

A review of social recognition in pinnipeds

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Abstract

A substantial amount of research has been carried out on recognition behaviour in natural populations of pinnipeds. This work includes detailed anecdotal and quantitative descriptions in addition to *in situ* experimental tests of recognition. The goals of this review are to summarize this research, and by doing so, to point out apparent patterns of social recognition among the pinnipeds, as well as important gaps in our knowledge. Following an introduction of the topic, the review is divided into three sections: (1) descriptive evidence, (2) experimental evidence, and (3) patterns of recognition in pinnipeds resulting from phylogenetic, ecological and life history constraints. The descriptive evidence mostly pertains to recognition between mother and offspring and includes vocal stereotypy, the use of other sensory modalities, and cases of adoption and allo-suckling. Further descriptive data include recognition among territorial males and between species. The experimental evidence is also weighted heavily towards tests of mother-offspring recognition. Recognition between pinniped mothers and pups, in at least one direction (i.e., mother recognizes pup or pup recognizes mother), has been experimentally demonstrated in seven pinniped species (4 otariids and 3 phocids), but is not the rule. Recent experiments have also been completed on recognition ontogeny and salient cues, as well as demonstrating long-term recognition. Such results provide the basis for complex social interactions among individuals. As with descriptive evidence, methodologies are an important aspect of these data. Finally, all the pinniped recognition data are synthesized with respect to the variability of intra- and interspecific pressures affecting the evolution of recognition behaviour.

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Introduction

Why study recognition behaviour?

Recognition is a fundamental and consequently ubiquitous biological process. It plays a key role in interactions among cells, among whole organisms, and ultimately in the process of evolution (Colgan, 1983; Sherman *et al.*, 1997). At the level of the organism, the rules of recognition are those that govern the process of assortment, whether between species, populations, kin, sexes, or individuals. Consequently, recognition plays a cornerstone role in all animal social interactions and thus, is central to the behavioural ecology and conservation of any animal species.

In one of the founding concepts of ethology, Von Uexküll (1934, 1957) asserted that to understand an animal one must understand its *Umwelt*: an animal's perceptual world (*Merkwelt*) and what is relevant within this world (*Wirkwelt*). An animal's social world necessarily exists within this larger perceptual framework and can be thought of as the '*social Umwelt*'; the social information that is: (1) available and (2) relevant (see also Greene, *et al.*, 2002). The resolution of conspecific identity is one of the most fundamental aspects of social information. Thus, to understand animal social interactions, we must have at least some notion as to the degree to which the individuals involved recognize each other.

Ultimate vs. proximate approaches to the study of recognition

Because of the ubiquity of recognition behaviour, investigators have taken an array of approaches to its study. To make valid comparisons of these studies, it is important to distinguish between

those that take evolutionary or 'ultimate' perspectives as compared to mechanistic or 'proximate' perspectives (Holmes, 1990).

Viewing social recognition from an ultimate perspective (i.e., an evolutionary timeframe), Sherman *et al.* (1997) developed a theoretical framework based on the nature of 'objects' being discriminated. Such a framework is useful for identifying the type of selection acting on recognition behaviour. Two basic and nonexclusive categories are whether the 'objects' are potential mates or whether they are kin. Kin recognition is the necessary ingredient for nepotism, where genetic relatedness is used to explain cooperation through kin selection (Hamilton, 1964; Sherman & Holmes, 1985; Fletcher & Michener, 1987; Hepper, 1991). Recognition between parent and offspring—maternal recognition in most mammals—is a special subset of kin recognition. Among other factors, the potential for kin selection would depend on the likelihood of relatives (e.g., mother and mature offspring) encountering one another during their lives. Mate recognition, on the other hand, is the key to assortative mating and possible sympatric speciation (Otte & Endler, 1989; Grant & Grant, 2002) and to the process of sexual selection via mate choice (Bateson, 1983; Andersson, 1994). The two types of recognition overlap in the area of optimal outbreeding, that is, obtaining a balance between inbreeding and outbreeding when selecting a mate (Bateson, 1978; 1983).

In contrast to investigations of how recognition behaviour might be adaptive, studies focusing on proximate aspects of recognition are likely to be testing for its existence, the cues used, or the level of resolution achieved. The cues that animals use for recognition of conspecifics can be grouped into four general categories: spatial location, familiarity, phenotype matching, and allele/genotype matching (Bradbury & Vehrencamp, 1998). The salient sensory cues used for recognition vary considerably among taxa. Although the process is often multimodal, most studies have focused on the acoustic/auditory channel using a limited number of taxa (e.g., Beer, 1970; Falls, 1982; Colgan, 1983; Beecher, 1991; Stoddard, 1996; Bradbury & Vehrencamp, 1998). A substantial amount of research also has focused on olfactory recognition, mostly with social insects and mammals (Halpin, 1980; Duvall *et al.*, 1986; Johnston *et al.*, 1999). In comparison, there has been considerably less research on electrical and visual recognition, and very little in the area of cross-modal comparisons of recognition (Partan & Marler, 1999; Rybak *et al.*, 2002).

Different organisms are capable of different degrees of recognition, referred to here as recognition resolution. These capabilities can be viewed

comparatively across taxa or from the perspective of an individual animal. For example, the existence of individual recognition, as compared to resolution of groups (e.g., castes of social insects, breeding colonies, etc.) or species, appears to be mostly limited to birds and mammals (Colgan, 1983). Individual recognition in the strictest sense can be defined as the ability to discriminate each individual in a group from every other individual (Beecher, 1989). A more functional definition of individual recognition is the differential treatment of an individual by other individuals based on individually distinctive cues (Beecher *et al.*, 1989). Individual recognition capabilities can be further thought of in terms of lateral and longitudinal resolution. Lateral resolution refers to the number of individuals one is able to resolve at a given point in time (e.g., immediate kin, more distant kin, cohort members, etc.; Rendall *et al.*, 1996). Longitudinal resolution refers to the durability of recognition over time (e.g., how long it lasts; Godard, 1991; Insley, 2000).

In sum, by understanding how recognition operates in any given species (e.g., modal bias and resolution) it becomes possible to isolate the parts of the system that selection processes act upon. We can then place the parts of the system into their functional contexts with the appropriate selective forces (e.g., kin or sexual selection, etc.) and attempt to measure the fitness benefits to the individual animal. This approach, with some luck, should provide a clearer perspective of how recognition behaviour is shaped.

Pinnipeds as a focal group

Pinnipeds (seals, sea lions, fur seals and walrus) have proven to be an excellent group for comparative studies of recognition. All species occupy either land or ice during parturition (King, 1983; Riedman, 1990; Trillmich, 1996) and during these periods detailed observations and even complex experimental procedures (e.g., vocal playbacks) are possible. The phylogenetic relationships among sister taxa within the pinniped group are reasonably well established (e.g., Berta & Wyss, 1994; Rice, 1998; Bininda-Emonds *et al.*, 1999; Wynen *et al.*, 2001; Heyning & Lento, 2002; Hoelzel *et al.*, 2002), and these relationships present numerous possibilities for comparative investigations of recognition. Many pinnipeds are exceptionally vocal in air and under water, and consequently, most evidence for social recognition is derived from studies of vocal communication (Tyack & Miller, 2002). The prevalence and importance of optical signalling in many pinnipeds, as well as their well-developed visual acuity, suggests that visual signalling also may be important (Schusterman, 1972, 1981; Miller, 1975a, 1991). Tactile abilities via facial vibrissae are extremely well developed (Renouf,

1991; Dehnhardt *et al.*, 2001), but the importance of this sense in recognition is unknown. Olfaction in pinnipeds, as with most mammals, appears to be well developed for use in air although its functional role in recognition and other aspects of communication essentially is untested (Miller, 1991; Dehnhardt, 2002).

A substantial amount of research has now been carried out that pertains to recognition behaviour in natural populations of pinnipeds. This work includes detailed anecdotal and quantitative descriptions in addition to experimental tests of recognition behaviour in natural populations. The goals of this review are to summarize this research, and by doing so, to point out apparent patterns of social recognition behaviour among the pinnipeds, as well as important gaps in our knowledge.

