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An Operant Method of Investigating Prey Selection in Seals

by

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Abstract

It is often concluded that seals respond opportunistically to changes in prey availability. In reality, however, the process of prey selection in seals is not understood. The lack of empirical information on prey selection in response to prey availability prevents the ability to understand and predict the dynamics of interaction between seal and prey populations.

There is considerable potential for contemporary foraging theory and operant conditioning techniques to contribute to the experimental study of prey selection in seals. These theoretical and experimental approaches are important means to understand how the behavioural constraints of predator perception interact with the environmental constraints of prey availability to modulate prey selection.

In an attempt to study the behavioural mechanisms that seals may use in prey selection, an apparatus has been constructed for use in feeding experiments on captive harbour and grey seals. The apparatus presents paired *combinations of fish* underwater and allows seals to choose between alternative prey by operant responses.

While operant feeding trials cannot accurately emulate the conditions in which wild seals forage, they can be used to examine behavioural abilities and responses that are relevant to diet selection in the wild.

Key words: Seal, prey selection, foraging theory, constraints, operant conditioning

Introduction

Assessments of ecological interactions between seals and commercial fisheries are often compromised by a lack of basic information on seal biology (Harwood and Croxall, 1988; Lavigne, 1995). In this respect, perhaps the most important absence in our current knowledge is an understanding of prey selection by seals (see Pierce *et al.*, 1990; Markussen and Øritsland, 1991; Lavigne, 1995). Feeding habit studies, which 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). Such inferences about foraging behaviour, however, remain speculative without crucial empirical information on the choices that seals make in relation to prey availability (Lavigne, 1995).

Recent discussions of prey selection in seals have made reference to contemporary foraging theory and models (Pierce *et al.*, 1990; Lavigne, 1995; also see Thompson *et al.*, 1993, regarding foraging tactics). Foraging theory, which has a substantial theoretical and empirical literature (reviews in Schoener, 1971; Pyke *et al.*, 1977; Pyke, 1984; Schoener, 1987), uses optimality models to predict aspects of foraging behaviour (Stephens and Krebs, 1986). Foraging models assume that feasible choices and benefits to an animal are limited by the constraints imposed by an animal's biology and environment (Stephens and Krebs, 1986). Moreover, specific information on constraints is essential to the development of realistic behavioural models (Cheverton *et al.*, 1985; Shettleworth, 1988; Real, 1990).

Optimality models of diving behaviour of aquatic and marine mammals have specified and incorporated physiological abilities as constraints on behaviour (Dunstone and O'Conner, 1979a, 1979b; Kramer, 1988; Fedak and Thompson, 1993; Thompson *et al.*, 1993). Thompson *et al.* (1993) showed 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). A similar approach can be taken with the study of prey selection in seals, by defining the behavioural constraints of predator perception (e.g. prey preferences) and modelling their interactions with constraints of prey availability (e.g. prey species). For empirical information about constraints on prey selection, however, an experimental methodology is required.

Historically, 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). Operant methods are being used increasingly in studies of perceptual constraints on foraging behaviour, which is consistent with their initial use in the study of behavioural mechanisms (Shettleworth, 1988). In addition, operant methods have been used in the study of feeding preferences (see Franco *et al.*, 1991). Given these two latter applications of operant methods, and the successful use of operant conditioning in studies of the sensory and cognitive abilities of pinnipeds (reviewed in Schusterman, 1981), it seems appropriate to employ operant conditioning as an experimental methodology in the study of behavioural constraints on prey selection in seals.

This paper outlines the design, construction, and use of an apparatus in feeding preference experiments with captive harbour and grey seals. The apparatus presents pairs of fish to seals and allows them to select between alternatives by operant responses.

Methods

The apparatus is designed for experiments that are intended primarily to test whether seals have preferences for different types of fish. A paired presentation design, which has been used commonly in studies of prey preferences (e.g. Smallwood, 1989; Swennen and Duiven, 1991), was selected because simultaneous (paired) presentation of stimuli gives a more sensitive measure of preference than successive (single) presentation (Bateson, 1990).

In essence, the experimental tank and apparatus (Fig. 1) together comprise a modified Skinner box, in which seals are presented with pairs of stimuli (fish prey) and receive differential reinforcement (fish delivery) following the operant of paddle pressing. In contrast to the traditional Skinner box, however, in which food is not seen until its delivery, the seal receives the same fish that is presented adjacent to the pressed paddle.

