J. Northw. Atl. Fish. Sci., Vol. 22: 115–117

NOTE

Studying Prey Selection by Seals: The Utility of Prey Preference Experiments

Glenn J. Boyle
Department of Zoology, University of Guelph
Guelph, Ontario, Canada N1G 2W1

Recent problems with the management of commercial fisheries in Atlantic and Pacific Canada have increased the importance of understanding and predicting ecological interactions between seals, as marine predators, and their prey. Seal feeding habit studies that document temporal and spatial variation in seal predation, often conclude that seals are opportunistic predators responding to changes in the relative abundance of prey (e.g. Beddington *et al*., 1985). In reality, these inferences are speculative, because crucial empirical data on the factors affecting prey selection by seals is not available (see Pierce *et al*., 1990; Markussen and Øritsland, 1991; Lavigne, 1995). As a result, feeding habit studies have limited utility in terms of understanding and predicting the feeding choices made by seals (Lavigne, 1995).

Recent field studies have documented intraspecific variation in the foraging behaviour of a number of seal species, but the factors influencing the development of such behavioural variation are not known (Boyd, 1993). Boyd (1993) suggests that new methods of diet analysis (e.g. fatty acid markers), and long-term, longitudinal study of diet in individuals, are required to document the development of individual variation in foraging and diet specializations. The fact remains, however, that these methods would also require accurate, concomitant measures of prey availability, and even then, would not necessarily improve our understanding of either the factors affecting individual variation in behaviour or the dynamics of prey selection.

To assess the choices that seals make in relation to prey availability, their functional responses to prey abundance, density and distribution, and their preferences for certain types (sizes, species) of prey have to be considered. Notably, none of these aspects of seal behaviour have received systematic research attention. The question, then, is how to proceed with investigating prey selection in seals.

Some researchers have suggested releasing seals into enclosed water bodies to feed on known fish populations (McLaren and Smith, 1985; Markussen and Øritsland, 1991). Despite the logistical and technical problems to be overcome, this type of ambitious approach – by direct measurement of the predatory response to prey availability – has intuitive appeal as a solution to the study of prey selection. Ultimately, this type of experiment has to be undertaken in order to be able to rationalize the decisions that seals make in the wild. If so, a theoretical framework, such as contemporary foraging theory, should be used to generate specific hypotheses to be tested during experiments. For example, the work of Thompson *et al*. (1993), which models how the optimal foraging tactics of seals may change as a function of the interactions between physiological constraints (costs of swimming) and constraints of prey availability (prey density and movement), is a good example of a model that needs to be tested empirically (Boyd, 1993).

A less ambitious, but equally promising approach is to focus on the role of prey preferences in seal feeding behaviour. Answers are needed to such basic questions as: Do seals have prey preferences (i.e. when prey availabilities are equal)? Are there differences in prey preferences between individuals of the same species, or between sympatric species? What are some of the important environmental influences on the development of prey preferences? Are preferences fixed or dependent on internal state (e.g. degree of satiation)? These are all key questions that need to be answered in order to gain a thorough understanding of why seals eat what they do. Certainly, if large-scale foraging experiments are to be attempted, information on the prey preferences of seals will be needed for the formulation and testing of models. This information will not come from conventional methods of assessing feeding habits. We can, however, begin to answer questions about prey preferences in a captive setting, using relatively simple techniques and equipment to gain powerful insights into the feeding behaviour of seals.

Operant conditioning has been used in the experimental analysis of proximate mechanisms of behaviour (Skinner, 1938), and in the psychophysical study of sensory function (Stebbins, 1970). Consistent with initial use in the study of behavioural mechanisms, operant methods have been used in more recent studies of perceptual constraints on foraging behaviour (Shettleworth, 1989), as well as in studies of feeding preferences of a variety of animals (e.g. Hutson and Wilson, 1984; Franco *et al*., 1991; Hou *et al*., 1991). Given the previously successful use of operant conditioning in studies of the sensory and cognitive abilities of pinnipeds (reviewed in Schusterman, 1981), it would seem appropriate to employ operant conditioning in experimental studies of the prey preferences of seals.

The experimental approach of using operant conditioning techniques to train an animal to respond to and select between prey alternatives has recently been used with a captive California sea lion (Cox *et al*., 1996). The sea lion was trained to respond to the simultaneous presentation of abstract symbols used to represent different types of food (whole and cut fish). This preliminary work identified the existence of distinct food preferences in the animal.

An extension of this work has already been undertaken in the design and construction of a feeding apparatus that presents pairs of fish to seals and allows them to select between alternatives by operant responses (Boyle, MS 1995). The experimental design used actual prey items instead of abstract symbols, so that animals could visually assess the quality of the prey alternatives presented. The apparatus has also been used successfully in feeding experiments with harbour and grey seals, in which seals expressed distinct prey size and species preferences (G.J. Boyle, unpubl. data).