Descriptive Evidence

The ability of individuals to recognize each other has been documented since the earliest descriptions of pinniped behaviour. For example, Bryant (1870) noted that the northern fur seal mother 'manifests a strong attachment for her own young, and distinguishes its cry among thousands'.

Recognition between mother and pup

The most obvious and well-documented evidence of recognition in the pinnipeds is between a lactating mother and her dependent pup, particularly in otariid species. Anecdotal descriptions of reunion behaviour in sea lions and fur seals suggest that mothers and pups are able to recognize each other using a combination of vocal and olfactory cues, with spatial and visual cues assisting in localizing individuals (sea lions: Peterson & Bartholomew, 1969; Sandegren, 1970; Stirling, 1972; Marlow, 1975; Trillmich, 1981; and fur seals: Bartholomew, 1959; Paulian, 1964; Rand, 1967; Bonner, 1968; Stirling, 1970; McNab & Crawley, 1975; Trillmich, 1981). Despite the high quality of many of these anecdotal descriptions, quantitative accounts of mother-pup reunion behaviour are few (e.g., Gisiner & Schusterman, 1991; Insley, 2001; Dobson & Jouventin, 2003; Phillips, 2003) and needed for most pinniped species.

Most descriptive mother-pup recognition studies in pinnipeds focus on the individual distinctiveness (i.e., stereotypy) of calls used between the pair. Below, we first examine vocal stereotypy in mother and pup calling behaviour. Next, we look at the existing data on the use of other sensory modalities in pinniped mother-pup recognition. Finally, we briefly review the descriptions of adoptive and allo-suckling behaviour of pinnipeds in light of recognition errors.

Vocal stereotypy of mothers and pups—A stereotypic signal is an important aspect of vocal recognition. Vocal stereotypy between mother-pup pairs has been examined, at least to some extent, in four of five sea lion, seven of nine fur seal, four of 19 seal species, and the one extant walrus species. This information is summarized in Table 1a. Diagrammatic and specific examples of vocal stereotypy are given in Figures 1 and 2. Figure 3 shows examples of the variability of breeding densities among different pinniped species, a factor likely directly related to recognition abilities.

The affiliative vocalizations used between otariid mothers and pups show individual stereotypy in all species that have been examined (Table 1a). This finding matches the expectedly high selective pressure acting on recognition behaviour in otariids consistent with their characteristic mating and maternal strategies (Insley, 1992; Trillmich, 1996). Specifically, all otariids breed in dense colonies and have relatively long periods (i.e., 4–24 months) of neonatal dependence (Riedman, 1990; Boness, *et al.*, 2002). In addition, all otariids forage throughout lactation (i.e., 'income' breeders; Bowen, 1991; Bowen *et al.*, 2002) and, as a result, must regularly relocate their offspring. The particular acoustic features that appear to be the most reliable indicators of identity generally are related to the fundamental frequency and to formant-like or 'peak' frequencies of the vocalizations (Fig. 1; Insley, 1992; Phillips & Stirling, 2000; Campbell *et al.*, 2002; Charrier *et al.*, 2002a; Page *et al.*, 2002a).

In comparison to otariids, phocid mothers and pups generally show more variability in their maternal and breeding strategies (Trillmich, 1996), and similarly, more variability in the stereotypy of their affiliative vocalizations (Insley, 1992; Table 1a). In many phocid species, mothers tend to vocalize infrequently to their pups and therefore, do not exhibit call stereotypy. In colonially breeding phocid species, such as elephant seals and grey seals, pups have individualistic calls and mothers reject strange pups most of the time, although adoption or allo-suckling (see next section) is not uncommon in either species (elephant seals: Bartholomew & Collias, 1962; Le Boeuf *et al.*, 1972; Riedman & Le Boeuf, 1982; and grey seals: Fogden, 1971; McCulloch *et al.*, 1999; McCulloch & Boness, 2000). Harbour seals are more dispersed within colonies and pups often accompany mothers on foraging trips from birth; mothers appear to be able to recognize their pups based on individualistic calls (Wilson, 1974; Renouf *et al.*, 1983; Renouf, 1984). Although Hawaiian monk seals breed in relatively close proximity to other seals and pups have individualistic vocalizations, mothers do not appear to be able to recognize their own pups, and nurse pups indiscriminately (Boness, 1990; Job *et al.*, 1995). In

Table 1. Summary of pinniped species for which vocal individuality (i.e., stereotypy) has been quantified. Note that although the degree of individual stereotypy varies among the pinniped species, it has been demonstrated in all species of pinnipeds examined.

Species	Common name	Individualistic vocalization tested	References
(a) Mother and pup calls			
<i>Callorhinus ursinus</i>	Northern fur seal	mother+pup calls	Lisitsina, 1973 ^a ; Takemura <i>et al.</i> , 1983 ^a ; Insley, 1992
<i>Arctocephalus gazella</i>	Antarctic fur seal	mother+pup calls	Stirling & Warneke, 1971 ^a ; Page <i>et al.</i> , 2002a
<i>Arctocephalus pusillus</i>	Australian fur seal	mother+pup calls	Stirling & Warneke, 1971 ^a
<i>Arctocephalus galapagoensis</i>	Galapagos fur seal	mother+pup calls	Trillmich, 1981
<i>Arctocephalus forsteri</i>	New Zealand fur seal	mother+pup calls	Stirling, 1970 ^a , 1971b ^a ; Stirling & Warneke, 1971 ^a ; Page <i>et al.</i> , 2002a
<i>Arctocephalus australis</i>	South American fur seal	mother+pup calls	Phillips & Stirling, 2000;
<i>Arctocephalus tropicalis</i>	Subantarctic fur seal	mother+pup calls	Roux & Jouventin, 1987; Charrier <i>et al.</i> , 2003; Page <i>et al.</i> , 2002a; Charrier <i>et al.</i> 2002a;
<i>Zalophus californianus</i>	California sea lion	pup calls	Schusterman <i>et al.</i> , 1992
<i>Zalophus wollebaeki</i>	Galapagos sea lion	mother+pup calls	Trillmich, 1981
<i>Otaria byronia</i>	S. American sea lion	mother+pup calls	Fernández-Juricic <i>et al.</i> , 1999
<i>Eumatopias jubatus</i>	Steller sea lion	mother calls	Campbell <i>et al.</i> , 2002
<i>Mirounga angustirostris</i>	Northern elephant seal	mother+pup calls	Insley, 1992
<i>Halichoerus grypus</i>	Grey seal	pup calls	Caudron <i>et al.</i> , 1998; McCulloch <i>et al.</i> , 1999
<i>Phoca vitulina</i>	Harbour seal	pup calls	Renouf, 1984; Perry & Renouf, 1988
<i>Monachus schauinslandi</i>	Hawaiian monk seal	pup calls	Job <i>et al.</i> , 1995
<i>Odobenus rosmarus</i>	Walrus	pup barks	Kibal'chich & Lisitsina, 1979 ^a ; Miller, 1985 ^a ; Kastelein <i>et al.</i> , 1995 ^a
(b) Adult male calls			
<i>Callorhinus ursinus</i>	Northern fur seal	roars	Antonelis & York, 1985
<i>Arctocephalus forsteri</i>	New Zealand fur seal	full threat calls ^a	Stirling, 1971a
<i>Arctocephalus australis</i>	South American fur seal	full threat calls ^a	Phillips & Stirling, 2001
<i>Arctocephalus tropicalis</i>	Subantarctic fur seal	full threat calls	Roux & Jouventin, 1987
<i>Otaria byronia</i>	South American sea lion	high-pitched calls, barks	Fernandez-Juricic <i>et al.</i> , 1999
<i>Mirounga angustirostris</i>	Northern elephant seal	clap-threat calls	Shipley <i>et al.</i> , 1981
<i>Mirounga leonina</i>	Southern elephant seal	aggressive calls	Sanvito & Galimberti, 2000a,b
<i>Phoca vitulina</i>	Harbour seal	roars	Hanggi & Schusterman, 1994; Van Parijs <i>et al.</i> , 2000
<i>Hydrurga leptonyx</i>	Leopard seal	Underwater call sequences (trills)	Rogers & Cato, 2002
<i>Odobenus rosmarus</i>	Walrus	diving vocalization, surface codas	Stirling <i>et al.</i> , 1987

^aAcoustic features in calls measured and presented, but no statistics performed.

ice-breeding seals, such as harp seals, pups typically are stationary and well dispersed on fast ice, such that vocal recognition is likely less important than spatial and olfactory cues (Terhune *et al.*, 1979; Kovacs, 1987, 1995). The hooded seal, with its incredibly brief lactation period (4 days), has little opportunity for mothers and pups to become separated, and there is no evidence that mothers can

recognize pups (Perry & Stenson, 1992; Ballard & Kovacs, 1995).

