

THE BEHAVIOR AND PHYSIOLOGY OF PINNIPEDS

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Experimental Laboratory Studies of Pinniped Behavior

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INTRODUCTION

This paper reviews the laboratory studies conducted to date on pinniped behavior and supplements this information with new and previously unreported data on Steller sea lions (*Eumetopias jubata*), harbor seals (*Phoca vitulina*), and the California sea lion (*Zalophus californianus*). In this way we hope to achieve some measure of understanding of the sensory, perceptual, learning, and motivational systems as they relate to individual and social behavior patterns of pinnipeds living in captivity as well as in their natural habitat. Even the most intensively studied species within a laboratory setting

(the California sea lion) has been subjected to a behavioral analysis which, at best, could only be described as being in its formative stages. For this reason any broad generalizations regarding the behavioral capabilities of the pinnipeds as a whole must be discouraged until more data are obtained both on the California sea lion and on other species.

The California sea lion is exhibited in most zoos, circuses, and marine-lands all over the world. Yet, except for a minor but informative investigation of this species by Spindler and Bluhm (1934), until 1963 information about their sensory perception, learning, and individual and social activity patterns in captivity was extremely meager (cf. Grandall, 1964; Hediger, 1955).

This dearth of laboratory behavioral studies of sea lions is even more surprising when we consider the rapid growth of conditioning techniques for the testing of animal capabilities. Many of these techniques, which have in the main been based upon one or more forms of reinforcement theory, have been available at least since the middle 1930's (cf. Kimble, 1961). It is perhaps because this methodology has been primarily developed and used by psychologists, who in the past have applied them to samples of small and relatively docile animals, that the widespread use of operant conditioning techniques has usually been limited to the experimental analysis of rat and pigeon behavior. Fortunately, a few psychologists like Robert M. Yerkes, Harry F. Harlow, and Winthrop N. Kellogg persisted in applying such training techniques to the experimental analysis of the behavior of mammals that are large and considered more difficult to handle, such as the chimpanzee, rhesus monkey, and the porpoise. It was the pioneering work of William A. Kellogg during the mid and late 1950's and the early efforts of William A. Schevill on the problem of echolocation in porpoises which eventually opened the way to the experimental analysis of the behavior of the porpoise (*Tursiops truncatus*) and finally to more systematic laboratory study of the behavior of the California sea lion.

Clues as to the sensory perception and learning capabilities of seals, sea lions, and walrus can be obtained through observational studies conducted in their natural habitat. However, in order to do a quantitative analysis of such abilities, these animals must of necessity be brought into the laboratory. Because sufficient individual and social behaviors exhibited in nature are also displayed in captivity, it is possible to experimentally analyze individual

activity patterns as well as some types of social communicative processes which are either difficult or impossible at this time to study under natural conditions. Some behavioral patterns displayed in captivity are unique to captive animals. The development of such abnormal behaviors is worthy of inquiry from the standpoint of zoo ecology and may help us to understand how such behaviors are generally developed under conditions of unnaturally restricted environments. One of the key factors in the recent interest in seals and sea lions is their unique adaptation to both a terrestrial and a marine existence. This is particularly true in the study of the refinements of their sensory perception.

#### MOTOR AND PERCEPTUAL TRAINING

In captivity, and probably in the wild as well (see Peterson, this book), the California sea lion is a rather continuous feeder. This aspect of its behavior, combined with a seemingly natural tendency to manipulate objects by tossing and catching them again, makes this sea lion an ideal specimen for being trained in the performance of tricks, such as balancing balls, catching thrown objects of various sorts, retrieving water-borne objects or objects on land, and a variety of other perceptual motor skills (Hediger, 1955).

Through the use of reinforcement principles, we have had excellent success thus far in training six California sea lions, two Steller sea lions, and two harbor seals for work on a variety of visual and auditory tasks. By reinforcing successive approximations of the ultimately desired response (response shaping), seals and sea lions are first trained to push a target in air or under water with sufficient force to trip a microswitch. A fearful animal is trained more readily if a piece of fish is attached to the target. Normally, however, placement of a target directly in front of the animal elicits intense investigatory responses with the mouth and nose. Immediate fish reinforcement of such responses usually leads to consistent target pushing within 15 to 30 minutes of the first target presentation. Target pressing, which often serves as an indicator response for perceptual tasks including those related to the use of active sonar or echolocation, may be "chained" to a sequence of motor acts to help ensure adequate observing or orienting responses. This is accomplished by making presentation of the target manipulandum

contingent upon the desired starting position. When the animal moves to the desired position, presentation of the target is immediate. The animal then swims to the target, pushes it, and receives a fish reward (see Figs. 1 and 2). Continued training of this sort results in an animal holding itself in a relatively fixed position for intervals up to 1 minute. The sea lion can be trained to hold this position with its head either submerged or in air.

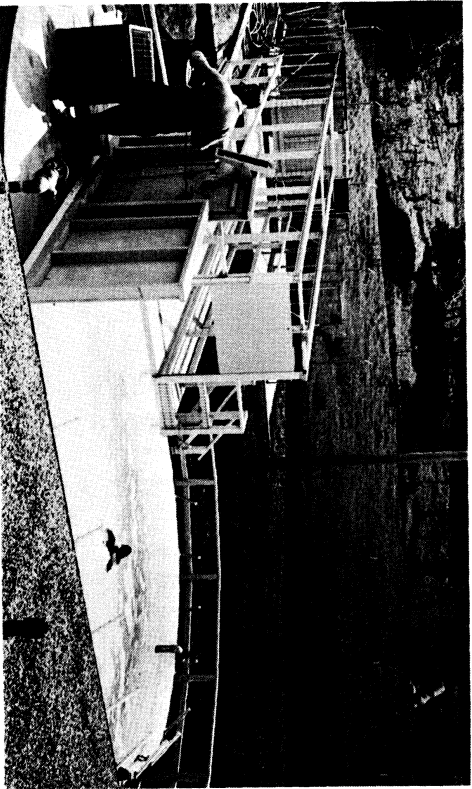


Fig. 1 SEA LION HOLDING ITS POSITION PRIOR TO TEST TRIAL.

The method of successive approximations for training motor responses can also be applied to the training of perception (Terrace, 1966). I have recently extended the use of this progressive training procedure to a series of discrimination reversals performed virtually without error by the California sea lion (Schusterman, 1965b, 1966b). The significance of this training procedure is that it virtually eliminates errors, i.e., responses to the negative or incorrect stimulus. Since the negative stimulus has been demonstrated to acquire aversive properties during discrimination learning, eliminating responses to the negative stimulus attenuates the emotional or nonest-oriented behavior that often accompanies nonreinforced responding and therefore ensures that the animal is attending to the discriminative stimuli. Thus,

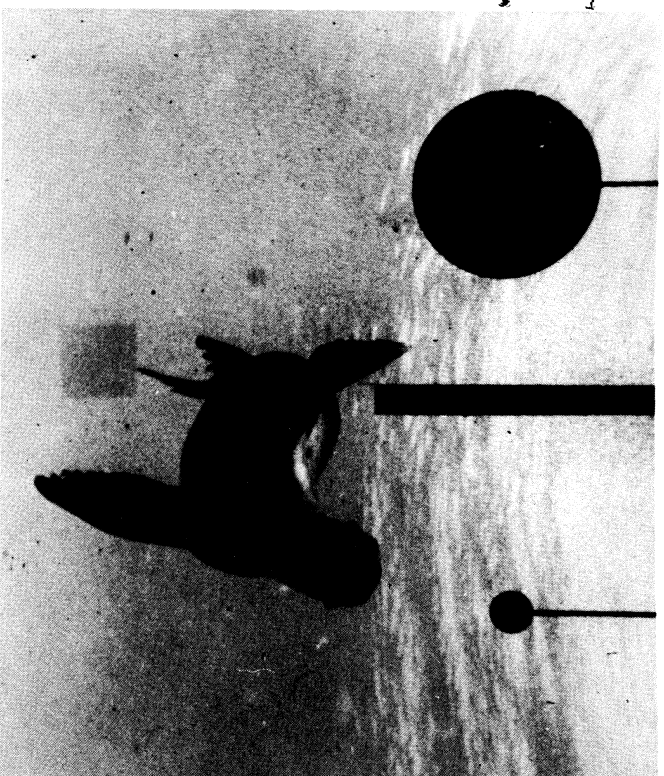


Fig. 2 SEA LION APPROACHING SMALLER OF TWO TARGETS.

when it is desirable, we are able to study perceptual processes in seals and sea lions that are relatively uncontaminated by emotional displays and by inattention.

This progressive training or "fading" technique relies on establishing a simple discrimination between stimuli within a single dimension, superimposing a new relevant dimension on the previous one, and then gradually eliminating the original dimension until it is no longer present.

The critical elements of training were the repeated combining of a previously well-learned size cue preference with the nonpreferred form cue, followed by the progressive reduction of the size cue. Figure 3 shows a prototype of the progressive training procedure used in a series of reversal tasks. The figure shows that the first form reversal may begin by having the nonpreferred form (circle) and the preferred size (small) constitute the positive or reinforced compound stimulus and by having the preferred form

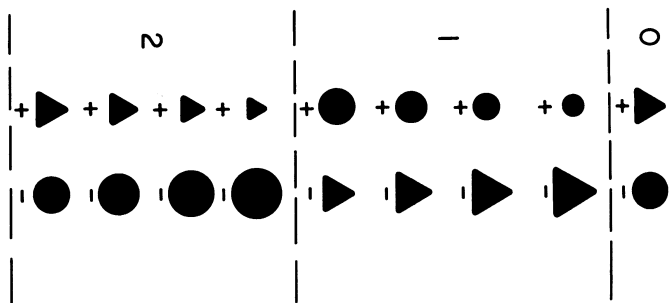


Fig. 3  
 PROTOTYPE OF PROGRESSIVE DIMENSIONAL-CHANGE TRAINING FOR OBTAINING ERRORLESS LEARNING ON TWO FORM REVERSALS. Pluses refer to the positive or reinforced stimulus and minuses refer to the negative or nonreinforced stimulus. Note that at the beginning of each form-reversal training series both size and form cues are correlated with reinforcement and that at the end of the series the size cue is eliminated.

(triangle) and the nonpreferred size (large) constitute the negative or non-reinforced compound stimulus. During succeeding training stages the area of the circle is gradually increased and the area of the triangle is gradually decreased until size is eliminated as a cue and only the circle and triangle serve as discriminative stimuli. Training on the next form reversal proceeds in a similar manner except that the small triangle becomes the positive compound stimulus and the large circle becomes the negative compound stimulus.

Application of this methodology has proved extremely fruitful in studying visual attention processes in two California sea lions (Schusterman, 1967b). Systematic insertion of probe trials, during which the size cue was not present, revealed that attention was primarily focused on the size dimension during early stages of training when size differences were large, and then was gradually shifted to the form dimension as a function of the increasing difficulty of the size discrimination.

### SENSORY AND PERCEPTUAL SYSTEMS

In this section, I will review past studies and present new data concerning the avenues by which seals and sea lions gain information about their environment and how they organize this information in a meaningful way for successful adaptation to both a marine and terrestrial existence.

The dominant modes of sensory perception useful in communication systems, navigation, and the detection and discrimination of prey and enemies, the augmentation of these dominant perceptual systems by other systems, the degree to which sensory avenues are acute, and the use of special perceptual systems such as echolocation for the detection and discrimination of underwater or aerial objects are topics which are currently being researched (Schusterman, 1967a). For the most part, attempts have been made in these studies to determine whether seals and sea lions use their sound production for purposes of echolocation or active sonar. The animal primarily used in these studies has been the California sea lion.

Because of the sparsity of information in this area, a number of questions have arisen. A few of these questions have caused some degree of controversy: Do most, if not all, pinniped species use an echolocation system under water? If pinniped visual discrimination in air is of as low an order as suggested by the observations of Peterson and Bartholomew (1967)

on the California sea lion, how does the aerial vision of these animals compare with their underwater vision? How acute is their vision under extremely low levels of illumination? Despite the fact that some species are extremely vocal under water, it has been suggested that the underwater hearing of at least one species--the California sea lion--is somewhat feeble (Bonnort 1951). How does underwater hearing compare to aerial hearing in some pinniped species? If there are certain deficiencies either in hearing or in seeing, are these deficiencies primarily a function of the mechanical or neurological aspects of the sensory system, or are they related to the perceptual system as a whole; i.e., are there selective attention mechanisms which play a crucial role in the responsiveness of these animals to various types of environmental stimulation? Unfortunately, complete or even partial answers to some of these questions have not as yet been obtained. However, there are now enough data available to suggest limitations in some of the hypotheses concerning the sensory perception of these animals. Furthermore, new and interesting lines of inquiry are beginning to be formulated. These may enable us to direct our efforts in a more fruitful manner than in the past.

#### Echolocation or Active Sonar

The use of active sonar or echolocation as a perceptual tool has been demonstrated in a relatively wide variety of animal forms, including man, and may in fact be a potential sensing device in any animal that can emit and receive vibrational disturbances of a mechanical nature. However, until recently there has been little interest in the relative importance and efficiency of a sonar system as compared with other perceptual mechanisms at an animal's disposal. For example, according to current knowledge, the insectivorous bats, Microchiroptera, apparently rely primarily on reflected sound for object detection and discrimination, with other sensory and perceptual mechanisms having only auxiliary functions. However, studies of the genus *Rousettus* of the suborder of fruit bats, Megachiroptera, indicate that in this bat echolocation is an adaptation to cave roosting where absolute darkness may occur, but that in semidarkness visual perception plays a major role during this animal's nocturnal activities. Perception of reflected sound is neither as important nor as well developed in *Rousettus* as in insectivorous bats, and presumably *Rousettus* depends primarily on visual information as long as some faint light is available (Griffin, Novick, and Kornfield, 1958;

Neuweiler, 1967). Aside from *Rousettus*, all other fruit bats rely on vision or possibly olfaction (Möhres, 1967). Among birds, cave swiftlets, *Collocalia*, and the oil bird, *Steatornis*, may also use echolocation, depending on the availability of visual cues (Griffin, 1958; Neuweiler, 1967; Medway, 1967). Although the data are still equivocal, shrews, tenrecs, and rats may use echolocation under special circumstances and may rely on this perceptual mode of object detection considerably less than on smell, hearing (passive sonar), vision, touch and other skin senses, and kinaesthesia (Gould, Negus, and Novick, 1964; Gould, 1965; Neuweiler, 1967; Riley and Rosenzweig, 1957).

Active sonar as the predominant and possibly the most highly developed means of object discrimination is well established for dolphins, particularly *Tursiops truncatus* (Evans, 1967; Kellogg, 1961; Turner and Norris, 1966) and *Phocaena phocaena* (Busnel, Dziedzic, and Anderson, 1965). Although there is very little information available on the visual capabilities of dolphins, one behavioral study on the visual discrimination of *T. truncatus* suggests that these animals have great difficulty in initially attending to visual forms and that they do not possess binocular stereoscopic vision, at least for short distances (Kellogg and Rice, 1966). On the other hand, tests in which visual cues and reflected sound cues were opposed offered no difficulty to *T. truncatus* (Kellogg, 1961); the animal depended solely on reflected sound cues. Apparently the behavior of these dolphins is primarily controlled by reflected sound and not by reflected light. Even when visual cues are readily available, dolphins emit "exploratory" sonar signals every 15 to 20 seconds. Such periodic signal emission suggests a sonar equivalent to glancing in the field of vision (Kellogg, 1961). Furthermore, threshold values of obstacle avoidance by *P. phocaena*, obtained when vision was eliminated, were not enhanced when visual cues became available (Busnel and Dziedzic, 1967).

In view of these results with dolphins, it was not surprising that a hypothesis was formulated suggesting that seals and sea lions also use active sonar as a dominant perceptual mechanism for object detection and discrimination. This notion was strengthened once it was demonstrated that the California sea lion and other forms of pinnipeds were capable of producing clicks under water in conjunction with feeding, regardless of whether visual cues were readily available (Poulter, 1963a, 1963b; Schewill, Watkins, and Ray, 1963). The evidence for this hypothesis is equivocal at this time (see Poulter, 1963a,

1963b, 1966, for evidence in support; and Evans and Haugen, 1963; Schevill, Watkins, and Ray, 1963; and Schusterman, 1966a, 1967a, for non-supporting evidence).

Observation of blind California sea lions in apparently good health (Poulter, 1966) has resulted in at best only circumstantial evidence for the use of an active sonar system in the detection and discrimination of food targets. Since these sea lions vocalize under water a good deal of the time while in a social group (Schusterman, Gentry, and Schmook, 1966) and have been observed in large groups when feeding on schooling fish (see Peterson, this book), it may be argued that blind individuals maintain acoustical contact with the group during feeding episodes and thereby locate food sources merely by means of passive listening. Furthermore, there is currently no information available regarding the incidence of healthy but totally blind sea lions, nor do we know whether blind individuals depend on the same types of food sources as do normally sighted animals.

In reviewing laboratory studies on echolocation, Evans (1967) reminds us that we still have very scanty information regarding the ecological determinants of the behavior of these animals in their natural habitat, and such studies of behavioral potentialities must be extremely speculative at best until more information is forthcoming from the field.

It is recognized that one of the chief positive features of experimental studies in the laboratory is that such studies can be nearly exactly replicated. Although on the basis of his data Poulter (1963a, 1963b, 1966) has concluded that numerous species of pinnipeds have a highly sophisticated active sonar system, especially the California sea lion, the published reports of these experiments unfortunately do not contain enough information which would enable replication of these studies. For example, little or no information is given in these papers regarding the age or sex of the animals used, the objective response criteria, the response latencies, the number of test trials presented, the techniques for tracking or observing the animal during test trials, the spatial relationship between the experimenter and the animal, the spatial location of the sonar objects in relation to the animal, the size of the testing tank relative to the size of the animal, or the amount of visual experience that the animal had in the tank prior to elimination of visual cues. A number of these questions relate to whether some of the results could have been accounted for in terms of the sea lion's spatial memory, especially if location

of the test objects were not strictly randomly determined, or whether tactual cues arising from any portion of the sea lion's body or from the stiff vibrissae (15 to 20 cm in length) of the sea lion were used in the detection and discrimination of objects. There is little question that the vibrissae play an important role as short-range tactile sensing devices. I have observed, for example, that a blind adult female harbor seal will show no reaction when a fish is held above her face. However, as soon as the fish just brushes against the whiskers, the animal responds within a fraction of a second and snatches the fish from the feeder's hand. Furthermore, observations indicate that the sea lion shows great concern whenever any type of material clings to its vibrissae. In such cases, the animal has been observed to vigorously wipe its whiskers either against its own furry body or that of a neighbor or against a rock or cement.

Since in none of these studies has sound reception or emission been blocked during the proposed echolocation tasks, they cannot be regarded as definitive. Some investigators have even had difficulty in obtaining sound production under conditions of darkness or other types of visual impairment (Evans and Haugen, 1963; Schusterman, 1966a, 1967a). It is worth noting that in one instance when the blocking of click emission from a dolphin, *T. truncatus*, was attempted by placement of an acoustically opaque head cover, the animal refused to swim forward and eventually rid itself of the head cover before continuing to swim forward (Norris, in press). In this regard, experiments that block signal emission should be considerably easier to accomplish with sea lions than with porpoises (see Norris, in press, for a review of the controversy on the origin of the porpoise's sound production), since *Zalophus* and presumably some other otariid species emit underwater clicks that have a known origin in the posterior portion of the vocal cords (Poulter, 1965). Therefore total removal of the vocal cords (Eiseman, Bilbone, and Slater, 1965) should cause these animals to lose their ability to emit underwater clicks, thereby enabling one to compare vocal and devocalized animals in sonar detection and discrimination tasks.

