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Note to reader: The following annotated bibliographies are organized in an order that addresses foraging behaviour of sea otters (*Enhydra lutris*) from proximate to ultimate causes. The underlying small-scale physiological and developmental mechanisms of foraging are described first, followed by larger-scale proximate causes of behaviour that encode the species' evolution and life history traits.

Reference:

Carss, D. (1995). Foraging behaviour and feeding ecology of the otter *Lutra lutra*: A selective review. *Hystrix, the Italian Journal of Mammalogy*, 7(1-2), 179-194. https://doi.org/10.4404/hystrix-7.1-2-4069

Summary:

Sea otters (*Enhydra lutris*, previously known as *Lutra lutra*,) are known to have diverse diets, foraging habitats, and a complex social system. This review article summarizes the prior knowledge of this species' foraging behavior and the feeding ecology of both adults and juveniles, as well as gaps in knowledge of how foraging efforts corelate to maternal-juvenile interactions during dependency periods. There are three objectives to this review: summarize recent advances in foraging behavior and feeding ecology, highlight gaps in knowledge in foraging-feeding behaviors, and implement a push to direct further research on this species' predator-prey relationships for conservation management. The review outlined the ontogeny of foraging behavior, based on observational trends of foraging distribution and diet. This revealed varying abilities of foraging performance and food choices amongst individuals that were age dependent. It was also concluded that foraging techniques must be learned through intensive learning from the mother early in life, which helped explain the long periods of parental care in sea otters. There is more research that needs to be done to assess the social organization of this species that affect varying levels of foraging efficiency. This paper emphasized a refinement of assessing diet through spraint analysis, analyzing the diet of sea otters over a short period of time. This method measures the frequency of occurrence of each food source. It was deemed reasonable to provide a general overview of diet, however, this technique often carries an unknown accuracy of estimates, suggesting unreliability. Overall, this paper highlights the need for more refined and rigorous studies of sea otters in conservation ecology and assembling wetland habitat mosaics, even with significant findings of otter foraging behaviors previously.

Contribution:

This review contributes to the science community by highlighting techniques used in the assessment of foraging behavior and suggesting a push towards technique refinement to assess foraging behavior and feeding ecology of sea otters for conservation management. This was included in my literature review to outline all known levels of social organization in maternal-juvenile relationships and studied foraging strategies amongst various age groups. Additionally, this review article outlined the various gaps in knowledge and techniques when assessing foraging behavior linked to parental care in the otter, which help highlight potential areas of research.

Reference:

Bodkin, J. L., Esslinger, G. G., & Monson, D. H. (2004). Foraging depths of sea otters and implications to coastal marine communities. *Marine Mammal Science*, *20*(2), 305–321. https://doi.org/10.1111/j.1748-7692.2004.tb01159.x

Summary:

Sea otters (*Enhydra lutris)* forage primarily on benthic invertebrates, organisms that live on the surface of ocean bedforms. As they bring their prey to surface of the water for handling and consumption, their dive function can be identified. Previously, diving behaviour related to sea otter foraging has been observed by scuba divers in water depths within ten meters. However, this does not cover the full depth and extent where foraging dives take place. The objectives of this study were to classify sea otter dives by function (travel or foraging dive), describe dive attributes (ascent/descent rates, mean dive depths, dive duration), and explore the distribution of sea otter foraging dive depths. The shore along Port Althorp, Alaska was selected as the study site, which provided sea otters with a range of water depths within their diving abilities, from zero to 200 meters. The sample size included a total of 14 individuals (nine female, five male) that were surgically implanted with a radio transmitter to track location, and a time depth recorder (TDR) to record dive time and depth. The number of dives decreased as deeper dives took place, suggesting greater chances of catching prey with increased depth. This presents the need for research that examines energy expenditure with respect to dive depth, to clarify relations between dive depth and the number of dives taken. Individuals with greater body mass had deeper dive depths, suggesting that sexual dimorphism that led to differences in body weight affected an individual's foraging technique. The use of TDR technologies can be explored in future studies to develop models to better understand trends to increased foraging success and selection for prey type.

