



Changes in glucocorticoids, IGF-I and thyroid hormones as indicators of nutritional stress and subsequent refeeding in Steller sea lions (*Eumetopias jubatus*)

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ABSTRACT

Physiological responses to changes in energy balance are tightly regulated by the endocrine system through glucocorticoids, IGF-I and thyroid hormones. Changes in these hormones were studied in eight captive female Steller sea lions that experienced changes in food intake, body mass, body composition, and blood metabolites during summer and winter. During a period of energy restriction, one group of sea lions was fed reduced amounts of Pacific herring and another was fed an isocaloric diet of walleye pollock, after which both groups returned to their pre-experimental diets of herring. Cortisol was negatively and IGF-I was positively associated with changes in body mass during periods of energy restriction (mass loss associated with increase in cortisol and decrease in IGF-I) and refeeding (body mass maintenance associated with stable hormone concentrations in summer and compensatory growth linked to decrease in cortisol and increase in IGF-I in winter). Cortisol and IGF-I were also correlated with changes in lipid and lean mass, respectively. Consequently, these two hormones likely make adequate biomarkers for nutritional stress in sea lions, and when combined provide indication of the energetic strategy (lipid vs lean mass catabolism) animals adopt to cope with changes in nutrient intake. Unlike type of diet fed to the sea lions, age of the animals also impacted hormonal responses, with younger animals showing more intense hormonal changes to nutritional stress. Thyroid hormones, however, were not linked to any physiological changes observed in this study.

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1. Introduction

Natural habitats are neither constant nor completely predictable, and animals must continuously adjust to these environmental variations (Wingfield and Kitaysky, 2002). Regulation of energy intake and expenditure is an essential part of these adjustments, and is linked to the survival and reproductive success of animals in their natural environment (Lavigne et al., 1982). Insufficient quantity or quality of food, conditions that Steller sea lions might chronically encounter in the wild (Trites and Donnelly, 2003), results in animals modifying their physiologies and behaviours to rebalance their energy budgets (Stini, 1969; Waterlow, 1986; Lawson et al., 1997; Schmidt-Nielsen, 1997; Boyd, 2002; Trumble et al., 2003). Ultimately these physiological changes are regulated by complex, interconnected endocrine systems. Determining how changes in hormone concentrations are influenced by external factors such as diet type, age, and season that all impact nutritional physiology of Steller sea lions during periods of energy restriction (Rosen and Trites, 2005; Kumagai et al., 2006; Jeanniard du

Dot et al., 2008), can help to understand the regulatory mechanisms behind changes in body composition, partitioning of the energy intake, and ultimately life history of these animals.

Endocrine response to nutritional stress (in terms of food quantity or quality) primarily, but not exclusively, involves the somatotrophic, glucocorticoid, and thyroid hormones (Hornick et al., 2000; Robson et al., 2002). Hormones from the somatotrophic axis, including insulin-like growth factor-I [IGF-I], are involved in protein and lipid metabolism as well as mineral metabolism and bone growth (Breier, 1999; Butler and Le Roith, 2001) while glucocorticoids (cortisol and free cortisol) are known to be involved in lipid metabolism, and correlate with unpredictable life situations such as energy intake shortages (Kitaysky et al., 2001b; Reeder and Kramer, 2005). Thyroid hormones (triiodothyronine [T3], and thyroxine [T4]) are essential for growth, metabolism, and thermogenesis in mammals (Kelly, 2000). During a negative energy balance, GH and glucocorticoids usually increase while concentrations of IGF-I and thyroid hormones decrease (Table 1) which are linked to a cessation of growth, a sparing of protein and an increase in lipolysis (Hornick et al., 2000), an overall decrease in energy expenditures through reduction in metabolic rates (Buonomo and Baile, 1991; Yambayamba et al., 1996; Weinsier et al., 2000), and a modification of development and behaviour in birds and mammals (Moberg, 1985; Ortiz et al., 2001a; Kitaysky et al., 2003).

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Table 1

Predicted and observed changes of blood concentrations of cortisol and free cortisol, IGF-1, total T3, total and free T4, BUN/creatinine, NEFA and β -HBA in 8 female Steller sea lions during period of energy restriction followed by periods of refeeding in summer and winter

Parameter	Predicted results ^a		Observed results				Related to loss of endogenous energy reserves
	Energy restriction	Refeeding	Energy restriction		Refeeding		
			Summer	Winter	Summer	Winter	
Cortisol	↑	↓	↑	↑ ^b	0	↓ ^b	– (lipids)
Free cortisol	↑	↓	↑	↑ ^b	0	↓ ^b	– (lipids)
IGF-1	↓	↑	↓ ^b	↓	0	0 or ↑ ^b	+ (proteins)
Total T3 (TT3)	↓	↑	↓	↓ or ↑ ^c	0	↑	NA
Total T4 (TT4)	↓	↑	0	↓	0	↑	NA
Free T4 (fT4)	↓	↑	0	0	0	0	NA
TT3:TT4	↓	↑	↓ ^c	↓ then ↑ ^c	↓	0	NA
BUN:creatinine	↑	↓	0	↑ or 0 ^c	↑	↓ or 0 ^c	– (proteins)
NEFA	↑	↓	↓ ^c	↑	0	↓	no
β -HBA	↑	↓	0	NA	0	NA	no

Significant relations between changes in blood variables and changes in endogenous energy reserves during the course of the experiments are also indicated.

