Interacting Physiological Constraints to Foraging Behavior in Marine Mammals

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Introduction

Marine mammals face distinct environmental conditions that can translate into unique physiological challenges. Studies of foraging behavior in marine (diving) mammals have primarily focused on how the physiological constraint of aerobic dive limits defines their strategies. However, there are other physiological constraints that shape foraging patterns in marine mammals that are often neglected. This paper discusses the interaction of three broad physiological processes that impose limitations on foraging patterns: the physiological demands of prey acquisition (foraging), prey processing (digestion), and thermoregulation. The theoretical framework presented in Figure 1 (and detailed below) allows us to review and synthesize the complex physiological interactions that shape foraging behavior at the individual level. Observed foraging behavior is an integration of a multitude of competing demands on an animal. The aim of this framework is to enhance our understanding of these processes and direct areas of future research.

Framework details

1. Prey acquisition is limited by the amount of time that an animal can spend foraging. The amount of time a marine mammal can spend at depth actively pursuing prey during a single dive, the frequency of those dives, and the inter-dive and post-dive recovery periods, are all related to its aerobic dive limit (ADL) (Costa et al. 2001). ADLs therefore represent a critical constraint to foraging behavior (Castellini 1991). An individual's ADL is dependent on internal oxygen stores, and is decreased by increased metabolic demands (metabolic overhead).

2. Prey processing is limited by the animal's physiological maximum capacity for consumption and digestion, and the amount of time that can be devoted to digesting acquired prey. Digestive constraints represent a finite limitation on the rate of energy intake (Karasov & Diamond 1988; Kirkwood 1983; Weiner 1992). Digestive capacity (sometimes referred to as "consumption capacity") is the amount of food that an animal can process over a sustained period. This rate is limited by two factors: the instantaneous content of the gastrointestinal tract ("gut capacity") and the mean length of time food takes to pass through the tract ("retention time"). Digestive capacity is therefore maximized when gut capacity is maximized and retention time is minimized (Altmann 1998).

Given sufficient decreases in the nutritional quality or availability of prey (or available foraging time), the required level of food intake will be greater than the digestive capacity of the animal. An alternate strategy (or an inevitable result) is for the animal to catabolise body tissues to fulfill energetic deficits. Therefore, maximizing prey quality is not just a strategy for minimizing foraging time but also a strategy for ensuring energy balance before digestive capacity is reached.

3. Foraging time and digestion time may be mutually exclusive activities, either due to behavioral or physiological constraints. This disjunction may result from incompatible circulatory adjustments required to maximize the efficiency of diving and digestion. The hypometabolism and vasoconstriction typical of longer, deeper dives (Castellini 1991) will limit blood flow to the digestive tract and suspend digestive processes. This physiological incompatibility of foraging and digestion can lead to behavioral partitions (Crocker et al. 1997).

4. The heat increment of feeding (Blaxter 1989) associated with digestion will potentially decrease foraging efficiency by increasing metabolic overhead during dives. This increased metabolism will result in decreased aerobic dive limits.

5. The amount and quality of food digested will directly affect the animal’s subsequent energy balance.

6. Energy deficits will result in catabolism of body structures. The anatomical source of that mass loss can be almost as important as the degree of tissue loss. The preferential utilization of either lipid or protein sources under certain conditions not only results in changes in relative body condition, but also reflects physiological ‘decisions’ resulting from numerous conflicting requirements and constraints. In marine mammals the preferential utilization of lipid reserves (Øritsland 1990) will lead to a decrease in body condition (see review in Castellini & Rea 1992).

7. The hypodermal lipid layer in marine mammals serves the dual (often contrary) role of energy reserve and thermoregulatory organ. If the lipid blubber layer is depleted too much due to energy deficits, the animal will have to contend with increased thermoregulatory costs.

8. Increased thermoregulatory costs will lead to an increased energy deficit. This can contribute to the onset of a downward spiral of reduced body condition and increased energy deficit, until thermal balance can no longer be maintained. Most studies of the direct thermoregulatory costs of changes in lipid mass have been completed on young phocid seals. Bioenergetic modeling can provide a vehicle to examine some of the constraints on thermoregulation that are otherwise difficult to collect on free-ranging animals (Hokkanen 1990; Kvadsheim et al. 1997).

9. Changes in relative body condition will also affect the animal’s buoyancy and swimming biomechanics.

10. Increased thermal costs will directly increase the total cost of locomotion. Additionally, the circulatory changes required for thermoregulation and diving may be in physiological conflict. Vasoconstriction during diving may limit heat dissipation abilities (Whittow 1987).

Animals may decrease heat flow to thermal windows during submergence and increase blood flow to peripheral sites after exercise in an effort to maximize heat dissipation rates (Noren et al. 1999; Williams et al. 1999). These studies suggest that the majority of heat dissipation is deferred until animals surface, thereby maximizing the oxygen-sparing mechanisms associated with diving. This may be limited by increases in body temperature observed during swimming in some species.