In one of the most recent studies dealing with echolocation in the California sea lion a technique was used which eliminated visual cues, allowed detailed observation of the animal while it performed, and still allowed the animal to approach as close to the targets as was necessary prior to making an objectively scored indicator response (Schusterman, 1967a). A three-year-old

female sea lion was simultaneously presented with two visually identical Plexiglas<sup>1</sup> discs, one of which was laminated and filled with air, the other solid. The sea lion was required to push the air-filled disc in order to receive a piece of fish. Even though these targets were grossly different objects acoustically, the sea lion continued to perform at a chance level for 2,050 trials. This occurred despite the fact that the sea lion emitted clicking sounds during virtually all target presentations. Further studies suggested that the California sea lion is much more efficient in finding food by visual means than by active sonar, and that although it has great difficulty, this animal can eventually find live fish under extremely poor visibility conditions regardless of whether it uses sound pulses. It was concluded that although such findings cannot be interpreted as proof that the California sea lion has no sonar system, they do raise a question as to the degree to which these animals rely on such a perceptual tool and the conditions that must prevail before the tool is brought into operation.

It should be borne in mind that these studies cannot be directly compared with those conducted by Poulter (1963a, 1963b, 1966) since they were primarily concerned with the identification of inanimate objects, whereas those of Poulter were more directly concerned with the echolocation of stationary and moving dead fish targets. Furthermore, Visicorder records of clicks taken from the experimental tanks of Poulter (4.3 by 3.1 by 1.2 m) and Schusterman (9.1 by 4.6 by 1.5 m) indicate a fivefold increase in reverberation time and a higher ambient-noise level in the larger tank (Feinstein, 1966). On the other hand, Feinstein (1966) also showed that human divers submerged in Schusterman's tank and placed 30.5 cm in front of a speaker emitting broad-band clicks at the rate of 27/sec were able to discriminate between an air-filled Plexiglas disc and a solid Plexiglas disc on the basis of reflected sound. These discs were the same ones used in the study of sonar discrimination in the California sea lion (Schusterman, 1967a).

In a series of studies related to the question of whether sea lions strongly depend on their sonar system for discrimination of objects, I attempted to determine under what conditions these animals produced clicking sounds

under water (Schusterman, 1967a). I found that vocalizations appeared to be related to uncertainty, novelty, arousal level or frustration, and social factors. Furthermore, they were easily conditioned. Perhaps, for the time being, we may be able to live with the apparently contradictory evidence on the use of active sonar by pinnipeds if we consider the crucial roles played by developmental processes, learning, and memory in any animal sonar system, and also the way the system may operate in relation to other forms of sensory perception.

The finding that vocalizations of *Zalophus* are variable under water, that they are elicited when the animal is aroused and in conflict induced by conditions of poor visibility, and that they are so readily conditioned leads to the hypothesis that selective pressures may be such that some pinniped forms are currently in the process of developing a biological sonar system, but that in the present state of its evolution this sonar system must be relatively primitive compared with that in the porpoise. Norris (in press) has recently suggested, however, that even click emission in some species of porpoises is variable, although there is even less evidence for this statement at our current stage of experimentation.

Placing the question of sea lion echolocation in comparative perspective, there may be some agreement with the notion that the echolocation of some sea lions is not in any discernible manner modeled along the same lines as that of the insect-eating bats or some of the porpoises. This is true not only with respect to the signals produced (in this regard, there are also great differences between families of insectivorous bats [Vincent, 1964]) but also--and possibly of even greater significance--with respect to the differences that exist in the interaction of active sonar with other sensory systems, mainly vision. Only some dolphins and the insect-eating bats, according to present knowledge, have developed to the point of making full use of the diverse information implicit in an echolocation system without obvious recourse to other perceptual mechanisms. Vision, however, appears to play an important role in the way some seals and sea lions receive and organize information from their immediate environments.

### Vision

*Auity.* Anatomical evidence (Walls, 1963) suggests that pinnipeds have compensated for the absence of the refractive power of the cornea under

<sup>1</sup> Tradename for thermoplastic poly(methyl methacrylate)-type polymers, Rohm & Haas Co.

water by having a large spherical lens that produces enough accommodation to form a reasonably well-defined image on the retina. Recent behavioral data on the underwater size discrimination ability of the California sea lion have confirmed this anatomical evidence (Schusterman, Kellogg, and Rice, 1965). Differential size thresholds under normal daylight conditions were obtained by the psychophysical method of constant stimuli. The sea lions responded to one of two circular targets and were required to make a decision at least 1.2 m prior to giving an indicator response.

Additional experiments of this nature have been conducted with two harbor seals (Feinstein and Rice, 1966) and two Steller sea lions. In all of these experiments the targets were black circular discs presented against a white background. The standard target (against which all other targets are compared) was approximately 108 cm<sup>2</sup> in area. Although the testing apparatus and procedures used across species were similar, there were some differences. For example, in order to reduce the nonest-oriented behavior of the Steller sea lions, a modified method of constants was used in which easy comparisons were always presented first at any given test session. Size differences were progressively reduced until the sea lion made two consecutive errors or three total errors in ten trials at the same size difference level. With this procedure the absolute number of errors at a given test session was effectively reduced and both Steller sea lions appeared to be attending to the stimuli throughout most of the experiment.

Figure 4 gives the comparative results of these studies. The curves for all animals show systematic increases in correct responses as a function of increased area differences. All animals but one (Steller sea lion, Ferd) were capable of discriminating area differences as small as 6 percent. If the discrimination of size differences may be taken as a gross measure of functional visual acuity, then *Z. californianus*, *P. vitulina*, and *E. jubata* may be said to have good underwater visual acuity. Indeed, comparison of these results of three species of pinnipeds with those of such "visual" animals as the Java monkey and the squirrel monkey reveals little difference in the size discrimination ability of these divergent mammalian forms (Klüver, 1933).

Despite Walls' (1963) claim that on the basis of the eye's corneal, pupillary, retinal, and choroidal properties the visual acuity of most pinnipeds should be nearly as sharp in air as it is under water, some observers have indicated otherwise (Hamilton, 1934; Peterson and Bartholomew, 1967).

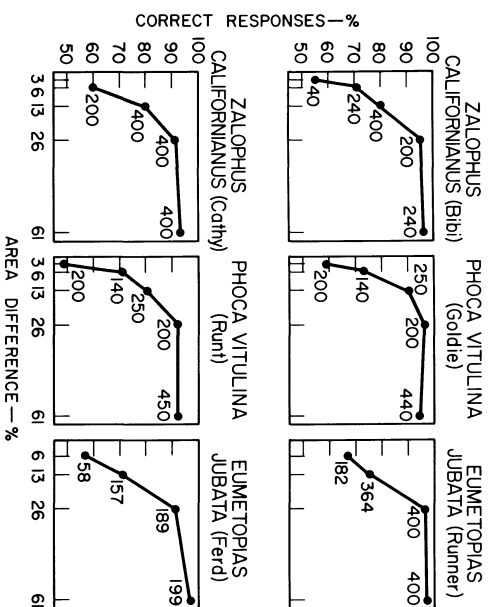


Fig. 4 PERFORMANCE CURVES COMPARING THREE SPECIES OF PINNIPEDS ON A SIZE OR AREA DISCRIMINATION TASK UNDER WATER. Numbers refer to trials given at each area difference.

For example, Peterson and Bartholomew indicate that, in terms of their reactions to man, the aerial visual discrimination of *Zalophus* in daylight is of a low order, whereas that of the harbor seals (*P. vitulina*) is considerably better. In support of this viewpoint Peterson and Bartholomew point to the fact that in broad daylight *Zalophus* displays little reaction to crouching and stationary human forms even at distances as close as a few meters, whereas harbor seals react to similar visual stimuli at considerably further distances. However, these differences in visual reaction between these two species may be due to physiological mechanisms involving selective attention such as the reticular formation (Hernández-Peón, Scherrer, and Jouvet, 1956; Hernández-Peón, 1961) rather than to visual acuity per se. This alternative hypothesis is in accord with the great amount of vigilance behavior shown by harbor seals both in the wild and in captivity (see "Vigilance" below). The harbor seal, in contrast to the California sea lion, is constantly searching its environment by means of vision as well as audition and is therefore much more likely to detect subtle environmental changes. Therefore, in order to compare the



visual acuity of *Zalophus* in air and under water, it is absolutely necessary to train the animal to attend to subtle differences. Only in this manner, i.e., by equating attention in the two media, can questions about the functional visual acuity of seals and sea lions be answered. We have recently subjected these areas of question to laboratory experimentation and found related behavioral evidence contradicting the views of Peterson and Bartholomew and supporting those of Walls. The experiment was conducted outdoors under normal daylight conditions with a California sea lion. Essentially the same procedures were used as those outlined for the underwater studies. The animal was first trained under water to discriminate between different sized circular discs by pushing the larger one. By gradually reducing the water level the animal was trained to hold its head out of the water and look at the aerial targets as it swam forward (see Fig. 5). Figure 6 presents a comparison of the animal's performance in air and under water. Clearly these results indicate that insofar as a size discrimination task reflects visual acuity, the vision of the California sea lion under normal daylight conditions is just as acute in air as it is under water.

All of these studies have been carried out under levels of high illumination. Therefore behavioral evidence on the important question of whether pinnipeds have a relatively superior visual acuity (either in air or under water) at night or in dim illumination is still lacking.

Walls (1963) points out that aerial accommodation by some pinnipeds may be accomplished by a much constricted pupil that closes down to a narrow vertical slit. Under water, however, where there is usually less light available, the pupil dilates to a very large circle. According to Walls the pupil remains dilated in this fashion as long as the eye remains under water. However it is unclear whether the pupil remains dilated in this fashion when the eye is in air and in extremely dim light. If this is the case, as it is incidentally with most nocturnally adapted eyes, then on the basis of the corneal astigmatism of the sea lion's eye one might expect limited aerial visual acuity in these animals when they are in very dim light. Currently, however, there are no physiological data available on this question.

Regardless of the physiological mechanisms responsible for sea lion visual discrimination in air and under water, we have recently conducted experiments with the California sea lion which suggest that visual discrimination of very fine line length differences remains relatively unchanged,

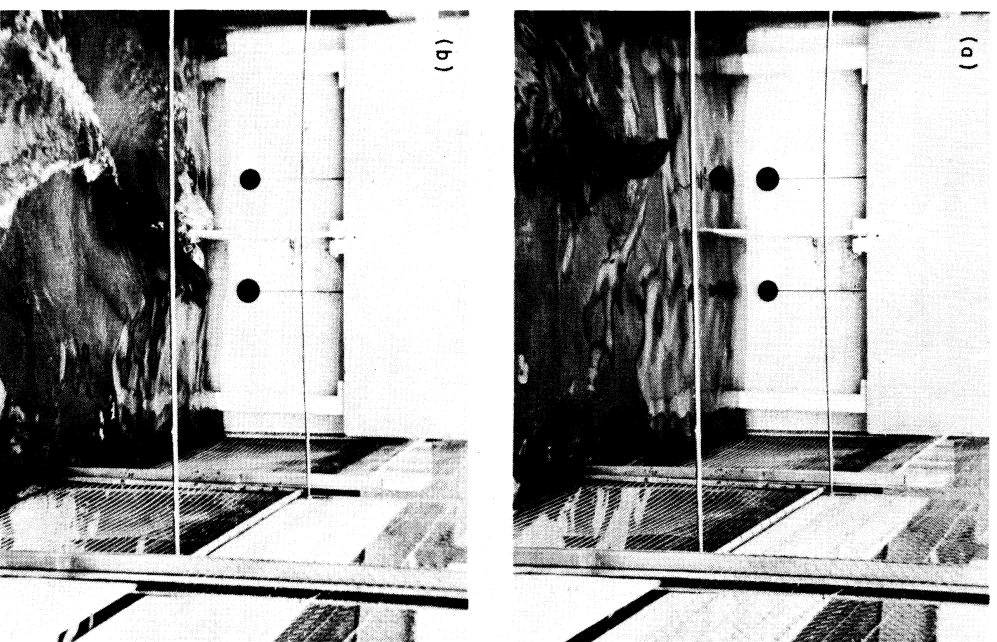


Fig. 5 SEA LION DURING A SIZE DISCRIMINATION TASK.  
 (a) Starting toward aerial targets.  
 (b) Approaching the larger target with head held out of water.

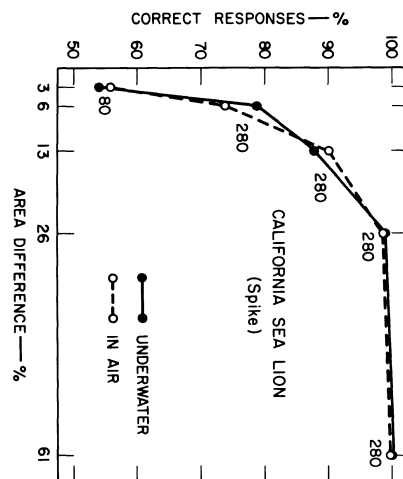


Fig. 6 PERFORMANCE CURVES COMPARING THE AERIAL AND UNDERWATER WATER SIZE DISCRIMINATION OF *Z. CALIFORNIANUS*. Numbers refer to trials given for each target area difference.

either in air or under water, with changes in background luminance varying from approximately 3.0 to 2.6 mV to 3.8 to 3.4 x 10<sup>-4</sup> mV (Schusterman and Dawson, in preparation). The experiments were conducted in a relatively light-tight tank. Critical features of the apparatus including the stimulus presentation panels are schematically shown in Fig. 7. The targets were made of transparent Plexiglas; upon each was painted a single black opaque vertical bar or line 1.5 cm wide. Background lighting was controlled by a series of neutral density filters in conjunction with a 500 w iodine cycle floodlight.

A California sea lion was first trained to choose the larger of two circles silhouetted against a high-luminance background. The animal was then easily transferred to a size discrimination task involving squares. By progressively narrowing the width and increasing the length of the formerly square silhouettes, the sea lion finally reached the point where it was choosing the longer of the two black lines with 100 percent accuracy. Throughout the entire training process, which took place under water, the animal did not make a single error. The water level was then lowered and the same training program was repeated while the animal kept its head out of water. The animal was then tested by the psychophysical method of constant stimuli under different intensities of background lighting, both in air and under water, in order to

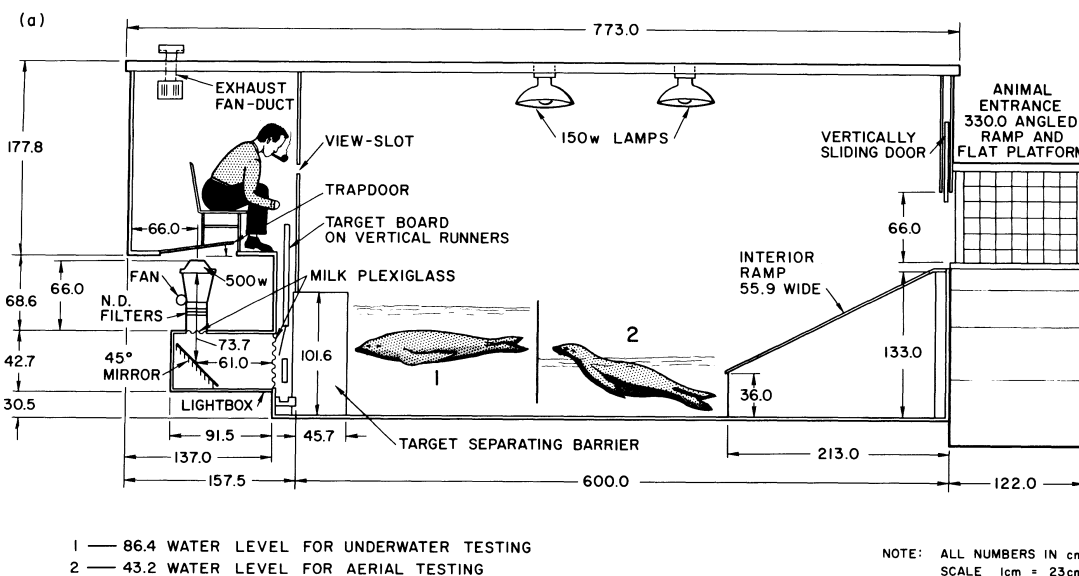


Fig. 7 SCHEMATIC DIAGRAM OF APPARATUS USED TO TEST SEA LION VISUAL ACUITY UNDER DIFFERENT LEVELS OF BACKGROUND LUMINANCE.  
 (a) Side view.

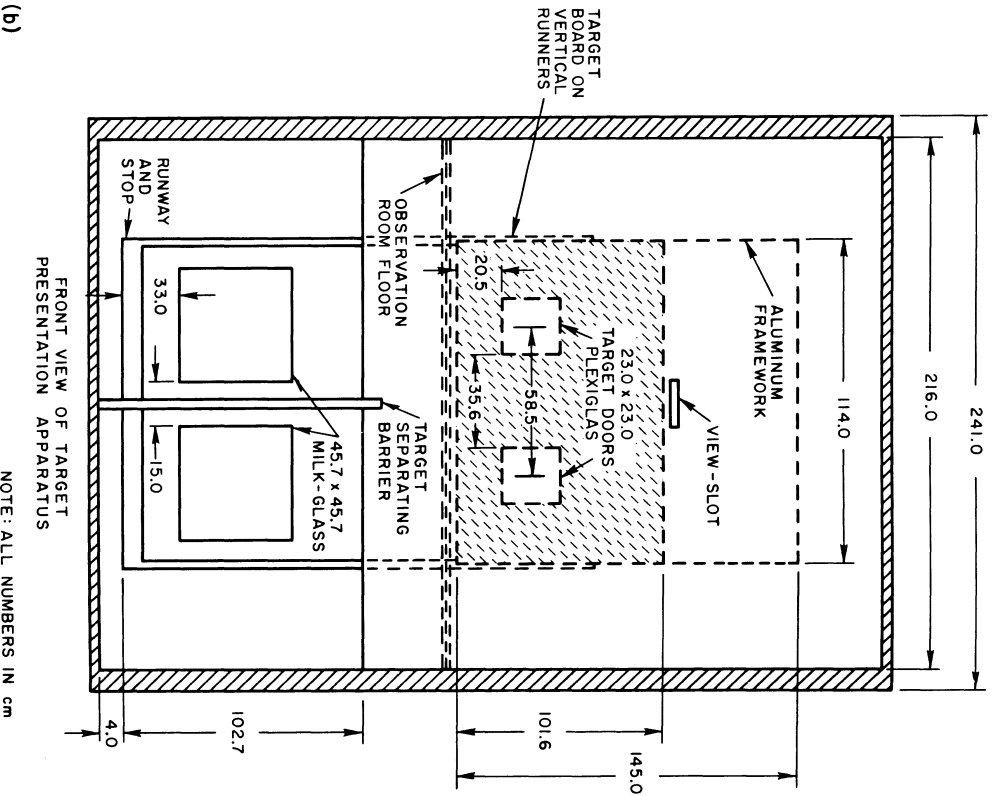


Fig. 7 SCHEMATIC DIAGRAM OF APPARATUS USED TO TEST SEA LION VISUAL ACUITY UNDER DIFFERENT LEVELS OF BACKGROUND LUMINANCE.  
(b) Front view.

determine how well it could discriminate the length of lines presented in the vertical plane. Prior to each experimental session, which lasted approximately 45 minutes, the sea lion was dark-adapted for a period of 5 minutes.

The series of graded line lengths and the levels of background luminance which were used along with the performance curves are shown in Fig. 8. These curves clearly show that discrimination of line length by the California sea lion remains relatively unchanged despite changes in media and background lighting.

