TERRITORIALITY AND AGGRESSIVE BEHAVIOR IN MALE PINNIPEDS

by

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TABLE OF CONTENTS

Introduction

The three families of pinnipeds include the Phocidae, "true seals", the Otariidae, sea lions and fur seals, and the Odobenidae, or walruses. It is remarkable that the evolution of polygyny in pinnipeds has generated such marked similarities in their behavior, while simultaneously creating extreme differences in the social and reproductive organization between the different taxa. The evolutionary relationship of the three families is not yet fully understood, for the fossil evidence is not complete. As a result, many ethologists theorize about the evolution of polygyny in pinnipeds while attempting to understand the evolutionary background of behavior. Most ethologists share a phyletic method of inferring behavioral evolution which has been described by Hinde and Tinbergen (1958) as follows, ..."by comparing the behavior traits of species whose phylogenetic relations are established (usually on the basis of morphology), it is possible to make hypotheses about the probable orgins of that behavior, and thus about the course of evolution."

The phyletic method is difficult to directly apply to the study of social organizations of pinnipeds, for there remain considerable differences in opinion as to whether pinnipeds are monophyletic or diphyletic (Davis 1958 ; McLaren 1960; Ling 1965; Mitchell 1967; and Sarich 1969a & b). It is difficult to infer relationships based on living genera and species. Present interpretations of the fossils that have been found are inadequate to provide a clear picture of their evolution (Peterson 1968). The most recent supporters of monophyly are Davies (1958), Ling (1965), and Sarich (1969a & b), while Scheffer (1958) states "It cannot be shown that any of the three families Otariidae, Odobenidae, or Phocidae is ancestral to another". The diphyletic view is also supported by McLaren (1960) and Mitchell (1967), and even though there has been no definite consensus it appears at this time to be the more widely accepted. The general form of the diphyletic theory is that the phocids evolved from a lutrine stock while the otariids were derived from an ursid stock; the odobenids supposidly diverged from the otariids at an early stage (Stirling 1975). Although the diphyletic explanation can be

helpful in understanding the evolution of pinniped social behavior, it is also important to remember that natural selection should act equally on the evolution of behavior independent of phylogeny.

Selective forces involved in the evolution of pinniped social behavior can be observered in the annual establishment and maintenance of the breeding system. All pinnipeds return to land or ice to give birth and at this time they breed on land or in adjacent waters. Pinnipeds disperse after the breeding season, some species move over great distances. Breeding site fidelity is a way of insuring that males and females can find each other. Thus producing the rookery breeding behavior in these offshore marine feeders.

Among and within the pinniped families there are varing patterns of reproductive organizations on the rookeries. The establishment and maintenance of territories by males is among the most diverse and important. Theoretical explanations for the complex behaviors demonstrated by male pinnipeds have

been proposed by Nutting (1891), Bertram (1940), and Bartholomew (1952). Since these papers were written, considerable new information has been collected. This paper focuses on recent (1930 to present) work on territoriality and aggressive behavior in pinnipeds, with the purpose of examining the complex phenomena symbolized by the term "territoriality" as observed in the reproductive organizations of pinnipeds. The intent of this paper is to identify and catergorize the reproductive organizations of the pinniped families with an emphisis on patterns of agonistic and aggressive behavior involved in the establishment and maintenance of territories.

Factors Involved in the Selection for Territoriality

In order to accurately identify which pinniped species establish and maintain territories, one must first define the term territory. It has been noted in much of the literature that the word is difficult to define and is often used loosely. Various criteria have been used to define the term territory, including any 'defended area' (Noble 1939), 'exclusive area' (Schoener 1968), or a 'fixed, exclusive area with the presence of defense that keeps out rivals' (Brown & Orians 1970). Emlen (1957) defines a territory as a space within which an animal is aggressive toward and usually dominant over certain intruders. In summary, the essential characterists underlying most definitions are: (1) it is a fixed area, (2) it is actively defended, and (3) the holder has exclusive use of it. In this paper I use the definition of territory as defined by Brown & Orians (1970). This definition includes the three essential characteristics as listed above.

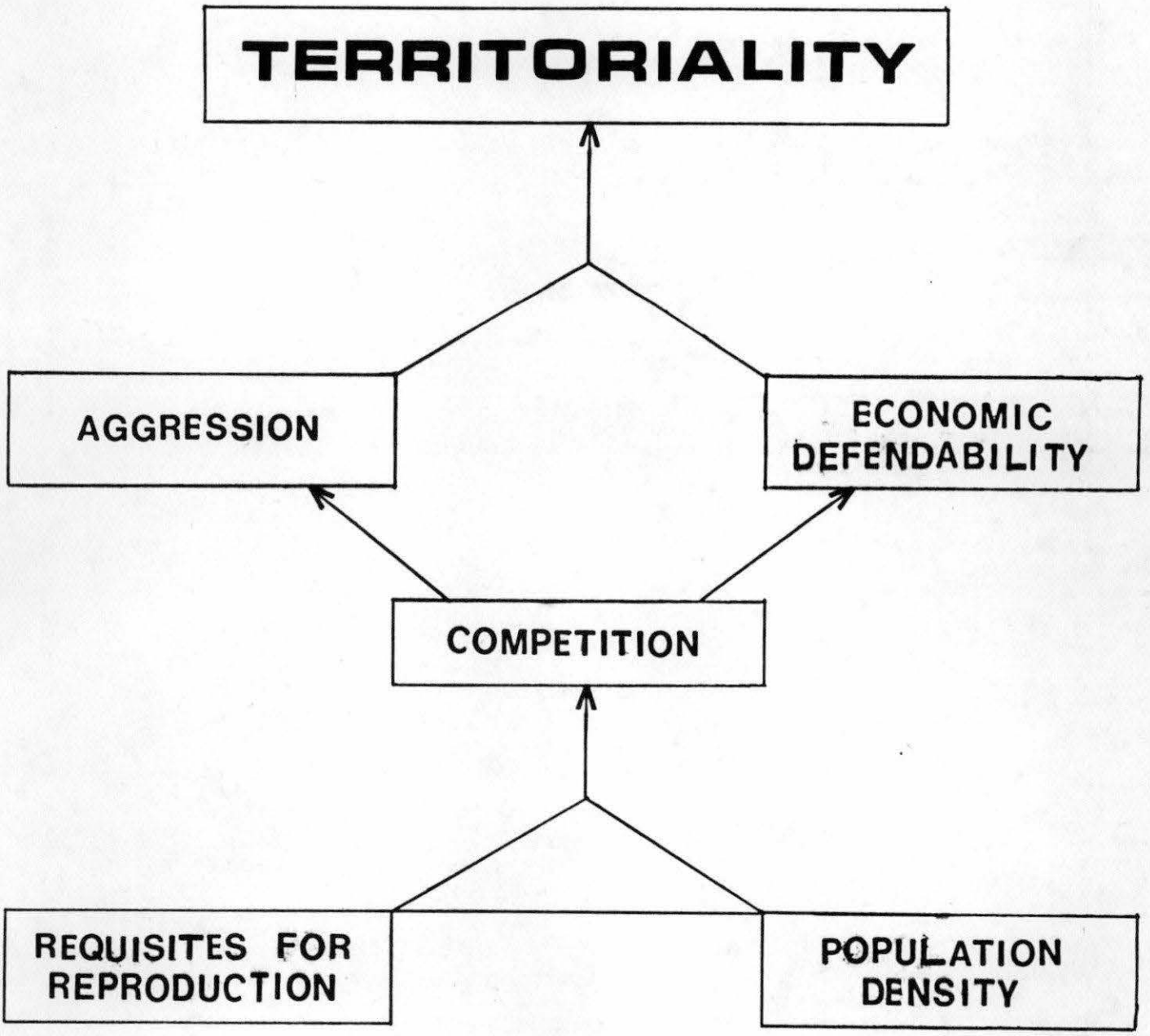

FIG. 1. A general theory of the evolution of territorial systems evolving from intraspecific interactions. (Redrawn from Brown, 1964).