Walrus mothers and calves associate closely with each other for 2–3 years and calves regularly follow their mothers closely and reunite with them after associating with other juveniles. Observations of behaviour and analysis of vocalizations, although not statistical, suggest that pups, at least, appear to

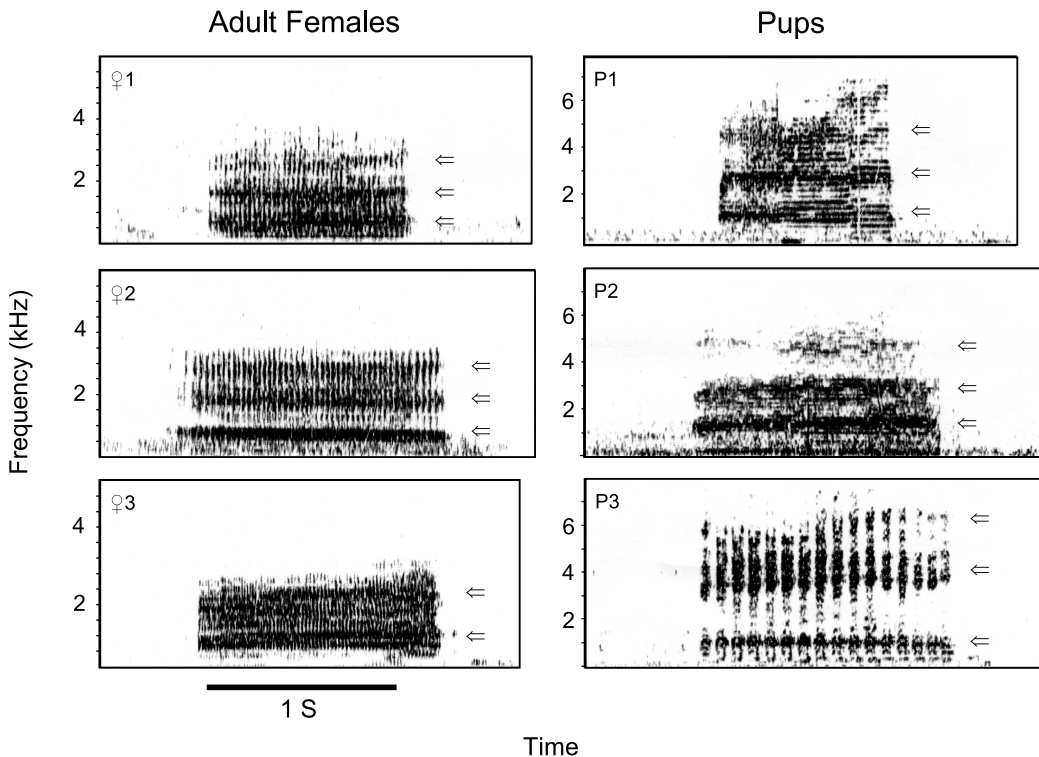


Figure 1. Example sound spectrograms of contact (aka ‘attraction’) calls from three different adult female and pup northern fur seals illustrating the individual distinctiveness inherent in many pinniped contact vocalizations. Note the frequency emphasized portions or ‘formant-like’ frequencies (approximate centre frequencies indicated with arrows).

have individualistic vocalizations and that mother–offspring recognition may be well developed (Kibal’chich & Lisitsina, 1979; Miller & Boness, 1983; Miller, 1985; Kastelein *et al.*, 1995; Sjare & Stirling, in this issue).

Use of other sensory modalities in mother–pup recognition—Most studies of mother–pup behaviour in pinnipeds have mentioned that they appear to use a combination of olfactory, visual, and geographical cues to facilitate reunion and recognition. However, no research has systematically addressed the relative contribution of the different modalities during the process of recognition.

In every species described, mothers make naso–nasal investigations of pups and appear to accept or reject pups using olfactory cues (e.g., Peterson & Bartholomew, 1967; Burton *et al.*, 1975; McCann, 1982; Kovacs, 1995). These observations suggest that olfactory recognition plays a crucial role in the reunion process. The presence of a well-developed vomero–nasal organ in pinnipeds, possibly functional for recognition purposes, is suspected, but has yet to be shown (Dehnhardt, 2002). Unfortu-

nately, experimental evidence of chemical recognition is lacking, as are histological research of chemical pathways and descriptions of the substances used.

Visual cues appear to play an important role in the sequence of behaviours leading to reunion between a mother and pup; however, these cues seem more likely to be priming and localizing devices rather than individual identifiers. For example, the stereotypical searching posture of female otariids, the shiny, dark pelage of wet females returning from the sea (see Fig. 3d), the purposeful movement of mothers and pups within the colony in response to vocalizations, and head-shaking while calling, are all important cues for localizing and orienting to searching individuals (Stirling, 1970; Terhune *et al.*, 1979; Miller, 1991; Kovacs, 1995; Insley, 2001; Phillips & Stirling, 2001; Phillips, 2003). Individuality of physical appearance may be expressed in external features such as size, shape, pelage patterns and facial characteristics (Stutz, 1967; Miller, 1975a; Kelly, 1981; Miller, 1991) and most pinnipeds have adequate visual acuity in air to distinguish optical

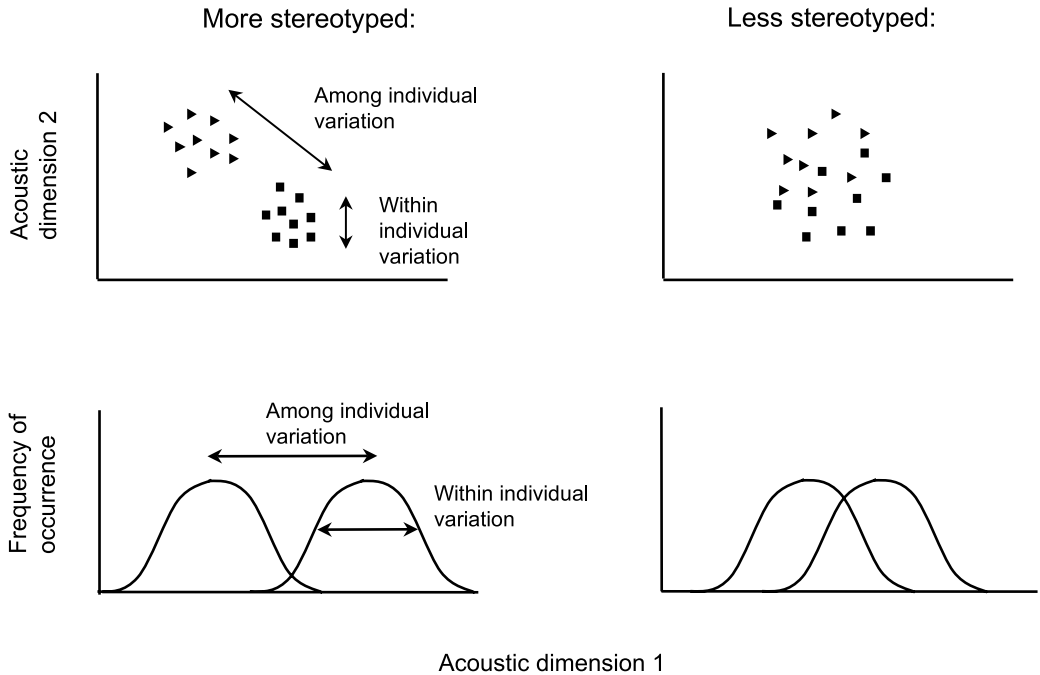


Figure 2. Signal stereotypy, or distinctiveness, is a key aspect of recognition and is essentially the relationship between the signal variation within and between individuals. This can be illustrated using bivariate (upper panels) or frequency (lower panel) plots. The variables, labelled Acoustic Dimension 1 and 2 here, could be a single feature (e.g., call duration) in the simplest case, or a composite variable (e.g., multiple features combined as in Principle Components Analyses) in more complex cases.

patterns at short distances (Schusterman, 1972, 1981; Renouf, 1991; Dehnhardt, 2002). However, currently there is no experimental evidence that visual cues play a role in the recognition of individual mothers and pups.