In our most recent experiments with the same sea lion, a "minimum separable" technique (i.e., the perception of a small gap between two parallel lines) was used which yielded a visual angle of between 4 to 6 min. at a luminance level of  $2 \times 10^{-4}$  mL under water, and a visual angle of 8 to 10 min. at approximately the same luminance level in air. Thus by using a more sensitive test of acuity, a shift can be observed in *Zalophus* toward better acuity under water than in air under conditions of very dim light. However the aerial figure of 8 to 10 min. compares very favorably with acuity figures given by Walls (1963) for such terrestrial nocturnal animals as cats (5.5 min.) and opossums (11 min.). In reporting these figures Walls makes no mention of illumination level, and it is probably safe to assume that moderate levels of illumination were used. Acuity tests conducted in air with a luminance of 3.0 mL yielded a visual angle in *Zalophus* of between 4 to 6 min. Therefore, until more behavioral tests are conducted and additional work has elucidated some of the physiological mechanisms involved, it may tentatively be concluded that the California sea lion has excellent visual acuity in moderate light, both under water and in air, with little or no change occurring in very dim light under water and only a moderate loss occurring in very dim light in air.

*Color and Brightness.* Currently there are only scanty data available regarding color vision in seals and sea lions. Walls (1963) states that seals probably have only rod vision. Nevertheless, recent behavioral research on the vision of the opossum, which Walls says has such a small proportion of cones as to seem useless, has demonstrated that this nocturnal animal does indeed have functional color vision (Friedman, 1967). This suggests that color vision research with animals having nocturnally adapted eyes such as the pinnipeds may not be a completely fruitless endeavor. However, Baldwin

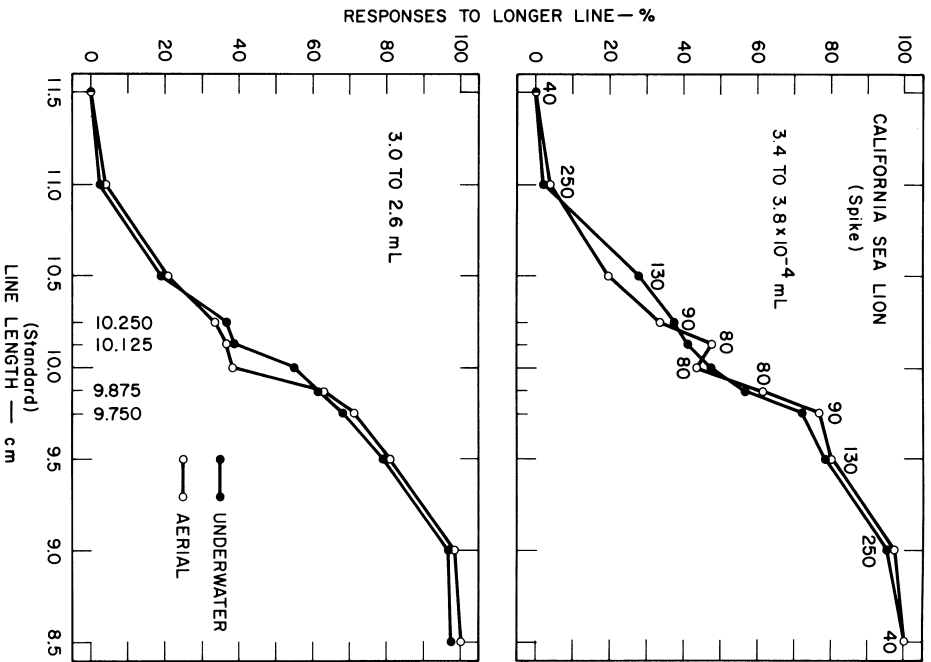


Fig. 8 PERFORMANCE CURVES COMPARING AERIAL AND UNDERWATER LINE-LENGTH DISCRIMINATION OF *Z. CALIFORNIA/US* UNDER TWO LEVELS OF BACKGROUND LUMINANCE. Numbers refer to trials given for each line length comparison.

(1966), using a tennis ball retrieval test, was unable to demonstrate color discrimination (orange vs. red) in a young California sea lion. This research was considered very preliminary, and without further detailed study of a variety of pinniped species it would seem premature, especially in light of the opossum results, to completely rule out functional color vision in the pinnipeds. In another preliminary experiment, Baldwin (1966) was able to show that a California sea lion could discriminate between rather small differences in brightness.

*Orientation.* Sea lions swimming in mildly turbid water, which completely occluded their vision as they began their approach toward a stimulus display, learned orienting responses of the head and body in order to discriminate visually between two target stimuli (Schusterman, 1965a). Discrimination performance remained perfect in both clear and turbid water but orienting responses occurred more frequently in the latter. Such results suggest that sea lions rely primarily on postural adjustments and fixating responses of the head and eyes in order to discriminate effectively between two objects of different sizes. Furthermore, in line with Hobson's (1966) recent observations regarding the tendency of seals and sea lions to approach from below and silhouette their prey against the ambient surface light even at night, all species tested in my experimental situation have approached targets from a position considerably beneath the targets.

*Shape Discrimination and Classification.* A recent study of the underwater discrimination ability of two California sea lions revealed efficient discrimination of stimulus figures differing only with regard to shape (Schusterman and Thomas, 1966). Many of these discriminations were maintained at a high level of accuracy even when positive, negative, or both shapes underwent changes in orientation of 45°, 90°, or 180°.

These results suggest that visual form input to *Zalophus* is classified with regard to general and not specific properties. Similar findings have been obtained with higher mammalian land forms such as cats and monkeys, but not with rats (Sutherland, 1961). Comparative studies of a similar nature with the Steller sea lion and the harbor seal reveal a similar type of adaptation for the processing of visual information. Table 1 gives the results.

Table 1

## COMPARATIVE RESULTS OF SHAPE DISCRIMINATION AND TRANSFER TESTS

The formula for the transfer index developed by Sutherland (1961) is  $(T - 50)/(O - 50)$ , where O is the percentage of correct responses given on the retraining trials and T is the percentage of times that the transfer shape is treated as equivalent to one of the original training shapes.

PAIR NO.	1	2	3	4	5	6	7	8	9	10	11	12
Original Stimulus Pairs	● ▲	⊕ ■	⊔ ○	♥ ◆	T =	S U	K C	^ D	∟ A	W Z	6 8	● ● ●
Transfer Stimulus Pairs	● ▼	⊗ ■	⊔ ○	▲ ◆	T ⊥	∩	× C	^ ∩	Y V	M Z	6 8	● ● ●
Shapes Reoriented	+	-	both	-	+	both	-	+	both	-	+	both
California Sea Lions (Bibi)												
Original Learning (Errors)	12	1	5	23	4	1	30	13	29	8	35	1
Retraining (% correct)	95	100	100	100	100	100	100	100	100	100	45	100
% Transfer	95	100	100	85	70	100	100	95	55	100	15	80
Transfer Index	+1.00*	+1.00*	+1.00*	+0.70*	+0.40	+1.00*	+1.00*	+0.90*	+0.10	+1.00*	--	+0.60*
Growler												
Original Learning	25	1	78	38	26	27	5	43	94	6	179	100
Retraining	95	100	95	90	100	100	100	95	95	100	75	90
% Transfer	85	100	75	95	20	75	100	80	45	95	80	85
Transfer Index	+0.78*	+1.00*	+0.56*	+1.11*	-0.60*	+0.50*	+1.00*	+0.67*	-0.11	+0.90*	+1.20*	+0.88*
Stellar Sea Lion (Runner)												
Original Learning	121	4	49	4	1	4	22	27	2	1	74	13
Retraining	100	100	100	95	100	100	95	95	100	95	90	95
% Transfer	35	95	30	90	70	100	85	100	45	100	40	95
Transfer Index	-0.30	+0.90*	-0.40	+0.89*	+0.40	+1.00*	+0.78*	+1.11*	-0.10	+1.11*	-0.25	+1.00*
Harbor Seal (Goldie)												
Original Learning	11	10	39	8	7	6	13	29	38	2	24	22
Retraining	95	95	95	100	100	100	100	90	100	100	100	100
% Transfer	60	100	55	95	75	80	100	70	50	100	55	80
Transfer Index	+0.22	+1.11*	+0.11	+0.90*	+0.50*	+0.60*	+1.00*	+0.50	0.00	+1.00*	+0.11	+0.60*

\* Designates significant transfer

There are several features of these results and the procedures used to obtain them which deserve some discussion. First, all four animals (representing three genera and two families of pinnipeds) received training on size discrimination tasks with triangles and circles and had perfected a cutout triangle-circle discrimination just prior to this study. However, the California sea lion (Bibi) was also given previous training on a series of reversal tasks (Schusterman, 1966b) and the harbor seal had previously learned to discriminate between a series of regular and irregular patterns (see "Learning Set and Visual Pattern Discrimination" below). For these and several other reasons, including the fact that the first two original pairs of shapes were considerably easier to discriminate between than some of the latter pairs (e.g., 9, 11, and 12), it is difficult to draw any firm conclusions regarding the relative rate of learning-set formation or the ability to "learn how to learn" on the 12 original pattern discrimination problems (see "Learning Set and Visual Pattern Discrimination" below). Second, in contrast to a previously drawn conclusion by the author (Schusterman and Thomas, 1966), the overall results of this study indicate that seals and sea lions show somewhat better transfer when the negative or nonreinforced shape is reoriented than when the positive or reinforced shape is reoriented. This is borne out by the finding that all four test animals showed significant positive transfer on all four shape discriminations when the negative shape was reoriented. A similar degree of transfer across species was not achieved on a single problem in which the positive shape alone was reoriented and on only two problems in which both positive and negative shapes were reoriented. Since, however, we have not as yet held the stimulus shape variable constant and systematically varied the reorientation of the positive and negative shapes, this interpretation is regarded as tentative. Third, despite some of the shortcomings alluded to above, in terms of the procedures which were used, the results shown in Table 1 suggest a considerable degree of consistency across several genera of pinnipeds in their equivalence responses to the reorientation of shapes over a relatively wide range of stimulus configurations.

#### Audition

Both Scheffer (1958) and King (1964) indicate that there is no information of an experimental nature regarding the underwater or in-air hearing of *Zalophus*, or for that matter of any pinnipeds. There has even been some

suggestion that their underwater hearing is "somewhat feeble" (Bonnor, 1951). However, the general belief of most investigators has been that, as in cetaceans, hearing is a very important sensory avenue in seals and sea lions. My own general impressions tend to support this view. On several occasions, brief sounds have inadvertently been introduced into a testing tank with a submerged California sea lion or harbor seal, and the animal has invariably been oriented to the sound source.

Investigations (Fraser and Purves, 1960) of the anatomy and physiology of the acoustic mechanisms of cetaceans indicate that they are superbly adapted for purposes of underwater hearing. A comparable anatomical analysis has yet to be worked out for the pinniped auditory mechanisms. On the other hand, Gentry (1967) conducted behavioral tests of sea lions' underwater directional hearing, or auditory spatial perception, similar to those conducted by Dudok van Heel (1962) with the porpoise, *P. phocaena*. The results showed that the California sea lion can reliably locate an underwater sound source at 10° azimuth when a 6 kHz tone is used and at 15° azimuth when a 3.5 kHz tone is used.

In order to test hearing directionality over a wider frequency spectrum range, a second experiment was conducted in which the auditory angle remained at a constant 25° azimuth and the frequency varied from 1.5 kHz to 6.5 kHz in increments of 1 kHz. Six frequency settings were presented for 15 consecutive trials at each test session until a total of 105 trials had been presented at each frequency. The results showed that at a constant azimuth of 25°, performance of the California sea lion improved as a direct function of increasing frequencies up to 6.5 kHz. Apparently, even at an angle as wide as 25°, *Zalophus* cannot locate a sound at frequencies much below 3.5 kHz. The reason for this is not yet clear, and obviously more data are needed. It may, however, be a function of a decreased sensitivity of *Zalophus* to low-frequency sounds, or an unfavorable signal-to-noise ratio at the low end of the spectrum, or the presence of standing waves. Interestingly, Dudok van Heel (1962) also found that the porpoise, *P. phocaena*, was not proficient at localizing a 2 kHz tone. Thus, at 6 kHz, the minimum auditory angle found by Dudok van Heel for the porpoise was 8° and for *Zalophus* it was 10°. At 3.5 kHz, the minimum angle increased for both species: 12° for the porpoise and 15° for *Zalophus*.

The ability of man and marine mammals to hear underwater sounds and the mechanisms that enable them to do so are currently subjects of great controversy (Feinstein, 1966; Reysenbach de Haan, 1966). The superior sonar system of the porpoise (*T. truncatus*) implies hearing in the ultrahigh-frequency ranges as well as an extremely acute perception of audiodirection or sound localization. With the very recent and extensive studies of Johnson (1967) we now have a better idea of the porpoise's auditory sensitivity. Using a staircase psychophysical method similar to that used by Tavolga and Wodinsky (1963) for obtaining auditory thresholds in fish, Johnson obtained an audiogram over the frequency range of 75 Hz to 150 kHz with a peak sensitivity near 50 kHz. As previously mentioned, in regard to the porpoise's (*P. phocaena*) perception of audiodirection, van Heel (1962) reports a threshold value of 8° to 12° azimuth. In view of this animal's excellent sonar ability, these values seem rather high; they appear to be indicative only of adequate sound localization and may have been a function of the relatively low frequencies (3500 and 6000 Hz) and test conditions employed, which did not allow this animal to use its full capabilities (Kenshalo, 1967). A personal communication from Bertel Møhl (1967) indicates that Søren Andersen has obtained a much lower auditory localization threshold with *Phocaena* (around 2° to 3° azimuth). Thus, porpoises obviously make full use of their auditory sensitivity and acuity for sonar detection and discrimination as well as for passive listening.

In terms of active sonar and passive listening, we now have evidence for adequate localization under water; but evidence regarding the auditory sensitivity and frequency range of the California sea lion is currently lacking. Except for Møhl's work (see Møhl, this book) on the aerial and underwater hearing sensitivity and sound localization of the harbor seal, there have been no reports of extensive experimentation on the hearing of other pinniped forms. Therefore, there is great need for systematic study of a comparative nature aimed at determining the underwater hearing abilities of seals and sea lions. The results from such studies should give us a much better understanding of the abilities of some pinnipeds to receive and organize information for perceptual guidance. Furthermore, since the little we know about the neuroanatomy of the pinnipeds' auditory system suggests that it is constructed and organized more along the lines of a terrestrial mammal than of a cetacean, results from these studies should help clarify the various auditory

mechanisms that tend to facilitate or impede underwater sound reception in other mammals, including man (see Møhl, this book).

### UNDERWATER SOUND PRODUCTION

A number of recent reviews have been or are in the process of being written which deal with various aspects of the underwater vocalizations and sounds produced by pinnipeds (see Evans, 1967; Norris, in press; Poulter, this book). Furthermore, a number of papers have recently been published dealing with the determinants of underwater vocalization in one species of pinniped: *Z. californianus* (Schusterman, 1967a). For these reasons, this section will be necessarily brief and will try to point out that it is unsafe at this time to draw any definite conclusions about the prevalence and function of this or that type of underwater vocalization or sound. The only firm conviction that may be held at the present time concerning underwater sound production of these animals is their extreme variability both within and between species. For example, the California sea lion produces a variety of vocal utterances and sounds including varying patterns of short duration pulses or clicks, barks, "whimpy" sounds, "bangs," and buzzes. Most, if not all, of *Zalophus*' underwater sounds appear to have a pulsed structure. All investigators who have recorded *Zalophus*' underwater sounds in captivity agree that the most widespread sounds are clicks or short-duration pulses. Such a conclusion may be premature.

My own recordings indicate that the dominant frequencies of these clicks range from 500 Hz to 4 kHz. However, there is one report indicating a great deal of energy in signals to 16 kHz (Schusterman, 1966a). Schevill, Watkins, and Ray (1963) found the emphasized frequencies ranging between 600 Hz and 1.5 kHz, and Evans and Haugen (1963) showed an upper frequency limit between 6 and 8 kHz. Poulter (1963) reports frequencies ranging from 5 to 13 kHz (1963a) or 3 to 13 kHz (1963b). Although other otariids such as the Steller sea lion and the fur seal have been reported to emit underwater clicks, detailed analysis of these sounds is still in progress (Poulter, 1963; Poulter, this book). Faint clicks are also produced in captivity by a variety of phocids including the harbor seal, *P. vitulina*, the ringed seal, *Phoca hispida*, the harp seal, *Phoca groenlandica*, the hooded seal,

*Cystophora cristata*, and the gray seal, *Halichoerus grypus* (Schevill, Watkins, and Ray, 1963). Schevill, Watkins, and Ray (1966) have also recorded underwater sounds from a captive Atlantic walrus, *Odobenus rosmarus rosmarus*. The most common sounds are rasps and clicks, but this animal also produces a very dramatic church bell sound.

Although there has been no systematic work regarding the earliest age at which pinnipeds are capable of underwater vocalization, at our laboratory I have recently heard three female walruses less than a month old emit underwater moans and barks. One infant produced these sounds in a submerged state while mouthing or sucking part of the body of another infant. These observations suggest that some pinniped forms may be capable of underwater vocalization at a very early stage of development.

Although clicks appear to be the most prevalent underwater sounds produced by those species of pinnipeds which have thus far been recorded either in captivity or in the field, further work may indicate otherwise. In all of these studies, little attention has been paid to the age and sex of the animals recorded or to the conditions under which the sounds were made. Although clicks were found to be the vocalizations most frequently produced by the California sea lion in an experiment dealing with the effects of social and mirror stimuli (Schusterman, Gentry, and Schmook, 1966), the animals involved in this experiment were young animals (two three-year-old females and a three- to four-year-old male) and the experiment was conducted during the nonbreeding season (winter, 1965-66). This experiment suggested that such vocalizations probably function in the underwater communication system of the California sea lion.

Since it is now established that barking by breeding males is at least partly a territorial vocalization in air and since it has also been shown that large portions of the bull's territory are submerged during high tides (Peterson and Bartholomew, 1967), it may be expected that in captivity as well as in his natural habitat, the male California sea lion may produce barks more frequently than any other type of underwater vocalization, especially during the breeding season (see "Barking, Dominance, and Territoriality" below). In addition, since the female California sea lion barks infrequently outside of the breeding season but barks frequently during the breeding season (Peterson and Bartholomew, 1967), the predominance of some types of underwater pinniped vocalizations may be assumed to be partly a function of hormonal

changes. Despite the scanty evidence on the functional properties of clicking sounds and other underwater vocalizations emitted by the California sea lion in captivity, there is enough circumstantial evidence pointing to the use of clicks, barks, and growl-type sounds as vocal communications. This, combined with the equivocal experiments implicating clicks as the first part of a highly sophisticated active sonar system, should lead us toward further investigation of *not* merely cataloging the sounds of pinnipeds but of relating the sounds to the behavior of the emitter and the receiver and thereby arriving at some understanding of the social significance or communication value of these signals.

## LEARNING AND CONDITIONING

### Learning Set and Visual Pattern Discrimination

As previously mentioned, seals and sea lions take advantage of surface light at night by viewing other animals from below for the purpose of either attacking or avoiding them. This maneuver has two advantages: First, the other animal is seen against the lighter water above. Second, there is less likelihood that the animal below will be visually detected by the other animal (Hobson, 1966). It therefore seems reasonable to suppose that some seals and sea lions learn to discriminate between a number of different patterns or silhouettes primarily on the basis of size and shape cues. Survival in terms of approach or avoidance movements may depend on how rapidly such silhouettes or patterns are associated with rewarding, nonrewarding, or punishing inputs, and how many such associations the animal can handle.

During the past year I have obtained evidence related to some of the foregoing hypotheses. In particular I have been interested in determining how proficient seals and sea lions are at solving two-choice pattern discrimination problems and whether they show progressive improvement in learning successive problems. This type of interproblem improvement has been called "learning how to learn," "deutero-learning," or "learning-set formation" (Harlow, 1949). These terms also apply to progressive improvement shown on a series of discrimination reversals in which the reinforced member of a single pair of stimuli is repeatedly alternated after each problem is learned to a criterion. Data have been obtained from seals and sea lions which are relevant to the acquisition of both types of learning set.