It is important to consider the economics of defense from which selection for territoriality has arisen (Fig. 1). An animal can afford to defend a territory only when the gains obtained from this activity exceed the expenses incurred. Because of the direct correlation between effective territorial behavior and reproductive success in polygynous pinnipeds (Bartholomew 1970), selective forces have favored territoriality. Therefore, competition for a limited resource, (mates or space in this case), provoking aggressive behavior has lead to the evolution of territoriality in pinnipeds. Aggressiveness leads to the establishment of high social rank within a group; and high rank frequently allows the aquisition of territories. Similarly, possession of a territory usually means social domination.

Territories are established by the formation of dominance relationships through agonistic interactions. Social rank is decided by fighting, bluffing, or passive submission at the initial encounter between any given pair of individuals, or by an early series of such encounters. These aggressive behaviors are not only essential in the establishment of a

territory but are also required in the defense and maintenance of the territory. There cannot be territories without boundaries of some description; there cannot be boundaries without disputes arising from those boundaries (Howard 1948). Therefore, it is important when determining whether territories are established and to also examine the patterns of aggressive and agonistic encounters involved in the formation of social structures among breeding pinnipeds.

Pinniped Social and Reproductive Behavior

Odobenidae

The family Odobenidae, walruses, consists of 1 species. They are among the largest and most robust of the pinnipeds. The adults are slightly sexually dimorphic, the males being about 20% longer than the females. Walruses occur around the Northern Hemisphere and are inhabitants principally of the moving pack ice.

The social behavior of the walrus is the least understood of all pinnipeds. This is primarily due to their inacessibility to humans as they inhabit moving pack ice over shallow waters of the continental shelf. They use the ice as a substrate on which to haul out for resting, moulting, and

bearing their young. Walruses in both breeding and non-breeding seasons are among the most gregarious of mammals, hauling out in herds of up to several thousands.

The social mechanism through which the spacial ordering of individuals (both male and female) is established is of considerable interest during the nonbreeding season. On the ice walruses lie in close physical contact and youngsters frequently lie on top of the adults (Fay 1981). In the non-breeding season body contact is essential since it aids in heat conservation in cold weather (Fay and Ray 1968). Heat savings attained through body contact should be maximal for walruses in the central location of a herd and decrease toward the periphery: on the edges of the herd, walruses are in less body contact with each other and are exposed to wind and splashing water. In addition, body contact among walruses along the seaward margin of a herd is often disrupted because of walruses hauling out and departing (Miller 1976). As a result subordinate walruses (male and female) generally occupy positions along the seaward edge of herds of males because the dominant males are assertive and aggressive. Dominants

preferentially threaten subordinates, dominants have greater success than subordinates at displacing residents, and resident dominants are displaced less often than are resident subordinates (Miller 1975b). The observed dispersion, therefore seems to be a straight forward result of numerous agonistic interaction with consequent 'sorting out' (Miller 1976).

Most social interactions between both male and female walruses while hauled out are soley of an agonistic nature. On land the males engage in frequent threats involving the visual presentation of the tusks or strikes with the tusks, or both (Loughrey 1959; Miller 1975b). These agonistic interactions occur because of jostling by other walruses, as well as from attempts to gain or maintain positions within herds. Studies have shown that individual social status in herds is based on the combined values of body size, tusk size, and aggressiveness (Miller 1975b). Salter (1979) found that dominance was also clearly related to age class and possibly to sex class in adults.

Most agonistic interactions which occur during the breeding and non-breeding seasons (in both the males and females) involve static visual tusk threats, in which the head of the sender is raised and thrown back so that the tusks are held roughly horizontal and point directly or obliquely toward the recipient (Miller 1975b). Visual tusk threats are common and are accompanied by leaning toward the recipient, especially when he is a subordinate, or if the sender is very aggressive. Striking with the tusks is done with a downward motion, so that the recipient is struck with the tips of the tusks (Miller 1975b). Strikes are common and usually draw blood, but rarely cause serious injuries.

The system of polygynous mating in walruses seems best defined as a "mobile lek" (Fay 1981). The walruses congregate on the ice in traditional breeding areas, the competitive interactions between males during the breeding season is for acess to the most favorable locations near the females. The successful males then undergo an elaborate visual and vocal display behavior in full view for the females. These displays involve repeated dives by males near the edge of the ice where

the females haul out. Rapid 'knocks', produced by forceful bringing together of the cheek teeth, and resembling the sound of castanets, are given underwater and are followed by the 'bell tone', which is somehow produced by means of the pharyngeal pouches (Fay 1960; Schevill et al. 1966). Before surfacing, another series of knocks is produced and, upon surfacing, a single knock is emitted (Miller 1975b). Individual females leave the resting herd to meet the choosen male. Females rub against the male and somtimes dives in unison with him. It is believed that copulation then takes place beneath the surface of the water.

Otariidae

Sea lions and fur seals are members of the family Otariidae (the eared seals). The otariids can be found from Alaska to the subantartic islands of South Atlantic and Indian oceans. There are 12 species of otariids and they appear to have similar reproductive organizations and social behavior, although upon closer examination of detailed descriptive studies variations are visible. Sea lions come to shore to breed on sandy beaches, flat surfaced slabs of rock and shores with small stones, while the fur seals typically breed on steep beaches, near cliffs or in places with big rocky boulders (Vaz-Ferreira 1965). In their densely populated colonies, huge males - sometimes ten times the size of females - control territories, creating a social structure of considerable interest.

Males and females of all sizes and ages interact in the annual establishment of breeding colonies. These interactions are mainly sexual and agonistic in nature, and involve a variety of behavioral elements. Through agonistic

interactions, dominance relations and reproductive roles are established among individuals, and a non-random social structure is created with non-random mating as a result (Gentry 1970, Sandegren 1970).

In addition to aggressive behaviors, vocalization also appears to be an important factor in determining social status. Vocal activity is prominent on the breeding grounds. Vaz-Ferreira (1971) identified the adult male challenge vocal signal in the South American sea lion, Otaria flavescens, which consists of a roar followed by 3 to 7 bellows. This sound produces a pronounced resonance which appears to be a significant factor in the establishment of dominance in the social hierarchy even without any previous struggle.

There are broad similiarities in the social organizations and behaviors in otariids. They are among the most polygynous and gregarious of mammals. Characteristics common to otariid societies have resulted largely from competition among males for access to oestrous females, and from the need for a

terrestrial habitat in which to give birth, nurse the young, and copulate (Bartholomew 1970). Therefore, the males each strive to establish and maintain a territory where copulation may occur. The territory is distinguishable by the ceremonial threat displays exhibited by a male with adjacent males at several points around the periphery. Encroachment beyond a line joining the points of display, considered the territorial boundary, precipitates a fight. Fighting here is refered to as an interaction between two males, in which the antagonist attempts to physically overpower another by the use of biting and shaking, pushing, and slashing. Such contests are distinct from ritualized threat dispays used by territorial males which, however, incorporate elements of behavior used in fights (Miller 1975a). Ritualised threat displays occur at points in space accepted by both interactants, and are not considered disputes or direct contests.

