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Heat Increment of Feeding in Steller Sea Lions, *Eumetopias jubatus*

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ABSTRACT. The heat increment of feeding (HIF) was measured in six captive, juvenile Steller sea lions (*Eumetopias jubatus*), fed meals of either 2 or 4 kg of herring. HIF was calculated as the post-prandial increase in metabolism above baseline levels, and was measured using open-circuit (gas) respirometry. It averaged 12.4 ± 0.9% (SE) of ingested energy intake for the 4-kg meal trials, and 9.9 ± 0.9% for the 2-kg meal size. The effect lasted 8–10 hr for the larger meal size. Metabolism peaked 3.7 hr after feeding, and was 2.13 times higher than baseline levels. For the 2-kg meal size, the effect lasted 6–8 hr, with metabolism peaking 2.8 hr after ingestion at 1.76 times baseline levels. Our estimates of HIF for Steller sea lions are at the lower end of estimates for terrestrial mammals, and are consistent with estimates for other marine mammals. COMP BIOCHEM PHYSIOL 118A;3:877–881, 1997. © 1997 Elsevier Science Inc.

KEY WORDS. Digestion, heat increment of feeding, pinnipeds, specific dynamic action, Steller sea lion, *Eumetopias jubatus*

INTRODUCTION

Not all of the energy ingested as food is available to an animal for growth, maintenance, and work. Some energy is invariably lost in the digestive process. Early studies on humans recognized that oxygen consumption increased after feeding, a phenomenon that was explained by Bidder and Schmidt in 1877 as the "work of digestion" (19). This increase in metabolism is thought to result from both the mechanical and biochemical processes of digestion, although the exact processes are poorly understood (5,33). The resultant "loss" of energy has been variously denoted as the heat increment of feeding (15), specific dynamic action (3,19), specific dynamic effect (38), heat of nutrient metabolism (34), and diet-induced thermogenesis (37).

The heat increment of feeding (HIF) is not a fixed amount, and is at least partly dictated by the size and composition of the meal (16,21), as well as by the core body/prey temperature differential (42), and the age and nutritional state of the animal (1,8). The energetic cost of processing food is lowest for lipid (4–15%) and carbohydrate (4–30%), and highest for protein (30–70%) (5). Several studies have demonstrated a relationship between protein (9,10,17,20) or lipid (4) meal content and the extent of the HIF effect. Unfortunately, studies have shown that HIF can not be calculated directly from a knowledge of diet composition, as mixed composition foods result in a lower than predicted HIF (16). It has also been suggested that HIF should increase curvilinearly with total ingested energy (6).

Pinnipeds have been described as "inefficient converters of fish flesh" (39), yet few studies have examined the physiological truth to such a statement. Most studies of marine mammal metabolism have undertaken to eliminate the effect of digestion from comparative baseline readings [see (24)]. Consequently, only a few studies have examined the cost of HIF among this group of animals (1,11–13,29,36), and no estimates exist for otariids. Accurate estimates of HIF are essential for constructing energetic models of marine mammal populations, and for making predictions about prey consumption [e.g., (14,27,28,35)].

The following investigates HIF and its relationship to meal size in six captive, juvenile Steller sea lions (*Eumetopias jubatus*). The estimates are, in turn, compared to other marine and terrestrial mammals.

MATERIALS AND METHODS

The study group consisted of six juvenile Steller sea lions (three males and three females; Table 1). All had been introduced to captivity as pups, and were 2.6–2.8 years old at the time of the study, except for one female who was 1.8 years old. The sea lions were held in an outdoor compound at the Vancouver Aquarium (British Columbia, Canada) with access to ambient sea-water and haul out space. Their normal diet consisted of thawed herring (*Clupea harengus*)

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TABLE 1. Estimates of the heat increment of feeding for six juvenile Steller sea lions, fed 2 and 4 kg of herring. The heat increment is expressed as a proportion of gross energy intake (kJ/kJ * 100)

			Heat increment of feeding (%GE)	
Subject	**Gender/age**	**Body mass (kg)**	**2-kg Meal**	**4-kg Meal**
1	M, 3	158.8	8.9	12.1
2	F, 3	116.3	8.5	12.3
3	F, 2	111.3	12.7	15.0
4	F, 3	113.0	6.9	8.5
5	M, 3	145.2	10.1	12.8
6	M, 3	166.9	12.5	13.6
		Average	9.9	12.4

fed *ad lib* twice per day, supplemented with vitamin tablets (5M26 Vitazu tablets, Purina Test Diets, Richmond, IN), and small quantities of other fish species.