In many pinniped species, spatial or geographical cues have been implicated in both reunion and recognition between mothers and pups. Small-scale site fidelity, or the repeatable preference of mothers for a particular location within a breeding colony, is widespread among pinnipeds. In the ice-breeding phocids, in which pups generally do not move far from their birth site, geographic location is a primary cue for reunion, as mothers orient to a particular breathing hole or ice lead to reunite with their pups (Tedman & Bryden, 1979; Terhune *et al.*, 1979; Kovacs, 1995). In pinnipeds in which mothers and pups are regularly separated, such as otariids and grey seals, studies have demonstrated that mothers consistently return to the spot where they last suckled, or to a particular feature such as a boulder, tidepool or mound of tussock grass to suckle their pups, and these locations are often defended from other females (e.g., Bartholomew, 1959; Sandegren, 1970; Fogden, 1971; McNab & Crawley, 1975; Boness & James, 1979; Trillmich,

1981; Lunn & Boyd, 1991; Pomeroy *et al.*, 1994; Phillips, 2003). Natal site fidelity increases the probability of mothers and pups encountering one another within a season while pups are still dependent, and also in future years when the pup is grown. Future encounters provide the opportunity for co-operation through nepotism if there is long-term recognition (Hanggi & Schusterman, 1990; Insley, 2000).

Adoption and allo-suckling as a potential indicator of recognition errors—Mother–pup recognition appears to be widespread in the pinnipeds, yet numerous incidences of adoption, fostering or allo-suckling (i.e., females nursing non-filial pups in addition to or in replacement of their own pup) have been described (summarized in Stirling, 1975; Riedman & Le Boeuf, 1982; Bowen, 1991). These behaviours are suggestive of errors in or lack of recognition between a mother and her pup. However, because adoptive behaviours may serve adaptive functions that are independent of recognition abilities (e.g., Roulin, 2002; 2003), it cannot be considered conclusive evidence of recognition errors. These potential benefits include both behavioural and physiological aspects of allo-suckling



Figure 3. Examples of variation in breeding densities among different pinniped species, a factor that likely plays a strong role in selection for recognition: (A) low density: monk seals on Spit Islet, Midway Atoll; (B) medium density: grey seals on Sable Island, Nova Scotia; high density: (C and D) wide angle and close up respectively of northern fur seals on the Pribilof Islands, Alaska. (Photo A by Leona Laniawe, National Marine Fisheries Service, B by Daryl Boness, Smithsonian Institution, and C and D by SJI).

using both proximate and ultimate explanations (e.g., indirect fitness benefits realized through nepotism, reciprocal altruism, maternal experience, milk evacuation, and prolactin stimulation). Ultimately, lack of recognition is difficult to demonstrate conclusively because of the problem of motivation.

Although adoption and allo-suckling cannot be conclusively tied to a lack of recognition, its occurrence does correlate with the expected patterns of recognition abilities. That is, adoptive and allo-suckling appears to be rare among the otariids where mother–pup recognition appears to be better developed. Adoptive behaviour is most common in phocids, especially in Hawaiian monk seals, elephant seals and grey seals; species in which mothers and pups frequently are separated, but where mother–pup recognition may not be well developed, as evidenced by their lack of vocal

stereotypy and also by playback experiments (Klopfer & Gilbert, 1966; Fogden, 1971; Eley, 1978; Fay, 1982; Riedman & Le Boeuf, 1982; Boness, 1990; Job *et al.*, 1995; McCulloch *et al.*, 1999). Less commonly, adoption has been observed in the ice-breeding Weddell seals and spotted seals (*Phoca largha*; Burns *et al.*, 1972; Kaufman *et al.*, 1975), but these instances were likely related to disruption of the mother–pup bond by human-related disturbances (Stirling, 1975; see also Fogden, 1971). In harbour seals and otariids, adoption has been documented on rare occasions and although the proximate cause likely is recognition error on the part of the mother, allo-suckling in these species ultimately may be a consequence of environmental conditions and/or maternal inexperience (Bowen, 1991; Boness *et al.*, 1992; Lunn, 1992; Georges *et al.*, 1999). Finally, there are some accounts of potential

adoptions and allo-suckling in Pacific walruses (Fay, 1982; Eley, 1978), although these accounts have not been substantiated.

A similar behaviour, 'milk-thieving', refers to suckling by pups on unrelated females that either remain unaware of the nursing bouts or reject the non-filial pup as soon as it is discovered. This situation is more likely to represent milk supplementation by nutritionally stressed pups, rather than recognition errors (Roux, 1986; Lunn, 1992).

Recognition among territorial males

In most pinniped species, males exhibit a complex repertoire of threat calls, many of which are graded and vary both in acoustic structure and apparent meaning (Stirling & Warneke, 1971; Miller, 1991; Phillips & Stirling, 2001). Of these, the calls that appear to convey the highest level of intensity or threat (variously named roars, full threat calls, clap threats, etc.) are associated with formalized visual display behaviour and tend to be individualistic, particularly in the colonially breeding otariids and elephant seals (Bartholomew & Collias, 1962; Stirling, 1971*a*; Miller, 1975*a*, 1991; Table 1*b*). It is not known whether stereotypy in adult male calls is functional, and if so, what the primary selective pressures may be.

Call stereotypy in male pinnipeds may function in male–male competition (i.e., neighbour–stranger discrimination) and/or in mate choice. The ability of males to recognize one another has obvious importance in dominance relationships and territorial display behaviour in elephant seals (Bartholomew & Collias, 1962; McCann, 1981; Shipley *et al.*, 1981) and many otariid pinnipeds (Peterson & Bartholomew, 1969; Miller, 1975*b*; Stirling, 1971*a*; Stirling & Warneke, 1971; Roux & Jouventin, 1987). Anecdotal evidence suggests that territorial males of some species respond differentially to neighbours than non-neighbours, by decreasing the rate of threat calls used to familiar (i.e., recognized) males (Bartholomew & Collias, 1962; Gentry, 1975; McCann, 1980; Gisiner, 1985; Fernández-Juricic *et al.*, 2001).

When territorial males have individualistic vocalizations that are used frequently in male–male competition, the potential arises for females to discriminate among males for mate choice. Although no studies have shown that females can recognize individual males, some circumstantial evidence has been documented. First, females of most species have the neural capacity to recognize individualistic vocalizations, as evidenced by mother–pup recognition. Second, female choice has been implicated by molecular genetic studies of grey seals and fur seals (Amos *et al.*, 1995; Goldsworthy *et al.*, 1999; Gemmell *et al.*, 2001) and by behavioural observations of South American fur seals (Majluf

et al., 1996). Finally, male harbour seals, walrus, and most ice-breeding phocids engage in complex underwater vocal (and visual) displays that might act as advertisements of individual fitness for females (Thomas & Kuechle, 1982; Stirling *et al.*, 1987; Cleator *et al.*, 1989; Ballard & Kovacs, 1995; Rogers *et al.*, 1996; Sjare & Stirling, 1996; Van Parijs *et al.*, 2000). At present, the role of male vocalizations in mate recognition and mate choice remains to be directly tested.

Species recognition

Although some species of pinnipeds occur sympatrically, the breeding systems of overlapping species usually are distinct enough that recognition of species to avoid interspecific mating is not necessary. However, at Macquarie Island, post-sealing recolonization has resulted in sympatric populations of Antarctic, Subantarctic and New Zealand fur seals that breed in mixed species territories, mate interspecifically and produce hybrids (Goldsworthy, *et al.*, 1999). Similarly, at Marion Island, Antarctic and Subantarctic fur seals breed in separate colonies, but females of each species mate and produce hybrids with males of the other species (Kerley, 1983). Despite what appears to be recognition errors, females in both situations apparently are able to assess the species identity of males (Goldsworthy *et al.*, 1999). Page *et al.* (2002*b*) and St. Clair Hill *et al.* (2001) found that males of the above three fur seal species all produce 'barks' that exhibit species-specific differences. Most male otariids have a bark-like vocal signal that is typically used in male–female interactions, particularly during investigations of female sexual receptivity (Stirling & Warneke, 1971; Miller, 1991; Phillips & Stirling, 2001). It is therefore possible that this class of vocal signal ('bark calls') is the subject of sexual selection via female mate choice (Page *et al.*, 2002*b*).

