



HAL
open science

Mother–pup recognition mechanisms in Australia sea lion (*Neophoca cinerea*) using uni- and multi-modal approaches

Isabelle Charrier, Benjamin Pitcher, Robert Harcourt

► **To cite this version:**

Isabelle Charrier, Benjamin Pitcher, Robert Harcourt. Mother–pup recognition mechanisms in Australia sea lion (*Neophoca cinerea*) using uni- and multi-modal approaches. *Animal Cognition*, 2022, 25 (5), pp.1019-1028. 10.1007/s10071-022-01641-5 . hal-03822079

HAL Id: hal-03822079

<https://hal.science/hal-03822079v1>

Submitted on 21 Oct 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **REVIEW**

2 **Mother-pup recognition mechanisms in Australia sea lion (*Neophoca cinerea*) using uni- and**
3 **multi-modal approaches.**

4 **Isabelle Charrier^{1*}, Benjamin J. Pitcher^{2,3} and Robert G. Harcourt²**

5

6 1. Université Paris-Saclay, Université Paris-Sud, CNRS, UMR 9197, Institut des Neurosciences
7 Paris-Saclay, 91405 Orsay, France.

8 2. School of Natural Sciences, Macquarie University, Sydney, Australia

9 3. Taronga Institute of Science and Learning, Taronga Conservation Society, Sydney, NSW,
10 Australia

11 ***corresponding author: isabelle.charrier@cnr.fr**

12

13 Isabelle Charrier Orcid: 0000-0003-4873-2342

14 Robert Harcourt Orcid: 0000-0003-4666-2934

15 Benjamin Pitcher Orcid: 0000-0002-8580-0343

16 **Abstract**

17 Communication is the process by which one emitter conveys information to one or several
18 receivers to induce a response (behavioral or physiological) by the receiver. Communication
19 plays a major role in various biological functions and may involve signals and cues from
20 different sensory modalities. Traditionally, investigations of animal communication focused
21 on a single sensory modality, yet communication is often multimodal. As these different
22 processes may be quite complex and therefore difficult to disentangle, one approach is to first
23 study each sensorial modality separately. With this refined understanding of individual senses,
24 revealing how they interact becomes possible as the characteristics and properties of each
25 modality can be accounted for, making a multimodal approach feasible. Using this framework,
26 researchers undertook systematic, experimental investigations on mother-pup recognition
27 processes in a colonial pinniped species, the Australian sea lion *Neophoca cinerea*. The
28 research first assessed the abilities of mothers and pups to identify each other by their voice
29 using playback experiments. Secondly they assessed whether visual cues are used by both
30 mothers and pups to distinguish them from conspecifics, and / or whether females
31 discriminate the odor of their filial pup from those from non-filial pups. Finally, to understand
32 if the information transmitted by different sensory modalities is analyzed synergistically or if
33 there is a hierarchy among the sensory modalities, experiments were performed involving
34 different sensory cues simultaneously. These findings are discussed with regards to the active
35 space of each sensory cue, and of the potential enhancements that may arise by assessing
36 information from different modalities.

37

38 **Keywords:** communication, sensory modalities, multimodal recognition, Australian sea lion

39 Introduction

40 Animal communication is the process by which one emitter conveys information to
41 one or several receivers that elicits a response (behavioural or physiological) that is beneficial
42 to the emitter, the receiver or to both (Shannon and Weaver 1949). Communication plays a
43 major role in crucial biological functions such as parental care, mate choice, anti-predator
44 behaviour and in the regulation of social interactions (Bradbury and Vehrencamp 2011). One
45 or multiple senses can be involved in such communication: e.g. hearing, vision, touch, and
46 olfaction. The use of a particular sensory modality will mostly depend on the expected range
47 for such communication (short- or long range), intended receivers (public vs private
48 communication), the physical properties of sensory cues or signals (propagation, localization,
49 nocturnal use, persistence in the environment) and the physical structure of the environment
50 in which the information is transmitted (Alcock 1998).

51 Investigations of animal communication have traditionally focused on a single sensory
52 modality, although communication is likely to involve multiple modalities (Partan and Marler
53 2005; Partan et al. 2013; Starnberger et al. 2014). As these processes can be complex and
54 therefore it is difficult to disentangle the relative importance of each sensory modality, a first
55 step is to study each sensory modality separately. With a refined understanding of individual
56 senses, it is then possible to examine interactions between modalities while accounting for
57 the characteristics and properties of each modality.