Metabolism was measured using open circuit (gas) respirometry. The sea lions were fasted at least 18 hr prior to the start of the experiment to ensure they were post-absorptive. They entered a cage within a sealed opaque chamber, through which air was drawn at a constant rate (153 L/min), sufficient to prevent extreme changes in gas concentrations (specifically, $O_2 \geq 19.0\%$, $CO_2 \leq 1.0\%$). The chamber was equipped with a fan to ensure air circulation, a water cooling system, and a video camera and fluorescent lighting to continuously monitor the sea lion's activity. Oxygen and carbon dioxide concentrations within a desiccated subsample of expired air were determined by a S-3A/I solid oxide (stabilized zirconia) cell analyzer (Ametek Inc., Pittsburgh, PA) and an AR-60 infrared gas analyzer (Anarad Inc., Santa Barbara, CA), respectively. Barometric pressure and expired air temperature were also monitored (Airguide Instruments, Chicago, IL). The expired air current was continuously subsampled, and a Sable data acquisition system (Sable Systems, Salt Lake City, UT) calculated an average concentration (from 200 subsamples) every second. Gas concentration readings were verified every 2 hr during the tests, and the entire system was recalibrated through the course of the experiments with gases of known concentration.

The study was conducted between 23 January and 18 April 1996. Each sea lion was run twice: once with a meal of 2 kg of herring, and once with 4 kg of herring (normal meal size was 3–5 kg). Each run began by measuring resting metabolic rate (RMR), which was used as a control measurement for each HIF determination. This was obtained after a 25-min acclimation period, and consisted of an 8–30-min period of stable oxygen consumption which satisfied standard criteria for measuring basal metabolic rate (i.e., sea lions were postabsorptive, quiescent, and within their thermoneutral zone; 19), with the exception that the animals were still growing. The sea lions were subsequently fed a meal of known size. Oxygen consumption continued to be monitored through its post-prandial rise, until it returned to the prefeeding baseline level. Changes in oxygen concentration were converted to oxygen consumption (equation 3b, 43) and then to energy utilization using the equation: $1 \text{ l } O_2 = 20.1$ kJ.

The HIF has been estimated in some studies solely as the maximum increase in metabolism over a basal level (36). However, it is more accurately calculated as the total increase in metabolism induced by digestion, expressed as a proportion of the ingested meal. In this study we calculated HIF as the total increase in energy consumption above RMR, expressed as a percentage of gross energy intake (GE).

Gross energy intake was calculated from ingested mass, given that the energy density of the herring was 9414 kJ/kg wet weight (determined through oxygen bomb calorimetry). Proximate composition of the herring was 14.3% lipid [modified Bligh-Dyer technique (7)], 15.8% protein (Kjeldahl nitrogen extraction), 2.3% ash content, and 67.3% water, as determined from analysis of representative samples (West Vancouver Science Lab, Department of Fisheries and Oceans).

Each of the 6 sea lions were subject to both feeding conditions (i.e., 2- and 4-kg meal sizes). Individual feeding trials were rerun at a later date if the animals were active in the metabolic chamber, as the quantitative effect of activity upon HIF is unknown.

RESULTS

The HIF of the six sea lions averaged 12.4 ± 0.9% (mean ± SE) of gross energy intake for the larger meal size (4173.2 ± 631.5 g, or 41134 ± 6225 kJ), and 9.9 ± 0.9% for the smaller meal size (2037.7 ± 133.4 g, or 20085 ± 1314 kJ) (Table 1). While the absolute difference between the two treatments was relatively small, it was statistically significant (paired t-test = 5.992, 5 df, $p = .002$).

Meal size also appeared to affect the duration of the HIF effect. For the larger meals, HIF lasted from 8–10 hr. Peak oxygen consumption averaged 2.13 ± 0.14 times baseline levels, and occurred about 3.7 hr after feeding (Fig. 1, Table 2). In contrast, HIF lasted only 6–8 hr with the smaller meal size. This treatment condition produced a peak oxygen consumption 1.76 ± 0.16 times resting levels, about 2.8 hr after feeding.