The most important single factor in the reproductive performance of the adult bulls is an uncomprimising aggressiveness which is associated with territorial maintenance (Bartholomew 1953). This aggressiveness is

expressed by vocal threats, threatening charges, and fights between pairs of bulls. All of these behaviors are strongly affected by the spatial location of the animals. The attachment to a restricted territory is probably more strongly developed in the otariids than in any other mammal, since the successful establishment and maintenance of a territory on the rookery is a prerequisite for effective reproductive performance by a bull.

In both sea lions and fur seals, territories are established by the males before the arrival of females. Fur seals stay on the territories until females arrive, a period of approximately 1 month. In contrast sea lions are not continuously present, they may leave the rookeries for short periods to feed or to cool themselves. Boundary adjustments occur as new bulls arrive. Territorial males typically fast while holding a breeding territory, a period which may exceed 2 months (Miller 1974b). All fur seal territories have access to the sea, so that the bulls can enter the water to cool off and drink.

A seasonal transition to and from rigid territoriality, that is influenced by the timing of the breeding season and the presence of females, occurs in otariids (Bonner 1984). Before the first females arrive at the rookeries, few territorial displays occur. As the season progresses intense territorial maintenance takes place and then diminishes as the breeding season comes to an end.

Fluid territorial behavior where male's will not leave the territories the during the begining of the breeding season has been noted for the Australian sea lion, Neophoca cinerea (Marlow 1968), the stellar sea lion, Eumetopias jubatus (Gentry 1970), and the Northern fur seal, Callorhinus ursinus (Kenyon 1960). This fluidity is also present in late summer, for example territorial Callorhinus ursinus (Peterson 1965), Eumetopias jubatus (Gentry 1970), and the Antartic fur seal, Arctocephalus gazella (Bonner 1968) show increased tolerance of the presence of subadult males at this time. New Zealand fur seals, Artocephalus forsteri show a decrease in territory maintenance at the end of the breeding season (Bonner 1984). In this instance territorial males will temporarily abandon

their stations during the heat of the day, though they had remained on the station under similar temperature conditions through the peak of breeding (Bonner 1984).

Intensity of territorial maintenance also decreases in late summer in Callorhinus ursinus (Peterson 1965). In contrast, territoriality in Eumetopias jubatus remains rigid in late summer, but the frequency of boundary delimitation displays declines (Gentry 1970). It can be inferred from these observations that territorial maintenance decreases as the breeding season comes to an end. Accordingly, males that challenged territory - holders late in the season are more likely to attain territorial status because of a decline in aggressiveness and tenacity of a tenured males.

In some otariid species the establishment and distriburtion of territories is related to, and modified by, the presence of females. In some species females must be present for territorial behavior to be initiated and maintained. The presence of females is essential for the

successful establishment of a territory in Neophoca cinerea. In the early stages of territorial defence, Neophoca cinerea bulls will defend an area for 4 or 5 days, but if no females have entered and settled in this area after this time, the bull will then desert the territory and move off to try to establish himself eleswhere (Marlow 1975). Territories in the Californian sea lion, Zalophus californianus, appear to be held only where females are present (Peterson and Bartholomew 1967), and a single female Eumetopias jubatus is adequate stimulus for territorial behavior by an adult male (Gentry 1970). Otaria flavescens will maintain a territory without females but will only defend a territory in which female's are present (Vaz-Ferreira 1975). In contrast, Hooker's sea lion Phocartos hookeri, maintains its territorial defence of an area irrespective of whether it contains females or not (Marlow 1975). Phocartos hookeri bulls do not leave their territory once they have establishes their position on the beach. They do not enter the sea to feed or to cool themselves, but continue to lie in their territory flipping sand over themselves to keep cool (Marlow 1975). Male Zalophus californianus are attracted to a particular area by

the presence of females (Peterson and Bartholomew 1967 and Odell 1975). As the number of females increased, the number of territorial males also increased. In some instances the distribution of females seemed to act as a proximate factor for expansion of territorial size, throughout the breeding season. Although some territories have been noted to be held by males before the number of females in them is high. Miller (1975a) has suggested that males can predict to some degree which areas will contain females as he noted in Arctocephalus forsteri. This has also been noted in the grey seal, Halichoerus grypus (Hewer and Backhouse 1960) and Eumetopias jubatus (Gentry 1970).

In other species of otariids the presence of females is not required for territorial maintenance. Individual male Callorhinus ursinus have been found to occupy particular geographically located spots rather than locations likely to attract many females (Peterson 1965), this supports the interpretations made by Bonner (1968) and Paulian (1964) that the territory is more important than the presence of females. From these observations it suggests that otariids perfer to

maintain a territory over retaining females. This behavior may have arisen because of the process of equating territoriality with access to females. Miller (1975a) states, "It is undoubtedly advantageous for male otariids to remain somewhat labile in their territory - establishing behavior, to permit opportunistic increases in the frequency of copulation." Therefore the amount of reproductive activity by a male is related to the males' success in holding a territory of a size and location such that it always contains a large number of females.

The position of the males in the social hierachy may also be a significant factor involved in the establishment of territories, since subordinate animals are often evicted from their territories by more dominant males. In some cases subordinates take flight into the sea without offering any retaliation to the dominent intruder. This characteristic flight action of a subordinate animal has been frequently observed in Neophoca cinerea (Marlow 1975a) but is completely absent in the adult males of Phocarctos hookeri (Marlow 1975a). In this species any charge evokes either a ritualised

territorial boundary displays or an aggressive retaliation (Marlow 1975a). The difference in the behaviors of these two species can be explained by the social status of the bulls that initially claim territories. Only the dominant males in the social hierarchy in P. hookeri are able to establish themselves in territories and therefore, being equally matched, they respond to any challenge by territorial defense. In contrast, subordinate N. cinerea bulls take up territories and leave without defending them, as if recognizing the challenger as a more dominant male.

Intra - sexual competition among male otariids has been a strong selection force for the evolution of a number of characteristics. These characteristics are summarized by Miller (1975a) as follows: sexual dimorphism in size, strength, and social behavior; greater mean age of breeding in males than in females; shorter reproductive life in males than in females; greater per capita genetic contribution to each generation by breeding males than by breeding females; positive allometric growth in some characters used in inter-male strife (e.g. teeth); and narrowing of phenotypic variance

for certain structural, physiological, and psychological character states in territorial males. Therefore, in order for bulls to acheive a dominant status they must be of large body size, able to fast for prolonged periods, be aggressive, and demonstrate a prowess in fighting ability.

Fighting ability appears to be a requisite for prolonged territorial status in otariids. Fights are intense, often producing wounds, although few result in serious injury. Bulls attempting to establish a position on an already occupied beach are always challenged and may suffer serious injury. But there are no records of bulls being killed in the course of a fight (Bonner 1981).