By extension, recognition of hybrid individuals in areas of interspecific breeding also is important for mate choice, since hybrids may have depressed fitness. At both Macquarie Island and Marion Island, the acoustic characteristics of vocalizations—and the pelage patterns—of hybrid animals are intermediate to those of their parental species (Goldsworthy *et al.*, 1999; Page *et al.*, 2001; St. Clair Hill *et al.*, 2001). Whether these cues affect the breeding success of hybrids is unknown.

Studies of hybrids also provide an opportunity to examine heritability of individualistic traits, such as vocalizations. At the species level, at least some aspects of the call structure of hybrid fur seals appear to be genetically inherited, as hybrid calls exhibit acoustic characteristics distinctive to both parental species (Page *et al.*, 2001; St. Clair Hill *et al.*, 2001). However, within a species, South American fur seal pup calls did not resemble those

of their mothers (Phillips, 1998). These findings provide mixed evidence with regard to phenotypic matching as a mechanism for kin recognition. Further investigations into the genetic basis of inheritance of call structure would also be valuable to determine the relative contributions of parents vs. species to vocal individuality.

Methodological considerations

There are three main methodological issues that need to be mentioned in our efforts to quantify and compare the cues used for pinniped recognition behaviour. Our recommendations relating to standardization of nomenclature, choice of measurement variables, and statistical analyses are briefly noted as follows.

First, in general, efforts must be made to standardize the nomenclature of visual and vocal cues to enable cross-species comparisons (Miller, 1991; Miller & Job, 1992; Phillips & Stirling, 2001). Investigators should attempt to use descriptive, as compared to interpretive, labels whenever possible (Martin & Bateson, 1993). Call descriptions should also, whenever possible, include the degree to which call categories are discrete or graded. This practice throughout the animal acoustic communication literature would avoid unnecessary new categories being created from variants of existing categories. Finally, if new labels are adopted in place of existing labels, the originals should always be referred to in the methodology.

Second, the choice of measurement variables is especially important for results to be meaningful and comparable. These choices often are dictated by the available methodology and, to date, have mostly concerned acoustical analyses of vocal data. There are numerous pitfalls to be avoided in acoustic measurement (far beyond the scope of this review) and investigators should make themselves familiar with the available literature in this area (e.g., Hopp *et al.*, 1998). For example, care should be taken to measure acoustic features that are biologically relevant (e.g., 'highest harmonic', a commonly measured characteristic, is a function of analyzing bandwidth, sampling rate and attenuation with distance) and that do not vary under the influence of external factors (e.g., maximum frequency) unless the external factors are carefully recorded and reported. Also, calls that are presented in bouts or series should not be treated as independent from each other in subsequent analyses. A full reporting of analysis methodology is always essential if the data are to be useful for comparisons.

Third, related to the choice of measurement variable, is the choice of statistical analyses. Until very recently, most statistical analyses of vocal

individuality in pinnipeds have used multivariate approaches such as ANOVA, DFA and PCA, which have limitations relating to sample size and assumptions of normality. These methods also rely heavily on the researcher's ability to decide which variables are useful for detecting individuality (Janik, 1999; Terry *et al.*, 2001). Newer and potentially more objective classification techniques such as neural networks (Campbell *et al.*, 2002) and nonlinear analysis (Tokuda *et al.*, 2002) should be explored further, particularly in their application to the characteristically noisy or complex calls of pinnipeds.

For future studies, the advent of more automated detection and classification techniques should allow broader comparisons across taxa. However, as a technique becomes increasingly automated, the analysis decisions for each technique often become less apparent and more important to report. Similarly, it is increasingly important to report the limitations of the different techniques. For example, the prediction coefficients of DFA and neural net mathematical models remain a function of sample size, thus the coefficient alone is not necessarily a meaningful statistic. Finally, it is particularly important that future studies in this area make their work comparable to previous investigations. The investigations of vocal stereotypy provide a good example. Whether or not a class of animals has stereotyped calls alone is not particularly meaningful (refer to Table 1; every pinniped measured to date has stereotyped calls). Instead, among the most important aspects of descriptive studies of vocal stereotypy are the relative degrees of stereotypy among species. Making one's data comparable does not imply using dated technology for future studies, but simply keeping comparative issues, standing hypotheses and previous data in mind.

Experimental Evidence

Experimentally testing for recognition

Quantitative acoustic analyses have demonstrated call individuality for mothers, pups and adult males in a number of species (see Table 1). The presence of vocal stereotypy, however, is not sufficient to show that social recognition occurs in any of the pinniped species, nor how, or to what degree, recognition is achieved. Testing for the expression of recognition behaviour, not merely its potential, allows assessment of the complexity of pinniped social systems, as well as understanding how such a trait evolves.

Experiments using vocal playbacks in natural settings have now been carried out on four otariid and three phocid species of pinnipeds. The results of these experiments are summarized in Table 2.

Table 2. Summary of experimental playback studies of individual vocal recognition in pinnipeds.

Species	Common name	Type of recognition tested	Finding	References
(a) Otariidae				
<i>Arctocephalus galapagoensis</i>	Galapagos fur seal	Mother by pup	Present	Trillmich, 1981
<i>Arctocephalus tropicalis</i>	Subantarctic fur seal	Mutual mother–pup	Present	Roux & Jouventin, 1987; Charrier <i>et al.</i> , 2001, 2002a
<i>Arctocephalus tropicalis</i>	Subantarctic fur seal	Male–male (neighbour)	Present	Roux & Jouventin, 1987
<i>Callorhinus ursinus</i>	Northern fur seal	Mutual mother–pup	Present	Insley, 2000, 2001
<i>Zalophus californianus</i>	California sea lion	Mother by pup	Present ¹	Hanggi, 1992
<i>Zalophus wollebaeki</i>	Galapagos sea lion	Mother by pup	Present	Trillmich, 1981
(b) Phocidae				
<i>Halichoerus grypus</i>	Grey seal	Pup by mother	Absent ² Present ³	McCulloch <i>et al.</i> , 1999 McCulloch & Boness, 2000
<i>Mirounga angustirostris</i>	Northern elephant seal	Pup by mother	Present	Petrinovich, 1974
<i>Monachus schauinslandi</i>	Hawaiian monk seal	Pup by mother	Absent	Job <i>et al.</i> , 1995
<i>Phoca vitulina</i>	Harbour seal	Pup by mother	Present	Renouf, 1985

¹Captive study. ²Island of May, Scotland. ³Sable Island, Nova Scotia, Canada.

The primary focus of each study was vocal recognition between mothers and their pups. Mother–pup recognition appears to be consistently present in all otariids and more variable among phocids. Although apparent bi-directional ('mutual') mother–pup recognition is widely observed in otariids (Trillmich, 1981; Gisiner & Schusterman, 1991), it has been experimentally demonstrated in only two species, the Subantarctic fur seal (Roux & Jouventin, 1987) and the northern fur seal (Insley, 2000, 2001).

Tests of individual vocal recognition between neighbouring territorial males (i.e., neighbour–stranger recognition; Falls, 1982; Stoddard, 1996) are needed for pinnipeds. Despite the apparent existence of this form of recognition (e.g., the New Zealand fur seal; Stirling, 1971a; Gisiner, 1985), experiments have only been conducted on two species, the Subantarctic fur seal (Roux & Jouventin, 1987) and the northern fur seal (Insley, 2003). To date, there have been no tests of mate recognition in pinnipeds that we are aware of.