Further studies of this type, by offering combinations of many species of fish, would be able to show how consistent preference hierarchies are, and, by careful manipulations of diet over time, how experience affects choices. It would also be instructive to test the preferences of a number of animals with the same experience to identify individual variation, and then to test the responses of these different animals to the same diet manipulations.

In an impoverished, artificial environment, in which other factors (such as prey density and abundance) have been deliberately abstracted, prey preference experiments with a captive seal do not (and should not be expected to) test hypotheses about its free-ranging feeding behaviour or the behaviour of wild seals in general. Nonetheless, the utility of prey preference experiments is still considerable, in terms of being able to answer many relevant questions about the abilities and propensities of feeding seals. For example, for seals to express prey preferences using their vision, they have to be able to discriminate between (and perhaps recognize) different prey. The ability of a seal to discriminate between different prey types is an intrinsic constraint on the choices that it makes in the wild. Similarly, if preferences are state-dependent, changing with the degree of satiation of the seal, this is crucial information for the modelling of foraging behaviour.

In conclusion, prey preference experiments with captive seals offer the opportunity to produce important new information on the perceptions and abilities that seals have and may use during prey selection. This information could provide the basis for the design and interpretation of more ambitious experiments and observations under semi-naturalistic and free-ranging conditions, and would help to define the context within which seals make decisions about food.

Acknowledgements

I thank M. D. Boyle, D. M. Lavigne, E. H. Miller, G. B. Stenson, R. Werner, and an anonymous reviewer for helpful comments, criticisms and discussions. This work was supported by a Norman James Aquatic Mammalogy Fellowship to the author, and an NSERC operating grant to D. M. Lavigne.

References

BEDDINGTON, J. R., R. J. H. BEVERTON, and D. M. LAVIGNE (eds.). 1985. Marine mammals and fisheries. George Allen and Unwin Publ., London. 354 p.

BOYD, I. L. 1993. Introduction: trends in marine mammal science. *Symp. Zool. Soc., London*, **66**: 1–12.

BOYLE, G. J. MS 1995. An operant method of investigating prey selection in seals. *NAFO SCR Doc.*, No. 89, Serial No. N2611, 15 p.

COX, M., E. GAGLIONE, P. PROWTEN, and M. NOONAN. 1996. Food preferences communicated via symbol discrimination by a California sea lion (*Zalophus californianus*). *Aq. Mamm.*, **22**: 3–10.

FRANCO, J., A. D. F. JOHNSTONE, and A. M. MACKIE. 1991. Studies of bait preference in the cod, *Gadus morhua* L.: characterisation of feeding stimulants using an operant conditioning technique. *Fish. Res.*, **10**: 229–242.

HOU, X. Z., A. B. LAWRENCE, A. ILLIUS, D. ANDERSON, and J. D. OLDHAM. 1991. Operant studies on feed selection in sheep. *Proc. Nutr. Soc.*, **50**: 95A.

HUTSON, G. D. and P. N. WILSON. 1984. A note on the preference of sheep for whole or crushed grains and seeds. *Anim. Prod.*, **38**: 145–146.

LAVIGNE, D.M. 1995. Ecological interactions between marine mammals, commercial fisheries and their prey: Unravelling the tangled web. International Marine Mammal Association Inc. Tech. Rep., 95-02. 26 p.

MARKUSSEN, N.H., and N.A. ØRITSLAND. 1991. Food energy requirements of the harp seal (*Phoca groenlandica*) population in the Barents and White Seas. *Polar Res.*, **10**: 603–608.

McLAREN, I. A., and T. G. SMITH. 1985. Population ecology of seals: Retrospective and prospective views. *Mar. Mamm. Sci.*, **1**: 54–83.

PIERCE, G. J., P. R. BOYLE, and P. M. THOMPSON. 1990. Diet selection by seals. *In*: Trophic relationships in the marine environment, M. Barnes and R.N. Gibson (eds.). Aberdeen University Press, p. 222–238.

SCHUSTERMAN, R. J. 1981. Behavioral capabilities of seals and sea lions: A review of their hearing, visual, learning and diving skills. *Psychol. Rec.*, **31**: 125–143.

SHETTLEWORTH, S.J. 1989. Animals foraging in the lab: Problems and promises. *J. Exp. Psych. Anim. Behav. Proc.*, **15**: 81–87.

SKINNER, B.F. 1938. The behavior of organisms. Appleton-Century-Crofts, New York. 457 p.

STEBBINS, W.C. 1970. Principles of animal psychophysics. *In*: Animal psychophysics: the design and conduct of sensory experiments, W. C. Stebbins (ed.). Appleton-Century-Crofts, New York, p. 1–19.

THOMPSON, D., A.R. HIBY, and M.A. FEDAK. 1993. How fast should I swim? Behavioural implications of diving physiology. *Symp. Zool. Soc., London*, **66**: 349–368.