*Reversal Learning.* Two relatively naive California sea lions were tested on a series of 60 discrimination reversal problems. The stimuli were a cutout triangle and a circle having the same surface area and painted black. During the initial 20 reversals, each problem was presented until solved to an average criterion of 12 consecutive correct responses. During the next 40 problems, the average learning criterion was 10 consecutive correct responses.

As Fig. 9 clearly shows, both sea lions demonstrate rapid learning-set formation after the first or second reversal, eventually attaining a level of performance that averages approximately nine errors per reversal problem. Since the original problem was the last trained form discrimination task in which the progressive dimensional change technique was applied (see "Motor and Perceptual Training" above), both animals learned this problem with a minimum of errors. The first reversal, however, resulted in a large number of errors committed by both animals.

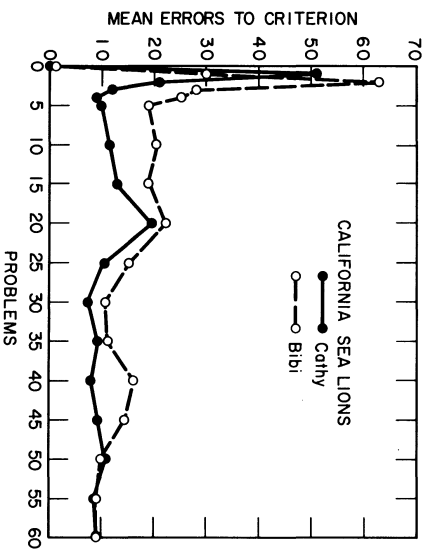


Fig. 9 INTERREVERSAL LEARNING BY TWO CALIFORNIA SEA LIONS FOLLOWING ERRORLESS REVERSAL LEARNING BY MEANS OF PROGRESSIVE DIMENSIONAL CHANGE TRAINING.

Despite differences in procedure, apparatus, and deprivation schedules, comparative studies of serial discrimination-reversal learning and interproblem learning have resulted in what some view as a fairly systematic phyletic trend



toward an increasingly greater learning capacity within the vertebrate series (Warren, 1965). Comparison of the interversal learning curves of the California sea lion with those of other mammalian species suggests that this marine mammal's proficiency on a series of visual discrimination reversals, although superior to that of rats and squirrels (data by A. R. Rollin as cited by Warren, 1965) is within the range of proficiency achieved by cats, rhesus monkeys, and chimpanzees (Schusterman, 1964; Warren, 1965). However, the California sea lion, in contrast to chimpanzees (Schusterman, 1962, 1964), shows no sign of eventually reaching a level of one-trial learning in such tasks.

*Multiple Pattern Discriminations.* Progressive improvement or learning-set formation on a series of pattern discrimination problems has been demonstrated by a California sea lion (Sam) and a harbor seal (Goldie). The stimulus patterns and the sequence in which the problems were presented to the California sea lion are shown in the top row of Table 1. The interproblem learning curves for both errors and trials to criterion are shown in Fig. 10 and indicate that, despite the fact that the last few configurations appear more difficult than the earlier configurations, this sea lion formed a rather efficient pattern discrimination learning set. It is worth noting that the data of Table 1 indicate that if we eliminate stimulus pair 11, the Steller sea lion may also be considered to have formed a learning set.

The first 28 pattern discrimination problems presented to the harbor seal were generated from all possible combinations of eight stimulus patterns taken two at a time (excluding reversing polarity of reward). This type of experimental design has been termed "learning set from minimal stimuli" (Riopelle, 1955). The next 30 problems were made up of stimulus configurations with which the animal had never had experience in the laboratory, each differing in size and shape. In order to determine the effects of initial pattern preference the rewarded member of each stimulus pair was determined by the seal's response on the first trial (trial 1) of each problem. Whereas on half of the problems response to either stimulus pattern was reinforced on the first trial (+) and the stimulus chosen by the animal on trial 1 continued to be reinforced on subsequent trials, on the other half of the problems response to either stimulus pattern was not reinforced on the first trial (-) and that pattern not chosen on trial 1 was thereafter reinforced on all subsequent trials. Interproblem performance curves are shown in

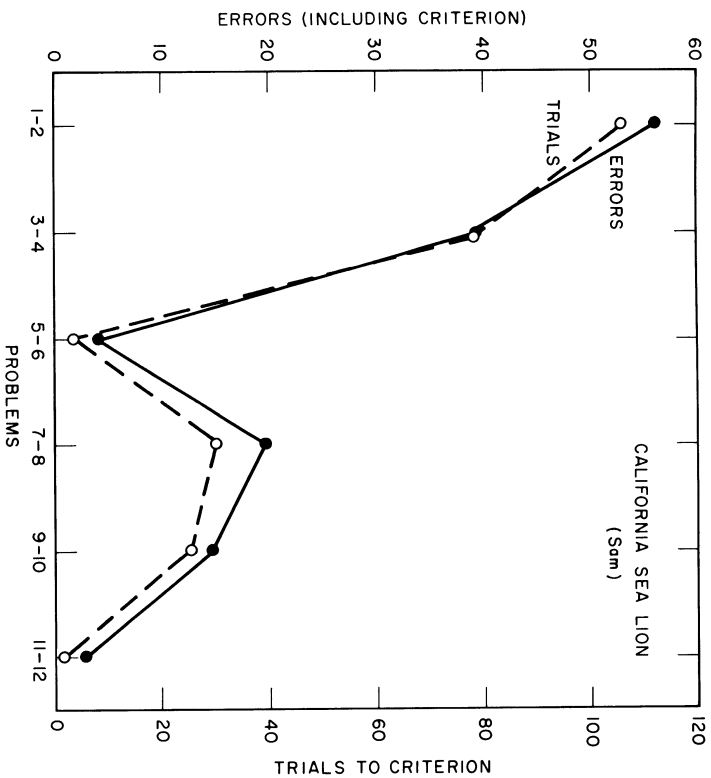


Fig. 10 INTERPROBLEM PERFORMANCE CURVES FOR *Z. CALIFORNIANUS* ON SERIES OF INITIAL PATTERN DISCRIMINATIONS.

Fig. 11 with trial 1 (+) and trial 1 (-) data plotted separately. As the figure shows, performance was generally better on those problems in which initial pattern preference continued to be reinforced. As in the case of the California sea lion, a learning set on pattern discrimination problems was formed rather rapidly by the harbor seal. The presumably asymptotic performance level shows that when the reinforcement contingencies coincided with its initial choice, this harbor seal was capable of solving most problems with less than 10 errors, and in some instances almost immediately upon presentation. Even though forcing the harbor seal to shift from its initial preference led to greater error production, even these problems were usually solved with an error level of less than 20.

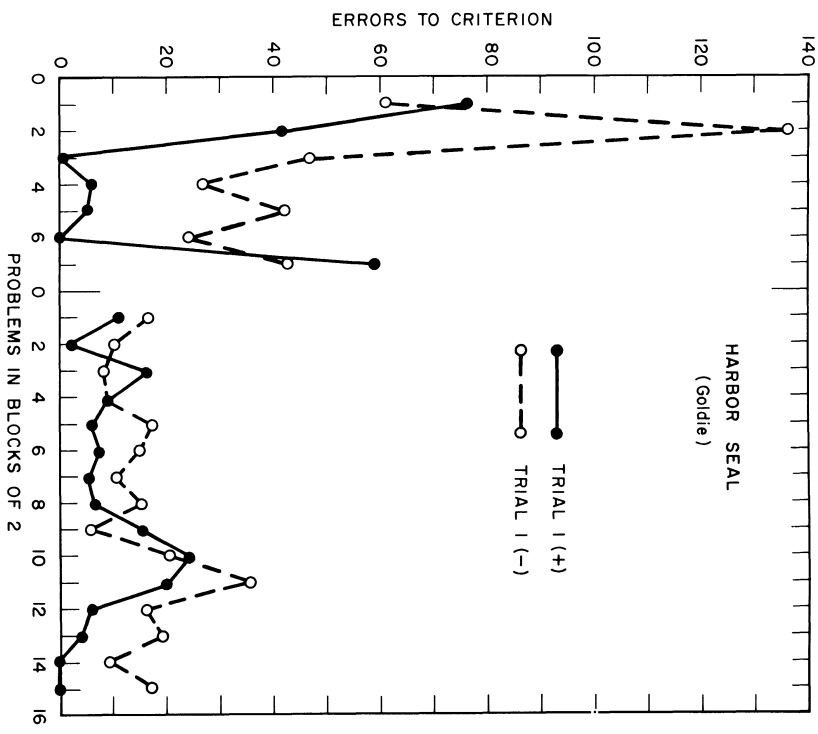


Fig. 11 INTERPROBLEM PERFORMANCE CURVES FOR *P. VITULINA* ON SERIES OF PATTERN DISCRIMINATIONS.

*Six-Trial Problems.* One way to find out how efficiently an animal can solve a series of discrimination problems is to present each problem for a limited number of trials (Warren, 1965). In conducting such tests with pinnipeds I hoped to gain some information relevant to the following questions:

(1) Are some seals and sea lions capable of discriminating between a variety of patterns primarily on the basis of shape differences only, when their experience for each discrimination problem is limited to six trials? (2) How important is initial stimulus preference under such training conditions?

(3) Do different pinniped forms differ with regard to learning proficiency and in the strategies they use?

Two California sea lions, one Steller sea lion, and one harbor seal were each tested under nearly identical conditions. All four animals had been trained and tested in a shape discrimination and transfer experiment (see "Shape Discrimination and Classification" above) just prior to this experiment. A total of 190 new and distinct problems were constructed from all possible recombinations of 20 different stimulus patterns taken two at a time. The stimulus shapes used were the first 20 appearing in the top row of Table 1. Thus, although all animals were familiar with the individual stimulus shapes, each problem was a presentation of a distinctly novel combination. Ten additional problems (for a total of 200 problems) were added by reversing the polarity of reward of 10 previously presented stimulus pairs. These pairs were selected randomly and were intermixed with the other stimulus pairs during the last 20 problems.

Each animal received 10 different problems of six trials each at a given test session. The animals had no information as to which stimulus shape would pay off on the first trial of each problem. However, following the first trial of a problem, fish reinforcement was consistently associated with one or the other of the stimulus shapes for the next five trials. Stimulus preferences were controlled as before; i.e., on half of the problems, reinforcement continued to be associated with the stimulus chosen on trial 1 (+), and on the other half of the problems, neither choice was reinforced on trial 1 and reinforcement was then associated with the stimulus *not* chosen on trial 1 (-).

The interproblem performance curves for each animal are shown in Fig. 12 with the results from trial 1 (+) and trial 1 (-) plotted separately. Better than chance performance, in terms of correct responses, for each block of 20 problems would be 65 percent or more (0.05 level of confidence, two-tailed test). The salient features of these curves may be summarized as follows: First, all of those animals having already formed a discrimination learning set for patterns (California sea lion, Sam; Steller sea lion, Runner; and harbor seal, Goldie) demonstrated immediate and significant persistent choice of the shape which paid off or was reinforced on the first trial of a discrimination problem. Second, all animals failed over the course of 100 six-trial problems to acquire any consistent discriminative skills when their

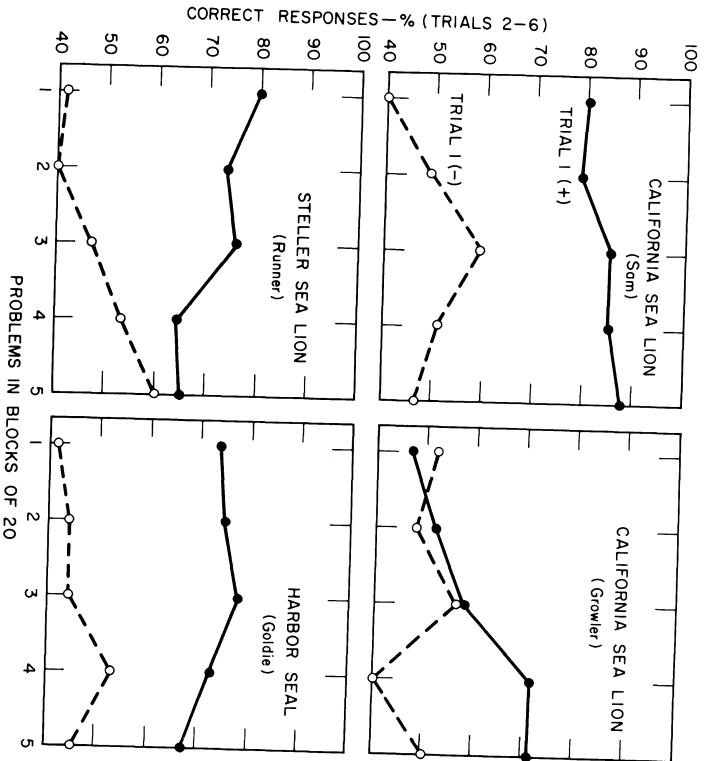


Fig. 12. PERFORMANCE CURVES COMPARING THREE SPECIES OF PINNIPEDS ON SERIES OF 200 SIX-TRIAL PATTERN DISCRIMINATION PROBLEMS.

initial choice was not reinforced. Third, the California sea lion, Growler, who showed little sign of learning how to learn during a previous shape discrimination experiment (see "Shape Discrimination and Classification" above) did demonstrate significant interproblem improvement on six-trial problems, but only on those problems in which initial choices were reinforced.

Stimulus combinations were randomly assigned to the trial 1 (+) and trial 1 (-) conditions throughout the course of the experiment, and none of the stimulus shapes were consistently associated with reinforcement. Beyond the first 100 problems, it was impossible to predict an animal's initial choice on the basis of the algebraic summation of reinforcement and nonreinforcement associated with one or another of the stimulus shapes. Thus, although

it would appear that several genera of pinnipeds are capable of acquiring pattern discriminations even when their experience is limited to only six trials per problem, such capability is strongly affected by initial stimulus preference and presumably the consequences of such preference, i.e., whether the initial choice is positively reinforced or nonreinforced. On the basis of the experiments reported in this section and those dealing with shape discrimination and transfer, it is suggested that some seals and sea lions may learn to approach silhouettes or patterns associated with a rewarding input more efficiently than they learn to avoid silhouettes or patterns associated with a nonrewarding input. However, systematic experimentation regarding the truth or falsity of this notion has not yet been attempted, nor have we attempted to conduct any experiments dealing with the effects of punishment on pattern discrimination learning.

An additional experiment was conducted in order to determine whether a sea lion was capable of learning pattern discrimination problems limited to six trials despite the fact that the initial choice was nonreinforced. The animal selected for study was a California sea lion (Sam) whose performance during the previous experiment was superior to that of the other animals (see Figs. 10 and 12). The stimulus pairings were the same as those used in the previous experiment except that the sequence of presentation was changed. Again, 10 six-trial problems were presented at each test session. Instead of using a trial 1 (+) and a trial 1 (-) procedure as before, only the latter procedure was used. Thus, in order to consistently receive fish reinforcement on trials 2 through 6 for each of the problems, the sea lion had to shift away from its initially preferred choice which was always nonreinforced.

The results of this experiment are plotted in Fig. 13. During the first 100 problems performance remained at a chance level. However, after 100 problems performance became significantly better than chance and remained that way through 120 additional problems. Thus, at least in the case of one California sea lion, we see the formation of a learning set with six-trial problems, even though trial 1 responses were never reinforced and the animal was forced to shift from its initially preferred stimulus choice. A clue as to the way this learning set may have been acquired lies in the development of a particularly interesting behavior pattern. Despite the fact that the first-trial presentation of each problem always resulted in a nonreinforced response, the animal never balked on such trials. Instead of balking or refusing to respond by pushing one or the other stimulus patterns on trial 1,

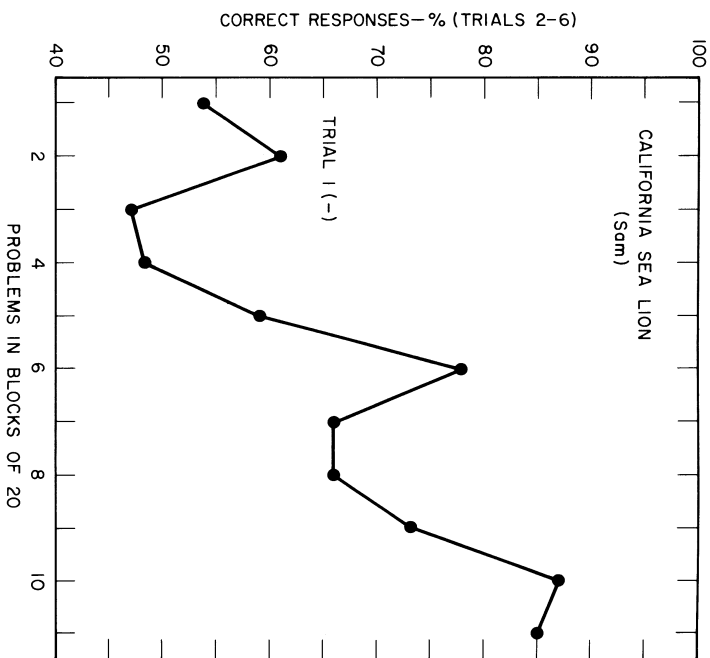


Fig. 13 INTERPROBLEM PERFORMANCE OF *Z. CALIFORNIANUS* ON SERIES OF 220 SIX-TRIAL PATTERN DISCRIMINATION PROBLEMS IN WHICH ONLY A NONPREFERRED PATTERN WAS CORRECT FOR ALL PROBLEMS.

the sea lion indicated its choice by simultaneously pushing and biting the stimulus. Figure 14 shows the differential development of this aggressive display toward trial 1 stimuli and toward the stimuli presented on trials 2 through 6 and indicates that the sea lion learned to distinguish between the reinforcement contingencies of trial 1 and trials 2 through 6. These results, therefore, suggest that any stimulus chosen on the first trial of a problem had acquired unusually strong aversive properties which ultimately led to its being more readily distinguished and avoided during trials 2 through 6.

In summary, these initial experiments on pattern discrimination and the formation of a learning set indicate, first, that seals and sea lions learn how to

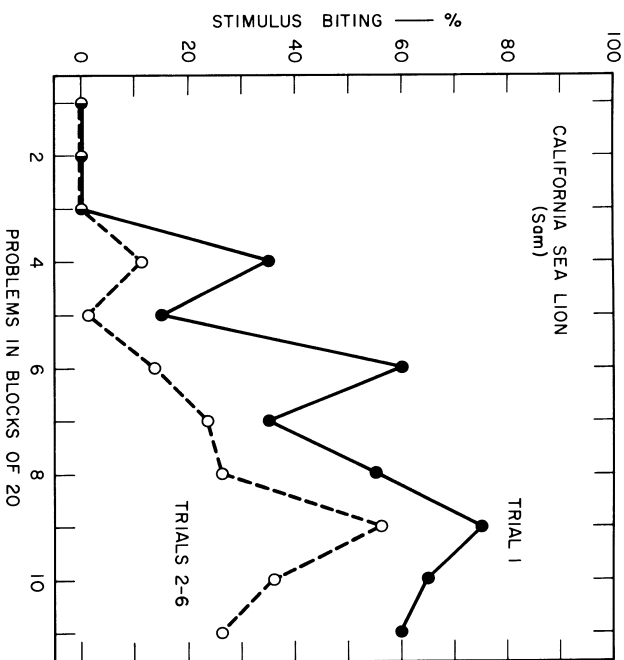


Fig. 14 ACQUISITION OF TARGET BITING BEHAVIOR BY *Z. CALIFORNIANUS* WHILE PERFORMING ON SERIES OF 220 SIX-TRIAL PATTERN DISCRIMINATIONS IN WHICH THE FIRST TRIAL OF EACH PROBLEM WAS NONREINFORCED.

learn quite rapidly when compared to some other mammalian forms (Riopelle, 1960; Warren, 1965), particularly when we consider the great difficulty that even such an intelligent primate form as the rhesus monkey has in learning a series of pattern discriminations (Chow, 1954); and, second, that initial stimulus preference significantly affects discrimination learning; as it does in terrestrial carnivores (Riopelle, 1960; Warren, 1965). Thus, in general, there is initial confirmation of the notion that some seals and sea lions can learn quite efficiently to visually discriminate between a large variety of different patterns or silhouettes primarily on the basis of shape and size cues. Moreover, there appears to be little difference between each of the species tested in their ability to acquire such underwater discriminations.

