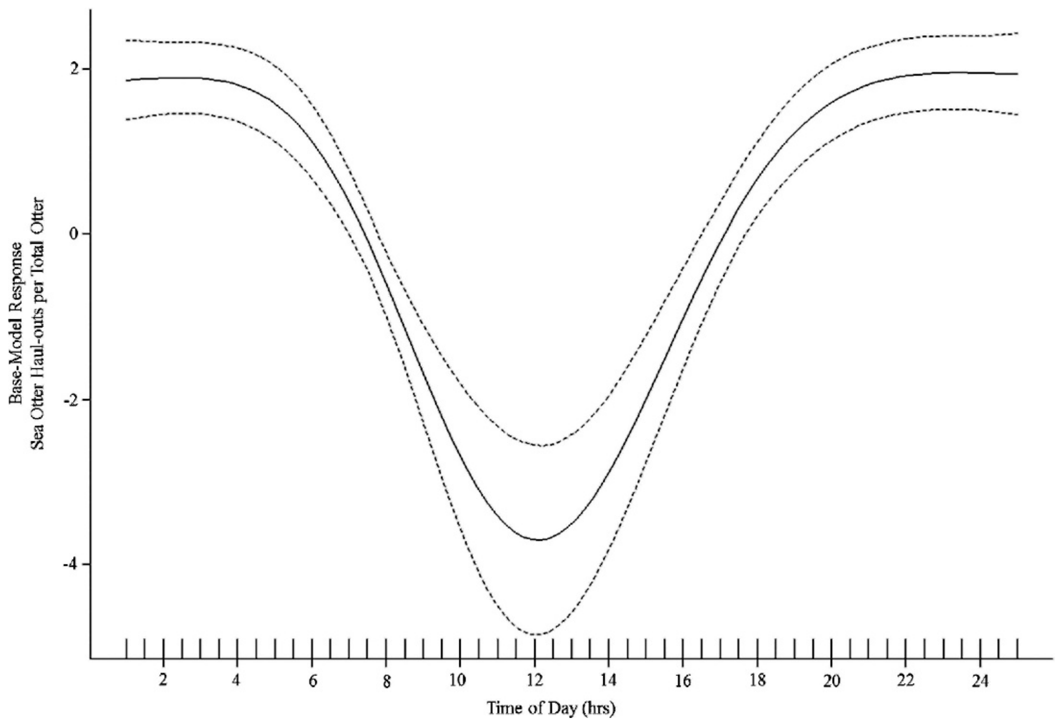

FIGURE 3. Base-Model response graph showing a significant effect of time of day on the proportion of Sea Otters hauled out.

Sea Otters hauled-out during 30-min observations, with an offset for the log of the count of all Sea Otters present in the study area, which modeled the proportion of all Sea Otters which were hauled-out.

In what we defined as the 'base-model', we included a variable for time of day, with a smooth-plate regression spline for time (6 degrees of freedom), plus an intercept. Time of day was deemed important because large numbers of Sea Otters left the study area between 08:00 and 17:00 each day. This was reflected in the strong U-shaped hourly trend in the number of Sea Otters hauled-out over a 24-h period (Fig. 3).

In what we defined as the 'full-model', we used 7 explanatory variables which included 30-min estimates of (1) air temperature, (2) water temperature, (3) wind-speed, (4) wind direction, (5) tide-height, (6) tide change, and (7) minimum daily water temperatures (Table 1). Our Hierarchical Partitioning analysis ran through all possible combinations of variables in the 'base-model' and the 'full-model' to partition the goodness-of-fit statistic among variables. The analysis results in estimates of 'independent contributions' and 'joint contributions' for each variable.

'Independent contributions' were the proportion of the goodness-of-fit statistic uniquely attributable to each variable. 'Joint contributions' were the shared contributions of (1) the variables to the goodness-of-fit statistic due to their collinearity, and (2) the U-shaped hourly trend in the data.

In order to assess the significance of the results of Hierarchical Partitioning, we performed 100 randomizations of the 7 explanatory variables and repeated the Hierarchical Partitioning procedure for each randomization to calculate each variable's 'independent contributions'. We then calculated the Z-score of the actual independent contributions versus the distribution of independent contributions in the 100 randomizations.

RESULTS

General Results

We completed 1187 h of observation. During the sampling period, air temperatures ranged

TABLE 1. Independent contribution of each of the 7 explanatory variables in the Full-Model (* signifies significance at < 0.05; ** signifies significance at < 0.01).

