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Low prey abundance leads to less efficient foraging behavior in Steller sea lions

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ABSTRACT

Breath-hold divers should adjust their dive behaviors to maximize the benefits and minimize the costs of foraging on prey patches of different densities at different depths. However, few studies have quantified how animals respond to changes in prey availability (depth and density), and how this affects their foraging efficiency. We tested the effects of changes in prey availability on the foraging behavior and efficiency of Steller sea lions (*Eumetopias jubatus*) by measuring diving metabolic rate, dive durations, and food intake of 4 trained sea lions diving in the open ocean on controlled prey patches of different densities at different depths. Sea lions completed bouts of 5 consecutive dives on high- or low-density prey patches at two depths (10 m and 40 m). We found that the rate of energy expenditure did not change under any of the imposed foraging conditions (mean ± SD: 0.22 ± 0.02 kJ min^{-1} kg^{-1}), but that the proportion of time spent consuming prey increased with prey patch density due to changes in diving patterns. At both depths, sea lions spent a greater proportion of the dive bout foraging on prey patches with high prey density, which led to high rates of energy gain (4.3 ± 0.96 kJ min^{-1} kg^{-1}) and high foraging efficiency (cost:benefit was 1:20). In contrast, the sea lions spent a smaller proportion of their dive bout actively feeding on prey patches with low prey density, and consequently had a lower energetic gain (0.91 ± 0.29 kJ min^{-1} kg^{-1}) and foraging efficiency (1:4). The 5-fold differences in foraging efficiency between the two types of prey patches were greater than the 3-fold differences that we expected based on differences in food availability. Our results suggest that sea lions faced with reduced prey availability forage less efficiently and therefore would have greater difficulty obtaining their daily energy requirements.

1. Introduction

Animals should forage optimally such that they maximize net energy gain relative to the time and energy spent foraging (Charnov, 1976; Krebs, 1978; MacArthur and Pianka, 1966; McNamara, 1982). This means that foraging animals should alter their behavior to balance the energy they spend to catch prey against the energy they acquire through feeding to meet their daily energetic requirements (i.e., minimizing costs while maximizing benefits). Time spent foraging is also an important consideration, given that minimizing the time needed to acquire sufficient energy minimizes overhead costs and predation vulnerability and maximizes time available for other behaviors.

Breath-hold divers feed at depth, but must return to the surface to breathe and exchange gases. Their foraging decisions are thus constrained by their physiological ability to remain submerged, the distance between the surface and the food source, and the quality of the prey patch on which they forage. These factors impact both the time and energy spent foraging, as well as the potential energetic gains. Several long-standing models have been developed to predict how dive duration and behavior might vary in relation to the depth and abundance of prey, taking into account aspects of prey distribution and predator physiology (Carbone and Houston, 1996; Houston and Carbone, 1992; Kooyman, 1989; Kramer, 1988; Thompson and Fedak, 2001). However, none of these models have been tested experimentally.

Understanding how differences in prey distribution and abundance affects individuals is important for determining the larger-scale impacts these factors may have on the health of entire populations. Steller sea lions (*Eumetopias jubatus*), as well as several other marine mammal and bird species in the Gulf of Alaska and Bering Sea, have experienced significant population declines that may be related to reduced prey availability (Trites and Donnelly, 2003). Several studies have tested how changes in the quality or quantity of prey affect the physiology of individual sea lions (Atkinson et al., 2008; Gerlinsky et al., 2014; Jeanniard du Dot et al., 2009; Rosen and Trites, 2000, 2004; Rosen et al., 2000). However, only a few studies have investigated how such

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Abbreviations: MR_S, surface metabolic rate; AMR, average metabolic rate over a dive cycle; ADL, aerobic dive limit; cADL, calculated aerobic dive limit.

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changes in prey may also impact foraging behavior and efficiency, and how they relate to the predictions of foraging models.

Tests of foraging models on marine mammals include studies where dive behavior of wild animals have been compared to model predictions (Costa et al., 1989; Doniol-Valcroze et al., 2011; Mori and Boyd, 2004; Nolet et al., 1993; Thums et al., 2013) and controlled experiments with captive animals swimming in pools in simulated foraging conditions of varying quality (Cornick and Horning, 2003; Sparling et al., 2007). Both types of studies have examined aspects of foraging behavior, but no studies have evaluated the role that foraging energetics, including foraging efficiency, plays in formulating these observed patterns. Specifically, no studies have yet measured both the costs and benefits of a particular foraging strategy for Steller sea lions foraging at realistic depths.

Our study tested how prey depth and abundance affect dive behavior and foraging efficiency by measuring diving metabolic rate, dive behavior, and food intake of 4 trained Steller sea lions diving in the open ocean on simulated prey patches of different densities at different depths. We thus empirically tested optimal foraging models for breath-hold divers by measuring energy gain and expenditure for animals diving in realistic conditions. Our results provide insights into the foraging success and bioenergetic consequences of Steller sea lions in the wild faced with changes in prey availability, as well as the implications this may have for population recovery.