Apparatus design and construction

The apparatus is fixed at one end of a rectangular tank (4.5 m long x 2.5 m wide x 1.6 m deep) (Fig. 1). Constructed of water-resistant plywood and reinforcing metal struts and fittings, the apparatus comprises two major sections of plywood, fixed at 90° to each other (Fig. 2). The front-facing board has two presentation windows (50 cm apart) with plexiglass paddles mounted adjacently; the bottom-facing board is fitted with hinged trapdoors (Fig. 2 and Fig. 3). The windows (50 cm x 13 cm) are fitted with plate glass (8 mm thick). When the tank is filled with water the centre of each window is approximately 33 cm below the surface.

A stainless steel treadmill, mounted on a wooden frame and suspended from an aluminum bar behind the front board, rests on the bottom-facing board at an angle, with the two steel tracks positioned in the middle of the windows (Fig. 4). Fixed at set distances along both steel tracks are plexiglass plates with steel hooks, upon which experimental fish are impaled for lateral presentation at the windows.

A plastic screen hanging behind the front board (Fig. 5), hides the experimenter from view during fish presentation but, at the same time, allows fish that are loaded by the experimenter to be transported down on the treadmill. Adjustable, board-mounted mirrors (Fig. 5) allow the experimenter to see the fish after they pass the plastic screen into presentation position at the windows. The selected fish is peeled off the treadmill by raising the trapdoor on that side as the treadmill is advanced; the fish is delivered to the seal as the trapdoor closes. The unselected fish remains on the treadmill as it advances to the underside, where it is peeled off by a fixed plate into a collecting bucket. An opaque plexiglass screen mounted behind the windows covers the window aperture when fish are not presented, and is lifted to present fish; as soon as the selected fish is delivered, the screen is lowered again.

The front-mounted paddles operate by magnetic leaf switches when the paddles are pressed. This operation sounds a buzzer (0.3 sec. duration) via a mains-operated relay box. A manual on-off switch connected to the relay box resets the circuit after each paddle press, just prior to the next fish presentation.

The presentation and delivery of fish is operated by the experimenter, who can see the movements of the experimental animal in the tank via an overhead mirror, and a monitor linked to a camcorder mounted at the opposite end of the tank.

Conditioning of seals and experimental design

Operant *conditioning* of seals follows standard procedures of behavioural shaping (see Reese, 1964). Paddle pressing with the nose is the desired operant, as in much of the previous work with pinnipeds (Schusterman, 1981). This operant is shaped by selective food reinforcement of successive approximations to the required behaviour.

Once paddle pressing is established, a sequence (chain) of behaviour preceding the operant is built by using discriminative stimuli (S^Ds) as conditioned reinforcers for preceding responses (Reese, 1964). In this way, a two-component heterogeneous chain is established:

$$S^D_1 \text{ -----> } R_1 \text{ -----> } S^D_2 \text{ -----> } R_2 \text{ ----->} S^R \qquad (1)$$

In this chain, food reinforcement (S^R) is contingent upon the response of paddle pressing (R_2) following the discriminative stimulus of fish presentation at the windows of the apparatus (S^D_2), which is a conditioned reinforcer for the response of stationing at the far end of the tank (R_1) following the stimulus of no fish presentation S^D_1 (plexiglass screen at windows).

An experimental session includes 8-10 trials, each trial comprising a single presentation of fish pairs; the left-right orientation of fish types is randomized within and between sessions. The seal is required to station at the far end of the tank prior to each trial in a session (see chain above). After each selection, the window apertures are covered and the seal is again required to station at the far end of the tank until the next trial.

Preliminary prey size selection experiments, using Atlantic herring (*Clupea harengus*) of two size classes, have been conducted with 3 harbour seals.

Results

The conditioning of harbour seals for feeding preference experiments has been relatively quick, which *confirms* previous conclusions that pinniped species are generally amenable to operant conditioning (Schusterman, 1981). The desired sequence of behaviour for experiments was established in each of 3 harbour seals within 10 training sessions, over a period of a few weeks (Boyle, unpublished data).