58 Signals or cues? In the literature, the difference between cues and signals is linked to
59 their origin (Bradbury and Vehrencamp 2011). Signals have evolved for the purpose of
60 communication, whereas cues can provide information on the emitter but they have not
61 specifically evolved to transmit such information. Information provided by cues are the result of a

62 by-product of inherent anatomical characteristics to the emitter ([Bradbury and Vehrencamp](#)
63 [2011](#)). In regards to Australian sea lions, vocalizations are clearly signals that have evolved for
64 communication purposes and they transmit information about the emitter to the receiver. For
65 olfactory information, it is difficult to conclude on their origin and thus if they have evolved to
66 transmit information or they are a by-product of the animals' physiology and microbiota.
67 Olfactory information can be either a signal or a cue. Visual information described in our
68 review are related to the color of the pelage, so it can be clearly defined as a cue. Since all
69 signals are cues, but all cues are not signals, to facilitate the discussion in a multimodal
70 context, we will use the term "cues" throughout this review.

71 The information obtained by a receiver from multimodal cues is likely to be greater
72 than from a unimodal cue. Multimodal cues can contain redundant information across
73 channels or nonredundant information. Redundant cues are more likely to transmit
74 information if one channel is noisy or occluded (e.g. high background noise, confusion arising
75 from seeing multiple individuals in a crowded colony), and a secondary channel is less
76 constrained. Redundancy of information, within and among sensory modalities, is a way to
77 ensure the detectability of accurate information, and thus increase the reliability of
78 information transfer (Partan and Marler 2005). By contrast, nonredundant cues permit more
79 information to be transmitted per unit time (Partan and Marler 2005). How a detected cue
80 will modify receiver behavior is likely to be influenced by whether it contains redundant or
81 nonredundant information. For example, a redundant cue may elicit an equivalent response
82 to its unimodal components, or it may trigger an enhanced response where multiple
83 modalities exist (Partan and Marler 1999). Similarly, when nonredundant information is
84 present independent responses to each component may occur, or a response to one
85 component may be dominant over the other. Further there may be modulation of a response

86 (similar to enhancement) or a different response type could emerge (Partan and Marler 1999).
87 How an individual responds to a multimodal cue is likely to be influenced by the sequence in
88 which it encounters the components of the cue, which may be governed by the active space
89 of that modality. Components that are encountered first are typically processed ahead of
90 other signals and may dominate other cues. It is also likely that long-range components of
91 cues serve to attract individuals for closer assessment of shorter-range components (Uy and
92 Safran 2013).

93 Cues in different sensory modalities are likely to be subject to different production and
94 propagation, and perceptual constraints, and thus have different active spaces in the
95 environment. Acoustic cues have a short temporal component, can be degraded and
96 attenuated by complex physical structure, but can have high information content and
97 localizability. Visual cues have a long temporal component, can transmit over long distances
98 again subject to physical impediments, and have moderate information content and
99 localizability. Olfactory cues have a moderate to high temporal component, may disperse
100 through complex topography and retain high information content but variable localizability.

101 Using this framework, our team undertook experimental investigations of the mother-
102 pup recognition processes in a colonial pinniped species, the Australian sea lion *Neophoca*
103 *cinerea*. This species has a unique breeding cycle among pinnipeds and mammals, as they do
104 not breed annually but every 18 months, with breeding colonies being asynchronous (Marlow
105 1975; McIntosh and Pitcher 2021). Like all otariid species, females nurse only their filial pup,
106 reject any non-filial pup, and leave their pup only a few days after parturition to forage at sea.
107 This means that rapid development of mother-pup recognition is under strong selection so

108 that mother and pup can successfully reunite after the female returns from her first foraging
109 sea trip. Reunions are a step-by-step process involving acoustic, visual and olfactory cues.

110 Here we review the different field-based experimental studies undertaken to
111 investigate mother-pup recognition in Australian sea lions, its establishment and processes
112 using both unimodal and multimodal investigations. We review the experiments that have
113 been conducted involving multiple sensory modalities individually and simultaneously to
114 better understand if information transmitted by different sensory modalities are analyzed
115 synergistically by the receiver or if there is a sequential process among the sensory modalities
116 used during individual recognition. These findings are discussed within the context of the
117 active space of each sensory signals/cues, and of the potential enhancement arising from
118 assessing information from different modalities. The mother-pup communication system of
119 the Australian sea lion is one of the most comprehensively studied mammalian
120 communication systems and so provides a comparative basis from which to investigate other
121 mammalian communication systems.