Despite these fights much of the agonistic behavior involved in territory maintenance is highly ritualized. Various characteristic postures have been described for Arctocephalus forsteri (Stirling 1970 and Miller 1974b) which are essentially similar to those of A. gazella (Bonner 1968) and appears to apply generally to all members of the otariids

(Fig. 2). In A. forsteri the most aggressive posture is the "full neck display', where the male sits upright with the chest out, the head back and the nose vertical. This is characteristic of territorial males and probably enlarges the appearance of the size of the neck to an opponent (Stirling 1970). Encounters between territorial males begin by both animals giving a full neck display when in close proximity to one another, and often touching chests. If one animal does not back away, the two males begin "neck waving", the head and neck being waved from side to side, out of phase with each other. Submission is indicated by a general lowering of the profile of the body. An "open mouth display", in which the bared canine teeth are presented in a threatening fashion, may be given as an aggressive or submissive display. Displays are more frequent than actual fights. However, when fights take place, the bulls face one another and make slashes at their opponent's neck. Occasionally a bull will aim at the unprotected skin at the base of the flipper. Bulls sometimes are seen pushing at their opponents with their chests, driving them back by sheer strength. At the end of a contest, whether a fight or merely a threat, adjacent territorial bulls usually end up facing away from each other.

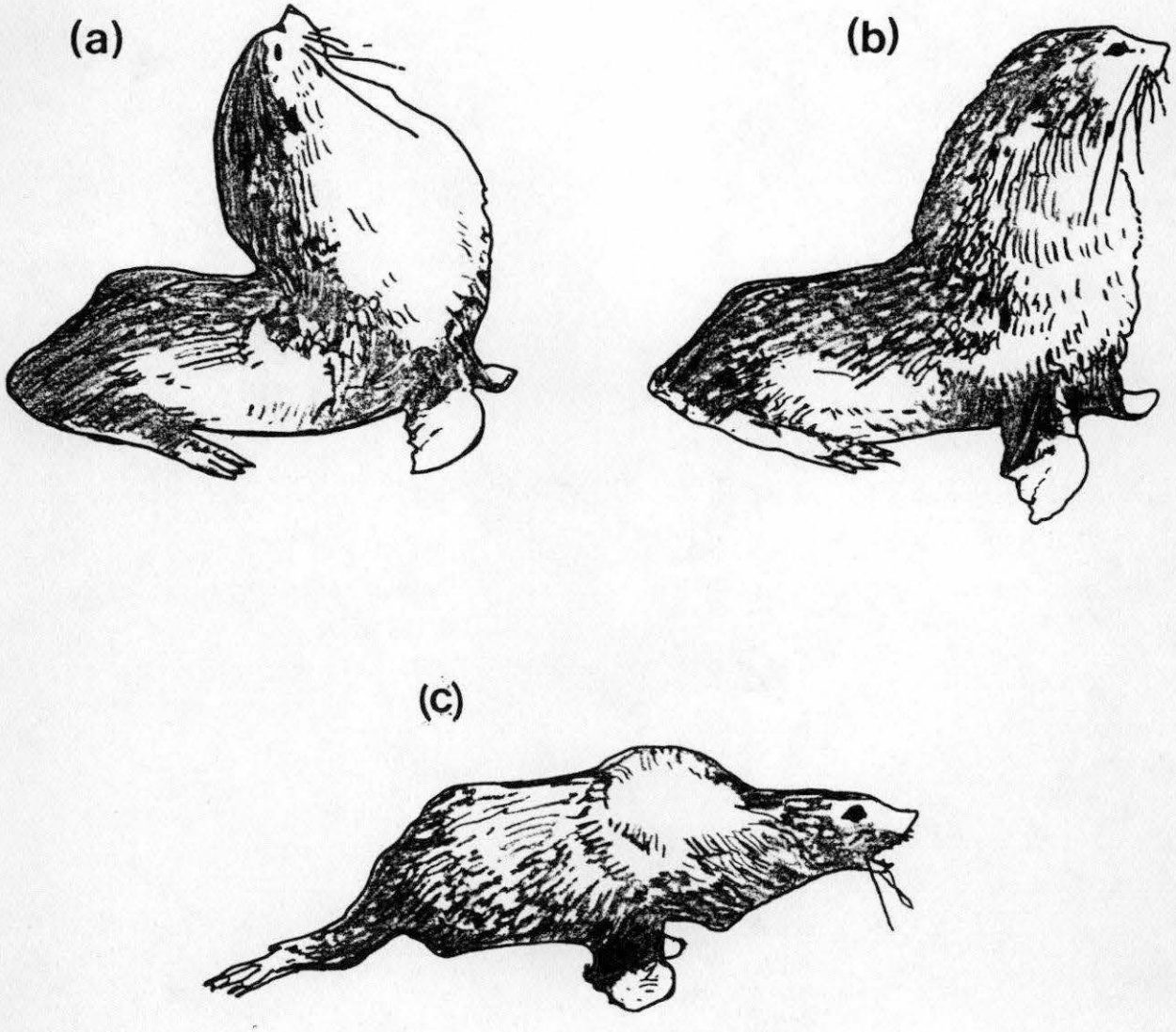

FIG. 2. Postures of Arctocephalus foresteri redrawn from Stirling (1970) drawings. (a) Full neck display; (b) alert posture; (c) submissive posture.

Oestrous females are sometimes, but not always, identified by olfactory investigation of perineal region. Bonner (1981) found that the "open mouth" display may also serve as a function in identifiction of an oestrous female. Some males mount immediately on finding that a female is sexually receptive; others may continue to sniff at the perineal or facial regions for up to 15 min before mounting (Miller 1974b). There may be multiple mountings before copulation is terminated. Copulation can take place on land or in shallow water, with the female in contact with the bottom.

Phocidae

Among the pinniped families, the Phocidae (true seals) are the most diverse family in terms of body size and habitat occupied, as well as one of the most widely distributed. Their members are more completely anatomically adapted to the marine aquatic environment. Such that, they do not move as fluidly on land as do otariids and odobenids, because their hindlimbs are extended posteriorly, incapable of forward rotation, and their frontlimbs are used only for support (Howell 1930; Vaughan 1975).

There are 18 species in eight genera in the family Phocidae. A similar advanced degree of adaptation to an aquatic mode of life is exhibited by each species. Reduced terrestrial mobility and instability of hauling grounds due to tidal changes (Loughlin 1974; Sullivan 1980) or unstable sea-ice (Stirling 1975; Beier and Wartzok 1979), preclude maintenance of territories on land or ice. The establishment of a stable aquatic territories in which females can aggregate is prevented by the high levels of mobility in water,

coupled with the difficulty of maintaining a territory in aboundaryless, three-dimensional medium, and the need to breath air (Bertram 1940; Bartholomew 1970; Stirling 1975). Only in the Weddell seal, Leptonychotes weddelli, do adult males seem to defend underwater "territories" (Stirling 1975; Kaufman et al. 1975; Siniff et al. 1977) or at least monopolize breathing holes (a resource in short supply) where females come to breath or haul out. Despite these constraints, there are a variety of mating systems in the Phocidae which range from pair bonding promiscuity to polygyny (Bartholomew 1970). Since members of the family Phocidae breed primarily in water (Stirling 1975) mating systems of these species must be attributed to some mechanism other than polygynous territoriality.