The apparatus worked successfully in preliminary experiments on prey size selection in harbour seals. The results of these experiments indicate inter-individual variation in the responses of seals, with one animal showing a significant tendency to select the larger fish of the pair in the first trial of successive sessions (Boyle, unpublished data).

Discussion

This operant approach to the study of choice has several merits. By separating the seal from the experimenter, for example, observer effects are minimized. Furthermore, because the apparatus presents prey under standardized conditions, this facilitates the study of intra- and inter-individual differences in behaviour (Hall, 1951). Individual variation in animal behaviour is common (Hall, 1951; Slater, 1981), though its study has generally been neglected in favour of generalizations about groups of animals (Slater, 1981; Bekoff and Jamieson, 1990).

Recent field studies of seals have documented intraspecific variation in ranging behaviour between sexes and individuals, 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), that allow long-term, longitudinal study of diet in individuals, are required to document the development of individual variation in foraging and diet specializations. Without concomitant measures of prey availability, however, these methods do not contribute to an understanding of either the factors affecting individual variation in behaviour, or the process of prey selection. In this respect, operant studies of choice in captive seals have the potential to help, by identifying individual variation in behaviour and perceptual constraints on prey selection.

This study of feeding preferences in seals is not the only novel experimental approach to the study of foraging behaviour and prey selection in pinnipeds. Operant experiments on food discrimination, for example, have been carried out with captive otariids (Eric Gaglione, pers. comm., Buffalo Aquarium, Buffalo, New York, U.S.A.), in an analogous experimental design to that described in this paper, in which symbols were used to represent fish types.

More ambitious suggestions for the experimental study of prey selection in seals have included releasing seals into enclosed water bodies to feed on known fish populations (McLaren and Smith, 1985; Markussen and Øritsland, 1991). Despite their logistical and technical problems, these approaches have intuitive appeal as direct solutions to the study of prey selection. Their utility, however, is limited if they are used without a theoretical framework (e.g. contemporary foraging theory) that generates specific hypotheses to be tested during experiments. In this context, the work of Thompson *et al.* (1993) on optimal foraging tactics of seals in relation to prey availability is an example of a model that needs to be tested empirically (Boyd, 1993).

Although behavioural mechanisms identified in operant experiments may be analogous and functionally equivalent to those used in the wild (Shettleworth, 1988; Dallery and Baum, 1991), results from operant feeding experiments should be treated with caution when attempting to translate from the laboratory to free-ranging conditions. Accordingly, the objective of the present experiments is not to test hypotheses about free-ranging feeding behaviour, but to test whether seals have preferences when different prey types are equally available. Choices that seals may make in such an impoverished, captive environment are context specific, because other factors that may influence prey selection (such as prey abundance and density) are deliberately abstracted. However, because we do not understand the process of prey selection in the wild, a logical first step is to identify if and how perceptions of seals, including prey preferences, comprise potential behavioural constraints on prey selection. This helps to define the context in which wild seals make decisions about food.

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References

BATESON, P. 1990. Choice, preference, and selection. *In:* Interpretation and explanation in the study of animal behavior Vol. I: Interpretation, intentionality, and communication, pp. 149-156. M. Bekoff and D. Jamieson (eds.). Westview Press, Oxford.

BEKOFF, M., and D. JAMIESON. 1990. Recognition, choice, and play: Introduction. *In:* Interpretation and explanation in the study of animal behavior Vol. I: Interpretation, intentionality, and communication, pp. 119-122. M. Bekoff and D. Jamieson (eds.). Westview Press, Oxford.

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

BOYD, I.L. 1993. Introduction: trends in marine mammal science. *Symp. zool. Soc. Lond.*, **66**: 1-12.

CHEVERTON, J., A. KACELNIK, and J.R. KREBS. 1985. Optimal foraging: Constraints and currencies. *In:* Experimental behavioral ecology and sociobiology, pp. 109-126. B. Holldobler and M. Lindauer (eds.). Fischer Publ., Stuttgart.

DALLERY, J., and W.M. BAUM. 1991. The functional equivalence of operant behavior and foraging. *Anim. Learn. Behav.*, **19**: 146-152.

DUNSTONE, N., and R.J. O'CONNOR. 1979a. Optimal foraging in an amphibious mammal. I. The aqualung effect. *Anim. Behav.*, **27**: 1182-1194.