Explanatory variable	Model Coefficient	Standard Error	P-value
1. Air temperature	−0.046	0.034	0.183
2. Water temperature	−0.156	0.048	0.001**
3. Wind speed	0.015	0.007	0.033*
4a. Wind direction (North-South)	0.025	0.037	0.495
4b. Wind direction (East-West)	0.050	0.043	0.247
4c. Wind direction (NS-EW interaction)	−0.038	0.012	0.002**
5a. Tide level (quadratic term)	−3.366	1.683	0.046*
5b. Tide level (linear term)	−0.883	2.312	0.703
6. Tidal change	0.020	0.049	0.682
7. Minimum daily water temperature	−0.155	0.068	0.023*

from 9° to 18.5°C and water temperatures from 9° to 22°C. Tidal range in the study area was approximately 2.13 m between Lowest-Low-Tide and Highest-High-Tide. Conditions requiring wind chill correction to air temperatures occurred only twice and fog prevented data collection 3 times.

Sea Otters were present in the study area at all times during observations and their numbers ranged from a minimum of 1 animal (only twice, on 12 June 2008 at 12:00 and on 13 May 2009 at 10:00, respectively) to a maximum of 149 animals (twice, on 27 March and 12 April 2008, both at 05:30). Thirty-minute counts averaged 42 (SD ± 0.58) Sea Otters present in the entire study area during daylight hours and 66 (SD ± 0.88) Sea Otters at night.

Sea Otters hauled-out on land during 70% of days surveyed. Overall, the average number of Sea Otters hauled-out in the study area per 30-min sampling interval was 22 (SD ± 0.71) and the maximum was 93 (SD ± 0.52). The proportion of the total Sea Otters present in the study area that was hauled out per 30-min interval ranged between 0% and 96% for day and night combined. However, this proportion averaged 3% during daylight hours and 21% at night.

Sea Otters tended to haul out in the same general area often within touching distance or less than 1 body length apart. The majority (98%) of Sea Otters hauled out were inactive and resting. Occasionally, bouts of activity were recorded, most lasting 56 to 123 s. These bouts of activity consisted of interactions between 2 or more Sea Otters, or of active self-grooming. Interactions consisted of chases and reciprocal biting. During chases, animals ran from the beach to the water and back to the beach. A chase generally ended with animals entering the water and not returning to shore.

Explanatory Variables

Most explanatory variables were measured every 30 min for 24 h during each survey day. The data revealed 2 different temporal structures: a daily–hourly pattern (Fig. 3) and a long-term seasonal trend in the number of hauled-out Sea Otters (Fig. 4). To account for the seasonal trend, we conducted a preliminary analysis of environmental variables at the level of days (Table 1) using daily maximums, minimums, and means for each survey day. This resulted in there being only 48 observations available for a preliminary analysis of seasonality patterns. We therefore restricted the candidate variables to four: (1) maximum tidal difference; (2) minimum daily water temperature; (3) minimum daily air temperature; and (4) minimum daily tidal level. Other summaries, such as daily maximums and means, closely followed the daily minimums with correlation coefficients of >0.80, and were ignored.

A preliminary Hierarchical Partitioning analysis suggested that only minimum daily water temperature had a significant contribution to the daily maximum number of Sea Otters hauled-out. Therefore, we included minimum daily water temperature into further analysis of 30- min intervals as an attempt to model seasonality trends in the number of Sea Otters hauled-out. Although the full-model accounted for two-thirds (R^2 = 0.673) of the variation in the number of hauled-out Sea Otters, much of this variation was explained by the base-model