Contribution:

This article was selected to understand the effects of sexual dimorphism, body condition and individual foraging strategy on foraging behaviour. As the first study to employ TDR technology to quantify dive depth and time relations beyond an observable range, the classification of unknown dive types through time and depth was now discretely classified through a new standardized method. This study highlights potential for further research, such as how gathering information on foraging energetics and success will clarify the correlation between foraging dive time and depth, to develop models that outline prey type and foraging success.

Reference:

Payne, S. F., & Jameson, R. J. (1984). Early behavioral development of the sea otter, *Enhydra lutris*. *Journal of Mammalogy*, *65*(3), 527–531. https://doi.org/10.2307/1381114

Summary:

Previous analysis of maternal sea otter (*Enhydra lutris*) behaviour has provided descriptions and quantification of daily activity budgets in maternal care and pup development. However, the behaviour of juvenile sea otters has not been studied with pups of known age. The objective of this study is to quantify the early ontogeny of sea otters, providing researchers with a method to estimate and determine juvenile age. This study was conducted observationally, via observation from the study site shore with binoculars and telescopes. The sample size consisted of fifteen pups from the Californian coast, who were tagged to allow for reidentification. Young pups are distinguishable from adult sea otters by their outer coat colour. Young pups are seen to transition from resting to active swimming at four to five weeks of age. By six weeks of age, pup independence is achieved, through observations of independent swimming to the mother, soliciting of solid food in their diet, and successful foraging dives comparable to an adult sea otter. Tool use became first evident at five weeks of age. By nineteen to twenty weeks of age, successful tool use is observed in cracking open snails. Nocturnal foraging was not observed in this study, but previous studies have shown that this technique is most valuable and common in maternal foraging. Ontogenetic data from this study concluded a dependency period of six to seven weeks, a slightly shorter period that those recorded in previous studies. Future directives could examine trends inferred by this study, checking for reliability and consistency. Ultimately, there must be more insight on pup dependency periods and inference on how replicable these foraging behaviours are in other otter populations.

Contribution:

This article provided a summary of foraging behavioural trends in maternal and juvenile sea otters (*Enhydra lutris*), which has rarely been studied. Observational trends on tool use were relevant my literature review, as I explore all forms of foraging behaviour. A new method of estimating juvenile age was conducted by recording correlations known-age individuals to its early ontogeny. Ontogenetic data in previous studies showed variation when describing durations of dependency periods in pups, to which this study further examined. Further research could implement a technologically enhanced study design beyond human observation to better understand maternal and juvenile foraging behaviour.

Reference:

Ostfeld, R. S. (1982). Foraging strategies and prey switching in the California sea otter. *Oecologia*, *53*(2), 170–178. http://doi.org/10.1007/bf00545660

Summary:

Sea otters (*Enhydra lutris)* have a single motivation when selecting prey and are highly asocial when foraging. Their diet undergoes rapid changes when they first encounter a new foraging ground, before diversifying and stabilizing their prey. Sea otters are known to be generalized predators, meaning that have a strong preference for one food to which they deplete before choosing another food choice. This study addresses common foraging strategies and prey switching trends of sea otters, and whether observations from this study follow previously developed optimal foraging theories. Results from this study were recorded through observations of foraging and feeding behaviour on a kelp (*Macrocystis pyrifera*) forest shore east of Point Santa Cruz, California. Feeding patterns were observed through a spotting telescope from shore, via continuous sampling of one focal individual. Results from this observational study revealed that sea urchins were highly selected for in their initial diet. This suggests a preference for sea otters to consume the food source with the highest energy intake per unit of foraging time, as predicted by trends of optimal foraging theory. There was a strong correlation of dietary switching with foraging success rate: as they choose a rarer prey species, poorer foraging success rates will follow, leading them choose another prey species. This is evidence of search image formation and patch selection working simultaneously.

Contribution:

This paper was selected for review to outline the foundational concepts of sea otter foraging strategies and diet specialization. Previous laboratory studies have displayed trends of optimal foraging theory, but this is the first study to be conducted in a free-living environment. Their preference to replace their next ranked food source after depletion of the primary food choice is consistent with previous studies surrounding this theory. The effects of diet specialization on sea urchins have increased species diversity of kelp forests in Alaska, though future research could examine if Californian kelp forests will yield similar results.