DUNSTONE, N., and R.J. O'CONNOR. 1979b. Optimal foraging in an amphibious mammal. II. A study using principal component analysis. *Anim. Behav.*, **27**: 1195-1201.

FEDAK, M.A., and D. THOMPSON. 1993. Behavioural and physiological options in diving seals. *Symp. zool. Soc. Lond.*, **66**: 333-348.

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.

HALL, C.S. 1951. Individual differences. *In*: Comparative psychology, 3rd edition, pp. 363-387. C.P. Stone (ed.). Prentice-Hall, Englewood Cliffs, New Jersey.

HARWOOD, J., and J.P. CROXALL. 1988. The assessment of competition between seals and commercial fisheries in the North Sea and the Antarctic. *Mar. Mamm. Sci.*, **4**: 13-33.

KRAMER, D.L. 1988. The behavioral ecology of air breathing by aquatic animals. *Can. J. Zool.*, **66**: 89-94.

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 pp.

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, pp. 222-238. M. Barnes and R.N. Gibson (eds.). Aberdeen University Press.

PYKE, G.H. 1984. Optimal foraging theory: A critical review. *Ann. Rev. Ecol. Syst.*, **15**: 523-575.

PYKE, G.H., H.R. PULLIAM, and E.L. CHARNOV. 1977. Optimal foraging: A selective review of theory and tests. *Quart. Rev. Biol.*, **52**: 137-154.

REAL, L.A. 1990. Predator switching and the interpretation of animal choice behavior: The case for constrained optimization. *In*: Behavioural mechanisms of food selection, pp. 1-20. R.N. Hughes (ed.). Springer-Verlag, Berlin Heidelberg.

REESE, E.P. 1964. Experiments in operant behavior. Appleton-Century-Crofts, New York. 209 pp.

SCHOENER, T.W. 1971. The theory of feeding strategies. *Ann. Rev. Ecol. Syst.*, **2**: 369-404.

SCHOENER, T.W. 1987. A brief history of optimal foraging ecology. *In*: Foraging behavior, pp. 5-67. A.C. Kamil, J.R. Krebs, and H.R. Pulliam (eds.). Plenum Press, New York.

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. 1988. Foraging as operant behavior and operant behavior as foraging: What have we learned? *In*: The psychology of learning and motivation: Advances in research and theory, pp. 1-49. G.H. Bower (ed.). Academic Press.

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

SLATER, P.J.B. 1981. Individual differences in animal behavior. *In*: Perspectives in ethology, Vol 4, pp. 35-49. P.P.G. Bateson and P.H. Klopfer (eds.). Plenum Press, New York.

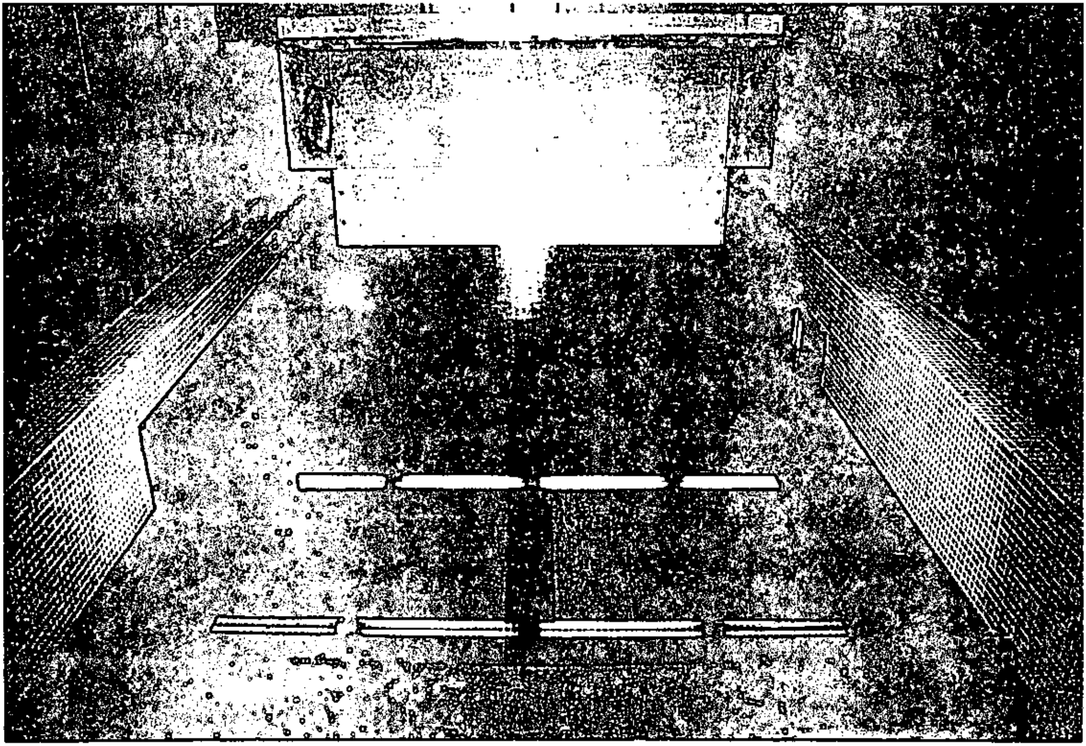
SMALLWOOD, J.A. 1989. Prey preferences of free-ranging American kestrels, *Falco sparverius*. *Anim. Behav.*, **38**: 712-714.