### Conditioned Vocalizations

Until recently, animal vocalizations were considered to be well-defined emotional behavior subject to modification only by classical conditioning procedures (Mower, 1948; Skinner, 1957; Thompson, 1958) and therefore to be distinct from human vocalizations, which may be brought under discriminative control by operant or instrumental reinforcement techniques (Skinner, 1938). However, operant control of vocalization has now been demonstrated in a variety of avian and mammalian species—budgerigars, mynah birds, chickens, dogs, cats (see Warren, 1965, for review), cebus monkeys (Myers, Horel, and Pennypacker, 1965), and dolphins (Lilly and Miller, 1962; Turner, 1962).

The relative ease with which the California sea lion's underwater vocalization may be brought under discriminative control has also been demonstrated experimentally. In one experiment, repetition of conditioning and extinction sessions resulted in a progressively more rapid transition between high and low degrees of vocal behavior (Schusterman, 1967). In another experiment, a sea lion was trained to make an underwater vocalization (clicks). This animal was further trained to conceptualize size by vocalizing when it saw a "large" target and inhibiting its vocalizations when it saw a "small" target, despite changes in the shape of the targets. The error level associated with this performance was extremely low (Schusterman and Feinstein, 1965).

Most recently the aforementioned experiment was repeated with another California sea lion. Using a counter-conditioning paradigm, a clicking vocalization in the presence of a small (16 cm<sup>2</sup>) circular target was reinforced and clicking in the presence of a large (736 cm<sup>2</sup>) circular target was not reinforced. The targets were presented successively in a random sequence within blocks of 100 trials; each was presented on 50 occasions at each test session. Figure 15 compares the previous counter-conditioning curves obtained from Cathy with those most recently obtained from Bibi. The similarities are quite striking and indicate the reliability of such vocal conditioning techniques with the California sea lion.

Demonstrations showing that previously neutral stimuli can acquire discriminative control over a sea lion's vocalizations are important from several standpoints. First, they indicate that learning may play a role, at least in terms of sheer vocal output, in the development of a vocal communication

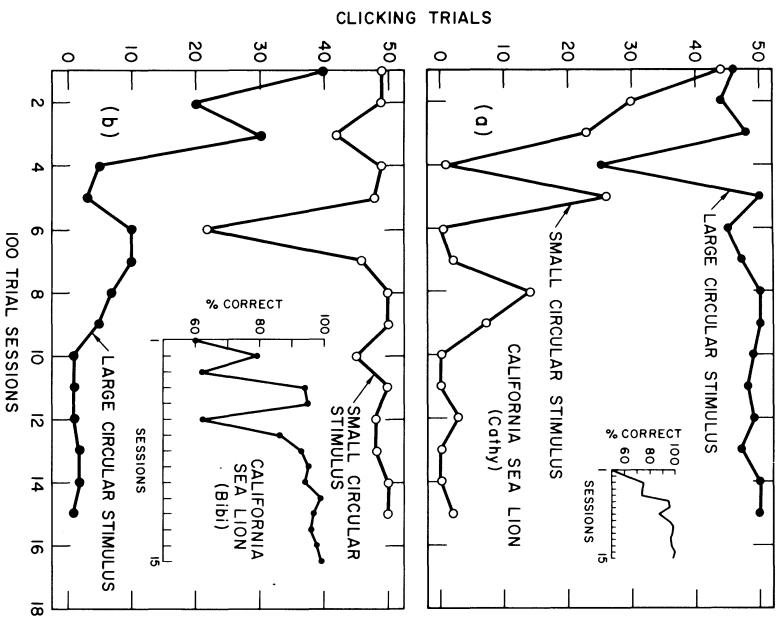


Fig. 15 ACQUIRING AND MAINTAINING DISCRIMINATIVE CONTROL OVER UNDERWATER CLICK VOCALIZATIONS. Inserts show acquisition of correct response (vocalizing or not vocalizing).  
 (a) Sea lion Cathy was reinforced for clicking in presence of large circular stimulus and for not clicking in presence of small circular stimulus.  
 (b) The opposite was true for sea lion Bibi.

system. Second, such studies suggest the necessity for revising our older notions about principles of conditioning and learning (Rescorla and Solomon, 1967; Salzinger and Waller, 1962). Third, such techniques can be used as a tool for studying sound production as well as other phenomena. For example, by using vocalization as an indicator response, we may well be able to determine the sea lion's differential or absolute sensitivity to certain selected aspects of its environment. By means of well-placed hydrophones, this can

be done while the sea lion is swimming freely and despite great distances between the experimenter and the sea lion and between the sea lion and the discriminative stimuli.

### INDIVIDUAL AND SOCIAL BEHAVIOR PATTERNS

During the past three years we have maintained a colony of seals and sea lions in several large compounds. For the most part, four different species of pinnipeds have lived in an integrated fashion in a 7.6 by 13.7 m compound containing a 3.4 m<sup>2</sup> pool, a 4.3 m long concrete slide, and a graded rocky slope running along one side of the compound. The four species (representing two genera of otariids and two genera of phocids) include the California sea lion, the Steller sea lion, the harbor seal, and the northern elephant seal. Daily maintenance of the living area generally consists of hand feeding individual animals and cleaning the pool and compound. Although the primary purpose of this living arrangement is to keep animals available for physiological and behavioral experimentation as well as for studying pinniped husbandry techniques (see Hubbard, this book), the maintenance of such a colony has afforded us the opportunity to observe several interesting individual and social behavior patterns. It is the purpose of this section to present quantitative and qualitative observational and experimental data dealing with conspecific and interspecific social behavior and individual activity patterns of seals and sea lions in a captive condition.

Table 2 gives pertinent information regarding individual members of the group. Although we were interested in describing the characteristic modes of behavior for each of the species under consideration, the table shows quite clearly that any observation of behavioral similarities and differences between species may be strongly influenced by such uncontrolled variables as sex, age, and age at capture. For example, the harbor seal group was composed only of females and included two fully adult animals, whereas the *Zalophus* group was composed only of males, none of which were fully grown. Both Steller sea lions, both elephant seals, two harbor seals, and one California sea lion were captured within one-half to three months of birth and may be considered laboratory-reared animals. Despite these shortcomings, it is hoped that some of the social and individual activity patterns displayed under these conditions are relevant to a comparative analysis of pinniped behavior.

**Table 2**  
CHARACTERISTICS OF ANIMALS COMPRISING THE GROUP USED FOR  
STUDYING SOCIAL AND INDIVIDUAL ACTIVITY PATTERNS

Animal	Species	Sex	Wt. (kg)	Approx. Age	Duration of Captivity	Remarks
M	California sea lion	M	150	5-6 yr	3 yr	
W	"	M	70	3 yr	11 mo	
P	"	M	60.1	3 yr	2 yr	
K	"	M	50	2 yr	11 mo	
T	"	M	43.2	2 yr	1 yr	
S	"	M	41.1	2 yr	23 mo	Forced fed and weaned at 7 mo
59	Steller sea lion	M	48.6	1 yr	10 mo	Forced fed and weaned at 6 mo
63	"	F	45	1 yr	10 mo	
J	Elephant seal	M	213.3	2 yr-5 mo	2 yr-2 mo	
Ma	"	M	146.3	1 yr-5 mo	1 yr-2 mo	
A	Harbor seal	F	70.5	7+ yr	2 yr	
B	"	F	69	7+ yr	1 yr	
Pi	"	F	45	3 yr-1 mo	3 yr-1/2 mo	Captured with mother and weaned at 1 mo
Ph	"	F	34.1	1 yr-2 mo	1 yr-1-1/2 mo	Forced fed and weaned at 2 mo

#### Baseline Observations and Comparisons

The animals were observed from a blind about 2.1 m above the top of the rocky slope. Observations were usually made between 1030 and 1100 hr and again between 1430 and 1500 hr on a five days per week schedule. The data obtained from these observations cover the period from May 26, 1967, to June 15, 1967. This time period covers the early stages of the California sea lion's breeding season off the California coast (Peterson and Bartholomew, 1967). Generally, the animals were relatively undisturbed during the observational periods and with two exceptions all 14 animals were always observed as a group. The incidence of various social and individual activity patterns was quantified by taking 1-minute samples of behavior every 5 minutes. There was a total of between 132 and 144 1-minute samples taken for

each individual in the group. During the 1-minute period each individual was scored for the one activity pattern which was predominant or most characteristic of the individual during that minute period. Since locomotion on land normally occurred in conjunction with another activity, this category was rarely scored. All individuals participating in a social interaction were noted. Definitions of the behavior categories and distinctions between classifications are described below:

- *Social Play and Aggression.* In general, social play is said to occur when two or more animals indulge in spirited motor activities usually culminating in the vigorous manipulation of one another's body parts (Welker, 1961). In several species of pinnipeds these play patterns include chasing, porpoising over one another, pushing, gentle biting, especially of the flippers, neck or back, claspings, mounting including copulatory movements, and jousting or mock-fighting (see Fig. 16). Since much of the social play by seals and sea lions is aggressive, it was important to distinguish between play encounters and agonistic encounters. This distinction could usually be made on the basis of the types of postures and vocalizations which were displayed as well as whether the biting was gentle or powerful.

- *Resting, Basking, and Orienting.* An animal was scored for resting when its eyes were closed and it was lying on its belly, side, or back with little body movement (see Fig. 17). In the case of the otariids, rest was also scored when an animal was sitting up with its eyes closed and with its head held parallel to the ground (see Fig. 18). If, however, the animal was in this exact same position but its head was tilted up in the characteristic way shown in Fig. 19, then the sea lion was scored for basking. If an animal was in a resting position but looked around briefly, then it was scored as resting. If, however, looking around was the predominant activity, then orientation was scored. An animal floating in the pool and constantly looking around was also scored as orienting (Fig. 20).

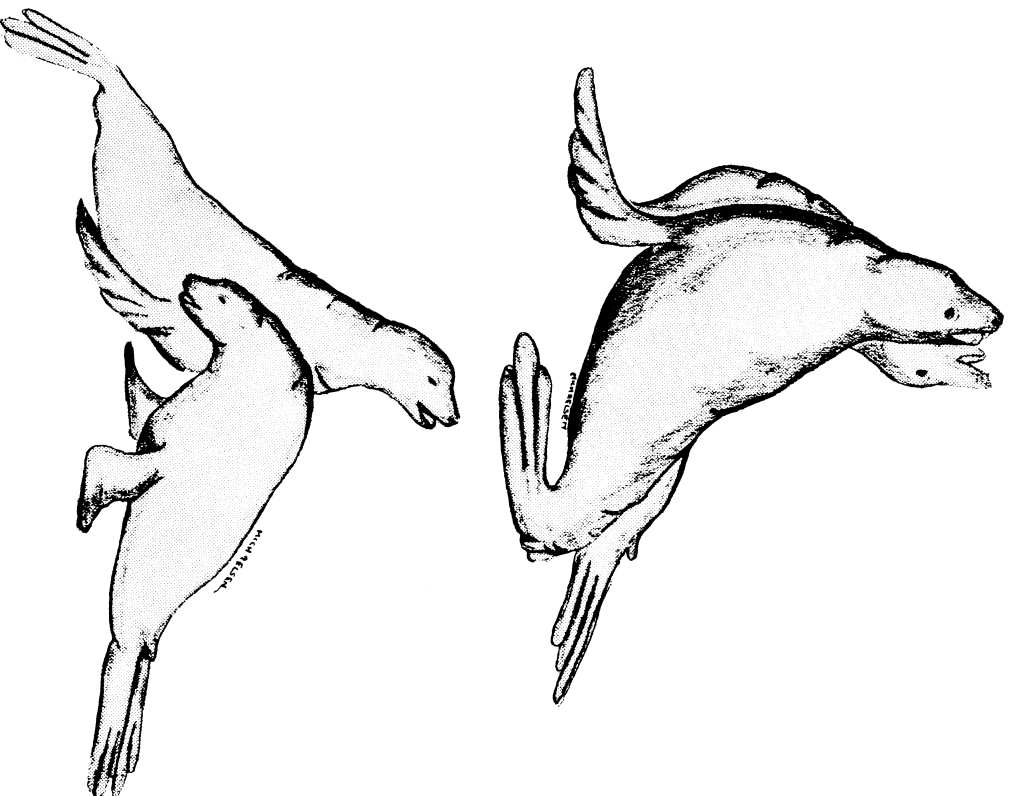


Fig. 16 SEA LIONS JOUSTING.

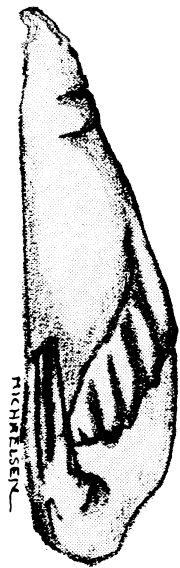


Fig. 17 TYPICAL RESTING POSITION OF *Z. CALIFORNIANUS*.

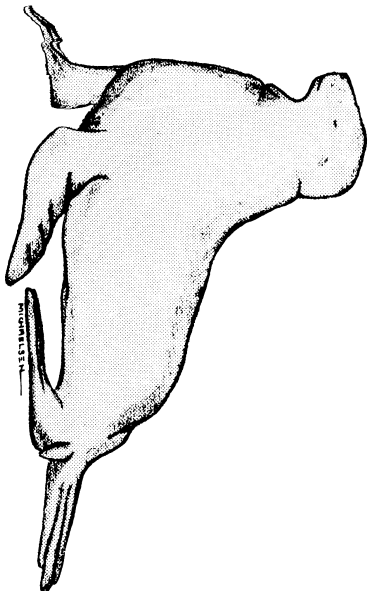


Fig. 18 A SEA LION RESTING IN SITTING-UP POSITION.

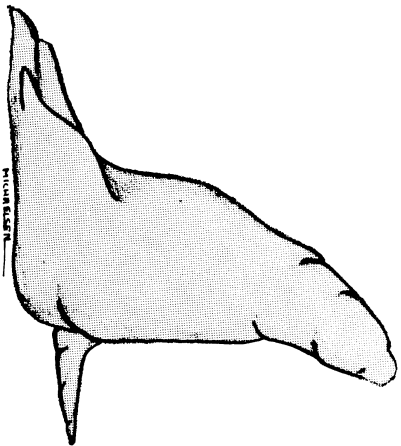


Fig. 19 SEA LION IN BASKING POSITION.



Fig. 20 VISUAL ORIENTATION BY HARBOR SEAL.

- *Aggregate and Contact Rest.* A distinction was made between resting alone and in groups. This category was scored if an animal met the requirements of rest but also had most of its body in direct contact with one or more other animals.
- *Grooming.* Grooming patterns differed widely between the phocids and otariids. The otariids typically cleaned their pelage by scratching with their clawed hindflippers, rubbing with the foreflippers, and nuzzling or biting their pelage (see Fig. 21). In contrast to the otariids, the phocids employed their clawed front flippers for scratching the flank and head regions (see Fig. 22). Both phocids and otariids rubbed their backs and sides against the ground either in or out of water. Furthermore, *Zalophus* rubbed its whiskers against its own body, that of another animal, or against a rock or the ground. *Zalophus* also rubbed parts of its body against another animal. All such self-manipulatory activities were classified as grooming and scored as such if the activity was relatively sustained during a 1-minute sampling period.
- *Individual Play and Environmental Manipulation.* This behavioral category was scored whenever an animal not



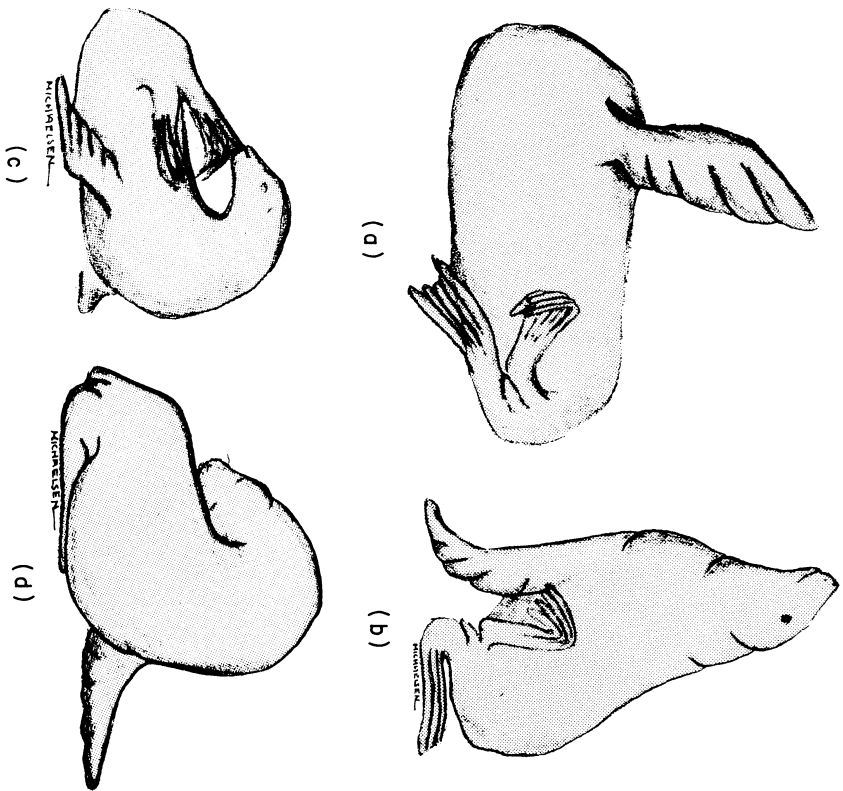


Fig. 21 SEA LION GROOMING VARIOUS PARTS OF BODY WITH REAR FLIPPERS (a) (b) (c) AND MOUTH (d).

in association with another animal was observed to repeatedly leap in and out of the pool, chase after its rear flippers, blow bubbles in the water, spit water, or repeatedly change the position or characteristics of environmental objects.

- *Swimming, Floating, or Submerging.* This was used as a catchall category and referred to animals in the pool that

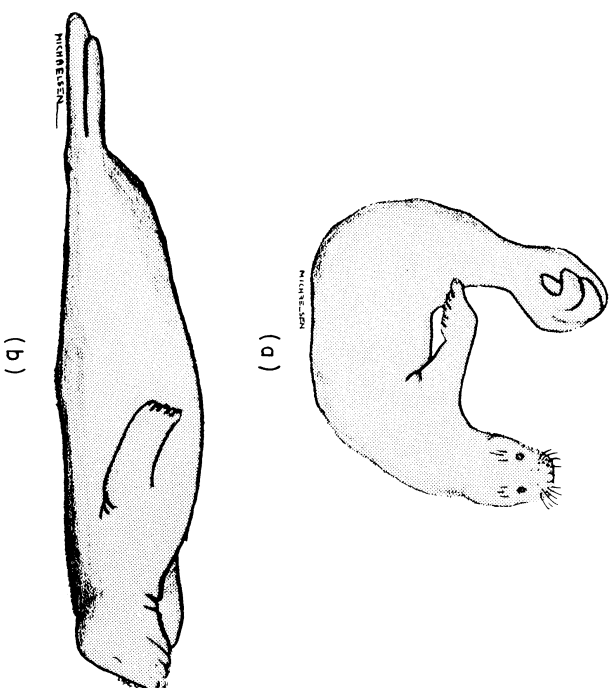


Fig. 22 GROOMING OF LOWER (a) AND UPPER (b) EXTREMITIES BY USE OF CLAWED FRONT FLIPPERS IN *M. ANGUSTIROSTRIS*.