Conversely, the heat generated through muscular activity may serve to offset thermoregulatory costs. The importance of heat generated by muscular activity for offsetting thermoregulatory costs has been demonstrated in a range of homeotherms. Studies have suggested that the level of thermal substitution varies with levels of activity (heat production) and rates of potential heat loss (Hind & Gurney 1997; Williams 1986).Thermal substitution of heat from activity may not be possible in many cases. Decreases in metabolism during diving (Hastie et al. in press; Hurley & Costa 2001; Sparling & Fedak 2004) would limit the potential for this type of interaction.

11. Changes in buoyancy and gait can alter the metabolic cost of locomotion and diving. Changes in gait (active strokes or gliding) are one strategy that animals use to optimize locomotion, but its effectiveness depends partly on the relative buoyancy of the animal in the medium (Biuw et al. 2003; Webb et al. 1998). Changes in swimming costs resulting from changes in body tissues can serve to decrease the aerobic dive limit, limit dive time, and decrease foraging efficiency through increased oxygen depletion rates.

12. Increases in diving costs will also increase the amount of total energy that the animal requires. This, in turn, feeds back into the amount of foraging activity or the degree of tissue catabolism required.

13. The heat increment of feeding generated during digestion may help to offset thermoregulatory demands. Homeotherms might be able to utilize the increase in heat production from digestion to offset concurrent thermoregulatory costs (Kleiber 1975; Lavigne et al. 1982). While there is evidence to support thermal substitution among some aquatic mammals, other experiments have failed to support this hypothesis (reviewed in Rosen & Trites 2003). To some extent, the circulatory alterations required to maximize thermoregulation and digestion may be in conflict.

Literature Cited

Altmann, S. A. 1998. *Foraging for survival: yearling baboons in Africa*. Chicago, IL: University of Chicago Press.

Biuw, M., McConnell, B., Bradshaw, C. J. A., Burton, H. & Fedak, M. 2003. Blubber and buoyancy: monitoring the body condition of free-ranging seals using simple dive characteristics. J. exp. Biol. 206, 3405-3423.

Blaxter, K. 1989. *Energy Metabolism in Animals and Man*. Cambridge: Cambridge University Press.

Castellini, M. A. 1991. The biology of diving mammals: Behavioral, physiological, and biochemical limits. Adv. Compar. Environ. Physiol. 8, 105-134.

Castellini, M. A. & Rea, L. D. 1992. The biochemistry of natural fasting at its limits. Experientia 48, 575-582.

Costa, D. P., Gales, N. J. & Goebel, M. E. 2001. Aerobic dive limit: how often does it occur in nature? Comp. Biochem. Physiol. A 129, 771-783.

Crocker, D. E., LeBoeuf, B. J. & Costa, D. P. 1997. Drift diving in female northern elephant seals: Implications for food processing. Can. J. Zool. 75, 27-39.

Hastie, G. D., Rosen, D. A. S. & Trites, A. W. in press. Oxygen consumption decreases during dives by Steller sea lions (*Eumetopias jubatus*). Mar. Mamm. Sci.

Hind, A. T. & Gurney, W. S. C. 1997. The metabolic cost of swimming in marine homeotherms. J. exp. Biol. 200, 531-542.

Hokkanen, J. E. I. 1990. Temperature regulation of marine mammals. J. theor. Biol. 145, 465-486.

Hurley, J. A. & Costa, D. P. 2001. Standard metabolic rate at the surface and during trained submersions in adult California sea lions (*Zalophus californianus*). J. exp. Biol. 204, 3273-3281.

Karasov, W. H. & Diamond, J. 1988. Interplay between physiology and ecology in digestion. BioScience 38, 602-611.

Kirkwood, J. K. 1983. A limit to metabolisable energy intake in mammals and birds. Comp. Biochem. Physiol. A 75, 1-3.

Kleiber, M. 1975. *The Fire of Life: An Introduction to Animal Energetics*. New York: Robert E. Krieger Publ. Co.

Kvadsheim, P. H., Gotaas, A. R. L., Folkow, L. P. & Blix, A. S. 1997. An experimental validation of heat loss models for marine mammals. J. theor. Biol. 184, 15-23.

Lavigne, D. M., Barchard, W., Innes, S. & Øritsland, N. A. 1982. Pinniped bioenergetics. In *Mammals in the Seas*, vol. IV, pp. 191-235. Rome: FAO.

Noren, D. P., Williams, T. M., Berry, P. & Butler, E. 1999. Thermoregulation during swimming and diving in bottlenose dolphins, *Tursiops truncatus*. J. Comp. Physiol. B 169, 93-99.