122

123 **Individual recognition in a unimodal context**

124 **Vocal recognition**

125 As with other pinniped species, Australian sea lion mothers and pups produce a typical
126 vocalization unique to mother-pup interactions, while in close contact or when reuniting after
127 a separation. These contact calls, namely the pup attraction call (PAC) produced by mothers,
128 and the mother attraction call (MAC (Figure 1) are produced as soon as at birth. These calls
129 have been shown to be individual-specific, with spectral features and the frequency

130 modulation pattern being the most individually stereotyped acoustic variables (Charrier and
131 Harcourt 2006).

132 Using playback experiments where natural or synthetic calls are broadcast and the
133 behavioural response of tested subjects is measured (Figure 2), we demonstrated that vocal
134 recognition is mutual between mothers and pups in Australian sea lions. Mothers are able to
135 perform vocal discrimination within 48 hours after parturition (Pitcher et al. 2010), but pups
136 were not able to learn to identify their mother's voice before the end of the perinatal period
137 when they experience their first separation from their mothers (Pitcher et al. 2009). However,
138 when tested at 2-months old, pups were able to recognize their mother's voice. This means
139 that during the first weeks after birth mother-pup reunions are led by mothers only and pups
140 only participate more actively in reunions at a later stage when they have developed their
141 vocal discrimination abilities. The density of most breeding colonies is relatively low compared
142 to those found in fur seal breeding colonies, and Australian sea lion pups usually stay near
143 their birth site for the first two months of life (Marlow 1975). These characteristics facilitate
144 the localization of the pup (birth site acting as spatial cues) and thus the success of mother-
145 pup reunions as the risk of confusion between individuals is reduced in low density colonies
146 (Insley et al. 2003).

147 Using playback tests with modified and synthesized calls, our team investigated the
148 individual vocal signatures involved in mother-pup recognition, and showed that both
149 mothers and pups use the absolute frequency values of the call as well as amplitude and
150 frequency modulations (Charrier et al. 2009; Pitcher et al. 2012b). Fast amplitude modulations
151 present in their calls facilitate the localization of the emitter in the colony, and frequency
152 modulations are quite resistant to degradations during propagation. Propagation tests

153 revealed that calls can reliably propagate in their natural environment up to 32 meters
154 (Charrier et al. 2009; Pitcher et al. 2012b), a functional distance as females always return to
155 their birth site or the last suckling spot when returning from their foraging trip at sea.

156

157 **Olfactory recognition**

158 During reunions with their young, otariid females always perform nose to nose
159 contacts to check the identity of their pups before accepting the pup to suckle (Riedman 1990;
160 Insley et al. 2003). These final checks using olfactory cues are also performed by Australian
161 sea lion mothers during reunions with their pups (Marlow 1975). Females presented with a
162 two-choice test using pup models, one impregnated with the scent of the filial pup and
163 another with those of a non-filial pup, were able to discriminate their own pup's scent from
164 those of a non-filial pup (Pitcher et al. 2011b). It is likely that pups can recognize their mother's
165 scent as it is quite common to see pups sniffing asleep females while searching for their
166 mother in the colony. However, it remains necessary to assess if such individual recognition is
167 also found in pups, and when such olfactory discrimination is established after parturition.
168 Some preliminary tests have been done on pups in a two-choice test where pups had to
169 approach and sniff two pieces of cotton gloves, one impregnated with the mother's body scent
170 and the other one with the scent of another female of the colony. Pups were scared of the
171 experimental apparatus and did not approach the gloves to sniff it, so further experimental
172 designs have to be developed and tested. Female models can not be used as a pup would
173 never approach a female that is not the mother, as they can get bitten by non-mother females.