- *Sucking.* This response refers to the placing of the mouth on a protuberance (in terms of the present observations this was always part of another animal's body) and then producing sucking sounds. In all instances true sucking was observed and not merely mouthing or swallowing (see Fig. 23).

Table 3 shows the percentage of time spent in major activities by individuals. Several features of these and other figures along with qualitative notes describing the behavior patterns are quite striking from a comparative-developmental standpoint, and each will be discussed separately.

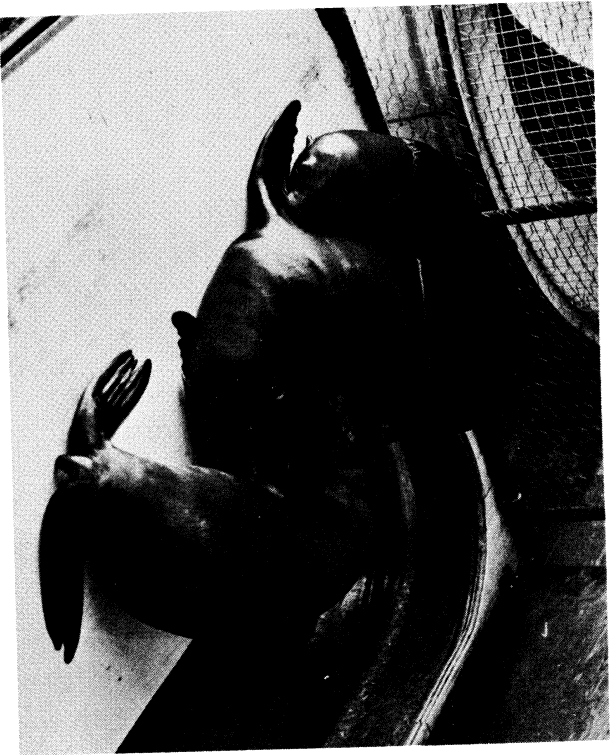


Fig. 23 TRIPARTITE NONNUTRITIVE SUCKING BOUT BETWEEN THREE CALIFORNIA SEA LION PUPS RAISED BY HOWARD BALDWIN, SENSORY SYSTEMS LABORATORY, TUCSON, ARIZONA.

*Homogeneity of Activity Patterns.* Although the individual activity patterns of the Steller-yearling pair, the young elephant seal pair, and the varying-aged, all female, harbor seal quartet were all fairly homogeneous within each of the generic groupings, such was not the case for the varying-aged, all male, *Zalophus* sextet. The considerable variation in individual activity scores was largely due to the highly developed social structure of this captive *Zalophus* group. Experimental evidence bearing on the issue of vocal communication and social structure in the male *Zalophus* group is presented in a later section. Suffice it to say that within this group there was a clear-cut dominance structure in which aggression was usually directed at the next animal in the status hierarchy. Consistent unidirectionality of *Zalophus* agonistic encounters clearly indicated a recognition of status.

Table 3  
PERCENTAGE OF TIME SPENT IN MAJOR ACTIVITIES BY  
INDIVIDUAL SEALS AND SEA LIONS

Animal	Social Play	Agonistic	Aggregate Contact Rest	Sucking	Swimming Floating Submerging	Orientation	Resting Alone	Basking	Grooming	Stereotypy	Environmental Manipulations
California Sea Lions											
M	7.0	4.6	17.1	...	61.0	...	6.5	3.0	0.7	...	...
W	16.0	5.2	36.1	...	1.5	...	35.3	2.2	3.0	...	...
P	9.6	5.4	8.5	...	49.2	...	21.7	4.6	1.0	...	...
K	43.2	5.2	24.3	...	3.0	...	12.0	1.5	3.0	7.7	...
T	44.3	...	18.6	...	1.4	1.4	23.6	7.1	2.9	...	0.7
S	46.0	0.7	26.7	3.4	6.2	2.1	6.2	4.6	2.7	...	1.4
Steller Sea Lions											
59	33.2	3.7	8.4	23.7	11.1	...	8.0	7.4	3.8	...	0.7
63	32.3	4.6	7.7	24.6	11.5	...	7.7	4.5	3.9	...	3.1
Elephant Seals											
J	18.3	1.6	23.0	...	14.3	3.2	36.3	...	0.8	...	2.4
Ma	15.2	2.4	28.3	...	15.8	0.8	35.2	...	1.6	...	0.8
Harbor Seals											
A	...	1.5	...	...	22.4	41.2	33.2	...	1.5	...	...
B	...	0.8	...	...	28.9	38.3	28.0	...	3.9	...	...
Pl	...	1.5	...	...	13.5	66.8	16.5	...	0.8	...	0.8
Pl	...	3.8	...	...	7.6	39.7	42.8	...	4.6	...	1.5

*Rest.* All animals, regardless of sex, age, or species, showed a pronounced tendency to rest, either alone or in aggregates. The reduced rest scores for the Steller pair may have been a function of their strong tendency to suck one another's appendages (see below).

*Vigilance.* Looking or glancing around was the most frequent activity of the harbor seals. Although individual members of each genus tended to orient briefly to a variety of sights and sounds, especially those characterized by a sudden onset, only the harbor seals were observed to consistently sustain such orienting postures, either when floating in the water or assuming a resting position. On the average, the harbor seal group showed orientation 20 times as much as any of the other three genera. It was frequently the case that when a loud sound was produced, such as a gun shot or a car door slamming, all animals within the compound would orient toward the sound. Following the disturbance, the harbor seals continued to remain vigilant for as

long as 5 or 10 minutes while the other animals generally resumed their interrupted activities. The tendency of the harbor seal to react alertly and remain vigilant in its natural habitat has frequently been acknowledged (Scheffer and Slipp, 1944) and is consistent with their hauling out locations, which are always close to the water's edge. The fact that the harbor seal group was maintained in a captive situation at least as long as any of the other generic groups, and had reached a presumably peak level of adaptation to its environment where all physical requirements including feeding and protection from natural predators were met, strongly suggests that vigilance or wariness of harbor seals is fundamentally an endogenous trait of this species and cannot be primarily attributable to any obvious needs arising from immediate exogenous factors.

*Contact.* California and Steller sea lions as well as the northern elephant seals frequently rested in aggregates with any given animal having direct contact with one or as many as four or five other animals. Individuals of these species frequently pressed close together, with smaller animals occasionally being on top of a tightly packed aggregate of three or four larger individuals. The tendency for California sea lions and elephant seals to be strongly thigmotactic while resting on land has previously been noted for wild living groups (Bartholomew, 1952; Peterson and Bartholomew, 1967). Occasionally our captive groupings were disturbed momentarily, resulting in the display of mild threat patterns. Normally such disturbances resulted in only brief (unscorable) agonistic encounters, and the individuals involved soon resumed their resting positions with former contacts only slightly changed. This behavior was in striking contrast with that of harbor seals, which never assumed a position, resting or otherwise, that placed them in direct contact with another animal for any length of time.

Certain combinations and groups of individuals were consistently observed to be resting in direct contact. Table 4 is a matrix indicating the frequency with which individuals were in contact with one another while resting. The table clearly shows that definite partner preferences were established when animals assumed resting positions. Such preferences may have been in part related to other social activities which were either cohesive (e.g., play or sucking) or disruptive (aggressive) in nature. For example, the lack of direct contact between W and P was probably a function of the unidirectional aggression within the *Zalophus* group and the high frequency of

Table 4

## PLAY PARTNERS OR ASSOCIATES OF INDIVIDUAL SEALS AND SEA LIONS

Animals	California Sea Lions					Steller Sea Lions		Elephant Seals	
	M	W	P	K	T	S	J	Ma	
M	—					59	63		
W	3	—							
P	1	3	—						
K	2	3	4	—					
T	2	4	5	41	—				
S	3	9	5	29	24	—			
59	1	8	0	0	3	17	—		
63	2	7	0	0	4	11	36	—	
J	0	2	0	0	0	4	3	3	—
Ma	0	0	0	0	0	0	0	0	17

rest contact between S and W was probably a function of S's sucking activities which were directed only at W (see "Sucking" below).

Despite the fact that the compound was sufficiently large so that individuals did not have to remain for any length of time in direct contact with each other, if we include scores from such categories as social play and sucking, where there was a great deal of direct contact, then except for the harbor seals all individuals spent from between 20 to 80 percent of their time in direct contact with one or more animals. Thus, the tendency for a high degree of gregariousness on land by California sea lions, elephant seals, and Steller sea lions is noted for captive individuals as it has been for wild living individuals of these species (Bartholomew, 1952; Peterson and Bartholomew, 1967; Peterson and Gentry, 1967).

Individuals of our captive harbor seal group were not nearly as gregarious as the California sea lions, the Steller sea lions, or the elephant seals. However, they frequently did remain within 1/2 to 1 m of another individual.

Aside from naturalistic observations related to sexual behavior and mother-infant interactions (Scheffer and Slipp, 1944; Venables and Venables, 1957), I am unaware of any mention in the literature of harbor seals maintaining a resting position or even a vigilant but sessile position in direct contact with one another outside the breeding and pupping seasons. And the lack of contact within our captive harbor seal group is consistent with observations that I and others have made on Año Nuevo Island (Orr, 1965). In this respect it would seem that harbor seals are similar to the Hawaiian monk seal, *Monachus schauinslandi* (Kenyon and Rice, 1959).

*Social Play.* Although the concept of play has never been well understood (see Beach, 1945; Loizos, 1966), either in terms, causation, or function, with few exceptions the playful activities of animals (and this seems to be as true of at least some seals and sea lions as it is of most nonhuman primate forms) may usually be determined and described especially by a trained observer primarily because as Loizos (1966, p. 7) says, "there is a fundamental similarity with the same kind of activity in human beings." She goes on to say, "This similarity lies in the exaggerated and uneconomical quality of the motor patterns involved. Regardless of its motivation or its end-product, this is what all playful activity has in common; and it is possible that it is all that it has in common, since causation and function could vary from species to species."

Social interactions characterized by playful activities were observed in all California and Steller sea lions as well as in both elephant seals, but were never observed in any of the harbor seals. Overall, social play was the overriding activity pattern for the three youngest California sea lions and for both Steller yearlings. For these animals various forms of social play occupied between 32 and 46 percent of their time. Although they rested more than they played, play bouts were a rather conspicuous aspect of the elephant seals' activity patterns.

Although in the quantification of our observations we did not distinguish between different types of social play, both genera of sea lions were involved in several play patterns which could be differentiated. These included a type of jousting or mock fighting, clapping, sexual mounting with or without copulatory movements, swimming and porpoising over one another, chasing, and wrestling and biting. The only type of social play observed in the elephant seals was that of jousting or sparring.

As is true of most pinniped activities, social play continued for long periods of time and it was not unusual for such episodes to last for 1/2 hr or longer. Although normally two animals participated in a play bout, occasionally a third animal joined in sporadically. Table 5 is a matrix showing the frequency with which individuals played with one another. The table clearly shows that there were definite partner preferences and that the most frequent play interactions took place among the three youngest *Zalophus* (K, T, and S) and the two Steller sea lion yearlings. The most common form of play was the mock battle in which two individuals stood chest-to-chest, pushing, feinting with the head and neck, falling prostrate, and making rapid head lunges. Frequently the lunges terminated momentarily when one individual gently grabbed the neck or flank of another with its teeth and then slowly turned loose. These make-believe battles apparently resemble the combat that occurs between territorial bulls during the breeding season (Peterson and Bartholomew, 1967; Orr and Poulter, 1967) except that there was no attempt to actually wound an opponent. In contrast to the young California sea lions, the Steller sea lions were quite vocal during these mock battles.

Gentle biting of the flippers of a resting sea lion frequently served as an invitation to play (see Fig. 24). Even though the soliciting animal may have been initially rebuffed by a series of open-mouthed threats, it would frequently persist in its invitation until finally the solicited animal gave chase and a prolonged vigorous play bout was thus begun. Gentle biting, clapping with the front flippers, wrestling, and rolling on the back frequently characterized the play between participants of widely disparate age and size (e.g., M and S, and G and T). During such play bouts the larger individual clearly controlled and coordinated the vigor and strength of its movements to match those of the smaller partner. Recently, Poole (1966) described in detail a similar phenomenon in polecats and concluded that in contrast to real aggression in which the stronger and more vigorous animal terrorizes its opponent, play-fighting is adapted to the strength and quickness of the opponent.

These examples of social communications between sea lions, i.e., signals regarding the nature of succeeding signals, involve communication about communication and have been called metacommunication (Altmann, 1962; Bateson, 1955). Thus, play encounters are frequently preceded and

Table 5  
CONTACT-REST PARTNERS OR ASSOCIATES OF INDIVIDUAL  
SEALS AND SEA LIONS

Animals	California Sea Lions					Steller Sea Lions		Elephant Seals		
	M	W	P	K	T	S	59	63	J	Ma
M	—									
W	4	—								
P	10	0	—							
K	0	27	0	—						
T	0	17	0	19	—					
S	5	34	0	10	8	—				
59	1	4	0	4	2	2	—			
63	6	1	0	1	2	3	6	—		
J	0	2	0	2	2	0	0	0	—	
Ma	0	0	1	0	1	0	0	0	27	—

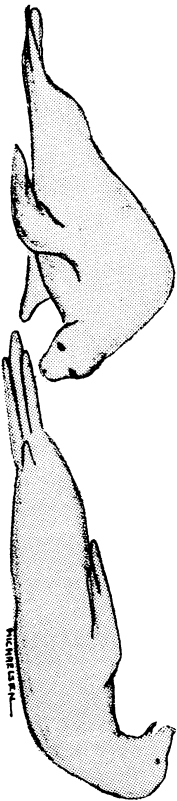


Fig. 24 "INVITATION TO PLAY."

accompanied by signals that inform members of the group that the battle is make-believe. Apparently a wide variety of mammalian species is capable of this form of metacommunication, including many primate species, dogs, cats, polecats, porpoises, and cows (e.g., see Altmann, 1967; Brownlee, 1954; Loizos, 1966; McBride and Hebb, 1948; Poole, 1966).

Virtually all the maneuvers performed during these mock battles between our young sea lion and elephant seal contestants were nearly identical to those described in the young of the same species in their natural habitat (Bartholomew, 1952; Peterson and Gentry, 1967; Peterson and Bartholomew, 1967; Orr and Poulter, 1967). Bartholomew (1952) and Peterson and Bartholomew (1967) have noted that these play patterns anticipate many of the activities of the adult elephant seal and California sea lion, particularly in fighting and copulatory behavior.

The lack of any social play by our harbor seal group may have been a function of the group composition which consisted only of one yearling and no males. Finch (1966) reports play by two captive pups which was characterized by gentle flipper biting and chasing in the water, and Bishop (1967, p. 20) reports that the young harbor seals of Tugidak Island were "more sociable than adults and often played among themselves." At any rate my preliminary observations are consistent with some field reports that indicate only sporadic observations of more mature harbor seals engaged in social play and most of these may in fact have been courtship bouts. Since courtship and copulatory activities by harbor seals are frequently carried out under water (Scheffer and Slipp, 1944; Venables and Venables, 1957) it would not be surprising to find that many harbor seals in similar fashion limit their social play to the same hydrospheric conditions.

*Sucking.* Due principally to the efforts of Bartholomew and his associates, there is a fair amount of information regarding the suckling patterns of young seals and sea lions. For several species, including the California sea lion, the Steller sea lion, and the northern elephant seal, the suckling patterns of newborn pups are marked by their periodic nature. The timing of these nursing patterns, however, may differ sharply for different species (Peterson and Bartholomew, 1967). A pup quickly learns the location of its mother's teats and lies at her side sucking intermittently until the mother goes to sea for several days of feeding. Since under normal conditions most mothers are believed to feed only their own pups, all pups are deprived of

nutritive sucking for periods lasting at least several days. (This may be less true for elephant seals since a recent report [Klopfer and Gilbert, 1966] indicates that females are very tolerant of alien young and in some instances even allow them to suckle, regardless of whether their own pup is near them.) Pups often utter distress calls when separated from the mother and upon her return such calls are frequently followed by suckling.

Infantile suckling is an important early social response in mammals (Collias, 1962) and there have been ample demonstrations across several mammalian species indicating that the need to suck, whether primarily acquired or innate, may be quite independent of nutritional intake per se (see McKee and Honzik, 1961, for a review of this material). Currently, however, there are no data from the field suggesting that the mother-infant bond in pinnipeds is other than nutritional. However, in view of the recent findings with dogs and monkeys (Scott, 1962; Harlow, 1959) showing that tactual, visual, and auditory contact may be an important factor in the infant's socialization, it would be surprising not to find ties other than nutritional which hold the developing sea lion pup to the mother and to the rest of the herd. Furthermore, Rosenblatt et al. (1962) have emphasized the importance of social experience in the sucking of domestic kittens. In this regard recent findings show that in contrast to kittens separated from their mothers, forced, and raised in individual isolation, those treated similarly but raised in groups learn to suck on each other's fur and genital areas and thus are able to initiate sucking on the mother when returned at the age of 30 days (Kovack and Kling, 1967). Excessive sucking on the body parts of littermates has also been found in puppy dogs separated from their mothers (Levy, 1934; Ross, 1951).

There is now a sufficient number of observations indicating that in contrast to harbor and elephant seal pups, which are completely weaned at approximately one month, some California and Steller sea lions may suckle beyond their first year (Peterson and Bartholomew, 1967; Peterson and Gentry, 1967; Orr and Poulter, 1965). Thus, the time of weaning and probably the deprivation of sucking opportunities appear to vary among several pinniped forms. It is therefore of some interest to observe and compare the sucking patterns of pups of different species that have been separated from the mother and reared in the laboratory. A look at Tables 2 and 3 reveals that of the seven animals reared in the lab from the time they were

approximately one-half to three months of age, only the otariids displayed consistent nonnutritive sucking. Indeed, sucking of one another's body parts ranked only second to social play in the daily activity patterns of the Steller sea lion pair.

Aside from the animals listed in Table 2, approximately 10 elephant seal pups and approximately 80 Steller pups have been captured and brought to our laboratory about two weeks to two months after birth. Despite adequate nurturing by forced-feeding techniques, almost all Steller pups indulged in nonnutritive sucking soon after capture while none of the elephant seals ever did. Nonnutritive sucking was normally social in nature; i.e., the pups sucked one another's pelage and appendages rather than sucking parts of their own bodies. It is noteworthy that despite the great incidence of nonnutritive sucking by the Steller pups, of the seven animals who survived their first nine months to a year of life, only one was successfully adapted to nursing on an artificial nipple. Thus, field observations taken together with our observations of captive pinnipeds suggest that species variation in nursing patterns and time of weaning are related in some as yet unspecified manner to the level and persistence of nonnutritive sucking.

The importance of the interplay between nonnutritive sucking as a social behavior and the ontogeny of a signaling system is nicely illustrated by a description of the sequence of acts by the yearling Steller pair which frequently led to their sucking of one another's body parts. If both animals were relatively dry, a mutual sucking episode was usually initiated when the male member of the pair began following the female, persistently emitting a belching vocalization (Orr and Poulter, 1967). Following several seconds of continuous following and calling by the male, the female approached the pool, immersed her head fully, and returned to the male who was at this point usually standing by the pool. Then both animals began wiping their muzzles together vigorously for several seconds with the male's face, especially the area around the mouth, having become quite wet. After 10 or 20 seconds of mutual face wiping, each member of the pair positioned itself, such that the male sucked on the female's left external ear while the female simultaneously sucked on the male's prepuce. Vigorous sucking usually continued for over a minute, during which time sucking sounds were clearly audible. On signal, both animals almost simultaneously ceased sucking, raised themselves up and the female again immersed her head in the pool and the sequence of behaviors was again repeated with little variation (see Fig. 25).