Øritsland, N. A. 1990. Starvation survival and body composition in mammals with particular reference to *Homo sapiens*. B Math Biol 52, 643-655.

Rosen, D. A. S. & Trites, A. W. 2003. No evidence for bioenergetic interaction between digestion and thermoregulation in Steller sea lions, *Eumetopias jubatus*. Physiol. Biochem. Zool. 76, 899-906.

Sparling, C. E. & Fedak, M. 2004. Metabolic rates of captive grey seals during voluntary diving. J. exp. Biol. 207, 1615-1624.

Webb, P. M., Crocker, D. E., Blackwell, S. B., Costa, D. P. & Le Boeuf, B. J. 1998. Effects of buoyancy on the diving behavior of northern elephant seals. J. exp. Biol. 201, 2349-2358.

Weiner, J. 1992. Physiological limits to sustainable energy budgets in birds and mammals: Ecological implications. Trends Ecol. Evol. 7, 384-388.

Whittow, G. C. 1987. Thermoregulatory adaptations in marine mammals: interacting effects of exercise and body mass. A review. Mar. Mamm. Sci. 3, 220-241.

Williams, T. M. 1986. Thermoregulation of the North American mink during rest and activity in the aquatic environment. Physiol. Zool. 59, 293-305.

Williams, T. M., Noren, D. P., Berry, P., Estes, J. A., Allison, C. & Kirtland, J. 1999. The diving physiology of bottlenose dolphins (*Tursiops truncatus*). III. Thermoregulation at depth. J. exp. Biol. 202, 2763-2769.

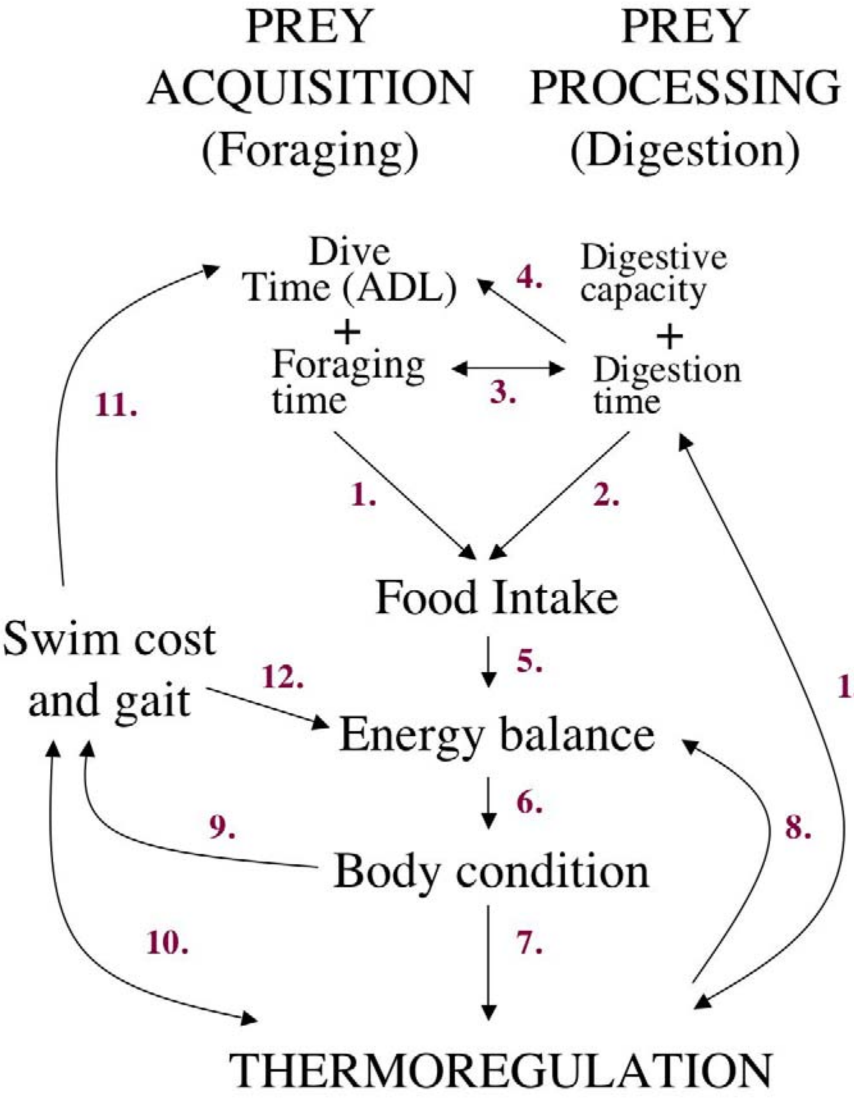

Figure 1. Schematic of the interactions between the processes of prey acquisition, prey processing, and thermoregulation.