Reference:

Esslinger, G. G., Bodkin, J. L., Breton, A. R., Burns, J. M., & Monson, D. H. (2014). Temporal patterns in the foraging behavior of sea otters in Alaska. *The Journal of Wildlife Management*, *78*(4), 689–700. http://doi.org/10.1002/jwmg.701

Summary:

The foraging efforts of sea otters (*Enhydra lutris*) is density-dependent response that is often used to assess the status of predator population status, in relation to resource limitation or carrying capacity. Previous studies have shown that sea otters have varying activity patterns that are affected by weather conditions, reproductive status, and time of day. As sea otters feed on benthic prey, all diving behaviour is described as a direct effort to forage. The objective of the study was to describe patterns of foraging behaviour and the effects of reproductive status and environmental conditions on activity budgets. Time-depth recorders (TDRs) were implanted into nineteen sea otters (fifteen female, four male) from Prince William Sound, Alaska. This study aimed to examine how foraging effort varies across time, how foraging efforts varied amongst individuals, and if environmental conditions affected daily foraging activities of females caring for pups. The results of the study revealed a preference for sea otters to forage more during the day, adjusting foraging efforts to relative amounts of available daylight. Post-partum females were the only group to be found foraging at night, likely to avoid predation of pups by eagles. Multi-level mixed regression models were used to assess the contribution of environmental factors to variation in daily activity budgets. There was a small percentage of variance quantified from this model, meaning foraging efforts were consistent amongst the population. However, this raises the question of how variation in foraging efforts could be detected if analysis was done on time scales that considered periods of time (hours or days) of known biological rhythms. This study reveals the importance of considering environmental and reproductive effects when population status is being assessed by using activity budgets.

Contribution:

This study provided further insight on sea otter foraging using activity patterns and temporal scales, which was useful to understand how density-dependent sources cause variation in foraging effort amongst individuals. Estimates for temporal trends of foraging in female sea otters were consistent with previous studies on populations on neighbouring islands. Previously, the extent to which weather conditions, reproductive status, and time of day affect activity patterns in sea otters remained unclear. This study was the first to assess and examine the impact these factors have when using activity budgets to assess the carrying capacity of a population.

Reference:

Thometz, N. M., Tinker, M. T., Staedler, M. M., Mayer, K. A., & Williams, T. M. (2014). Energetic demands of immature sea otters from birth to weaning: Implications for maternal costs, reproductive behavior and population-level trends. *Journal of Experimental Biology*, *217*(12), 2053–2061. https://doi.org/10.1242/jeb.099739

Summary:

Sea otters (*Enhydra lutris)* have the highest mass-specific metabolic rate of any marine mammal. They are known as extreme income breeders, who must forage throughout lactation, even with minimal energy reserves. This article was written to assess the energetic demands of lactation in maternal sea otters and of immature sea otters who require maternal care prior to becoming independent. To assess oxygen consumption of various age classes, seven wild sea otters placed into captivity were measured for their activity levels in both in-air and in-water conditions. Unweaned pups were found to have the highest consumption of oxygen, due to increased energy demands. The daily-activity budgets of 26 free-ranging sea otters were measured and compared between different age groups. Older individuals spent more time doing energetically expensive behaviors such as swimming and foraging, while young individuals invested more in grooming. Field metabolic rate (FMR) was measured to categorize metabolic rates by developmental stages. Weaned pups had the greatest FMR, mostly due to swimming and foraging for food, shortly after maternal care ended. Additionally, this study further confirmed a previous study, where high energetic demands of maternal investment led to decreased body mass, condition, and life expectancy for adult females' post-lactation. This study could aid in future scientific research on the implications of sea otter life-history decisions, population dynamics, and parental provisioning strategies.

Contribution:

This article provides a detailed description of the metabolic demands of sea otter pups and is the first evaluation of developmental and maternal investment costs for sea otters (*Enhydra lutris)*. This study quantified the energetic demands of pups in five developmental stages, to assess the varying energetic challenges mothers face in pup rearing periods that contribute to their poor maternal condition. This is particularly relevant to my study of interest by means of how maternal foraging behaviour influence trends of parental dependency periods.