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

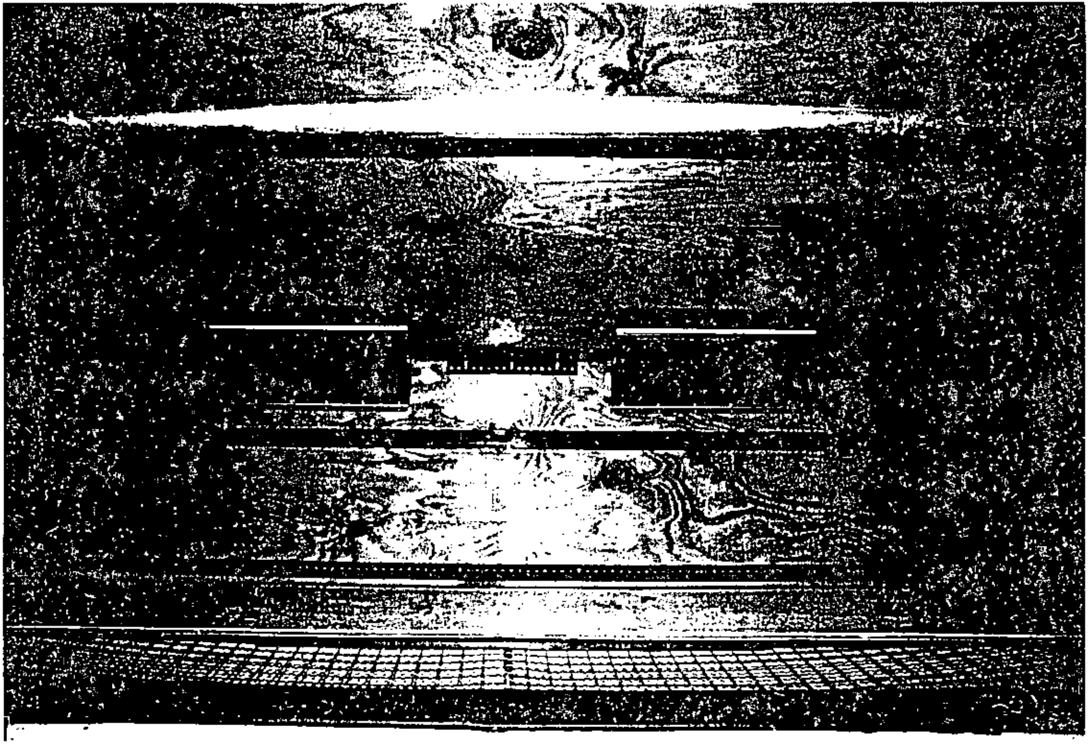
STEPHENS, D.W., and J.R. KREBS. 1986. Foraging theory. Princeton University Press. 247 pp.

SWENNEN, C., and P. DUIVEN. 1991. Diving speed and food-size selection in common guillemots, *Uria aalge*. *Neth. J. Sea Res.*, **27**: 191-196.