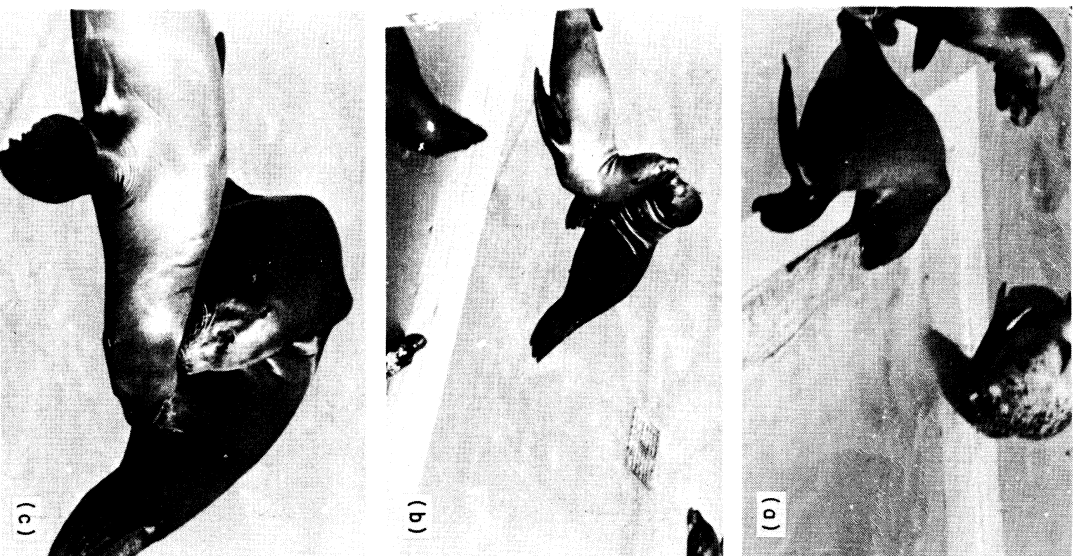


Fig. 25 SEQUENCE OF ACTS BY STELLER YEARLING PAIR, CULMINATING IN SUCKING.

- (a) Male (59) at left calls to female (63) who ducks her head in water.  
 (b) Mutual face wiping.  
 (c) Mutual sucking—female at left sucks male's prepuce while male sucks female's left ear.

Such sucking episodes, punctuated by periodic head dunking and face wiping, frequently lasted from 10 to 20 minutes. The specific events leading to the termination of these mutual sucking episodes were unclear, but frequently the approach and contact of a third animal were involved. The general impression of the roles that each played was that the male had a greater controlling influence over the female throughout the sequence. The male did not always vocalize at the start of each episode but he did usually appear to initiate the activity by approaching her in such a way as to signal that it was "sucking time." The particular bodily parts that were sucked and the positions assumed by the pair were highly stereotyped, in that there was never a deviation from the aforementioned description; the male sucked no other part of the female's body other than the left external ear and the female sucked no other part of the male's body other than the male's prepuce. Sucking was never unidirectional. Since these animals never engaged in non-nutritive sucking while each of them was dry, it must be assumed that the wetting of the female's head, followed by mutual face wiping, functioned as a lubricant that facilitated sucking. However, this highly stereotyped series of acts may have acquired certain reinforcing characteristics independent of their initial function, since even when both animals appeared to the observer to be quite wet they still preceded each sucking bout by head wetting and face wiping. The only instance in which such acts did not invariably precede sucking was when both animals had just previously been in the pool.

Unfortunately, despite the fact that others at the laboratory had noticed the Steller pair sucking one another prior to the time of our more systematic observations, no attention had been paid to the behavioral events preceding sucking. For this reason one can only speculate as to how these two sea lions learned to coordinate this complex series of communicative acts for their mutual benefit.

Since Steller pups in their natural habitat begin to form groups of four or five to a dozen or more where they play and "sleep together in many different positions ranging from prone to supine" (Orr and Poulter, 1967, p. 213), one wonders whether close and detailed observations of such "sleeping" postures may not reveal that some of these pups are engaged in mutual nonnutritive sucking.

As previously mentioned (see "Contract" above) a two-year-old California sea lion (S) was occasionally seen to engage in nonnutritive sucking. As in the case of the Steller yearlings, the sucking pattern was social and highly stereotyped. This sea lion directed all of his nonnutritive sucking at W and sucked no part of W's body other than the posterior aspect of the left axillary region. During these sucking episodes W was in the prone position with both foreflippers extended and S was positioned alongside of W. The latter rarely reacted to S's sucking. Frequently S preceded his sucking by calling. The sound resembled the "mother-response" calls of *Zalophus* pups as described by Peterson and Bartholomew (1967). However, these calls did not appear to lead to any specific reaction by W. These sucking episodes by S, unlike those of the Steller yearling pair, were brief and sporadic, usually lasting only 1 to 5 minutes.

*Manipulative Play.* Despite living in an environment in which manipulable objects were far from plentiful, most subadults within the group, regardless of species, displayed some degree of manipulative play with a variety of objects. Manipulation by all animals was primarily accomplished with the mouth and included the picking up, biting, carrying, pulling, shaking, and tossing of objects. The types of objects that were sporadically available included leaves, weeds, a piece of rope, fecal matter, and a broom handle. Aside from the period of time covered by these observations, several seals and sea lions at our laboratory have been observed to playfully manipulate such dead creatures as birds, rats, mice, and a garter snake. We were never able to determine whether the seals and sea lions actually had a hand in killing these animals.

In line with Hediger's reports of object manipulations by captive sea lions (1955), a rather interesting manipulative skill occasionally displayed by several young California sea lions and a young elephant seal (J) was that of repeatedly picking up an object with the mouth, tossing it high in the air with a vigorous twist of the neck and head, and then retrieving the object. The objects used by the sea lions were usually small rocks or bits of debris. The elephant seal favored fecal matter which it repeatedly tossed and retrieved (both on land and in the water) until the fecal matter had so fragmented that the pieces became too small to manipulate.

These qualitative observations of manipulative play by captive subadult seals and sea lions are consistent with naturalistic observations of similar

activities by individuals of the same four species (Bartholomew, 1952; Peterson and Bartholomew, 1967; Peterson and Gentry, 1967; Scheffer and Slipp, 1944). Furthermore, pebble and rock tossing have been observed in *Zalophus californianus wollebaecki* (the Galapagos sea lion) in its natural habitat by Eibl-Eibesfeldt (1955).

In addition to using the mouth as a manipulative organ, the California sea lion shows a marked tendency, in captivity at least, to handle large objects by clasping them with their front flippers (Schusterman, 1967) and also to skillfully swat small objects around with the front flippers. One California sea lion (S) has been observed to play with a rock by bating it back and forth between his front flippers as if he were playing a game of hockey with himself.

Our lack of knowledge of the underwater environment and of feeding habits makes it extremely difficult to relate these observations of the manipulative skills of young seals and sea lions to the requirements of their biotype. Undoubtedly, manipulative play is beneficial to these animals in the searching and seizing of food prey. For example, there have been numerous observations of sea lions surfacing with a large fish in their mouth and then proceeding to shake and toss the fish until it has broken into small pieces. Another and possibly better example of the importance of manipulative skills for feeding comes from a laboratory study dealing with the mother-pup relationship in harbor seals. Finch (1966) observed that mouth and foreflipper manipulation by the pup of fish, including biting, shredding, and throwing of fish, preceded the actual first ingestion of fish by four days. Furthermore, investigation and manipulation of nonedible objects by this harbor seal pup were seen to occur approximately five to ten days after birth, whereas the eating of fish did not begin until the pup was about five weeks old.

It has been suggested that manipulative play is an important preadaptation for intelligence toward objects (Jolly, 1964; Gluckman and Stroges, 1966) and that manipulative play tendencies "can interact with intelligence to open up new possibilities to the animal—possibilities as simple as eating a new kind of food. . . ." (Jolly, 1964, p. 569). Although there are probably many exceptions, sustained exploration and manipulatory play frequently lead to the skillful manipulation of objects eventually resulting in a successful adaptation. Several such examples may be cited from the literature dealing with nonhuman primate behavior in both natural and captive settings (Devore,



1968; Birch, 1945; Bolwig, 1959). Moreover, it has recently been pointed out that persistent manipulatory tendencies of some species of nonhuman primates has necessitated rather sophisticated procedures designed to prevent the picking of cagedoor locks (Rumbaugh, in press). In this regard, it is worth noting that several sea lions in our laboratory (both California and Steller), following vigorous and sustained manipulatory investigation of the gate entrances, have learned to skillfully and efficiently manipulate the latches by lifting them up with their muzzle or mouth and thereby release themselves from an enclosed area.

*Stereotypies.* In captivity, a variety of animal forms is reported to develop a series of repetitive movements that apparently serve no obvious function (Hediger, 1950; Berkson and Mason, 1964; Davenport and Menzel, 1963; Sargent and Keper, 1967). Such behaviors have been called "stereotypies" (Hediger, 1950), and, as Table 2 indicates, one California sea lion (K) spent nearly 8 percent of its time stereotyping. The most dramatic forms of stereotypies in sea lions take place on land. From a standing position the animal shifts its weight back and forth between its front flippers in a rocking motion and then falls down on its side hitting or banging its neck against the ground two or three times before again raising itself to a standing position. As the animal repeats these movements over and over, it frequently moves back and forth retracing its steps each time it turns around. Such stereotypies invariably occur within a meter or less of a wire fence. Preliminary observations indicate a pronounced increase in the level of stereotypies when a sea lion is isolated, especially while it is viewing other animals. Furthermore, the level of stereotypies tends to increase just prior to feeding time. Neither harbor seals nor elephant seals have yet been seen to stereotype on land.

Several factors have been hypothesized to account for the acquisition of stereotypies and these include level of physiological arousal, interference or blocking of goal-directed behavior, and habit formation (Hediger, 1950; Berkson, Mason, and Saxon, 1963). Experiments currently being conducted on monkeys (Harlow, 1959) and canaries (Sargent and Keiper, 1967) suggest that in addition to these factors, the acquisition of stereotypies is probably related to early rearing conditions. Our preliminary observations do suggest that arousal level, frustration, and habit formation do play a role in stereotypy development in captive California sea lions. Persistent nonnutritive sucking (a form of stereotypy) by captive California sea lions (see "Sucking" above) and

stronger and possibly more durable mother-infant ties in this species than in the elephant or harbor seals, for example, suggest that early rearing conditions may also be a factor in the development of stereotypies in California sea lions.

*Interspecific Interactions.* Combinations and grouping of individuals resting in direct contact or engaged in play are presented in Tables 4 and 5, which show that although there was a fair degree of interspecific interaction during rest and play, especially between Steller and California sea lions, individuals tended to interact and be closely associated with members of their own species rather than with extraspecies animals. As previously mentioned, although individual harbor seals tended to congregate together, they did not participate in social play nor did they remain in direct contact with one another or for that matter with any extraspecies animals. Regardless of species, accidental or intentional contact initiated by another animal invariably resulted in either avoidance or threat by any and all harbor seals (see Fig. 26). On the other hand, one elephant seal (J) did interact playfully, albeit infrequently, with several different sea lions.

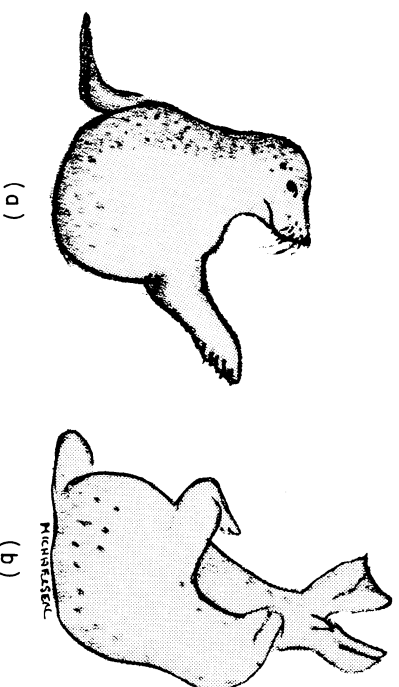


Fig. 26 HARBOR SEAL IN (a) THREAT AND (b) AVOIDANCE POSTURES.

Interspecific aggressive behavior was minimal and generally occurred less frequently than did conspecific aggressive behavior. On Año Nuevo Island (about 50 miles south of San Francisco off the Central California coast) where all four of these species may be observed at one time, Orr (1965) also reports some contact between the different species in which only a minimal amount of animosity is displayed.

Despite the fact that several of the young animals in the group (63, 59, J, Ma, S, Ph, and Pi) were only limited to a month or two after birth for the establishment of ties with the mother and others of their own species before being captured and brought to the laboratory, there was still a marked tendency, even in a captive setting, to associate with a like species member. This suggests that if there is a critical period for socialization in some species of pinnipeds, it probably occurs within the first two months of life. On the other hand, within this group of captive pinnipeds, an individual's preference to associate with a like species member may have been influenced by the establishment of a mutually beneficial relationship that may have been age dependent rather than species dependent, such as the reciprocal nonnutritive sucking by the Steller yearling pair.

#### **Barking, Dominance, and Territoriality**

Social structure, territoriality, and vocal signaling are useful concepts for describing the ways in which aggressive behavior is controlled in vertebrate social groups. Inferences regarding the important role that these factors play in vertebrate social organizations have been summarized for natural living and captive animal groups (Carpenter, 1958; Hediger, 1964). For several species of pinnipeds, field observations during the breeding season suggest that breeding males signal and defend territorial possessions primarily by means of a highly stereotyped series of vocalizations (Bartholomew, 1952; Bartholomew and Hoel, 1953; Kenyon, 1960; Bartholomew and Collins, 1962; Mansfield, 1967). It is thought that vocal signaling reduces actual fighting during the establishment and maintenance of territories.

It has been shown that the California sea lion produces a variety of underwater sounds, including barks, clicks, bangs, buzzes, and growls. All of these sounds are apparently a function of the social and investigatory responsiveness of this sea lion (Schusterman, Gentry, and Schmook, 1966, 1967).

During the course of these investigations, it was noticed that on several occasions introduction of a relatively large male *Zalophus* (about four years old) to smaller males (between two and three years old) almost invariably resulted in initiation of barking by the larger animal and cessation of barking by the smaller animal. This phenomenon took place under water as well as in air and appeared to be related to a dominant-subordinate relation with the larger male chasing, generally intimidating, and restricting the movements of the smaller male, especially when an incentive condition prevailed such as access to food, resting positions, swimming pool, and females. Furthermore, in November 1965, a survey of the aerial calling (consisting primarily of barks) of four male California sea lions living together in a large compound containing a pool revealed that of the two largest and oldest animals, G barked nearly 40 percent of the time while M barked less than 3 percent of the time; the two younger animals received barking scores of between 4 and 12 percent (Schusterman, 1967). During these observations, G was clearly the dominant animal of the group, directing most of his barking, open-mouthed threats, chases, and slashing lunges at M. The barking by G from a position in the pool, reinforced on occasion by direct physical aggression, appeared to deter M from entering the pool.

These relatively informal observations suggested that barking by individual males may be related to the group social structure and territoriality. If this is so, then manipulation of the social structure should lead to changes in the amount of barking by individual male sea lions within the group. In accordance with this hypothesis, a series of experiments was conducted in which group composition was modified by removing and reintroducing individual animals and recording the frequency of occurrence of barking and attack by 10-second intervals on a time-ruled check sheet.

All experiments were conducted in the two outdoor rectangular compounds enclosed and separated from each other by a cyclone fence. Compound 1, where the animals were usually housed, was described previously. Compound 2 was approximately 10.7 by 13.7 m. The fence separating the two compounds had three gates. Entrances for two of the gates located in the adjoining corners of the compounds were 1.7 m wide, and a center entrance was 1.2 m wide. The animals were observed from a blind about 2.1 m above the top of the rocky slope. Six male *Zalophus*, living together for at

least three months, took part in all experimental sessions, and a seventh animal (G) was introduced during the last experimental sessions. (Characteristics of individual animals are listed in Table 6.) All but one (S) of the sea lions were always fed prior to the experimental sessions which usually took place between 1300 and 1900 hr. Except for one experimental session, sea lions were removed from compound 1, placed in compound 2, and reintroduced one at a time. Observations and recordings usually began approximately 30 seconds after an animal's removal or return. In addition to the California sea lions, there were three other species of pinnipeds living in the compounds during the experiments, including two young elephant seals, one yearling, one two-year old, and two adult harbor seals, and two yearling Steller sea lions.

Table 6

ATTACK-WITHDRAWAL SCORES AND CHARACTERISTICS OF THE MALE CALIFORNIA SEA LIONS IN THE SOCIAL GROUP

Age (yr)	Wt. (kg)	Attacking Animal	Withdrawing Animal						
			G	M	W	P	K	S	T
5-6	136	G	-	8	1	0	0	0	0
5-6	153	M	0	-	42	1	0	0	0
3	68	W	0	0	-	104	54	6	4
3	58	P	0	0	0	-	6	3	1
2	50	K	0	0	0	0	-	10	1
2	40	S	0	0	0	0	0	-	2
2	38	T	0	0	0	0	0	0	-

Results from a series of three experimental sessions are shown in Fig. 27. During the first experimental session (6/19/67), alternately removing and reintroducing the most mature animal (M) led to the expected result, that the largest sea lion (M) produced the greatest amount of barking in the group;

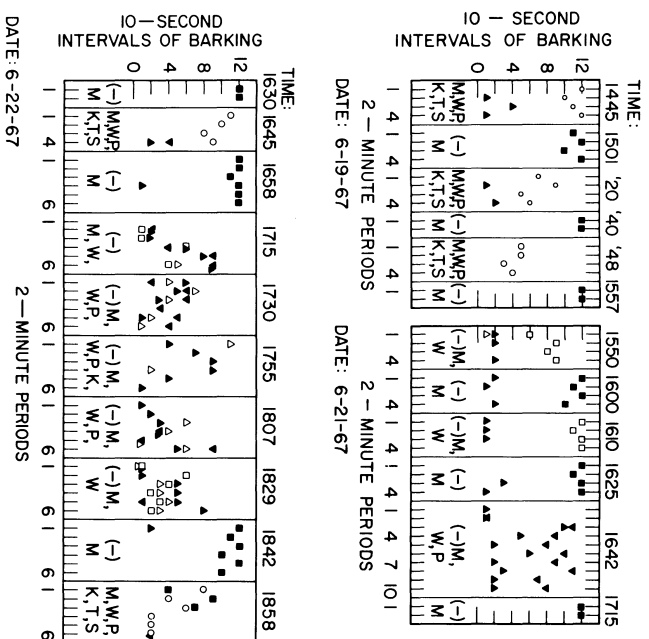


Fig. 27 AMOUNT OF BARKING BY MALE *Z. CALIFORNIANUS* AS FUNCTION OF GROUP COMPOSITION IN COMPOUND 1. Letters following minus sign refer to sea lions removed from compound 1 and placed in compound 2. Times refer to start of each experimental period.

upon his removal to compound 2, the next largest sea lion (W) produced the greatest amount of barking. During the next experimental session (6/21/67) removal of M and W resulted in a dramatic increase in barking by P, and P's subsequent removal led to an increase in K's barking. Reintroduction of W produced a complete reversal; i.e., W barked continuously whereas P and K remained silent. The removal of M during the first two phases of the third experimental session (6/22/67) resulted in continuous barking by W; upon the reintroduction of M, W immediately ceased barking. Although these results are consistent with the two previous sessions, removal of M and W during the third session increased not only the probability of P's barking,

but also that of K, S, and T as well. Again the return of W completely reversed this trend. Furthermore, despite M's return to compound 1 (time: 1858), W did not immediately cease barking as in all previous experimental phases; rather, W continued to bark at a relatively high rate for the first 6 minutes before stopping.