Reference:

Yeates, L. C., Williams, T. M., & Fink, T. L. (2007). Diving and foraging energetics of the smallest marine mammal, the sea otter (*Enhydra lutris*). *Journal of Experimental Biology*, *210*(11), 1960–1970. http://doi.org/10.1242/jeb.02767

Summary:

Sea otters (*Enhydra lutris*) are the smallest and most recently evolved marine mammals. They face large costs associated with foraging and daily energy budgets due to their small size and lack aquatic adaptations due to their recent evolutionary lineage to the marine environment. This study aimed to examine the effects these challenges have on sea otter energetics, by measuring the energetics of foraging, diving, resting, and grooming in captive and free-ranging adult males. Activity patterns and dive duration measurements were collected for wild sea otters through field observations on the coastline of Point Piedras Blancas, California. Metabolic measurements assessed aerobic and anaerobic diving costs of captive sea otters in a laboratory setting at the University of California. A clear acrylic dome was placed on top of the surface of water, in which captive sea otters foraged under. This method, known as open flow respirometry, assessed levels of oxygen consumption and energetics when exhibiting various foraging behaviours. Together, these results were standardized with activity budgets measured in wild sea otter populations to determine field metabolic rates (FMR). Results from this study revealed an increase in FMR when foraging occurred in submergence of water. Foraging dives of sea otters were twice as costly compared to phocid seals, due to their locomotive and swimming abilities, but most of their time was spent resting and feeding. When the mean FMR across all behaviours were quantified, FMR values matched with other marine mammals ranging in body sizes. This revealed the presence of counterbalancing behaviours that allow for high foraging costs to be mitigated by prolonged periods of time resting on the water surface.

Contribution:

This study was selected as it provided knowledge on the effects of evolutionary lineage on foraging adaptations that determine sea otter survival. Previously, the daily energetic balance of larger marine mammals, such as seals, have been studied. This study was the first to compare sea otter energetics to previous studies and revealed new knowledge on how energetically costly behaviours of sea otters are counterbalanced by increased resting behaviours. However, it is still unclear if the mechanisms of oxygen conservation used by other marine mammals are also present in sea otters.

Reference:

Cortez, M., Wolt, R., Gelwick, F., Osterrieder, S. K., & Davis, R. W. (2016). Development of an altricial mammal at sea: I. Activity budgets of female sea otters and their pups in Simpson Bay, Alaska. *Journal of Experimental Marine Biology and Ecology*, *481*, 71–80. https://doi.org/10.1016/j.jembe.2015.05.020

Summary:

Parental care is a requirement for the survival of most mammals and is especially important for newborn sea otters (*Enhydra lutris*), who require the help of their mother for predatory protection and feeding. This study examines the behaviour of female sea otters and their young in their first three months postpartum. A population of sea otters were present at Simpson Bay, Alaska at the time of the study; a site that provided sea otters protection from rough seas and easy access for researchers to observe their behaviour. Full-day (24-hour) activity budgets were generated both mothers and their young. Young were grouped into three categories: C1 (0-4 weeks of age), C2 (4-8 weeks of age), and C3 (8-12 weeks of age), and their activity budgets were determined. Results obtained from both boat and shore observations revealed changes in pup and maternal behaviour throughout pup development. Foraging efforts from the mother increased as pups aged, reflecting the increased nutritional need of pups as they grew bigger in size. Swimming behaviour in the mother to protect her young decreased as pups moved from C1 to C3 groups, as their predation risk decreased. The time spent nursing and resting by mothers remained constant, and independent of pup category. As pups matured, they spent less time resting, and more time swimming and foraging, likely due to increased strength and independence. This study quantitively described changes in the activity patterns of mothers and their young, as they go through critical stages of their development. Behaviours displayed by the mother early in development are all in response to survival threats, until pups can develop their own survival behaviours.

Contribution:

This study was selected, as obtaining knowledge on how foraging behaviour in sea otters evolve over the course of development is required to fully understand how these behaviours are maintained in their lifetime. This study is the first to explain how activity patterns and energy budgets vary with age. However, it is not fully understood how the metabolic requirements of the mother can be met, with so much time invested in protecting their young. Future research could also examine how energy budgets vary by season, as they face variation in weather conditions and different periods of their reproductive cycle.