– and + means negatively and positively related to endogenous energy reserves (type in brackets).

^a Predicted results are based on literature information from (Bergendahl et al., 1996; Buonomo and Baile, 1991; Castellini et al., 1993; Eales, 1988; Hornick et al., 2000; Kitaysky et al., 2001a,b; Moberg, 1985; Rea et al., 1998; Reeder and Kramer, 2005; Renaville et al., 2002; Robson et al., 2002; Thissen et al., 1994; Weinsier et al., 2000).

^b means difference between age groups.

^c means difference between diet groups.

While somatotrophic, glucocorticoid, and thyroid hormones regulate lipid or protein metabolism during periods of energy restriction, changes in tissue catabolism should also be reflected in blood concentrations of relevant metabolite by-products. In fasting animals, concentrations of non-esterified fatty acids (NEFA) and ketone bodies (beta-hydroxybutyrate, [β -HBA]) usually indicate lipid catabolism while concentrations of nitrogen waste in the blood (blood urea nitrogen, BUN) reflect changes in protein catabolism (Castellini et al., 1993; Rea et al., 2000; Mellish and Iverson, 2001). However, these variables may not accurately reflect the source of tissue catabolism during a milder energy restriction (when the rate of mass loss is less than during a fast) and will be additionally affected by concentrations of dietary protein and lipid intake (Narayanan and Appleton, 1980; Ramsay et al., 1991).

Interpreting the relationship between hormones and responses to nutritional stress is complex. Metabolism and hormone concentrations of mammals in general, and Steller sea lions, in particular, may vary naturally throughout the year with photoperiod or breeding status, and by age of the animals independent of nutritional stress (Engelhardt and Ferguson, 1980; Little, 1991; Thissen et al., 1994; Hall et al., 1998; Haulena et al., 1998; Wingfield and Kitaysky, 2002; Kumagai, 2004b; Myers et al., 2006; Mashburn and Atkinson, 2007). Concentrations of glucocorticoids are generally greater during the breeding season in summer in vertebrate species (Sangalang and Freeman, 1976; Bartsh et al., 1992; Romero, 2002), while circulatory concentrations of IGF-1 are greater in younger animals (Aujard et al., 2004) and in humans (Lamberts et al., 1997). Type of diet (protein/lipid ratio) also seems to influence hormone concentrations (Nap et al., 1993) and physiological response to nutritional stress (Kumagai et al., 2006; Jeanniard du Dot et al., 2008). Consequently, it is essential to use controlled studies to separate the impact of each variable (diet quality, level of energy intake, season, and age of the animal) on the endocrine systems to understand the potential impacts of resulting physiological responses during periods of energy restriction.

The primary goal of this study was to investigate the impact of season, age, and type of diet on the endocrine regulation in Steller sea lions during and after nutritional stress. Hormone measurements were discussed in reference to changes in body mass, body composition, and energetic priorities. We hypothesized that the endocrine response to nutritional stress would differ between animals fed a different type of diet since it induces differential loss of lean and lipid mass (Kumagai et al., 2006; Jeanniard du Dot et al., 2008). We also expected the endocrine response to nutritional

stress would be more intense in winter when energetic demands are greater, and in younger animals that have greater mass-specific energetic needs compared with older sea lions (Winship et al., 2002). Efficacy of blood metabolites and hormones as tools to evaluate nutritional stress of the animals was also assessed. Defining the relationship between the endocrine system and metabolic and energetic status will expand our understanding of the mechanisms of energetic adjustments available to Steller sea lions, and ultimately shed light on how changes in diet quality and quantity may be affecting animals' health in the wild.

2. Material and methods

2.1. Experimental design

Our study was conducted with the approval of the University of British Columbia Animal Care Committee, under Permit No. A04-0169. Experiments were conducted at the Vancouver Aquarium (BC, Canada) in the summer (June–August) 2005 and winter (January–March) 2006, on 8 female Steller sea lions (*Eumetopias jubatus*) (five 3-year old juveniles and three 5-year old sub-adults). The animals were randomly assigned to one of the two experimental groups, Group H or Group P, which were kept identical for the two seasons.

Each trial consisted of three phases, starting with a 28-day baseline (B) during which all the animals were fed their usual daily ration (i.e. energy intake to maintain body mass or sustain a slow growth) of Pacific herring (*Clupea pallasii*). The sea lions were then placed on a 28-day restriction treatment (R) during which energy intake was reduced by approximately 20–30%. Juveniles in both diet groups were given 260 kJ kg⁻¹ d⁻¹ of food and sub-adults received 230 kJ kg⁻¹ d⁻¹ (to buffer age/size differences and to result in a maximum 15% change in body mass). The two diet groups were given the same restricted level of energy (isocaloric diets), but Group H was fed exclusively Pacific herring and Group P was fed only walleye pollock (*Theragra chalcogramma*). Lipid and energy contents were less for pollock than for herring which resulted in Group P eating 30% and 60% more fish than Group H during the summer and winter energy restrictions, respectively, in order to obtain similar energy intakes between the two groups. The restriction was followed by a 28-day controlled refeeding (CR) period during which each sea lion received the same diet and energy intake of Pacific herring as they had received during the baseline phase. Subsamples of the herring and pollock were analyzed for their proximate chemical composition by Northwest Labs (Surrey, BC, Canada) and the gross energy contents of the

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