174 Chemical analyses on pups' body scent revealed some differences in chemical
175 compounds between cephalic (eyes, mouth, nose) and non-cephalic (back) areas in both pre-

176 molt and post-molt pups (Wierucka et al. 2019b). The different cephalic areas were however
177 very similar. General body scent of pups also seems ~~also~~ to change with age, likely due to
178 differences in their behavior as older pups (post-molt) spend more time in water compared to
179 younger ones. Detection of chemical compounds linked to vegetation and microbiota activity
180 in their chemical profiles suggests that body odor is greatly influenced by environmental
181 compounds. This hypothesis has been reinforced by the fact that differences in chemical
182 profiles of Australian sea lions from two breeding colonies are also driven by environmental
183 compounds (Wierucka et al. 2019a). Finally, analysis of mother-pup pairs chemical profiles
184 revealed a lack of similarity (Wierucka et al. 2019a) in contrast to that found in Antarctic fur
185 seals (Stoffel et al. 2015). It appears that Australian sea lion mothers learn to recognize the
186 body smell of their young. Because of this lack of similarity between mother-pup pairs, direct
187 familiarization with the scent rather than phenotype matching seems to be the most likely
188 mechanism for olfactory individual recognition.

189

190 **Visual discrimination**

191 Australian sea lion have a prolonged pupping season that can last up to nine months
192 (Ling and Walker 1978; McIntosh and Pitcher 2021), thus pups of different age classes –
193 showing different body size and fur color pattern - can occur at the same time in the colony.
194 For their first two months of life, pups are small and have black pelage, between two to four
195 months, they become larger with a cinnamon to brown pelage, and around four-month of age,
196 they molt to a silver-beige pelage like adult females (Figure 3). These morphological
197 differences could be used by females to perform an initial discrimination when coming back
198 from sea and searching for their pups often gathering with others in crèches. In order to

199 investigate if Australian sea lion mothers do use these visual cues to facilitate the reunion with
200 their pup, females were presented a two-choice test, one pup model matching the size and
201 pelage color of their own pup and another pup model of a different age-class (different size
202 and pelage color). Females showed a clear preference towards the pup model matching their
203 own pup's age class, they approached it first and did not show any aggressive behaviors. By
204 contrast, if they approached the non-matching pup model, they were very aggressive towards
205 it (bites and/or aggressive vocalizations)(Wierucka et al. 2017). This experiment clearly
206 showed that Australian sea lion mothers can use visual cues to categorize pups' by their age
207 class, and this might facilitate the reunion with their pups. At this stage, it is still unknown if
208 body size and color pelage are both used by females, or if one visual cue might be more
209 important than the other. Further investigations are needed to address those remaining
210 questions.

211 Similarly, pups showed a different behavioral response when presented with a female
212 or a pup model. Pups were highly vigilant and moved away when presented with a female
213 model, whereas they stayed in a resting position when tested with a pup model. As shown
214 with females, pups could categorize age-class (adult vs pup) based solely on their visual
215 characteristics (Wierucka et al. 2018a) and behave accordingly. This visual discrimination can
216 be quite important for the pup's survival as approaching a non-mother female might induce
217 injuries. Indeed, as seen in most otariids, Australian sea lion mothers reject and can be very
218 aggressive towards non-filial pups that approach them (Marlow 1972; Harcourt 1992b, a).

219

220 **Multimodal Context**

221 **Bimodal experiments in pups**

222 Australian sea lion pups are highly responsive to their mother's calls. To assess whether adding
223 visual cues during a playback experiment of their mother's calls would enhance their vocal
224 responses pups were presented with either a female model (visual cue), their mother's call
225 (acoustic cue) or both cues simultaneously (Table 1). Models were constructed with synthetic
226 fur of suitable colors and polyester filling, and supported with an internal wire frame to
227 maintain an upright posture (Figure 5). The female visual cue alone did not elicit any vocal
228 response, and the mother's calls alone or paired with the female elicited strong vocal
229 responses. The vocal responsiveness of pups when a visual cue was added to the mother's
230 calls did not increase suggesting that the visual female model did not enhance the vocal
231 responses of the pups (Wierucka et al. 2018a).

232 Using artificial models as visual cues only provides information on the type of individuals, e.g.
233 adult vs. young, female vs. male, but not at the individual level (i.e. the mother of the tested
234 pup), so this explains why pups would not respond to the female model presented alone, as
235 pups risk being bitten by non-mother females. Acoustic cues carry information at an individual
236 level, allowing pups to identify their mother. It was expected that mother's calls combined
237 with a female model would have induced a stronger or faster response, as this would indicate
238 to the pup that the mother had returned from the sea. If the pup identified the female model
239 as a non-mother and thus as a potential threat, a strong response similar to those obtained
240 with calls alone, would not have been observed.