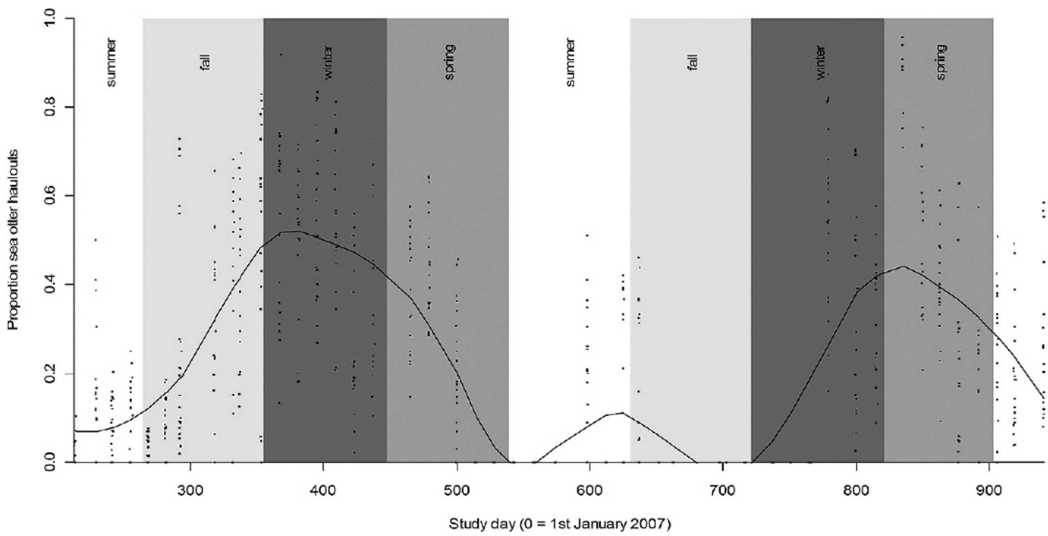

FIGURE 4. Relationship between seasonality and the proportion of Sea Otters hauled out.

(R^2 = 0.498). This variation was mostly explained by the prominent lack of haul-out behavior by Sea Otters during the day (Fig. 3). Water and air temperature showed the greatest independent contributions to the goodness-of-fit statistic (Table 2, Fig. 5). As expected, more Sea Otters hauled-out during colder temperatures, both over the hourly and daily time scales. The joint contributions of these variables to the goodness-of-fit statistic were also high, because of their correlation with each other and with the U-response-curve, fit with time as a variable.

Most of the explanatory variables were estimated as linear terms. However, we included a 2nd-degree polynomial transformation for tide-height, and a 2-way interaction for wind- direction. We split wind-direction into a North-South vector and an East-West vector, and included their interaction, resulting in 3 terms for wind-direction (Table 1). Transforming tide-height and wind-direction variables was necessary to adequately model the physical and behavioral phenomena of the marine-otter system. However, such transformations increased the number of parameters used to describe these variables and may have artificially inflated the contribution of tide-height and wind-direction to the goodness-of-fit statistics, regardless of the actual ecological importance of each of these 2 variables.

Visual inspection of tide-height data showed a quadratic response to the number of Sea Otters hauled-out (Fig. 6). The greatest proportion of haul outs occurred during the mid-range of tidal levels (Fig. 6), while lower and higher

TABLE 2. Results of Hierarchical Partitioning, with the independent and joint contributions of the explanatory variables of interest, as well as the percentage of their independent contributions.

Explanatory variable	Independent contribution	Joint contribution	Total contribution	Percent independent contribution	*P*-value
Tide level	8.9	22.5	31.3	8	0.000
Tide change	0.0	0.1	0.0	0	0.679
Wind speed	7.0	−2.4	4.6	6	0.000
Wind direction	0.0	2.3	2.3	0	0.687
Air temperature	33.1	43.5	76.7	29	0.000
Water temperature	33.6	51.7	85.3	30	0.000
Minimum daily water temperature minimum	30.6	53.5	84.1	27	0.000