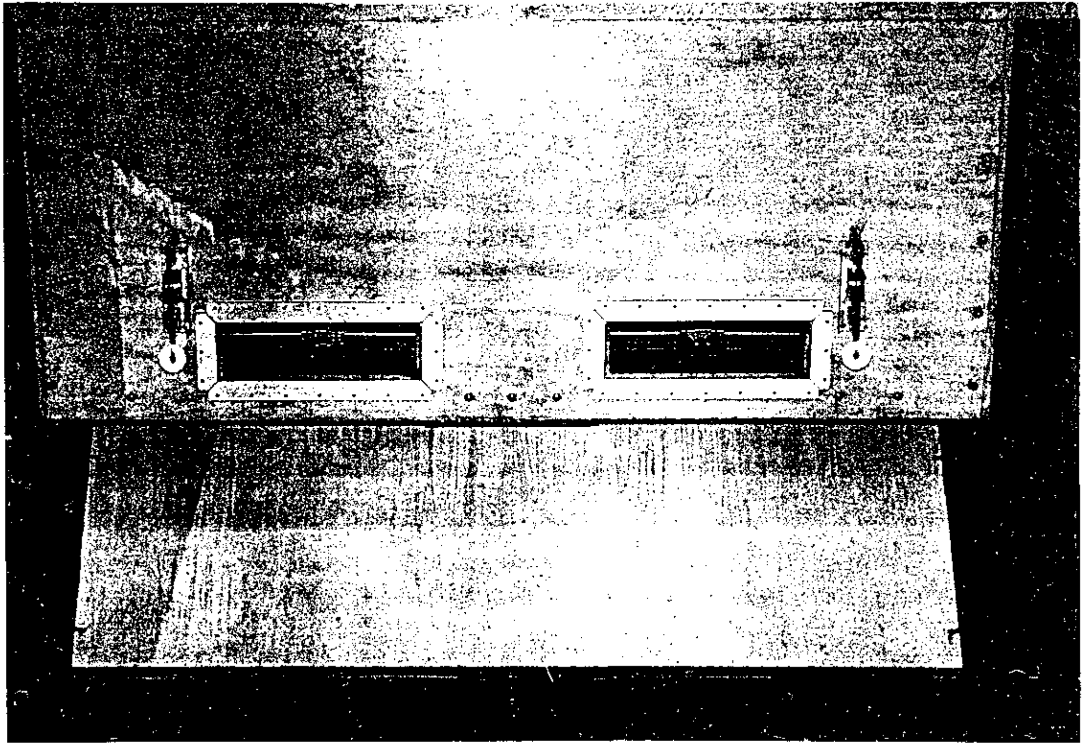
THOMPSON, D., A.R. HIBY, and M.A. FEDAK. 1993. How fast should I swim? Behavioural implications of diving physiology. *Symp. zool. Soc. Lond.*, **66**: 349-368.