241 Despite advances in our understanding of pinniped sensory systems, the visual capabilities of
242 pinnipeds to identify conspecific individuals remains unknown (Hanke et al. 2021). However,
243 it is most likely that their visual system will allow the pinnipeds to recognize individuals visually
244 especially in bright light conditions

245 **Multimodal experiments in mothers**

246 Having experimentally confirmed the use of acoustic, olfactory and visual cues in pup's
247 individual recognition and reunions, our team aimed to test combined effects, and then their
248 interactions and relative importance. Two series of experiments were conducted.

249 The first consisted of presenting different sensory filial cues to females in a similar way
250 to what they are naturally exposed to during mother-pup reunions: i.e. the acoustic cues are
251 the first cues received by mothers while searching for their pups, and then visual cues, and
252 finally they can check olfactory cues when in close contact with their pups. Females were
253 presented with acoustic cue alone, acoustic and visual cues, and acoustic, visual and olfactory
254 cues. Vocal and olfactory cues are individual cues whereas the visual cue is not an individual
255 cue (age-class cue only). The behavioral responses of females, such as investigations of a pup
256 model (i.e., sniffs) and vocalizations, were compared between these three different stimulus
257 combinations (Table 2). The number of sniffs towards the pup model increased with the
258 number of sensory cues presented to mothers, however this was not the case for the number
259 of calls produced by mothers in response. Accordingly, a clear enhancement effect was seen
260 for olfactory investigations (sniffs) but not for call production (Wierucka et al. 2018b).

261 In the second experiment, Australian sea lion mothers were presented with a pup
262 model matching the age-class of their filial pup (congruent visual cue, not varying) paired with
263 olfactory (filial or non-filial) and acoustic cues (filial and non-filial)(Table 3, Figure 4). As for the
264 first study, the recorded behavioural responses of females showed investigations of the pup
265 model (sniffs) and vocal production. Females mostly rely on acoustic cues as they only vocally
266 respond to filial calls independently of the identity of olfactory cues (filial or non-filial). The
267 presentation using both filial olfactory and vocal cues did not elicit stronger responses

268 compared to the presentation using filial vocal cues and non-filial cues. No difference in
269 investigations was observed between the four different presentations. There was no
270 enhancement effect of the vocal and olfactory cues, all females approached and sniffed the
271 pup model independently of the identity of the vocal and olfactory cues.

272 It is important to note the different interpretations of behaviors used by the
273 researchers across modalities and in these different experiments. From a mother's point of
274 view, calling may be used to prompt a pup to call in response, but it is not obligatory for the
275 mother to gather information if the pup is calling spontaneously. By contrast, the mother must
276 sniff the pup to gather olfactory information. In a choice test, where mothers chose between
277 two pup models impregnated with scent, our team observed a greater number of sniffs of the
278 filial than the non-filial model pup, and this difference in the number of sniffs was interpreted
279 as indicating the ability to differentiate between the cues. However in a sequential test, as
280 was used to examine the multimodal (visual/olfactory) cue (e.g. Wierucka et al. 2018b), the
281 number of sniffs was more likely to represent attempts to gain information than a recognition
282 response. This may explain why there was no differentiation in the sniffing response when
283 mothers were sequentially presented with filial and non-filial pup scents. In these cases, the
284 mothers must sniff the model to gather information but is not comparing the scent of two
285 pups. Further, in all the experiments involving the visual models (Figure 5), the inability to
286 present a model matching the pup's individual visual signature, as well as the static nature of
287 the models, likely contributed to limited responses from mothers. This highlights the
288 importance of context when designing and interpreting experiments to examine multimodal
289 communication.

290 Recognition is a step-by-step process with each sensory cue having its own active
291 space, and thus likely to become involved at different stages of the identification process
292 (Figure 6). Vocalizations are known to be efficient at long range, up to 32 m as measured by
293 propagation tests of Australian sea lion calls (Charrier et al. 2009; Pitcher et al. 2012a). Second,
294 visual cues can help females to sort pups in the colony based on the pelage color and body
295 size (Wierucka et al. 2017), and finally, when in close contact, mothers can confirm the identity
296 of the pup using olfactory cues (Pitcher et al. 2011a). Olfactory cues can be only assessed
297 when at very close range or in contact, at longer distance, they will be mixed with the odors
298 from other conspecifics, and thus difficult to assess and locate. In contrast to pups, Australian
299 sea lion mothers can approach pups to smell them, as there is no risk of injury. Thus they can
300 identify them if they are not calling as this behavior is frequently seen when females come
301 back from sea (Charrier, pers. obs). However, they will only vocally respond to their own pup's
302 calls.