Recognition in pinnipeds has not yet been thoroughly tested in any sensory modality apart from the acoustic/auditory mode. Chemical cues are the modality attracting the most obvious need for attention. As noted previously, nasal investigatory behaviour appears to play a role in maternal reunions in every species of pinniped described. Furthermore, females often reject alien pups only after nasal contact (Peterson & Bartholomew, 1967; Burton *et al.*, 1975; McCann, 1982; Kovacs, 1995), suggesting that olfactory cues are a key part of the

recognition process. Although conclusive evidence of olfactory recognition does not yet exist, several *ad hoc* experiments involving the application of chemical substances have been conducted (Fogden, 1971; Kaufman *et al.*, 1975; Terhune *et al.*, 1979; Roux & Jouventin, 1987).

Ontogeny, retention and salient cues

The more complex aspects of recognition behaviour that have been experimentally tested in pinnipeds include its ontogeny, the retention of identity over time, and the salient acoustic cues used. The ontogeny of an adult female's ability to recognize her offspring immediately after parturition has not been tested. Given the rapid development of pup mobility and the frequent mother–pup vocal and nasal interactions during this period (especially in otariids; Bartholomew, 1959; all authors, pers. obs.), it is probable that recognition by mothers develops relatively quickly. (Most otariid females leave on their first foraging trip 5–10 days post-partum.) The ontogeny of recognition for pups appears to be slower. Playback experiments demonstrated that Galapagos fur seal and Galapagos sea lion pups discriminate the calls of their mothers at 10 days of age (Trillmich, 1981) and Subantarctic fur seal pups at 2–5 days of age (Charrier *et al.*, 2001). Subantarctic fur seal pups develop the ability to recognize their mothers before the female's first post-partum departure (Charrier *et al.*, 2001), suggesting that recognition, in addition to other physiological and behavioural factors (e.g., transfer

of energy, timing of oestrous, copulation) constrain the female's departure.

Despite a large body of anecdotal accounts, studies of longitudinal resolution of recognition in the wild (i.e., recognition memory) are lacking for nearly all taxa, not just pinnipeds. The exceptions are hooded warblers (*Wilsonia citrina*; Godard, 1991), African elephants (*Loxodonta africana*; McComb, *et al.*, 2000) and northern fur seals (Insley, 2000). The research on northern fur seals showed that: (1) recognition is not affected by pup development from birth to weaning, (2) mothers recognize calls of their pups from the previous season, (3) pups recognized their mother's vocalizations recorded one year earlier, and (4) 4-year-old primiparous females still recognized their mother's vocalizations despite a low probability of contact since weaning. Although long-term affiliative associations between mother and offspring have been shown in captivity (Hanggi & Schusterman, 1990; Schusterman, *et al.*, 1992), such behaviour has yet to be shown in natural populations. Subantarctic fur seal mothers also have been shown to possess the ability to discriminate their own pup's calls from birth to weaning despite considerable change in pup's call structure during this period (Charrier *et al.*, 2003, in press). These findings suggest that a form of permanent vocal/auditory imprinting occurs between mother and offspring shortly after birth, and further, demonstrates the potential for complex interactions among individuals over long time frames.

The salient features of the vocal recognition process have been experimentally investigated across a wide range of taxa (e.g., Dooling & Hulse, 1989; Aubin & Jouventin, 2002), yet very little in pinnipeds. Playback experiments of acoustically modified calls to Subantarctic fur seals indicated that mothers and pups rely on multiple features for recognition, particularly frequency modulation and the spectral distribution of energy (Charrier *et al.*, 2002a; 2003). As the evidence of salient cues is investigated more broadly across taxa it will become possible to make comparisons that address the general issues of the ecological constraints shaping vocal recognition (e.g., breeding density, foraging trip duration, breeding area topography, etc.).

Methodological considerations

The design, procedure, and interpretation of playback experiments involve numerous choices that can directly affect the results. Several of the main issues that are directly applicable to the research with pinnipeds are outlined here (see McGregor, 1992 for a more thorough treatment of this area). First, the choice of the playback design must match the problem (Falls, 1992). Most playback designs

can be broadly grouped as serial or simultaneous presentations (Fig. 4). Simultaneous presentations have been primarily used during experiments that solicit choices between two signals when the sources can be widely spaced (e.g., neighbour-stranger recognition in passerine birds or playbacks conducted in temporary holding arenas). Serial presentations are widely used when repeated presentations are required (e.g., repeated measures, interactive and habituation/dishabituation designs) and during *in situ* presentations, where widely spaced sources are not possible.

Two factors that need to be considered during playback experiments are habituation rate and pseudoreplication. Habituation rate varies widely depending upon the nature of the stimulus (e.g., alarm or contact call) and the subject (e.g., dependent neonate or experienced adult). In determining the time between playback treatments, the probabilities of habituation and contextual change must be considered (i.e., increasing time between treatments decreases the chance of habituation, but also increases the chance of contextual change). Habituation rate is also an important determinant of the time between repeated treatments (e.g., repeating the same treatment when testing for recognition ontogeny). Because of these conflicting factors, methodologies will necessarily vary among investigations, making it all the more important for researchers to detail their procedural rationales. To prevent pseudoreplication (e.g., to ensure that responses to playback tests are not due to a particular call), treatment blocks should use multiple exemplars of each call (e.g., Fig. 4; Kroodsmas, 1989; McGregor *et al.*, 1992).

Related to habituation is the misinterpretation of a lack of response to an appropriate signal (i.e., a false negative) when motivation is a factor. Charrier *et al.* (2002b) demonstrated in Subantarctic fur seals that pup responsiveness to playbacks changes in relation to the duration of their mother's absence: during days 1–5 pups respond weakly to any female calls; during days 5–9 they respond strongly and specifically to their mother's calls; and after day 11 they respond more broadly to other females. Response motivation is apparently linked to satiety state in this species and the same might be true for other pinnipeds in which mothers leave to forage during lactation.

Patterns: Phylogenetic, Ecological and Life History Constraints

Interspecific variation

Although there are still many gaps in the evidence concerning recognition in pinnipeds, some patterns are apparent. At the most basic level, there is

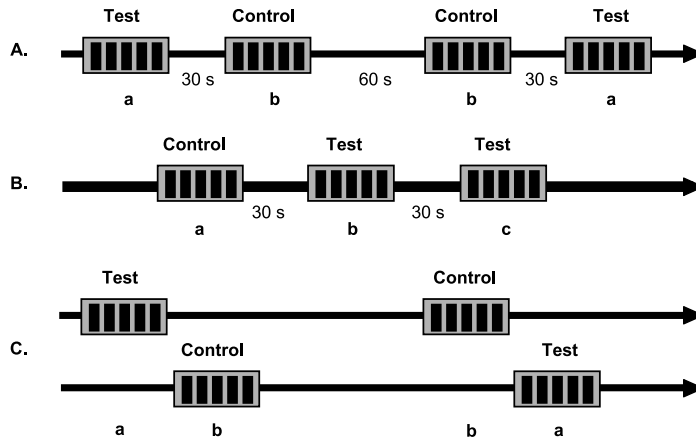


Figure 4. Schematic representation of three experimental designs for vocal playback experiments. A: a switchback serial design (a–b–b–a) used for presentation of two treatments (e.g., test and control) from a single source (e.g., one speaker). B: a repeated measures serial design (a–b–c) for presentation of more than two treatments (e.g., test1, test2 and control) from a single source (e.g., one speaker). C: a staggered simultaneous design for presentation of two treatments from two different sources. A true simultaneous design would present both treatments at the same time. For all three design types, multiple exemplars are used to avoid pseudoreplication problems. Here, vertical bars represent individual calls, in this case five different calls per treatment block. Times between treatments are variable and determined by factors such as how long reactions are sustained, the subject's habituation rate, and how quickly contexts change. In addition, for each design, the starting treatment is usually determined randomly and then alternated thereafter.

sufficient evidence to show that individual recognition, at least that between mothers and offspring, is widespread in pinnipeds (Tables 1 and 2). The evidence supporting recognition among territorial adult male neighbours (i.e., neighbour–stranger recognition) or among mates is primarily anecdotal, and although inconclusive, points to the same conclusion. The exceptions to this rule (e.g., apparent lack of maternal recognition in Hawaiian monk seals, Job *et al.*, 1995) provide clues as to the specific selective pressures driving recognition behaviour in pinnipeds. These primary factors are summarized in Table 3. As is the case during any comparison of multiple studies made over a number of years by different investigators, interpretive caution must be taken. Our intent here is to bring together the existing evidence to see what it suggests, not to be definitive in our conclusions. There is much work to be done, and in addition to filling gaps in the data, there are also many situations where revisiting a species with new techniques or increasing a previously small sample size would be of tremendous value.