igure 1: Front view of apparatus inside tank



igure 2: Rear view of main plywood sections of apparatus



'igure 3: Front view, showing positions of windows and paddle

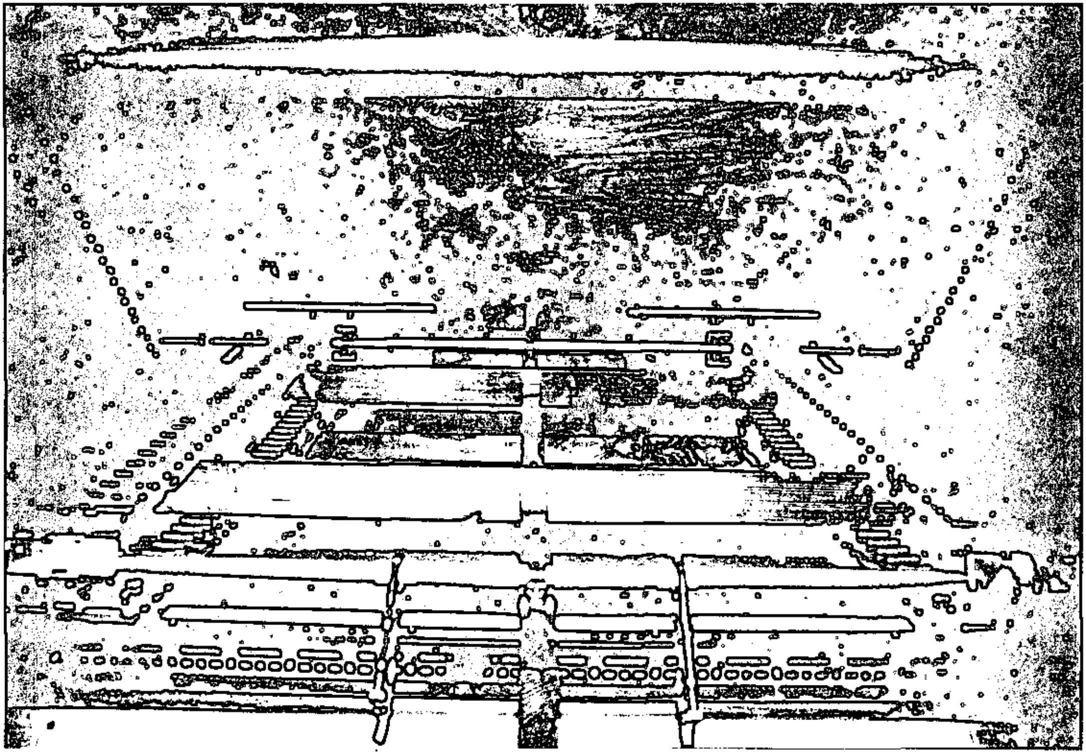


Figure 4: Rear view, with treadmill suspended in position

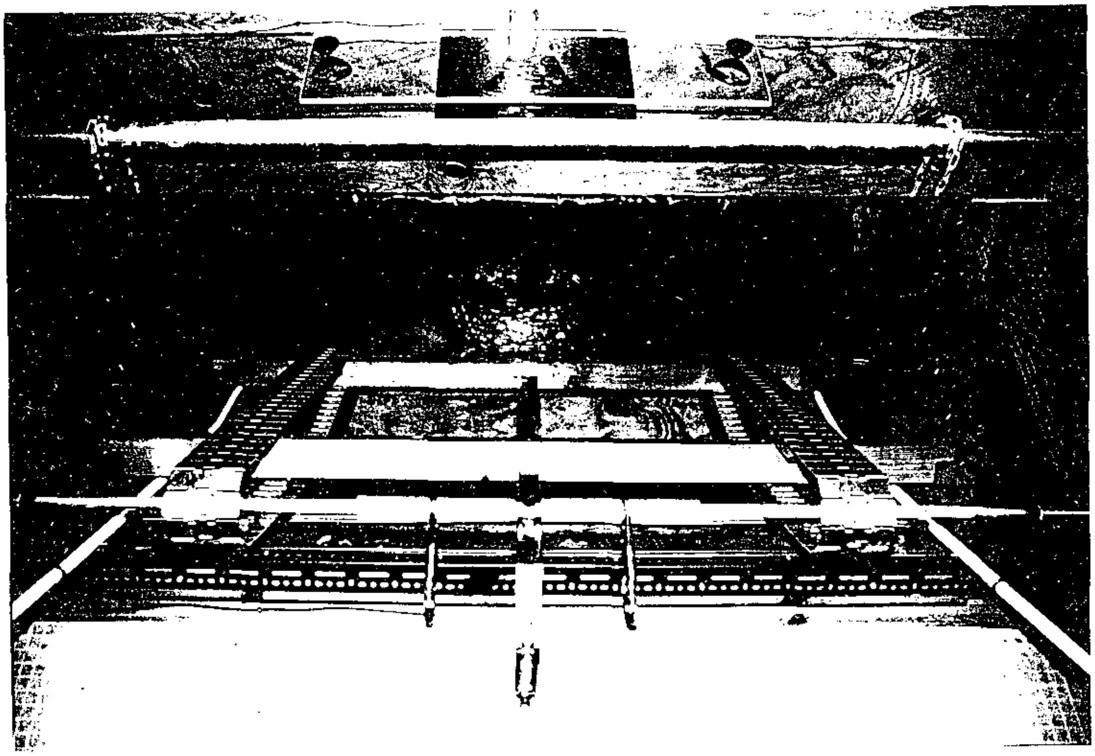


Figure 5: Rear view, with plastic screen and adjustable mirrors in place