Physiological and behavioral determinants of lactation efficiency in the northern elephant seal

The efficiency with which mothers convert acquired energy and body reserves into milk production is a key determinant of both the rate and magnitude of parental investment in mammals. Despite this, relatively few studies have examined lactation efficiency and its underlying physiological and behavioral characteristics in free-ranging mammals. Pinnipeds represent an ideal system with which to address these questions because the physiology of lactation in pinnipeds is significantly impacted by constraints resulting from the temporal separation of foraging and parental investment. This makes it possible to look at the costs of reproduction without the confounding variable of food intake. It has been suggested that one strategy available in the case of energy limitations on allocation toward reproduction is compensatory shifts in behavior that reduce energy spent on activity and reduce maternal energy requirements (Thompson 1992). From a physiological standpoint the key to lactation efficiency is the rapid mobilization of stored body lipids and their uptake and use in milk synthesis by the mammary gland. Lipoprotein lipase (LPL) is the primary enzyme involved in directing triglycerides mobilized from tissue stores to tissues for utilization. I propose to investigate these behavioral and physiological features in the northern elephant seal.

Background

Elephant seals spend the majority of their lives at sea but they are tied to the land for the birth and suckling of their young. When pregnant females arrive at the rookery they seek each other out for safety from the aggressive males and form harems. The fighting between the males results in a dominance hierarchy, with only the most dominate males having access to the females. Harems can range in size from a small group controlled by a single male to larger sizes where other males take up position in the periphery (LeBoeuf & Laws, 1994). During this period, elephant seals fast completely from food and water. Previous investigations of female reproductive energetics have revealed significant positive relationships between maternal age and lactation efficiency. It was suggested that this was because older females have more central harem positions and therefore expend less energy on agonistic encounters than younger females on the periphery (Crocker et al., in press). An alternative explanation for this increase in efficiency is that older females have higher levels of LPL that could increase the rate of lipid uptake by the mammary gland and increase the rate of milk synthesis relative to the females own maintenance metabolism. It has been suggested that Lipoprotein Lipase (LPL) activity plays an important role in high milk fat transfer from mother to pup in grey and hooded seals (Iverson et al. 1995, Mellish et al. 1999). The goal of this study is to determine which factors explain why older females are more efficient at milk synthesis than young females. I will test the following hypotheses: 1) Older females spend less time on agonistic interactions with other females and males and 2) Older females have higher LPL levels than younger females.

Methods

This study will be conducted at Año Nuevo State Reserve, San Mateo County, California, during the 2001 and 2002 breeding seasons. Known aged females will be identified by plastic flipper tags which were attached shortly after weaning in previous breeding seasons. Measurements will be collected on 10 mother-pup pairs with 4 year old females and 10 mother-pup pairs with 8 year old females.

Behavioral measurements - Behavioral observations of the selected females will be conducted daily throughout the lactation period. Time spent nursing, sleeping, and interacting with other females and males will be recorded using instantaneous scan sampling. *Ad libitum* sampling will supplement the instantaneous scan sampling to ensure than rare occurrences are not overlooked in the data (Martin &Bateson 1993). This data will be analyzed for differences in behavior between the younger (4 year olds) and older (8 year olds) seals using a log-likelihood contingency table analysis. *Physiological measurements* - Physiological measurements will be made at 3 days postpartum and just before weaning at 23 days postpartum. Females will be immobilized using Telezol and both the mother and pup will be weighed. Maternal body composition will be determined using an ultrasound scanner and morphometrics. (Gales & Burton 1987, Crocker et al. 1997, Webb et al. 1998) Maternal energy expenditure will be calculated from mass and body composition changes over the sampling period. The female will receive a bolus intravenous injection of heparin. Heparin causes tissues to release LPL into the blood. Post-heparin blood samples will be taken 10, 20, and 30 minutes following the injection and from these samples LPL activity will be determined. Blubber and mammary tissue samples will be taken from the first few females sampled to determine the specific LPL activity in the tissues as described in Mellish et al. 1999. If no LPL activity is present in the blubber we can assume that the post heparin LPL levels in the blood represent the LPL activity levels in the mammary gland (S.J.Iverson, pers. com.). If this is not the case, then mammary tissue samples will be taken from all the females sampled and the LPL levels will be measured in the mammary gland. Milk samples will be taken to determine fat content and it's

relationship to LPL levels. This data will be analyzed for differences in energy expenditure, LPL levels, and milk fat content between the two age groups using a t-test