In the majority of phocids, courtship and mating are rarely observed since these activities apparently take place in the water. The little information that is available comes primarily from observations of the harbor seal. According to Venables and Venables (1957) mating seems to be preceed and followed by periods of rolling and bubble blowing. Sulliven (1981) observed encounters between two harbor seals at the

surface of the water that involved rolling horizontally, splashing, scratching, riding in a mounted position venter to dorsum, biting, growling, and bubble blowing. When contact was made, both individuals oriented in a vertical position muzzle to muzzle. Each then exchanged a series of open -mouth thrusts, accompanied by growls, toward the head, neck, and cheek of the other. This exchange was found to initiate rolling, splashing, and lead to one seal maneurvering on to the back of the other in a riding position. These observations corroborated those of Bishop (1967) and Beier and Wartzok (1979) and were considered as courtship or copulatory behavior (Scheffer and Slipp 1944; Venables and Venables 1957; Bishop 1967; Hewer 1974). Aquatic encounters similar to those described by Sulliven (1981) were also reported in Leptonychotes weddelli (Kooyman 1968; Cline et al. 1975; Kaufman et al., 1975), the Hawaiian monk seal, Monachus schauinslandi (Kenyon and Rice 1959), and the Harp seal, Phoca groenlandica (Merdsoy et al. 1978).

Aquatic displays and aquatic interactions have also been observed between adult male phocids during the breeding season. Sulliven (1981) described these interactions between

adult male harbor seal, Phoca vitulina, as aggressive behaviors used in the establishment of dominance relationships required in establishing breeding privileges, e.g. acess to females. Dominance hierarchies in which males establish ranking by fighting were suggested for Leptonychotes weddelli (Ray 1967; Ray and DeCamp 1969; Kaufman et al. 1975) and for the ringed seal, Phoca hispida (Stirling 1973). These hierarchies were established bysplashing and lobtailing by dominant males. These behaviors may also function as visual display mechanism to attract estrous females. In addition to the dominance relationship established by fighting in water, an additional ranking may be established over access to landing and resting sites. Sulliven (1982) observed a strongly linear dominance ranking among Phoca vitulina. Ranking was related to size and sex; with adult males dominating females, sub-adult and juvenile males of all other age classes. Dominance based on size or aggressiveness was shown in the Alaskan Phoca vitulina (Bishop 1967) and in the male grey seal Halichoerus grypus (Hewer 1957). Sulliven (1982) described aggressive signals commonly used by the harbor seals, and phocids in general, on land (Table 1). These signals are responsible for setting up the dominance relationships.

Table 1. Aggressive signals of the Harbor Seal from Sulliven (1982).

1. The extended foreflipper : an aggressive, low-intensity, long-range threat, in which a sender elevates and orients its head and foreflipper toward an intruder.

2. The head - up - stare : an aggressive, long range threat in which a stationary seal raises its head toward the intruder, and stares with eyes open wide, nostrils flaring, mystacial vibrissae slightly erect and oriented forward.

3. The foreflipper wave : an aggressive medium-range threat involving single or multiple waving of the elevated and extended foreflipper directed at, but not contacting, an intruder (Fig. 3a).

4. Growling : an aggressive, close-range threat consisting of harsh, throaty gutteral vocalization (as noted by Sheffer and Slipp 1944; Bishop 1967; Knudtson 1974).

5. The foreflipper scratch : an aggressive contact threat involving single or multiple scratching of conspecifics using the sharp claws of the extended foreflipper (Fig. 3b) (also obsereved by Bishop 1967; Schusterman 1968).

6. The closed - mouth head thrust : an aggressive close-range threat consisting of rapid extensions and retractions of the neck with mouth closed (Fig. 3c).

7. The open - mouth head thrust : an extremely aggressive, close-range threat also involving rapid extension and retraction of the neck with the mouth open wide.

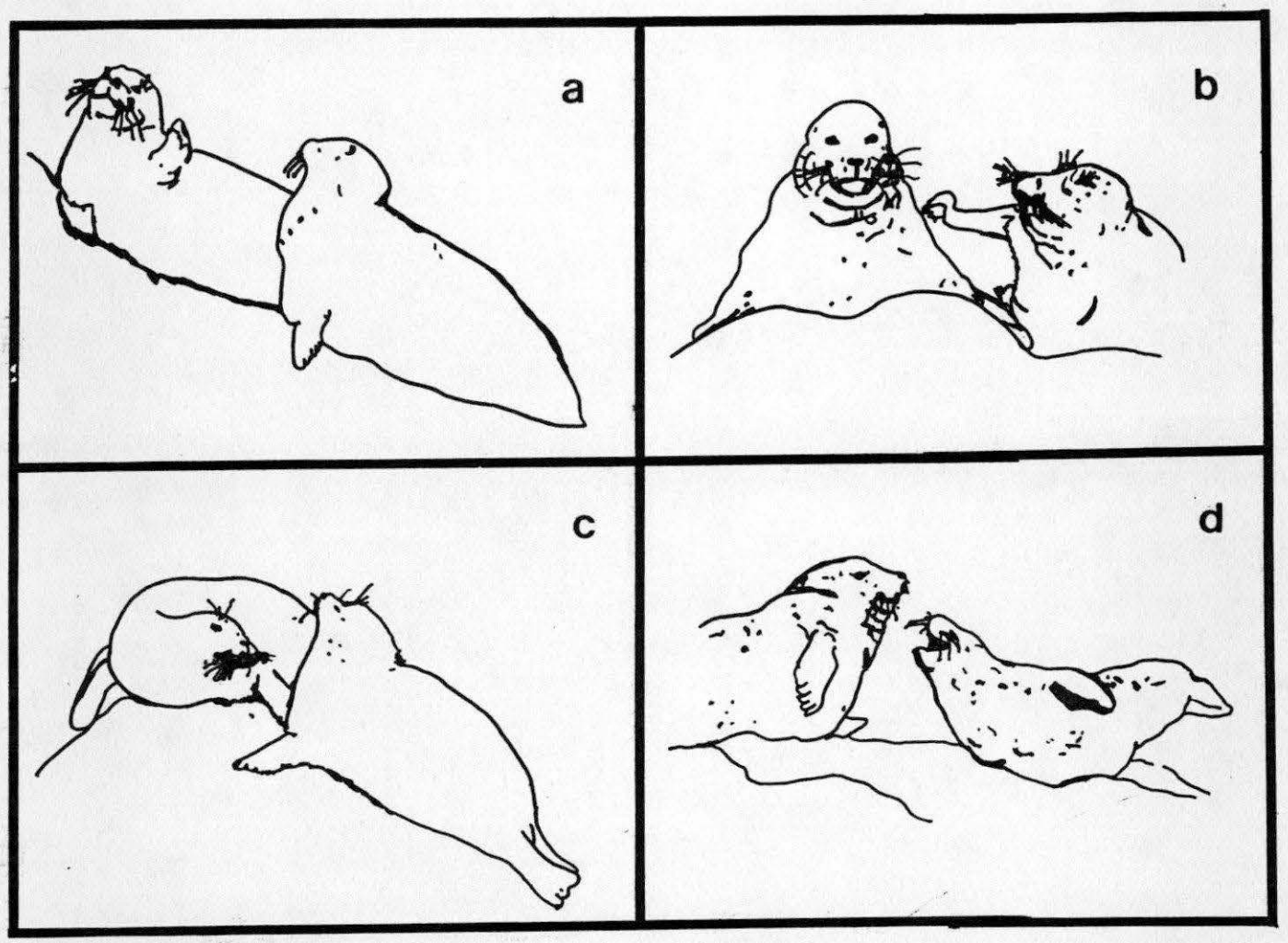

FIG. 3. Aggressive signaling in seals on land redrawn from Sulliven (1982). (a) A foreflipper wave by a seal reclined on its side in response to the ventral approach of an intruder. (b) A foreflipper scratch by a laterally-reclined seal directed at an approaching adult male. (c) A juvenile male giving a closed-mouth head thrust to an approaching juvenile male. (d) A juvenile male issuing an open-mouth head thrust to an approaching adult male.