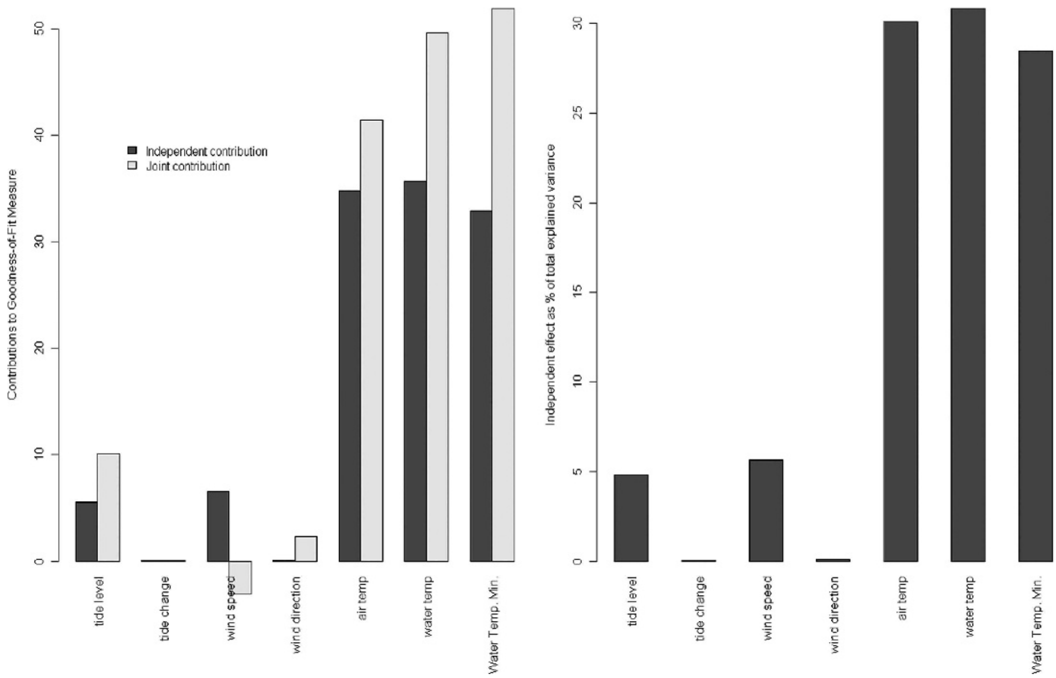

FIGURE 5. Results of the Hierarchical Partitioning analysis including 'independent' and 'joint contributions' of explanatory variables as well as the percentage of their independent contributions.

tide-heights resulted in a decline in this proportion. Tide-height also significantly contributed to the Hierarchical Partitioning of the goodness-of-fit (Table 2, Fig. 5). While the contribution of the variable Wind Speed was significant (Table 2), the variable Wind Direction contributed minimally to explaining Sea Otter haul-out patterns (Table 1 and 2).

In conclusion, both the Hierarchical Partitioning and the significance of the variables in the full-model suggested a significant effect of hourly and daily water temperatures, tide- height,

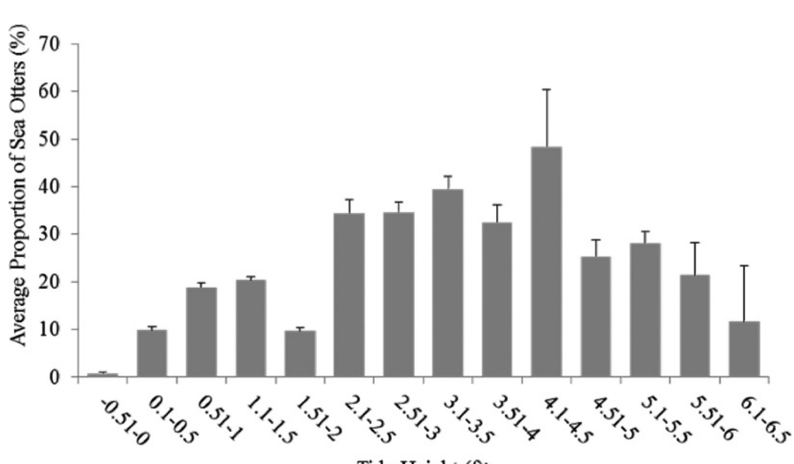

FIGURE 6. Proportion of Sea Otters hauled-out as a percent of total counted at different tide heights between August 2007 and July 2009. Bars represent the Standard Error (SE).

and wind speed on the number of Sea Otters hauled out. However, only Hierarchical Partitioning could tease out the significant contribution of decreasing air temperature to the increasing number of Sea Otters hauled out. The effect of air temperature was not adequately recognized in the full-model because of the model's inability to estimate the effects for highly collinear variables.

DISCUSSION

Haul-out behavior could be an important energy conservation mechanism for Southern Sea Otters and could compensate for limited food supplies. Haul-out behavior in other marine mammals such as Seals, Sea Lions and Walruses (*Odobenus rosmarus*) has been related to several proximal factors such as tide (Schneider and Payne 1983; Hayward and others 2006; Patterson and Acevedo-Gutierrez 2008), time of day (Beentjes 2006), wave intensity (Kovacs and others 1990), disturbance (Salter 1979; Lelli and Harris 2001), and wind chill (Andrews-Goff and others 2010).

The most significant differences we observed in Sea Otter haul-out patterns occurred between day and night. In general, Sea Otters tended to exit the harbor to forage in the Monterey Bay early in the day (Maldini and others 2010; Maldini and others, unpubl. data) and returned to the slough to rest at night. However, some resting Sea Otters were always present in the study area during the day, but were almost never on land. We believe the reason for this day–night difference was the presence of human disturbance during daytime, which caused Sea Otters to remain in the water, and that this disturbance mimicked the effects of predation by making it more costly to haul out than to spend time in the water. So the benefit of being on land during the day may not outweigh its cost. In fact, we observed that Sea Otters consistently left their land-based haul-out site at first light when the harbor became busy with human traffic and noise.