303 In a multimodal context, vocal cues have a primary role in mother-pup recognition
304 processes. Even if olfactory cues are individual-specific, and they can alone allow a reliable
305 identification, in a multimodal context, they are not as important as vocal cues. The primary
306 role of vocalization in the recognition of the pup is attributed to their long-range properties,
307 as in this system, calls are the first information to be detected and processed for both mothers
308 and pups. Indeed, even if all sensory cues are present simultaneously, they are not perceived
309 simultaneously but sequentially (Uy and Safran 2013). The active space of sensory cues
310 appears thus an evolutionary driver for the use of sensory cues and their relative importance
311 or hierarchy within a communication and recognition system (Higham and Hebets 2013; Uy
312 and Safran 2013; Wierucka et al. 2018b).

313

314 **Future Directions**

315 Studying multimodal communication in the field is a challenging task as detecting
316 sensory cues at the level needed is often not possible, especially when working at the
317 individual level. For instance, visual lures, such as animal models, are almost impossible to
318 replicate at an individual level, limiting some investigations. However, successful investigation
319 can be done at a lower level, and still allow researchers to answer interesting questions. In the
320 case of Australian sea lion, and pinnipeds in general, there is a dearth of investigation of their
321 visual acuity with regards to social communication and recognition. Pinnipeds show
322 differences in morphological traits between sexes, age-classes and individuals, but they also
323 display different postures during social interactions (Charrier 2021), all these visual cues are
324 likely to be used in social communication. The interactions of visual cues with acoustic and
325 olfactory cues need to be better studied as they likely enhance behavioral responses,
326 especially when occurring in agonistic interactions (e.g. competing males) that can be highly
327 costly for both receivers and emitters in the case of wrong assessment.

328 Additional work needs to be done on the distance of detection of acoustic and
329 olfactory cues. Assessing at which distance a mother or a pup can vocally recognize each other
330 could be carried out in the field. Propagation tests showed that individual vocal signature can
331 reliably transmit up to 16 or 32 meters, but the detection distance by the animals can be
332 greater depending on the hearing abilities. Similar experiments can be done with olfactory
333 cues: do mothers and pups need to be in contact (nose to nose) to assess the individual
334 information, or this can be done at further distance at least without physical contact?

335 Further investigations could be also done with acoustic and olfactory cues involved in
336 mate choice in Australian sea lions specifically and for pinnipeds in general. For instance,
337 investigating acoustic and olfactory similarities between genetically related adult individuals
338 might determine if such similarities are used to avoid inbreeding. For species showing either
339 low dispersal rate or low genetic diversity, this type of assessment could be particularly useful
340 to better understand mate choice strategies.

341 Assessing the active space of sensory cues allows for a better understanding of how
342 sensory cues can be detected and perceived by receivers. Even if presented simultaneously,
343 sensory information might be treated sequentially by receivers. For now, we don't have
344 enough knowledge on the analysis processes of sensory cues in Australian sea lion, and in
345 pinnipeds in general. Some neurophysiological studies would likely improve such knowledge,
346 including the sequence of perception and cognitive processing of cues (i.e. whether they are
347 perceived/processed sequentially or simultaneously). Finally, aiming to find common rules of
348 communication in mammals showing similar ecological and/or social constraints, comparative
349 experimental studies on other vertebrate species are needed. For instance, colonial seabirds
350 and mammals have shown to develop complex individual signature for individual recognition
351 between parents-offspring or between mates (Charrier et al. 2001; Aubin and Jouventin 2002;
352 Mathevon et al. 2003; Charrier 2020), so it will be interesting to conclude on the use of
353 multimodal sensory cues in such recognition processes. Would species showing more
354 ecological constraints for individual recognition use more sensory cues than species with
355 lower constraints? A study on wolf spider using a multimodal approach showed that the use
356 of multimodal signals (vibrational and visual signals) extended the range of communication in
357 complex environment (Uetz et al. 2013). The use of different sensory information allows the
358 wolf spider to compensate for their environmental constraints. Similarly, mating or warning

359 displays have been shown to be multimodal to be more efficiently detected by receiver or to
360 face environmental constraints (Preininger et al. 2013; Rowe and Halpin 2013).

361 Investigating these questions both in the natural environment of the study species and
362 in captivity, will help develop a general framework within which to fully elucidate the role of
363 sensory cues active space in animal communication.