Certain species of phocids are able to give birth and copulate on land or ice. Some examples include the elephant seal , the Harp seal, and the grey seal. The grey seals, Halichoerus grypus, breeding system is characteristic of the land breeding phocids. It resembles those of other pinniped species (fur seals, sea lions, and elephant seals) which give birth and copulate on land. Males physically compete for mating privileges (Miller and Boness 1979). Social interactions among breeding males are mainly agonistic, and involve many threats and fights. Spacing among breeding males is fairly uniform, but is not rigid as they attempt to stay near particular females or groups of females rather then maintaining territories.

The season begins with the arrival of the females and the birth of the first pups. The bulls arrive soon after and take up their positions. Where there are only a small number of cows in an isolated cove, it is usual for bulls to station themselves in the sea at the approach to the beach (Hewer 1957; Fogden 1971). Where the cows extend inland far from the beach, as at the larger and more crowded colonies (e.g. North Rona, the Farne Islands), the bulls station themselves

ashore (Hewer 1957; Anderson et al. 1975). Hewer (1957) suggested that the bulls with previous breeding experience choose the most advantageous positions on the beach forinsuring access to females and are rarely challenged. Hewer (1957) regarded this behavior as being associated with territoriality which has been observed in the Outer Hebrides, and occasionally at North Rona or the Farnes (Hicking 1962). Coulson and Hickling (1964), Hewer(1960), and Cameron (1967, 1969) have all described the male grey seal as highly territorial during the breeding season. However, there are no clear physically defined territories as noted in fur seals (Peterson 1968). The area dominated by the bulls has been observed to change from day to day (Bonner 1981). Bulls do not investigate individual females (as seen in the otariids), but once oestrous cows are present on the rookery, they will approach any female present and attempt to copulate. Therefore the reproductive strategy the grey seal bull uses is that of constant sexual activity, rather than territorial fighting or boundary displays (Anderson et al. 1975).

Another grade of organization of the social system in the family Phocidae is seen in elephant seals, Mirounga leonina and M. angustirostris, the largest of the

pinnipedia. The southern elephant seal, Mirounga leonina, males weigh over three tons (Laws 1953), while the northern species, M. angustirostris, is smaller weighing about two tons (Le Boeuf 1971). These two species are the only representatives of the genus and appear to have similiar behaviors (Laws 1956). Sexual dimorphism is pronounced with the males being about three times as large as the females (Laws 1953). In addition males display a heavily cornified integument shield on the chest and neck and possess an enlarged proboscis.

During the breeding season the main element in the social behavior of the adult female elephant seal appears to be gregariousness. The females haul out on the rookeries in dense aggregations which are often referred to as pods or "harems". A harem may be composed of 2 to 1000 females, their pups, and one or several males, one of which is dominant to all others (Laws 1956; Le Boeuf 1972,1974). Each female delivers one pup about 6 days after they arrive on the beach. The female then remains on land for approxiamately 35 days, and during the last 3-5 days of this period she copulates with one or more males (Cox 1981). Males, however, attempt to mate females long before they become estrous (Le

Boeuf 1972). Non - estrous females always respond with resistance in the form of threat vocalizations and attempts to escape, and estrus females typically respond in the same manner. This female "protest" alerts surrounding males to attempted copulation, and if there is a more dominant male in the vicinity, he threatens and displaces the mounting male (Cox and Le Boeuf 1977).

Males arrive at the traditional breeding grounds up to one month before the arrival of the first females, spending a total of over eight weeks on land during the breeding season. Immediately upon arrival the males begin fighting and threatening each other to establish rank in a social hierarchy which determines access to females. Dominance is expressed by the threatening gestures and are usually accompanied by loud vocalizations (Le Boeuf and Peterson 1969). There are a variety of aggressive movements, postures, and vocalizations used by males (Bartholomew 1952; Bartholomew and Collias 1962; Le Boeuf 1971, 1972; Sandegren 1976a). The following are descriptions of agonistic behaviors distinguished by Sandegren (1976a) for the behaviors of male M. angustirostris and adapted for the M. leonina by McCann (1981).

Table 2. Aggressive behaviors of the Southern elephant seal (M. leonina) as described by McCann (1981).

Proboscis Erection: from a dangling, relaxed state the proboscis increases in size and becomes firm and erect.

Frontal Approach: a bull orients and moves toward another.

Chase: one bull chases another.

Rear: the front half or more of the body is raised approximately to the vertical, with the fore - flippers off the ground.

Chest - to - Chest Pushing: From the Rear position a bull slams his neck and chest against his opponent.

Bite: a bull bites his opponent.

Table 3. Aggressive Vocalizations of the Southern elephant seal (M. leonina) as described by McCann (1981).

V0: a low-pitched sound apparently produced by inhaling through the open mouth.

V1: a low-pitched sound produced as air is exhaled through the relaxed or partially erected proboscis.

V2: commonly called the "roar", this is a low-pitched, loud vocalization capable of great carrying power which is emmitted from a stereotyped posture with the head and neck raised and proboscis erected.

Table 4. Submissive Behaviors of the Southern elephant seal (*M. leonina*) as described by McCann (1981).

Proboscis Retraction: the subordinate retracts and flattens his proboscis.

Open Relaxed Mouth: the subordinate opens his mouth maximally while retracting his proboscis.

Nip Bite: the subordinate makes short nipping of biting motions at the dominant's neck.

Retreat: the subordinate bull moves away from the dominant bull.

Table 5. Submissive Vocalization of the Southern elephant seal (*M. leonina*) as described by McCann (1981).

V3: a high-pitched, female - like sound, heard only in dominant - subordinate interactions.

The vocal challenge appears to be the prelude to nearly all fights and is used occassionally during fights. It is used as a threat and as an expression of dominance. It is frequently substituted for actual physical combat and is often effective in forcing the withdrawal of subordinate males when distance precludes physical contact or when the dominant male is otherwise occupied (Bartholomew 1953). The aggregate result of dominance relations established through threats and fights between pairs of males is a linear social dominance hierarchy (Cox 1981), in which each male attempts to gain access and to mate with as many females as possible, and to prevent other males from doing the same. As a consequence, there is a strong, positive correlation between aggressiveness, social rank, and the number of copulations a male engages in (Le Boeuf and Peterson 1969; Le Boeuf 1974).

Size appears to be a major factor in deciding the outcome of intrasexual competition through its effect on fighting ability. The largest, most dominant males gain high rank and high mating success. Superficially this situation does not appear to differ markedly from that found in the otariid seals in the establishment of territories. In

otariids (Bertram 1940) a territory with a dominant male is maintained as the reproductive unit by the aggressive activities of this dominant male, who defends his territory against other males attempting to displace him or to take individual females from him. In the elephant seal, however, the dominant males do not defend a fixed area (McCann 1981) or specific group of females against intrusion or theft so much as they defend their position among these females and attempt to keep other males from similarly locating themselves (Bartholomew 1953). Maintenance of position with regard to the females, rather than maintenance of a specific group of females, is the main preoccupation of the dominant males.