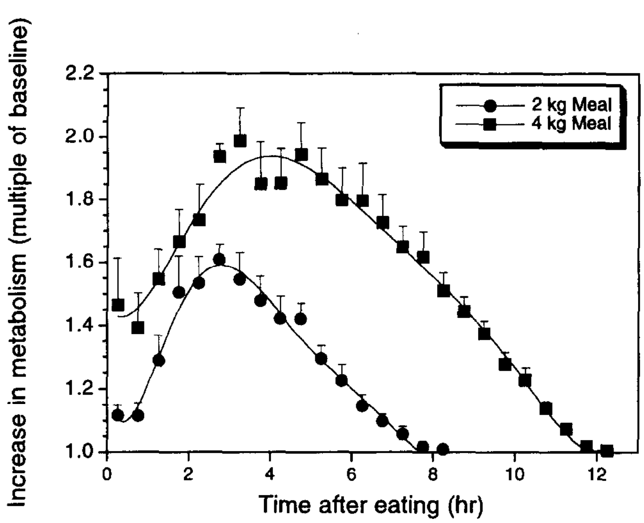

FIG. 1. Increases in metabolism after eating herring. Metabolic rate is expressed as a multiple of control baselines for each half hour period after feeding. Data points represent the average ± SE increase above prefeeding levels for the six Steller sea lions. Data are presented separately for the 2 and 4 kg meal size trials.

DISCUSSION

The estimated HIF for the Steller sea lions (9.9 and 12.4%) appears to be at the lower end of those reported for other mammalian species [see Table 12.1 in (5)]. No studies have investigated HIF in otariids, but comparative data are available from other marine mammals (Table 3).

Results from our study of Steller sea lions are higher than those reported for harbour seals. A yearling harbour seal demonstrated an HIF of 4.7% of GE (1). In comparison, HIF accounted for 9.0 ± 2.8% of GE in juvenile harbour seals (0–4 years) fed a diet of high-energy herring (10130–12560 kJ/kg), and 5.1 ± 2.3% of GE when fed herring of low-energy content (6575–8710 kJ/kg) (29). The sea lions in our study were fed a diet of intermediate energy density (mean = 9857 kJ/kg). This apparent effect of caloric density was also reported with sea otters which displayed HIF of 13.2% of GE when fed squid (3.60 kJ/g) and 10% of GE when fed clams (4.98 kJ/g) (11). No such effect was apparent with northern elephant seals fed either herring (6.6 kJ/g, HIF = 10.3% GE) or capelin (4.8 kJ/g, HIF = 12.3%

TABLE 2. Comparison of baseline (pre-feeding) and maximum metabolic rates (ml O_2/min), for 2 and 4 kg herring meals. Peak metabolism was calculated as the greatest 10 minute average

	2-kg Meal size		4-kg Meal size	
Subject	**Baseline RMR**	**Maximum MR**	**Baseline RMR**	**Maximum MR**
1	702	1060	532	1053
2	500	968	576	1255
3	825	1562	789	1624
4	699	1153	726	1461
5	576	1061	612	1372
6	631	1112	494	1153

TABLE 3. Estimates of the heat increment of feeding and peak metabolism during feeding for six species of marine mammals

Species	Food source	HIF (%GE)	Max. VO_2 (× RMR)	N	Source
Steller sea lion	2 kg Herring	9.9	1.76	6	This study
Eumetopias jubatus	4 kg Herring	12.4	2.13	6	
Northern elephant seal	2 kg Herring	9.1	1.46	4	(2)
Mirounga angustirostris	4 kg Herring	11.4	1.65	4	
	2 kg Capelin	11.5	—	3	
	4 kg Capelin	13.0	—	3	
Sea otter	Squid	13.2	—	3	(11)
Enhydra lutris	Clam	10	1.54	3	
Harp seal	1 kg Herring	16.82	1.40	1	(13)
Phoca groenlandica	2 kg Herring	15.74	1.67	1	
	3 kg Herring	—	1.64	1	
Ring seal	Unknown	—	1.80–2.00	2	(36)
Phoca hispida					
Harbour seal	Low energy herring	9.0	1.40	3	(29)
Phoca vitulina	High energy herring	5.1	1.31	4	
	1.8 kg Herring	4.7	1.90	3	(1)

The heat increment of feeding (HIF) is expressed as a percent of the gross energy intake. The maximum peak in post-feeding energy consumption is presented as a multiple of resting (RMR) levels. For example, the maximum observed metabolic rate for the Steller sea lions fed the 4 kg herring meal was 2.13 times resting levels. The peak increase for sea otters was calculated as the combined average peak for squid and clam trials, and the peak for northern elephant seals is the average for herring and capelin diets. The number of animals used in each study (*N*) is also listed.