2. Materials and methods

2.1. Data collection

We measured changes in dive behavior, metabolic expenditure, and energy intake in 4 adult female Steller sea lions diving in simulated prey patches of varying qualities. Data were collected between June and August 2013. Two sea lions were 13 years old and two were 16 years old and weighed between 163 and 239 kg at the time of the trials. All animals were collected from rookeries as pups, and were raised at the Vancouver Aquarium (Vancouver, BC, Canada). The sea lions were subsequently housed at the University of British Columbia's Open Water Research Station (Port Moody, BC, Canada) for 4–8 years, where they regularly dove in the open ocean for research purposes. The sea lions were previously trained to be familiar with the experimental equipment and protocols and all trials were performed voluntarily under trainer control. Experiments were conducted under UBC Animal Care Permit #A11-0397.

2.2. Diving metabolic rate

We measured diving metabolic rate via flow-through gas respirometry with the sea lions diving in a variety of imposed foraging conditions (see below). Metabolic rate was measured in a 100 L clear Plexiglas dome floating on the surface of the water. Air was drawn through the dome at a rate of 475 L min^{-1}. The excurrent air was continuously sub-sampled and scrubbed of water vapor via $CaSO_4$. Concentrations of oxygen and carbon dioxide were measured using Sable System FC-1B and CA-1B analyzers, coupled to a 500H mass flow generator and controller (Sable Systems, Las Vegas, NV, USA). Oxygen and carbon dioxide concentrations were recorded every 0.5 s (Sable Data Acquisition system, Sable Systems Inc.). Metabolic data was analyzed using LabAnalyst X (Warthog Systems, Mark Chappell, University of California) and oxygen consumption rates were calculated from changes in gas concentrations from baseline levels (using eq. 3b, Withers, 1977). Baseline gas concentrations were set using ambient air at the start and end of the trial to correct for drift during trials. The entire system was periodically calibrated with gases of known concentrations.

Pre-dive metabolic rate (MR_S) was measured for animals resting calmly at the surface in the metabolic dome before each dive trial. MR_S was calculated as the average rate of oxygen consumption during the last 2 min of a 5–10 minute period, during which oxygen concentrations were stable. Post-dive rates of oxygen consumption were measured to calculate oxygen consumed during the dive and to determine the amount of time it took to return to within 5% of MR_S (recovery time).

Average metabolic rate during the dive (AMR) was calculated as the total volume of oxygen consumed during a dive cycle, divided by the total dive cycle duration. A dive cycle was defined to begin with the first dive and end with the completion of the post-dive recovery, and includes all dives, inter-dive surface intervals in a bout, and the full post-dive recovery period. Thus, AMR accounts for all of the time and energy associated with a complete foraging bout, including the time spent at the surface as well as diving.

2.3. Trial protocol

The sea lions were trained to voluntarily dive between the metabolic dome at the surface and the end of two feeding tubes at depth, set either at 10 or 40 m. These depths were representative of dive depths observed in wild Steller sea lions (Merrick and Loughlin, 1997). During dives, 20 g pieces of Pacific herring (*Clupea pallasii*) were delivered to the sea lions at depth via the feeding tubes. Fish were alternately pumped out of each feeding tube to encourage movement between the tubes. Sea lions swam continually back and forth between the feeding tubes and consumed the fish pieces immediately as they came out of the tubes. Feeding was continuous and constant until after the animal chose to leave the bottom and resurface. This was monitored via a camera mounted on the feed tube. The rate of fish delivery was altered between trial types to simulate prey patches of different densities; prey delivery rates of 12 fish pieces per minute were used as the “high-density patches” and 4 fish pieces per minute as the “low-density patches”. Each animal completed three trials of each prey rate and dive depth combination, for a total of 48 dive trials under 4 different foraging conditions.

Animals were fasted overnight before trials and transported to the dive site by boat. During transport and measurements of pre-dive surface metabolic rates they received minimal food reinforcement (<0.8 kg) to reduce the potential impact of digestion on metabolic rate (Rosen and Trites, 1997). Sea lions performed bouts of 5 consecutive dives, wherein they chose both dive duration and inter-dive surface intervals. The sea lions were fed <0.2 kg during each surface interval to reinforce surfacing in the dome while minimizing the influence of the food at the surface on dive behavior. Each animal was outfitted with a tight-fitting harness holding a time depth recorder (ReefNet, Inc., Mississauga, ON, Canada) to record dive behavior. Total dive durations were measured as the time from when the animal left the metabolic dome to when the animal returned to the surface. Surface times were measured as the time spent in the metabolic dome between dives. Bottom and transit durations were extracted from the data on the time depth recorders.

2.4. Foraging efficiency

We calculated foraging efficiency in each of the four imposed foraging conditions using the equation from Weathers and Sullivan (1991):

$$\text{Mean gross foraging efficiency} = \frac{\text{energy intake}}{\text{energy expended}}.$$

Foraging efficiency thus represents the amount of energy gained, in kilojoules (kJ), for every kilojoule expended. Assuming that all fish