Discussion

The distinctiveness of the Pinnipedia from other mammals and the recognizable morphological simlilarities among the three families, Odobenidae, Otariidae, and Phocidae, support their being regarded as one of the orders of the class Mammalia. Whether the pinnipeds have evoled from a natural group derived from a single common ancestral carnivore or from two is still a matter for argument (Davis 1958; McLaren 1960; Ling 1965; Mitchell 1967; and Sarich 1969a & b). Most fossil evidence indicates a diphyletic orgin; true seals evolving from an otterlike ancestor which took to the water in North Atlantic and the eared seals and walruses from a doglike ancestor in the North Pacific (Repenning 1980). Recognizable eared seals and true seals both appear in the fossil record in the Miocene, with the walrus appearing a little later (Lipps and Mitchell 1976). Although consideration of pinniped social behavior in a diphyletic context can be helpful, the phyletic lines based on fossil pinnipeds are too limited to be of much use. Therefore, in order to understand the evoluion of the

social behavior it is important to examine the selective factors and characteristics involved in their formation.

The primary selection pressures leading to territorial behavior in pinnipeds appears to be a combination of many factors including: feeding patterns, the ablility to breed on land , the gregariousness of females, requisites for mates, males increased testosterone levels, and sexual dimorphism. It is important to note that all these factors are interelated and mutually reinforcing. Pelagic feeders, because of their wide dispersal over the surface of the ocean, survive as a species only through the evolution of a specific homing instinct. This leads to designated rookeries on which females aggregate, male competition for access to females, increased testosterone induced aggressiveness, sexual dimorphism, and the evolution of territoriality.

Bartholomew (1970) devised a schematic model to describe the evolution of pinniped polygyny (Fig. 4) which convincingly accounts for many of the observed

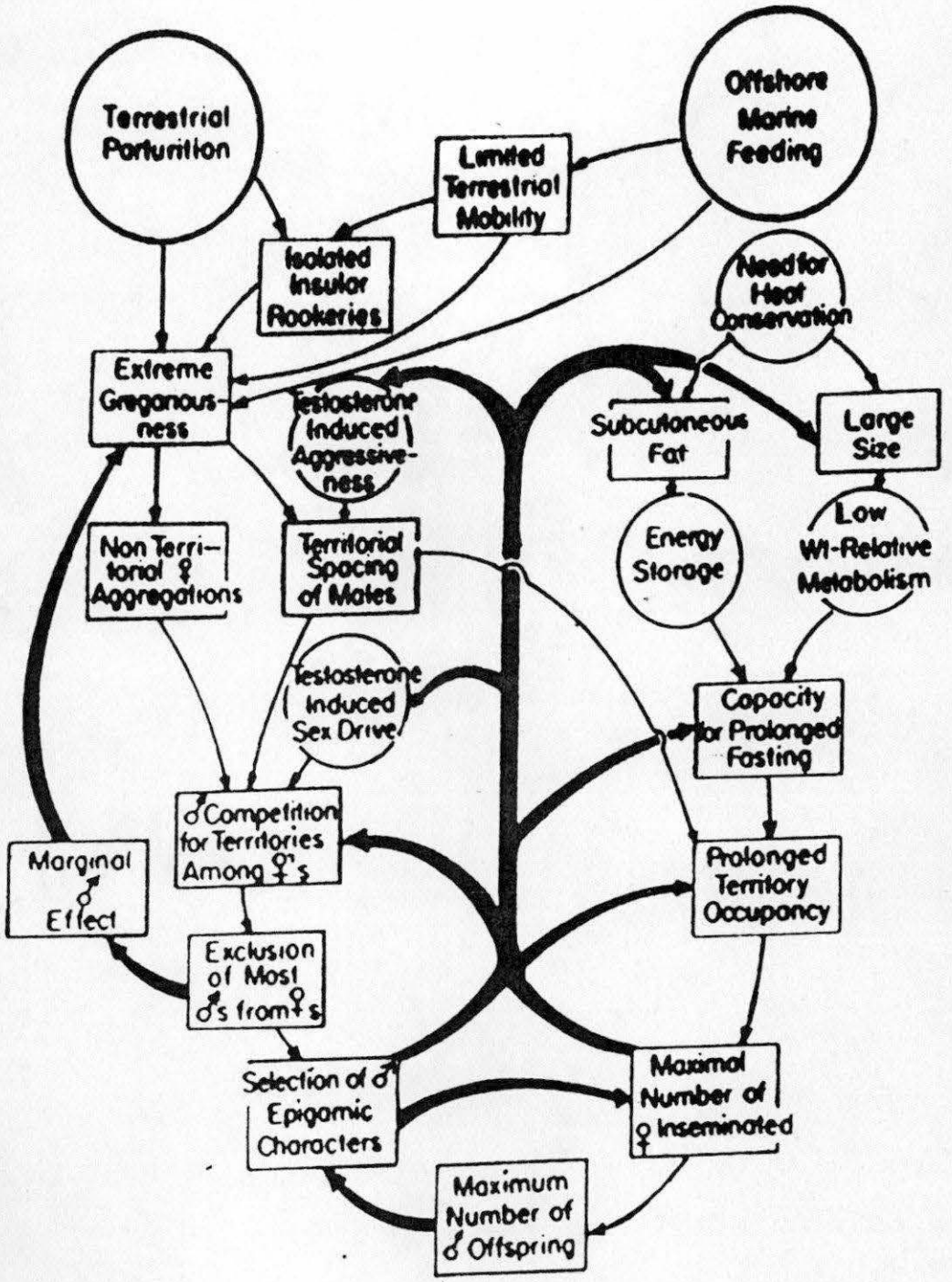

FIG. 4. A schematic model for the evolution of pinniped polygyny. The large circles represent to key attributes of pinnipeds; the smaller circles are attributes common to most mammals; the rectangles show attributes and functions typical of polygynous pinnipeds. The broad arrows show positive feedback loops. From Bartholomew, 1970.

characteristics. The concepts behind the model are complicated, but will be briefly summarized here. Bartholomew begins his model by starting from the two features that uniquely distinguish the group from the rest of the mammals - offshore marine feeding and terrestrial parturition. The reproductive cycles of local populations are synchronized and a high degree of fidelity for particularbreeding sites has developed to ensure that the sexes are reunited at the right place and time for breeding (e.f. C. ursinus, Kenyon 1960; M. leonina, Carrick et al. 1962; L. weddelli, Stirling 1969). The model accounts for the extreme gregariousness shown by pinnipeds when ashore. By adopting gregarious breeding habitats, animals which are widely dispersed when feeding at sea can make use of special situations, such as oceanic islands, where appropriate terrain and absence of terrestrial predators allow them to breed successfully on land. Despite the fact that their main adaptations are for an aquatic medium. In their breeding aggregations, males are more widely spaced than females, because of the males' testosterone - induced aggressiveness. From this it follows that many males are excluded from the

breeding females, resulting in competition between males. Those males which are most vigorous and aggressive can maintain the position on the beaches longest and can pass on a disproportionate number of genes to the next generation. Bartholomew calculated that in the Northern fur seal the fecundity of a territorial male, which might successfully impregnate about 80 percent of the 40 females in his territory in each of five breeding seasons, was about twenty-five times that of a breeding female, which would produce about six pups in her lifetime.

This results in a strong selection pressure toward the development of those characters which allow a male to successfully establish himself among the females and, once established, to maintain that position as long as there are estrous or pre-estrous females, in the vicinity. The relationships of some of these features are shown on the left side of figure 4.