The research to date also indicates that mother–pup recognition generally is better developed in otariids as compared to phocids. At present, the

evidence supporting this pattern is limited to the vocal/auditory sensory mode. Table 3 summarizes pinniped phylogenetic relationships along with the primary life history factors that are likely to affect mother–pup recognition (i.e., breeding density, the duration of the mother–offspring bond, and the likelihood of separation). There is a clear split at the family level for each of these factors. Otariids are ‘income’ breeders, regularly leaving their pups to forage throughout lactation. Phocids, in contrast, tend to be ‘capital’ breeders, mostly fasting throughout lactation and as a result normally remain close to their pups (Riedman, 1990; Trillmich, 1996; Boness *et al.*, 2002; Bowen *et al.*, 2002). Otariids also have substantially longer periods of dependence and breed in denser aggregations (on average) than phocids (Boness *et al.*, 2002). The result is a predictably more difficult recognition task for otariids compared to phocid pinnipeds and the descriptive research to date largely supports this prediction.

These patterns make both the phylogenetic position of the walrus and its relative recognition abilities of interest. Phylogenetic studies do not agree on whether walrus should be placed closer to the phocid or otariid clade, although it seems

Table 3. Pinniped phylogeny¹ resolved to genera, showing key life-history traits likely to affect mother-offspring recognition: (1) density of breeding aggregations, High, Medium or Low; (2) duration of offspring dependence in months; (3) maternal strategy, Income, Capital, or Intermediate (Bowen *et al.*, 2002); and (4) frequency of mother-pup separations, Infrequent, Frequent or Intermediate). Indirect and direct evidence for recognition includes: (1) prevalence of adoption and/or allo-suckling and (2) vocal recognition among mothers and pups). Note that the presence/absence of vocal stereotypy is not included as evidence because it has been demonstrated in all pinniped species where measured.

	<u>N Spp.</u>	<u>Density²</u>	<u>Duration of dependence (mo)²</u>	<u>Maternal Strategy</u>	<u>Separation²</u>	<u>Adoption/allo-suckling³</u>	<u>F/P Rec⁴</u>
<i>Neophoca</i>	1	H	18	Income	Freq	-	-
<i>Phocarcos</i>	1	H	6-12	Income	Freq	-	-
<i>Otaria</i>	1	H	6-12	Income	Freq	-	-
<i>Eumetopias</i>	1	H	11	Income	Freq	-	F↔P
<i>Zalophus</i>	1	H	10	Income	Freq	-	F↔P ⁵
<i>Arctocephalus</i>	8	H	4-24	Income	Freq	Rare	F↔P
<i>Callorhinus</i>	1	H	4	Income	Freq	Rare	F↔P
<i>Odobenus</i>	1	M	12-30	Income	Int	?	-
<i>Phoca</i>	7	L-M	.3-2	Capital-Int	Int	Some	F⇒P ⁶
<i>Halichoerus</i>	1	M	.5	Capital	Infreq	Reg	F⇒P
<i>Cystophora</i>	1	L	4 d	Capital	Infreq	-	-
<i>Erignathus</i>	1	L	.5	Capital	Infreq	-	-
<i>Hydrurga</i>	1	L	1?	-	-	-	-
<i>Lobodon</i>	1	L	1	-	-	-	-
<i>Leptonychotes</i>	1	M	2	Int	Int	Some	-
<i>Ommatophoca</i>	1	L?	1	-	-	-	-
<i>Mirounga</i>	2	H	1	Capital	Infreq	Reg	F⇒P ⁷
<i>Monachus</i>	2	L	1-1.5	-	-	Reg	Absent ⁸

¹Phylogeny adapted from Berta & Wyss (1994), Biniminda-Edmonds *et al.* (1999), Wynen *et al.* (2001) and Heyning & Lento (2002). Note the unresolved status of the walrus (*Odobenus*).

²After Boness *et al.* (2002), Riedman (1990).

³See text (Adoption and allo-suckling).

⁴See text (Table 2). F ⇒ P: mutual mother-pup vocal recognition. F ↔ P: vocal recognition of pup by mother.

⁵Evidence for *A. tropicalis* (Charrier *et al.*, 2001), and *A. galapagoensis* (Trillmich, 1981) only.

⁶Evidence for *P. vitulina* only (Renouf *et al.*, 1985).

⁷Evidence for *M. angustirostris* only (Petrinovich, 1974).

⁸Evidence for *M. schauinslandi* only (Job *et al.*, 1995).

likely that the split was relatively rapid and thus, difficult to resolve (e.g., Berta & Wyss, 1994; Rice, 1998; Bininda-Emonds *et al.*, 1999; Heyning & Lento, 2002; Hoelzel *et al.*, 2002). Walrus behavioural ecology suggests that mother–pup recognition is well developed. That is, they breed in dense groups, both mothers and offspring are vocal and they remain together for extended periods (Miller & Boness, 1983; Miller, 1985; Sjare & Stirling, 1996). The anecdotal reports of adoptions (Eley, 1978; Fay, 1982) are thus puzzling and may either be incorrect or indicate that adoptions are independent of recognition abilities.

Adoptive behaviour, although not alone indicative of recognition errors (Roulin, 2002; 2003), also tracks the phocid/otariid split. Adoptions and allo-suckling are regular occurrences in phocids, while appearing only incidentally among otariids (Stirling, 1975; Riedman & Le Boeuf, 1982; Bowen, 1991). One of the non-recognition related explanations for such non-offspring care is that it is a function of relatedness, presumably driven by indirect fitness benefits through kin selection. Specifically, high incidence of non-offspring care may correlate positively with relatedness among group members across populations. This possibility was directly tested in natural populations of grey seals (Perry *et al.*, 1998) and harbour seals (Schaeff *et al.*, 1999) where no relationship between relatedness and frequency of non-offspring care among different populations were found. Thus, although adoptive behaviours are not likely to be good indicators of recognition abilities across all taxa, the pattern of occurrence suggests that it may be related to recognition in pinnipeds.

The results of experimental evidence to date also support the contention that recognition is more refined in otariid pinnipeds. Playback experiments show a pattern of bi-directional (i.e., mutual) mother–pup recognition in most otariids (Trillmich, 1981; Roux & Jouventin, 1987; Insley 2001, 2002). The fact that this trait (i.e., mutual recognition) clearly is present in northern fur seals suggests that it was acquired early in the otariid lineage (see Table 3). Tests of phocids have demonstrated unidirectional recognition at most, that is, mothers recognizing their offspring, but not *visa versa*. Again, whether or not walrus show mutual mother–offspring recognition is of particular interest.

The degree of signal stereotypy is an additional means by which recognition could be enhanced (Beecher *et al.*, 1989). Although quantitative descriptions of vocalizations have demonstrated individual stereotypy in otariid and phocid pinnipeds (see Table 1), the degree of vocal stereotypy has not been broadly compared across the various pinniped species. A comparison of vocal stereotypy

between a colonial otariid and a colonial phocid (northern fur seals and northern elephant seals; Insley, 1992) showed the otariid vocalizations to be more stereotyped as per expectations. Although differences in methodology make it difficult to directly compare studies, broader comparisons are important. More automated acoustic analysis techniques may facilitate these sorts of comparisons.

An important caveat to the apparent pattern of more developed recognition in otariids compared to phocids, is that it is based solely on recognition in the acoustic/auditory modality. Clearly, pinniped communication relies substantially on non-acoustic modes, primarily olfactory, visual, and tactile modalities (see Table 1; Miller, 1991; Dehnhardt, 2002). As a result, we cannot discount the possibility of a phylogenetic split in modal preference, that is, phocids may rely more heavily on chemical cues for recognition purposes than otariids. Even if this were true, however, the more frequent occurrences of adoption and allo-suckling in phocids still support a more highly tuned discrimination ability in otariid pinnipeds.