364

365 **Acknowledgements**

366 Our research on Australian sea lion communication system began in 2005 and has benefited
367 from a large number of students, colleagues, guides and supporters. Here we would like to
368 thank them (in alphabetic order): Heidi Ahonen, Nicolette Armansin, Jessica Boomer, Justin
369 Clarke, Kym Collins, Rachael Gray, Clarence Kennedy, Scott Lindsay, Andrew Lowther, Rebecca
370 McIntosh, Tanya Rosewarne, Mel Stonnil, Adam Stow, Shannon Taylor, Kaja Wierucka and Seal
371 Bay Conservation Park staff. These studies have been funded by Macquarie University and
372 CNRS.

373 **Tables**

374 **Table 1** - Comparison of the behavioral responses of pups tested with three different
 375 treatments: audio only (mother's calls), visual only (female model) and both audio and visual
 376 cues. Data from Wireucka et al. 2018a.

Experimental treatment comparisons	Number of calls	Latency to call
Acoustic only vs Visual Only	Significant	Non-significant
Acoustic only vs Audio + Visual	Non-significant	Not assessed
Visual only vs Acoustic + Visual	Significant	Non-significant

377

378 **Table 2** – Pairwise comparisons of the behavioral responses of adult females tested with three
 379 different treatments: acoustic cues only (filial pup's calls), acoustic + visual (filial pup's calls +
 380 pup model matching age-class) and acoustic+visual+olfactory cues (filial pup's calls + pup
 381 model matching age-class+ filial pup's body scent). Data from Wierucka et al. 2018b.

Experimental treatment pairwise comparisons	Investigations (sniffs)	Vocal response (calls)
Acoustic vs Acoustic + Visual	NS	NS
Acoustic vs Acoustic + Visual + Olfactory	significant	NS
Acoustic + Visual vs Acoustic + visual + olfactory	significant	NS

382

383

384 **Table 3** - Pairwise comparisons of the behavioral responses of adult females tested with four
385 different treatments: filial acoustic cues paired with filial olfactory cues (AfOf), filial acoustic
386 cues paired with non-filial olfactory cues (AfOnf), non-filial acoustic cues paired with filial
387 olfactory cues (AnfOf), non-filial acoustic cues paired with non-filial olfactory cues (AnfOnf).

388 *NS: non-significant.* Data from Wierucka et al. 2018b.

Experimental treatment pairwise comparisons	Investigations (sniffs)	Vocal response (calls)
AfOnf – AfOf	NS	NS
AnfOf – AfOf	NS	Significant
AnfOnf – AfOf	NS	Significant
AnfOf – AfOnf	NS	Significant
AnfOnf – AfOnf	NS	Significant
AnfOnf - AnfOf	NS	NS

389

390 **Figures captions**

391 **Fig. 1** Spectrograms and oscillograms of a contact call produced by an Australian sea lion pup
392 (left) and a Australian sea lion mother (right) during a reunion.

393

394 **Fig. 2** Picture illustrating a playback experiment performed on an Australian sea lion pup (> 6-
395 month old) responding to the calls of its mother. Photo credit: Rob Harcourt.

396

397 **Fig. 3** Color pelage of Australian sea lion pups. A. pups younger than 2-month old have black
398 fur; B. between 2- to 4-month old, pups show a chocolate/brown fur; C. after molting pups
399 have a silver/beige fur similar to those of adult females; D and E: photographs showing pups
400 of different ages and thus different size and color fur pattern occurring in the breeding colony.
401 Photo credits: Isabelle Charrier & Benjamin Pitcher.

402

403 **Fig. 4** Behavioral test of Australian sea lion females tested in a multimodal set-up. The female
404 is presented with a pup model matching the size and the color pelage of her filial pup, and the
405 head model was fitted with a swab impregnated with a pup smell (either those from the filial
406 or non-filial pup). A speaker beside the model was playing pup's calls (filial or non-filial pup's
407 calls). The model is presented on the opposite side so that they are not in the same field of
408 view of the target female.

409

410 **Fig. 5** Visual models used in the different experiments on pups and females. A. A mother tested
411 with two pup models, one black model (less than two-month old pup) and one silver/beige
412 model (molted pup, older than 4 month old pup); B. A female tested with one black and one
413 chocolate/brown model (pup between 2 to 4-month old); C and D panels show pups being
414 tested with a female model (silver and beige adult pelage, and large size, in an upright
415 position).