Bartholomew's model is dependent on the maintenance of an advantage for a few of the available males through the establishment of territories where only the successful male

can exclude other males and mate with all the females in his territory. Such conditions exist for several pinnipeds, but are most obviously evident in the well developed social organizations characteristic of the otariids (e.g. Arctocephalus gazella, Bonner 1984; Eumetopias jubata, Sandegren 1975; Callorhinus ursinus, Kenyon 1960; and Zalaphus californianus, Orr 1967). Among phocids this type of behavior is true only of the northern elephant seal (M. angustirostris), the southern elephant seal (M. leonina), and the grey seal (H. grypus), in which the reproductive social unit consists of a group of females of reproductive age dominated by an aggressive male.

The most important single factor in the reproductive performance of adult bulls is an uncompromising aggressiveness which is associated with territorial maintenance. The aggressiveness is expressed in several ways; vocal threats, threatening charges, and fights between pairs of bulls. All are strongly affected by the spacial location of the animals; attachment to a restricted territory is probably the most strongly developed in the male fur seals

(e.g. Callorhinus ursinus, Bartholomew 1953). Successful establishment and maintenance of territory on a rookery is a necessary prerequisite to effective reproductive performance in pinnipeds in which copulation occurs on land (or packed ice).

To establish a territory and defend it in the face of the testosterone - induced aggressiveness of neighboring males and newly arrived competitors, a male must be well equiped with a suite of epigamic characters such as aggressivenesss, large size, large canines, a protective shield of hair or skin on the forequarters, and modified special structures used in threat display and vocal challenges. Males who possess these characters will mate with the most females and produce the most offspring.

The length of time a position among the breeding females can be maintained is also critical to the genetic success of the individual male. A seal lion, fur seal, or elephant seal in the breeding season will not feed for the entire period he remains on shore. To abandon his position on the beach to

feed would mean running the risk of having his females come in estrus and mate with another male. Additionally, a returning male would have to expend energy in re-establishing himself on the beach after an absence. Because of the correlation between prolonged territorial maintenance (or staying ashore in contact with breeding females) and the number of females fertilized, there is a strong selection pressure in favor of large size. This is demonstrated in Bartholomew's (1970) model by the positive feedback loops connecting these energy relationships (right side Fig. 4). Positive feedback loops are represented by broad arrows in the figure.

Bartholomew (1970) pointed out that, in Pinnipedia, selection will favor those characteristics which aid successful territorial behavior, namely aggressiveness and the ability to remain on land for a long period of time. In his model he appears to have ignored most phocids which exhibit little sexual dimorphism in size and copulate in the water (e.g. P. vitulina, Stirling 1975). High levels of mobility acheived by phocids in water coupled with the

difficulty of maintaining a territory or harem in a boundaryless, three - dimensional medium, in the absence of air to breath, prevents establishment of stable aquatic territories of harems in which females can aggregate (Bertram 1940; Bartholomew 1970; Stirling 1975; and Sulliven 1981).

Bartholomew did not address his analysis to seals that are not socially organized for designated rookery breeding and pupping, but still are well adapted to the two fundamental conditions of pinniped existence. Thus Bartholomew failed to make note of the poorly understood difference between coastal and pelagic marine feeding. Pelagic feeders because of their wide dispersal over the surface of the ocean, survive as a species only through the evolution of a very specific homing instinct. Coastal marine feeders have ready access to land or ice; they may haul out in groups at any time of the year just to rest but their grouping may be protective rather than for birth and breeding; they have evolved a relatively insignificant homing instinct and dimorphism; and they do not have designated rookeris for breeding and pupping. The exception is the

walrus, a dimorphic coastal feeder, whose ancestors were pelagic feeders. Therefore a logical explantion for the observed differences in the pinnipeds' breeding behavior may ultimately be explained by their differnces in feeding patterns.

In addition, an important question to address is why pinnipeds are not territorial in water? A possible explaination may simply be that since water is a 3-dimensional medium it precludes the establishment of stable aquatic territories in which females can aggregate. While male seals may wish to defend a 3-dimensional territory in the water, they must return to the surface to breath. Therefore males dependence upon a resource (air) outside the medium in which his territory is located (water) would limit his ability to sucessfully maintain a stable territory. Another important factor that has not been addressed is that of time constraints. Perhaps pinnipeds which mate in the water, namely phocids, do not need to form territories because they lalck the time constraint of a short estrus period placed on the otariids. The phocid females, such as

the harbor seals, are in estrus from 1 to 9 weeks. In contrast, the otariids have a much shorter estrus period. For instance, the Northern fur seal is only in estrus for 48 hours and the Australian fur seal is in estrus for about 3 days. Therefore in otariids, successful establishment and maintenance of a territory would be essential for effective reproduction by a bull.

An additional point to note is that in those species that give birth and copulate on land, space is a vital consideration. Not only is spacial separation limited by reduced agility on land, but often by habitat availability as well. Under such conditions, competition takes place between males in the establishment of territories as observed in the otariids. Hypothetically, it would appear that unlimited space for breeding results in the breakdown in establishment of territories. This argument is supported by those conditions in which space is not limited, as in the phocids. In the phocids, Phoca vitulina and Monachus schaunislandi, copulation takes place in the water where space is not limited and territories are not established (Stirling 1975).

Conclusion

"Territoriality" may mean different things to different researchers depending on their backround. These differences are especially important when examining phocid seals social systems as they do not fit the existing terminology in contrast to the otariids. Male "territoriality" is not a unitary concept. This is important to consider when speculating about the the roles played by various components of social behavior during the evolution of pinniped groups, as in Bartholomew's model (Bartholomew 1970).

"Territoriality" in reference to this paper is defined as a fixed area which is actively defended and used exclusively. According to the literature, territorial behavior appears only to exist in the otariids. Although in some species of the phocids, where only a single male is assiociated with a group of females, the behavior has been interpreted by some investigators to by territorial (e.g. L. weddelli, Ray 1967; H. grypus, Miller and Boness 1979; and M. angustirostris, Odell 1972). While it is true that the

dominant male of a harem, as in the case of the elephant seal, behaves aggressively towards males that approach him, this is not territoriality sensu strictu since males do not defend a fixed geographical area. Many sea lions are territorial; they adopt contiguous territories with stable well - defined boundaries. The Alaska fur seal male, C. ursinus, herds females into his territory and patrols the boundary of his territory directing aggressive boundary displays at adjacent males (Bartholomew and Hoel 1953). When a stellar sea lion female, E. jubata, moves through the territory of a male, the male may try to prevent her from leaving but he will not follow her into an adjacent territory (Gentry 1970). These behaviors are not characteristic of elephant seals or phocids in general. If the females shift their location, elephant seal males follow them. The location of a male in a harem is not fixed and inflexible as it would be in a territorial system. Rather it is determined by the location of males dominant to him (Bartholomew 1952).

In summary, it is becoming clear that no single behavioral pattern exists among the social and reproductive organizations of the polygynous pinnipeds. In the annual

establishment of breeding colonies males and females of all sizes and ages interact. Interactions are mainly sexual and agonistic in character and a great variety of behavioral elements are involved. In these polygynous species fighting among males determines access to females. Consequently, through agonistic interactions, dominance relations and reproductive roles are established among individuals and a non - random social structure is created with non - random mating as a result (Gentry 1970; Sandegren 1970).

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