Reference:

Thometz, N. M., Staedler, M. M., Tomoleoni, J. A., Bodkin, J. L., Bentall, G. B., & Tinker, M. T. (2016). Trade-offs between energy maximization and parental care in a central place forager, the sea otter. *Behavioral Ecology*, *27*(5), 1552–1566. https://doi.org/10.1093/beheco/arw089

Summary:

Sea otters (*Enhydra lutris*) are central place foragers, moving between resources of water and air. They capture prey in foraging patches in bodies of water, but return to the shore, known as the central place, to consume their prey and replenish their oxygen intake. Prey resource availability is the most important factor that limits sea otter population growth. However, mothers who invest in parental care are unable to respond to resource limitation that will maximize their energy intake. Previous studies have found differences in diving ability and parental investment between sexes that led to distinct foraging behaviours. The study objective of this article was to examine how foraging behaviour and habitat use in sea otters is influenced by the factors of reproductive constraints and prey availability. Data from 126 time-depth recorders (TDRs) were implanted into the sea otters over a span of 15 years and placed in five study sites along the Californian west coast that span various levels of prey availability. Results show a strong correlation of high fitness to energy maximization when foraging. However, foraging tactics amongst females with or without pups and between sexes differed. Females with pups did not dive as deep or as long to find food compared to males and females without pups. This suggests that pup care acts as a constraint of foraging behaviour, and mothers must face a trade-off between individual energy maximization and pup care to ensure their survival. Additionally, sea otters forage in deeper depths of water when prey resources become depleted. In all levels of resource availability, females with large pups increase their foraging efforts over pup care, even when under energetic constraints. Increased sensitivity to resource limitation in females with pups raises questions of how foraging behaviour may impact life-history decisions, population dynamics, and evolutionary trends.

Contribution:

This study was chosen in my literature review to examine how foraging behaviour can be influenced by prey availability and reproductive constraints. This study is the first to examine how diving and foraging behaviour is influenced by parental investment, sex, and prey availability. The results of the study support previous foraging theory, where energy maximization is the determinant of fitness. The study also brings new understanding of the trade-offs that occur between pup care and energy maximizing in females with pups. The extent to which these trade-offs occur can be further examined to produce models surrounding survivorship and population dynamics.

Reference:

Osterrieder, S. K., & Davis, R. W. (2009). Summer foraging behaviour of female sea otters (*Enhydra lutris*) with pups in Simpson Bay, Alaska. *Aquatic Mammals*, *35*(4), 481–489. http://doi.org/10.1578/am.35.4.2009.481

Summary:

Sea otter (*Enhydra lutris)* pups are dependent on their mothers for their survival for approximately five to six months. Their maternal-pup bond is necessary to acquire grooming and foraging skills. Females with pups must be able to sustain their own energetics, even when providing for pups. The shore of Simpson Bay, Alaska was chosen to be the study site of the study, a location that presents a manageable reliable population of sea otters, and easy to use observation sites. The objective of the study was to examine diving behaviour of females with pups in various age categories, and the effects this has on foraging technique. Researchers observed sea otters using binoculars from the study site, without approaching the individuals. When a foraging leap into the water was observed, the dive duration of the individual was recorded. Researchers also noted landmarks to which the individuals dived to, and used an instrument known as a bathymeter, to measure the depth of water at the landmark. Results from the study concluded no significance difference in foraging depths based on pup age but revealed an increase in dive duration with increasing pup age. Increased dive durations yield higher proportions of catching prey, necessary for larger pups. Females displayed a bimodal foraging strategy: mothers with young pups preferred shallow foraging depths, while mothers with larger pups preferred deeper foraging depths. Increased deep water feeding leads to higher caloric content of prey, beneficial for the survivorship of larger pups. This study highlights the need for further research to quantify available prey and caloric content with respect to water depth, and variation in habitat.

Contribution:

This article was selected to highlight foraging behaviours present in maternal-pup bonding and care. This is the first study to examine mother-pup foraging behaviour in Simpson Bay, Alaska, and how foraging depth is dependent on pup age. The preference for deeper diving depths in mothers with larger pups to obtain high caloric prey has not been quantified. Additionally, there is no data on the size, distribution, biomass, abundance, and depths of prey species in the Simpson Bay region. It is evident that this region could be a valuable study site in further research of sea otter foraging and population trends.