GE), although the relative energy density difference was similar to that in the sea otter study (2).

Other studies have suggested that HIF is dependent upon the protein composition of the food (9,10,17,20). Unfortunately, variation in experimental conditions (including age of the subjects) makes comparisons between studies of marine mammals difficult. Among studies using an adult harp seal (13), juvenile northern elephant seals (2), or juvenile Steller sea lions (this study) fed 2-kg herring meals, interspecific variation in HIF (15.7, 9.1, and 9.9% of GE, respectively) can not rationally be accounted for by either differences in protein content (15.5, 17.4, and 15.8% wet weight) or fat content (18.5, 8.7, and 14.4% wet weight).

It has been suggested that HIF should increase with meal size (6), as has been demonstrated in sheep (41). The results of our study support this hypothesis, although the difference is relatively small. Similarly, northern elephant seals demonstrated an effect of meal size (2 vs 4 kg) on HIF, when fed either herring or capelin (2). An adult female harp seal fed meals of 1 and 2 kg of herring demonstrated daily metabolic rates elevated by 11.14 and 20.77%, respectively, although this appeared to translate into a loss of 16.82 and 15.74% of gross energy through HIF (13). The authors noted, however, that the cost of HIF for the 2-kg meals was probably underestimated, as metabolism had not quite subsided to baseline levels by the end of the experiment.

The results of our experiment suggest that sea lions obtain a larger proportion of ingested energy from numerous smaller meals rather than from fewer larger meals. This appears to be consistent with the observed feeding habits of sea lions in the wild. However, such feeding patterns are probably more affected by prey distribution and related costs than by the small energetic benefit resulting from differences in HIF.

Most bioenergetic schemes characterize HIF as an energetic value removed from gross energy intake to calculate the net energy available to the animal. However, the energy generated via HIF does not necessarily constitute a "waste product" to the individual. The heat can be useful when retained by animals to stave off hypothermy when below their thermoneutral zone, thereby reducing the energy needed to maintain homeothermy (19). This mechanism has been demonstrated in both terrestrial (30,31) and aquatic endotherms (26). However, the opposite is true if HIF exceeds thermal maintenance requirements and contributes to hyperthermy (23). This can be partly attenuated by "dumping" excess heat into the water (26).

We tested our sea lions in air to obtain a "true" reading of HIF. There is no reason to assume that Steller sea lions do not avail themselves of the heat generated from HIF to decrease thermoregulatory costs. Care should, therefore, be taken when extrapolating these estimates of HIF to natural situations where Stellers are feeding in water, and may be outside of their thermoneutral zone.

It is important to use an accurate estimate of HIF in ecosystem bioenergetic models. Errors in HIF will directly affect estimates of the number of fish consumed by marine mammals. In the past, many models have assumed that HIF in marine mammals accounts for 17% of GE [e.g., (18, 22,28,35)], a value obtained from a single harp seal (13). This value is at the high end of estimates for marine mammals. As an example of its effect, if a model of harp seal predation on herring in the Barents Sea (27) had used a HIF value of 10% rather than 17%, their estimate of maximum herring consumption would have decreased by over 100,000 tonnes per year.

The Steller sea lion population has declined from over 300,000 in 1979 to current levels of less than 100,000 (25,32,40). The population continues to decline along parts of its range at a rate of 5% per year, and has been listed as a "threatened" species in the United States. Accurate bioenergetic models are an essential tool in making management decisions for ecosystems containing threatened pinniped or fish species.

The estimate of HIF derived for Steller sea lions is towards the low end of estimates for terrestrial mammals, and is consistent with estimates for other marine mammals. This suggests that sea lions, like other pinnipeds, are comparably efficient in utilizing ingested energy, contrary to the expectation that they are "inefficient converters of fish flesh."

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