The influence of human disturbance on haul-out patterns has been documented in other marine mammals such as Walruses (Salter 1979), Harbor Seals (Suryan and Harvey 1999; Henry and Hammill 2001; Lelli and Harris 2001), Steller Sea Lions (*Eumetopias jubatus*; Thørsteinson and others 1961; Harestad 1977; Lewis 1987; Johnson and others 1989), Australian Sea Lions (*Neophoca cinerea*; Orsini 2004), New Zealand Fur Seals (*Arctocephalus forsteri*; Boren and others 2002), and South American Fur Seals (*Arctocephalus australis*; Cassini 2001). Lelli and Harris (2001) found that boat traffic was the strongest predictor of Harbor Seal haul-out numbers at a haul-out site in Maine, accounting for 27% of their variability. In Steller Sea Lions, varied responses to disturbance have been reported ranging from abandonment of haul-out sites to almost immediate recovery after disturbance (Thørsteinson and others 1961; Harestad 1977; Lewis 1987; Johnson and others 1989). In other studies, hauled-out New Zealand Fur Seals and South American Fur Seals have shown strong fleeing responses to pedestrian and boat traffic (Cassini 2001; Boren and others 2002).

Boat traffic in Moss Landing North Harbor consists mainly of kayaks, increasing between 10:00 and 14:00 and being low in mornings and evenings (Maldini and others, unpubl. data). Although we have not measured decibel levels in the area at different times of day, it was clear to observers that spent the night at the observation site that the noise level at night was substantially less than during the day. At night, highway traffic was rare (the highway is 300 m from the haul-out site). However, occasional car and pedestrian traffic in the parking lot adjacent to the observation site often caused hauled-out Sea Otters to flush into the water. Additionally, circumstantial evidence for the influence of human disturbance was provided by our observations of Seas Otters hauled out in a remote area of the slough (where access is restricted and where there is no car or boat traffic). Here, we regularly observe hauled-out Sea Otters regardless of time of day (Maldini, unpubl. data).

In the absence of disturbance, haul-out behavior may help defray high metabolic costs incurred when environmental conditions are not optimal, such as during cold winter days when storms are frequent and foraging may be more difficult in certain areas. Our results support the expectation that a larger proportion of Sea Otters would haul out when temperatures are lower both seasonally and daily, by showing an increase in the proportion of Sea Otters hauled out with decreasing air and water temperatures. The range of air and water temperatures in our data, typical for the central California coast, is below core Sea Otter body temperature, and Sea Otters naturally compensate for this by foraging (Costa and Kooyman 1982, 1984). However, Tinker and others (2008) hypothesized that Sea Otters in California may have become food limited. If foraging is not optimal, increasing energy savings by resting, as suggested by Yeates and others (2007), could be further optimized by resting on land when conditions permit. In addition, resting on land in large groups may provide extra warmth by proximity and extra protection by increased collective vigilance (Powell 1974; Lima 1995; Rands 2010). Our data showed that groups of Sea Otters tended to haul out in close proximity and in groups as large as 93 animals. Also, a reaction by 1 animal was generally followed by a collective reaction.

Tide-height also affected haul-out patterns, with Sea Otters typically hauling-out at mid-tide ranges (Fig. 5). Based on empirical observations, extremely low tides increased the distance Sea Otters had to cross to reach the water. Because Sea Otters are awkward on land, covering long distances could be disadvantageous when escaping land-based predation or disturbance. Conversely, too high a tide decreased available haul-out space on the beach (the beach is narrow and abutted by a low cliff), limiting the number of animals that could haul out.

Although the variable wind direction contributed little to explaining haul-out patterns, the location of hauled-out Sea Otters in our study area relative to wind direction is of note. The main wind direction is from the northwest and the location of the haul-out site is such that Sea Otters are sheltered from a northwesterly wind when on the beach.

Conclusions

Sea Otters may maximize their energy savings by hauling out of the water when the benefits outweigh the costs. Seasonal and daily water and air temperature fluctuations are good predictors of Sea Otter haul-out patterns; however, the patterns are affected by the availability of haul-out sites at different tide levels. The cost effectiveness of the choice to haul out may be maximal at night because of the lack of human disturbance near the haul-out site during this time of day; whereas high levels of disturbance by vessels and foot traffic have been shown to decrease the rate of Sea Otter haul out, causing Sea Otters to incur higher metabolic costs during unfavorable weather conditions and when foraging may not be optimal.

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