Significance of results

The results from this study will contribute to the understanding of the underlying physiological and behavioral characteristics of lactation by investigating what causes the difference in lactation efficiency in the two age classes. A female can maximize the amount of energy available for milk production by minimizing the amount of energy expended on her own maintenance metabolism while on shore (Fedak and Anderson, 1982), thereby increasing the lactation efficiency. Two ways that a female can minimize her maintenance metabolism is by decreasing activity and through metabolic compensation.

The increased lactation efficiency in older female could be explained by behavioral modifications if it is found that older females spend less time than younger females involved in agonistic interactions with other females and males and/or if the older females are spending more time sleeping than younger females. In sleep the body temperature set point drops so the elephant seals do not expend as much energy on thermoregulation. In grey seals it has been found that lactation efficiency increased throughout lactation and that this increase in efficiency cannot be explained by behavioral modifications. It is suggested that the increase in efficiency is due to metabolic compensation (Mellish et al., 2000). A possible explanation for this metabolic compensation in grey seals could be an increase in LPL activity levels, which did show an increase from the beginning to the end of lactation. If it is found in the proposed study that the older females have higher LPL activity levels than the younger females it would suggest that LPL activity levels contribute to the metabolic compensation and thereby increases lactation efficiency in the older females. If it is found that, in addition to having higher LPL levels, older females produce milk with a higher fat content this would further support the hypothesis that increased LPL activity levels increase lactation efficiency.

References

Crocker, D.E., LeBoeuf, B.J., & Costa, D.P.. 1997. Drift diving in female northern elephant seal: Implications for food processing. *Canadian Journal of Zoology*. **75**(1):27-39

Crocker, D.E, Williams, J.D., Costa, D.P., & LeBoeuf, B.J. (in press) Maternal traits and reproduction effort in northern elephant seals. *Ecology.*

Fedak, M.A. & Anderson, S.S. 1982. The energetics of lactation: accurate measurements from a large wild mammal, the grey seal (*Halichoerus grypus*). *Journal of Zoology* **198**:473-479

Gales, N.J., & Burton H.R. 1987. Ultrasonic measurement of blubber thickness of the southern elephant seal, *Mirounga leionina* (Linn.). Australian Journal of Zoology **35**:207-217.

Iverson, S.J., Hamosh, M., & Bowen, W.D. 1995. Lipoprotein lipase activity and its relationship to high milk fat transfer during lactation in grey seals. *Journal of Comparative Physiology* **165**:384-395

Le Boeuf , B.J., & Laws, R.M. 1994. Elephant Seals: An Introduction to the Genus. Pages 1-26 in B.J. LeBouef & R.M. Laws, editors. *Elephant Seals Population Ecology, Behavior, and Physiology*. University of California Press, Berkely.

Martin P. & Bateson P. 1993. *Measuring behaviour, an introductory guide, second edition*. Cambridge: Cambridge University Press.

Mellish, J.E., Iverson, S.J., & Bowen, W.D. 2000. Metabolic compensation during high energy output in fasting, lactating grey seals (*Halichoerus grypus*): metabolic ceilings revisited. *Proceedings of the Royal Society Biological Sciences Series B*. **267**(1449):1245-1251

Mellish, J.E., Iverson, S.J., Bowen, W.D., & Hammill, M.O. 1999. Fat transfer and energetics during lactation in the hooded seal: the roles of tissue lipoprotein lipase in milk fat secretion and pup blubber deposition. *Journal of Comparative Physiology* **169**:377-390

Thompson, S.D. 1992. Gestation and lactation in small mammals: basal metabolic rate and the limits of energy use. Pages 213-259 in T.E. Tomasi and T.H. Horton, editors. *Mammalian energetics: Interdisciplinary Views of Metabolism and Reproduction*. Cornell University Press, Ithaca.

Webb, P.M., Crocker, D.E., Blackwell, S.B., Costa, D.P., & LeBoeuf, B.J. 1998. Effects of buoyancy on the diving behavior of northern elephant seals. *Journal of Experimental Biology* **201**(16):2349-2358