Intraspecific variation

Selective forces on recognition also will vary intraspecifically (e.g., among the different ages and between sexes) not only interspecifically. Two theoretical constructs that are applicable to recognition behaviour, parent–offspring conflict (Trivers, 1974) and signal detection theory (see Reeve, 1989; Sherman, *et al.*, 1997; Bradbury & Vehrencamp, 1998), help explain the variation in playback results between mothers and pups (Insley, 2001). From parent–offspring conflict theory, we expect unequal selective pressures acting on mothers and pups in regards to recognition. Specifically, pups have more to lose from a failed reunion than mothers (i.e., loss of life compared to loss of one of several potential offspring). At a proximate level of explanation, such a selective asymmetry would likely show up as different abilities or different response thresholds (these are difficult to distinguish in a playback paradigm). Signal detection theory provides a constructive way of viewing the trade-off in error types when such asymmetries exist.

Figure 5 illustrates how the trade-off between false alarms (e.g., responding to a wrong pup) and misses (e.g., not responding to the right pup) is a function of the response/rejection threshold. Placement of the threshold in turn, is a function of the cost of misses (e.g., for pups, no reunion with mother) relative to false alarms (e.g., danger from a non-mother). Following the expected cost asymmetry, we would predict for many pinnipeds that misses are more costly than false alarms for pups, and further, that misses are more costly for pups than mothers. As a result, we might expect pups to

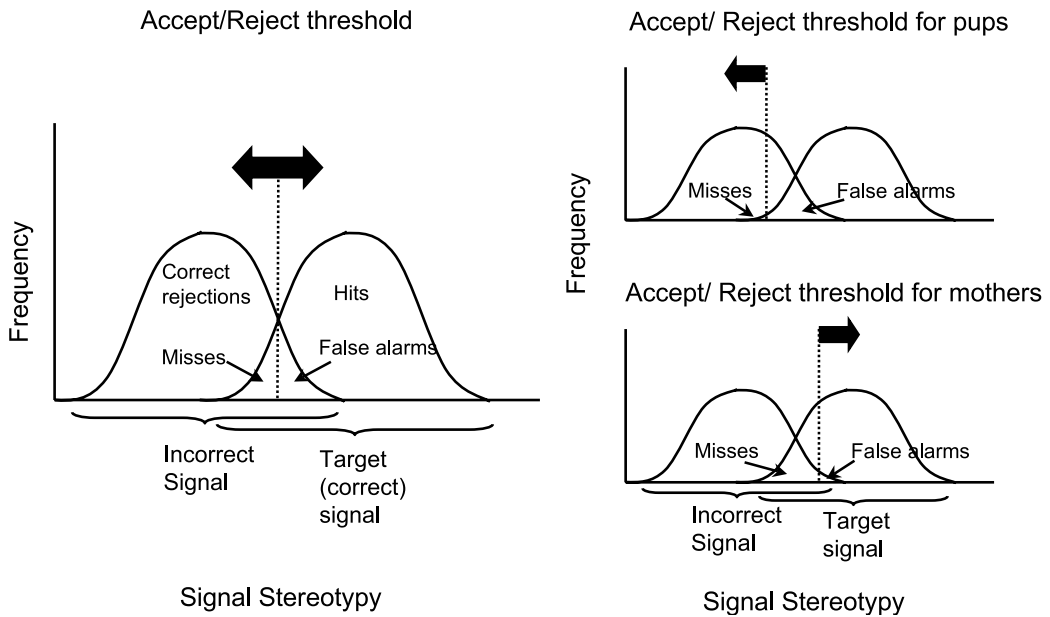


Figure 5. Illustration of how signal detection theory can be applied to animal recognition systems in order to formalize the decision rules that are part of the recognition process (see also Reeve, 1989; Sherman, *et al.*, 1997; Bradbury & Vehrencamp, 1998). Shown are two overlapping signal distributions where the amount of overlap is determined by signal stereotypy (consistent with Fig. 2). The signal on the right side of each panel is the correct or target signal and choosing it represents a hit. Similarly, not choosing the incorrect signal represents a correct rejection. The difficulty lay in the areas of signal overlap. There are two types of possible errors, misses and false alarms. A miss refers to rejecting a correct signal and false alarms refer to accepting an incorrect signal. There is a trade-off in these two types of errors, the relative amounts determined by the accept/reject threshold (dashed line with arrow). When the threshold is moved to the left, there are fewer misses but more false alarms; movement to the right results in fewer false alarms but more misses. The point is that depending on the costs and benefits of hits and misses, animals are likely to have different thresholds for accepting or rejecting a signal. Thus, if it is true that for pinniped pups, misses are likely more costly than for mothers, than pups are liable to be less discriminating (i.e., threshold optimized for minimal misses; upper right panel) than mothers (threshold optimized for minimal false alarms; lower right panel). A final cautionary consideration is that responding to an incorrect signal (i.e., a false positive) does not necessarily represent a lack of recognition.

be more liberal in their acceptance criteria than mothers, a result supported by the tests with northern fur seals (Insley, 2001). A final note, however, as in the case of a lack of response, responding to the 'wrong' stimuli (i.e., a false positive) does not equate with a lack of recognition. Although playback experiments can provide powerful positive assays for showing the existence of recognition, they are not a definitive method for showing a lack of recognition.

Summary

Although there is now a reasonable body of data on recognition abilities in pinnipeds and trends are apparent, there remain substantial gaps in our knowledge. The anecdotal and descriptive evidence strongly suggests that the different pinniped species vary tremendously in their recognition capabilities

and that multiple sensory modalities are employed. In most colonially breeding species, mothers and pups use vocal, visual, olfactory and spatial cues to relocate and reunite with each other. Although these species appear to recognize each other with individualistic vocalizations and probably scents, only vocal cues have been experimentally confirmed. Distinctive (i.e., stereotypic) vocalizations are widespread, but do not necessarily indicate individual recognition. Similar to calls of mothers and pups, some of the threat calls used by adult males are also individualistic, especially in species in which males compete for access to females in dense breeding situations. However, tests of whether or not these calls are used in neighbour-stranger, mate, or species (particularly in hybridizing species) recognition are few.

Recognition between pinniped mothers and pups, in at least one direction (i.e., mother recognizes pup

or pup recognizes mother), has been experimentally demonstrated in seven pinniped species (4 otariids and 3 phocids), but is not the rule. In some cases (i.e., northern fur seals), recognition of a parent may last multiple years, providing the basis for complex long-term social interactions. Whether or not there is an adaptive basis for long-term recognition is unknown. Mutual recognition between pinniped mothers and pups has only been demonstrated in otariids. Thus, at a gross level (i.e., taxonomic family) recognition ability appears to track phylogeny and tends to be more highly refined in otariids than in phocids. This pattern may be a secondary phenomenon, as several factors that would affect the difficulty of the recognition task (i.e., degree of coloniality, duration of dependence and the likelihood and predictability of separations due to maternal strategy) also vary at the family level. These factors tend to be more variable among the phocid species, and as expected, mother–pup recognition abilities also tend to be more variable in phocids than that demonstrated by otariids.

There are several important areas in which knowledge of recognition behaviour in the pinnipeds is sparse. Quantitative, baseline descriptions of the behaviours involved in reunion, male competition and female mate choice are needed for all species, particularly the walrus and the ice-breeding phocids for which such information is poorly known. Further investigations of these behaviours in hybridizing fur seals also are particularly important, as are studies of heritability of individualistic signals. Despite clear descriptive evidence of multiple modalities being used for recognition, essentially all evidence concerns the acoustic/auditory modality. Future studies need to quantify the use of non-vocal signals such as visual, olfactory and spatial cues, used in recognition. Studies of the salient cues used to code individual identity and recognition ontogeny need to be carried out with other pinniped species. Ultimately, interspecific comparisons of the cues used and other detailed aspects of the recognition process are necessary to understand the role of phylogenetic and ecological constraints shaping different recognition systems. All future studies, whether descriptive or experimental in nature, need to keep in mind the comparability of their data. It is through such broad comparisons that the patterns of recognition in pinnipeds will make a substantial contribution to the larger issues of recognition behaviour in all animals.

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