In an additional series of experiments we sought to determine the frequency of occurrence of barking by individuals in both compounds. In these experiments we systematically removed sea lions M, W, and P (in that sequence) and then returned each one in reverse order. The results are presented in the upper three pairs of bar graphs of Fig. 28. In general, these results are similar to those previously obtained. They also show that M's barking in compound 2 had little effect on the barking patterns of individuals in compound 1. Apparently the wire fence served as a signal to younger animals that barking and other aggressive displays by M could not be followed up by physical attack. When W or P was placed individually with M in compound 2, they immediately stopped barking and remained silent until returned to compound 1. Thus, regardless of which compound was used or how many sea lions were in the group, the amount of individual barking depended on the nature of the group's dominance structure.

The relation between barking and dominance is shown by the analysis of attack-withdrawal scores presented in Table 6. The scores represent the total number of 10-second intervals in which one sea lion was in the process of attacking another during the entire series of experiments. Attack by the more mature sea lion clearly occurred on a discriminative basis and was usually directed toward the next largest sea lion in the group. There were no instances of less mature animals attacking larger individuals, and there were only rare occurrences of the more mature sea lions such as G, M, and W attacking the two smallest individuals (S and T).

Removal or reintroduction of a dominant, or alpha, animal had a rather dramatic effect on the behavior of the next in line, or beta, individual in the social hierarchy. A dominant sea lion usually maintained a position within the pool, either swimming around the perimeter of the pool or holding a quadrupedal stance at the shallow edge of the pool while producing a rather continuous series of barks. The beta animal was usually positioned at or near the top of the rocky slope (see Fig. 29). This spatial relationship between alpha and beta animals was rather stereotyped; it was observed in

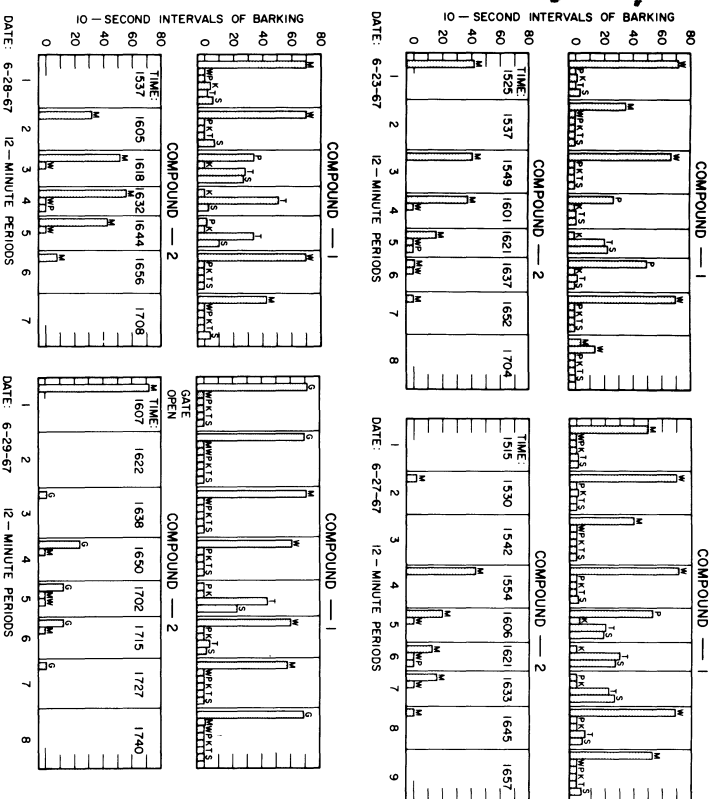


Fig. 28 AMOUNT OF BARKING BY MALE *Z. CALIFORNIANUS* AS FUNCTION OF GROUP COMPOSITION IN COMPOUNDS 1 AND 2.

the cases of G-M (see below), M-W, and W-P. Movement away from a position on top of the rocky slope by the beta animal usually led to attack and pursuit by the alpha animal which terminated only when the beta individual resumed its former position (see Fig. 30). Usually, upon its return to compound 1, a dominant individual immediately set up a barking pattern and locomoted directly to the pool while the beta animal immediately fell silent and scrambled out of the pool. However, in two instances at 1858 hr on 6/22/67 (Fig. 27) and 1704 hr on 6/23/67 (Fig. 29) instead of moving directly to the pool upon his return, M hauled out and rested in a shady corner of compound 1. Attack by a dominant individual usually consisted of pursuing the beta animal. The latter retreated up the rocky slope,



Fig. 29 ALPHA MALE IN POOL DIRECTING ITS BARKS AT BETA MALE LOCATED AT TOP OF SLIDE.

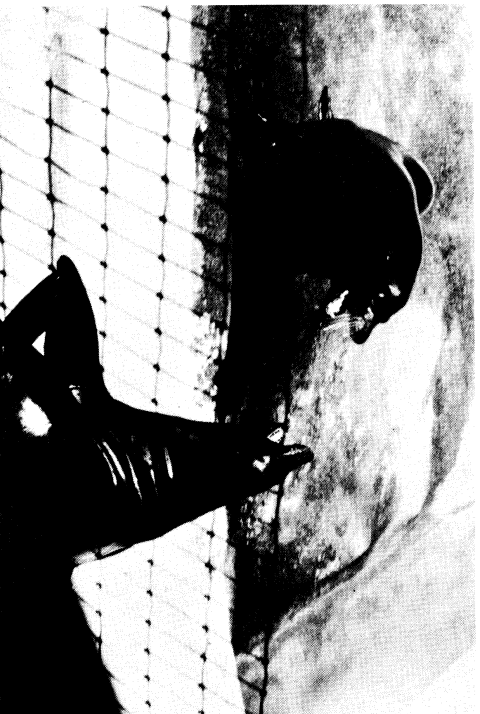


Fig. 30 ALPHA MALE (AT THE LEFT) RESTRICTING BETA MALE'S POSITION TO TOP OF SLIDE. Only alpha animal is barking. Note the postures of the animals as well as the forward position of their vibrissae.

occasionally turning to face its attacker and displaying an open-mouthed counterthrust while still withdrawing. During such encounters, the retreating animal never barked but the attacking animal emitted a constant series of barks intermixed occasionally with a rapid head lunge and a hard bite. The intensity of these agonistic encounters was directly related to the maturity or size of the animals involved.

In terms of vocal and agonistic behavior patterns, inspection of Figs. 27 and 28 and Table 6 suggests that the youngest sea lions, K, T, and S, were least affected by modifications in the social hierarchy. In general, the social activities of these animals may best be described as play-fighting and sexual play. On those occasions when the intensity of these social play patterns increased and these young animals began barking, a dominant animal (G, M, or W) would direct his barks toward them and rapidly move between the participants, who would in turn cease barking, nuzzle the head and neck region of the dominant animal, and disperse for a short time. With the removal of G, M, and W, the play patterns of K, T, and S invariably increased in intensity, with a corresponding increase in barking vocalizations. The decrease in K's barking during the last four experiments (see Fig. 28) was due to this sea lion's reacquiring a rocking and head-banging stereotypy (see "Stereotypies" above).

On 6/18/67, G, who nearly matched M in weight and in development of a head crest, was returned to compound 1 after an absence of about six months. In sharp contrast to M's continuous barking just prior to release from a cage into the compound, G remained silent. Upon release of G, the combatants rushed forward to stand chest-to-chest, emitting rapid series of barks. The violent fight which ensued lasted about 8 minutes and consisted primarily of chest and shoulder pushing, interspersed by whip-like head lunges, and hard biting. The struggle terminated when G pushed M into the pool. Following a short period of grappling in the pool, M suddenly ceased barking, leaped out of the pool, and fled up the rocky slope (see Fig. 31). After several chase sequences around and through the pool and up and down the rocky slope, during which M remained silent while G barked continuously, G was removed from the compound. Examination of M revealed several bloody cuts and wounds around the neck and flanks.

Except for a reduction in the duration and severity of the battle between G and M, reintroduction of G to compound 1 on 6/29/67 led essentially to

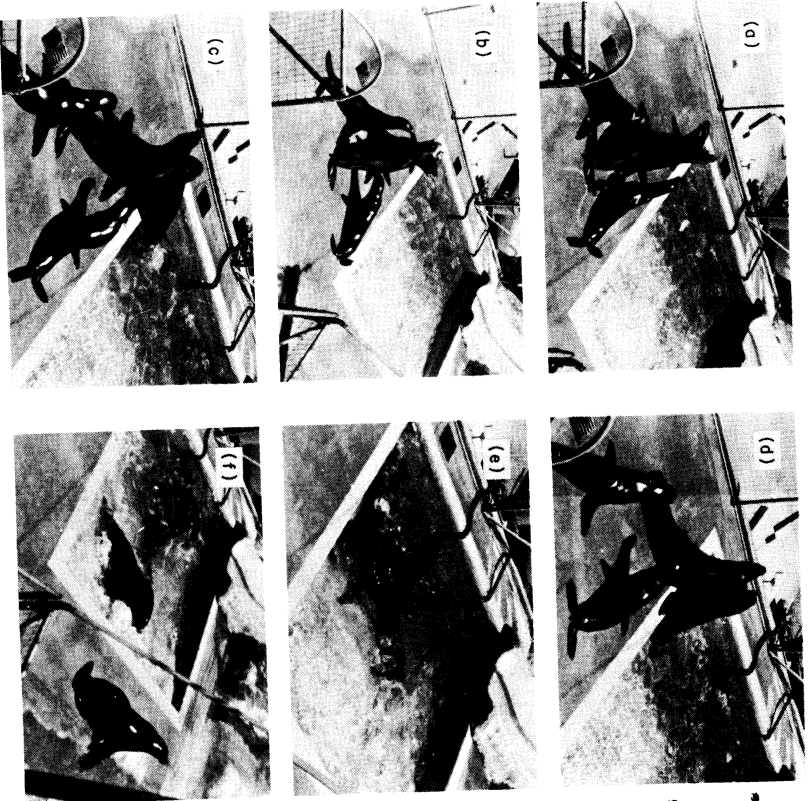


Fig. 31 FIGHT SEQUENCE FOLLOWING G'S IMMEDIATE RELEASE INTO COMPOUND 1.

- (a) (b) The combatants, G (with back toward camera) and M, stand chest-to-chest while pushing and barking. Note nuzzling of G's body by smaller males.
- (c) (d) G pushes M into pool.
- (e) G and M continue to bark while grappling in pool.
- (f) M is defeated and flees silently while G continues to bark.

the same outcome as before. However, this time the center gate was left open, and while M fled silently through the gate entrance, G terminated the chase at the gate threshold and remained in compound 1. For several minutes G patrolled the open gate area, moving back and forth between the pool and the border gate while emitting an almost continuous series of barks. This

was in sharp contrast to M, who stood silently in the center of compound 2 with his head held up in a basking position. As W passed through the entrance from compound 1 to compound 2, M began barking. Moments later M and G rushed toward the open gate and displayed what Peterson and Bartholomew (1967) have termed a "stereotyped boundary ceremony" in which little contact was made as the two combatants challenged each other with open mouth threats while staring sideways or obliquely at one another, barking rapidly, wagging and shaking the head, arching the neck, and falling prostrate (see Fig. 32). After nearly two hours of almost continuous barking by M and G from positions at the center of their respective compounds (G usually stood in the pool), punctuated by several series of boundary ceremonies at the open gate area, data were collected on barking and attack behavior in accordance with the procedures previously outlined.

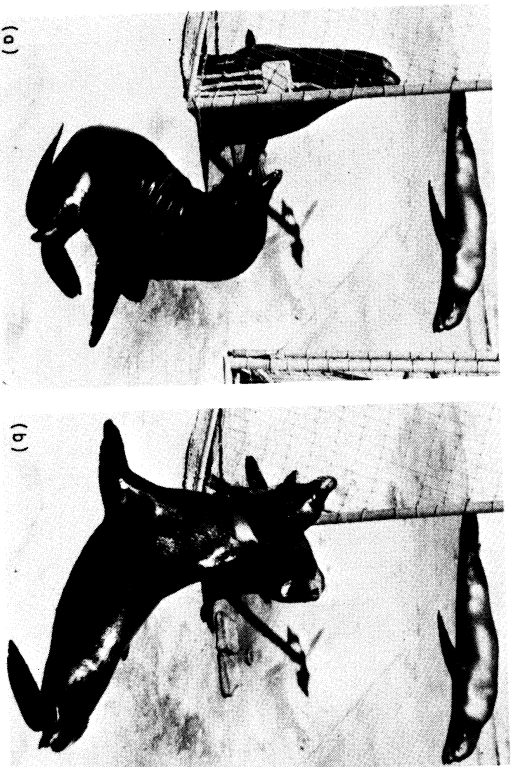


Fig. 32 DISPLAY OF THE STEREOTYPED BOUNDARY CEREMONY BY G (IN FOREGROUND) AND M AT OPEN GATE SEPARATING COMPOUNDS 1 AND 2. Both sea lions are barking.

- (a) G "neck arching."
- (b) "Oblique stare" pattern.

The results are presented in the bottom pair of bar graphs of Fig. 28 and are essentially in agreement with the results from the previous six experimental sessions. However, there are three aspects that deserve special mention. First, M and G barked and displayed at one another continuously during the first 12-minute period when the gate was left open. Second, despite the two previous fierce fights between M and G, no fighting broke out when M was returned to compound 1 with G, who merely restricted M's activities to the rocky slope. Third, G's forced presence in compound 2 eliminated M's original territorial defense. Reopening of the center gate resulted in renewed territorial displays by G and M within compounds 1 and 2, respectively. Although both animals were primarily active in territorial maintenance during most of July, on several occasions M was seen moving silently through the entrance from compound 2 and into the pool while G was resting or sleeping. Moreover, in several instances, G did displace M in compound 2.

It should be noted that throughout these experiments we saw *Zalophus* submerge and resurface in the pool while emitting a series of barks. On the basis of previous work, in which we have monitored their underwater sounds, it seems highly likely that during such vocal episodes *Zalophus* was barking while submerged (see "Underwater Sound Production" above).

Despite the great differences between captive and natural settings, there is a striking similarity between our observations of aggressive displays, especially by the two oldest males (M and G), and the field observations of Peterson and Bartholomew (1967) on the establishment and maintenance of territorial status of breeding males. Some examples of these similarities include: establishment, when possible, of partly aquatic territories; fights which are limited to two males; incessant barking by established territorial males; the use of physical force for displacement of an opponent; the stereotyped boundary ceremony between two territorial males; the lack of barking by smaller males who intrude into the resident male's territory and stay as long as they maintain silence and remain visually inconspicuous; and the interference by a dominant bull in "noisy squabbles" of females and pups.

These results thus support the hypothesis that barking by young male California sea lions is strongly related to dominance status and territorial defense. In our experiments, barking by a large male clearly served as a cue for restricting freedom of movement and inhibiting barking vocalizations by other

smaller males who were in the vicinity and were accessible to attack. Intra-specific status or class recognition was demonstrated by the fact that among the three more mature sea lions, barking and attack were primarily directed toward animals of most nearly equal size. The cues for identification among individual males are both visual and auditory. Although size is certainly an important cue, with growth males also develop a clearly discernible head crest as well as a lower-pitched bark.

Taken in conjunction with the recent field observations by Peterson and Bartholomew (1967), these experiments demonstrate that barking by immature *Zalophus* males (three to six years old in this study) plays a highly significant role in the development of social communication patterns leading to adult displays of aggressive and sexual behavior. There is experimental evidence available indicating that *Zalophus* is capable of learning to inhibit or emit its underwater click vocalizations in the presence of exteroceptive cues (Schusterman and Feinstein, 1965). That barking may also come under the control of exteroceptive cues, which are social in nature, is suggested by the finding that the sight and sound of a larger animal often suppressed vocalization and freedom of movement by the next smaller sized male, when a larger male was capable of physically attacking and punishing smaller males.

#### SUMMARY AND CONCLUSION

The experimental analysis of seal and sea lion behavior in the laboratory has had a very short history, beginning in the early 1960's. Well-controlled study and measurement of sensory perception, vocal communication, and learning capabilities of these animals has been extremely meager and has been limited to two species of otariids (the California sea lion and the Steller sea lion) and one species of phocid (the harbor seal). Nevertheless, when existing data from the laboratory are combined with field observations, there is enough information to indicate the inaccuracy of some previous notions. It is hoped, therefore, that future research efforts of an experimental nature may proceed in ways more sophisticated and productive than those of the past.

The initial impetus for much of the experimental work on behavior came from several investigators working independently who reported that many species of pinnipeds produce clicking sounds under water. These

findings immediately led to the speculation that, much like porpoises, some species of pinnipeds used such sounds for echo-ranging on food prey. However, some experiments with the California sea lion, in which all possible sensory cues have been eliminated as well as cues related to spatial memory and in which the sea lion has been tracked during the proposed echolocation task, have failed to find any evidence demonstrating the use of echolocation for object discrimination. Although sea lions have no difficulty finding food in clear water, this ability is severely curtailed when visibility is reduced to a few centimeters.

Attempts at recording consistent underwater sound production from the harbor seal and the Steller sea lion have been largely unsuccessful. Several studies with the California sea lion indicate that underwater clicks as well as barks and growls are likely to occur during social encounters and encounters with novel stimuli or when a state of conflict has been induced in the animal. Moreover, clicking vocalizations are easily conditioned. Aerial and underwater barking by male California sea lions is, among other things, related to a dominance structure and frequently occurs during the establishment and maintenance of territories. Further research of an experimental nature is sorely needed before we can arrive at a fuller understanding of the social communicative value of the underwater signals of seals and sea lions.

In addition, though much work remains to be done on the hearing capabilities of pinnipeds, the available data indicate that the harbor seal's peak sensitivity is about 12 kHz in air and 32 kHz under water with adequate pitch discrimination under water in the range from 1 to 60 kHz. Directional hearing under water in both the harbor seal and the California sea lion is probably adequate for localizing social communicative signals as well as some signals emanating from food prey.

The underwater vision of the California and Steller sea lions and the harbor seals is particularly well-suited for the detection and discrimination of food prey and predators as well as for the reception of social communicative signals. All three species are capable of consistently discriminating between circular targets differing in area by as little as 6 percent and are quite proficient in the discrimination of a variety of different shapes. Experiments dealing with shape classification suggest a considerable degree of consistency across the three species in their equivalence responses to the reorientation of

a wide range of configurations. In the California sea lion visual accommodation in air is about as good as it is under water. This is true in moderate light as well as very poor light. Controlled experiments have yielded visual angles of between 4 to 6 min. at light levels as low as  $2 \times 10^{-4}$  ml under water, with only a slight deterioration occurring at the same luminance level in air. Furthermore, all seals and sea lions that have been tested thus far are capable of improving their performance over a series of visual pattern discrimination problems; i.e., they are capable of learning how to learn.

Finally, preliminary quantitative and qualitative observations of a group of captive seals and sea lions indicated the following:

1. In contrast to California sea lions, Steller sea lions, and elephant seals, which are strongly thigmotactic while resting, harbor seals never rested in direct contact with another animal.
2. Harbor seals were characterized by a great deal of vigilance behavior.
3. Social play activities were most frequently initiated by young sea lions.
4. Sea lions developed play-partner preferences.
5. Nonnutritive sucking of another animal's body part occurred only in sea lions that were separated from their mother within the first three months of life. Intricate signaling systems were sometimes associated with social sucking.
6. Some California sea lions developed a series of repetitive movements or stereotypies, especially when frustrated.
7. Most subadults, regardless of species, displayed some degree of manipulative skill with a variety of objects.



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