416 **Fig. 6** Sensory cues involved in the mother-pup recognition process during reunion. Each
417 sensory cue shows different active space and is sequentially processed: acoustic cues are used
418 at first at long range, followed by visual cues to sort individuals (e.g., pups of different age
419 classes) and finally when in contact, olfactory cues allows a final verification. Even if multiple
420 cues are present, acoustic cues are processed as first, to identify the pup or the mother, and
421 to assess if a closer approach is necessary. Without acoustic cues, vision can be used and thus
422 olfactory cues when at short range. For pups, an approach will be performed only if the
423 acoustic cues are matching those of the mother. Approaching a non-mother can be costly for
424 pups as there is a high risk of injury (females can be quite aggressive towards non-filial pups).
425 In contrast, females can approach calling or non-calling pups to confirm or check the pup's
426 identity using olfactory cues as there is no cost for them.

427 **References**

- 428 Alcock J (1998) *Animal behavior: an evolutionary approach*. Sunderland, MA
- 429 Aubin T, Jouventin P (2002) How to vocally identify kin in a crowd: The penguin model. *Adv*
430 *Study Behav* 31:243–277
- 431 Bradbury JW., Vehrencamp SL (2011) *Principles of Animal Communication*. Sinauer
432 Associates, Inc, Sunderland, Massachusetts
- 433 Charrier I (2021) Non-vocal Communication in Otariids and Odobenids: The Involvement of
434 Visual and Olfactory Cues in Their Social Lives. In: Campagna C, Harcourt R (eds)
435 *Ethology and Behavioral Ecology of Otariids and the Odobenid*. Springer, Cham, pp 291–
436 304
- 437 Charrier I (2020) Mother–Offspring Vocal Recognition and Social System in Pinnipeds. In:
438 Aubin T, Mathevon N (eds) *Coding Strategies in Vertebrate Acoustic Communication*. pp
439 231–246
- 440 Charrier I, Harcourt RG (2006) Individual vocal identity in mother and pup Australian sea
441 lions (*Neophoca cinerea*). *J Mammal* 87:. doi: 10.1644/05-MAMM-A-344R3.1
- 442 Charrier I, Mathevon N, Jouventin P, Aubin T (2001) Acoustic communication in a black-
443 headed gull colony: How do chicks identify their parents? *Ethology* 107:. doi:
444 10.1046/j.1439-0310.2001.00748.x
- 445 Charrier I, Pitcher B, Harcourt R (2009) Vocal recognition of mothers by Australian sea lion
446 pups: individual signature and environmental constraints. *Anim Behav* 78:1127–1134
- 447 Hanke FD, Reichmuth C, Cook P (2021) The Sensory World of Otariids. In: Springer. pp 305–

448 321

449 Harcourt R (1992a) Maternal aggression in the South American fur seal in Peru. *Can J Zool*

450 70:320–325. doi: 10.1139/z92-048

451 Harcourt R (1992b) Factors affecting early mortality in the South American fur seal (

452 *Arctocephalus australis*) in Peru: density-related effects and predation. *J Zool* 226:259–

453 270. doi: 10.1111/j.1469-7998.1992.tb03838.x

454 Higham JP, Hebets EA (2013) An introduction to multimodal communication. *Behav Ecol*

455 *Sociobiol* 67:1381–1388. doi: 10.1007/s00265-013-1590-x

456 Insley S, Phillips A, Charrier I (2003) A review of social recognition in pinnipeds. *Aquat Mamm*

457 29:181–201

458 Ling JK, Walker GE (1978) An 18-month breeding cycle in the Australian sea lion? *Search*

459 9:464–465

460 Marlow B (1975) The comparative behaviour of the Australasian sea lions *Neophoca cinerea*

461 and *Phocarctos hookeri* (Pinnipedia: Otariidae). *Mammalia* 39:159–230

462 Marlow B (1972) Pup abduction in the Australian sea lion, *Neophoca cinerea*. *Mammalia*

463 36:161–165

464 Mathevon N, Charrier I, Jouventin P (2003) Potential for individual recognition in acoustic

465 signals: A comparative study of two gulls with different nesting patterns. *Comptes*

466 *Rendus - Biol* 326:. doi: 10.1016/S1631-0691(03)00072-6

467 McIntosh RR, Pitcher BJ (2021) The Enigmatic Life History of the Australian Sea Lion. pp 557–

468 585

469 Partan S, Marler P (1999) Communication goes multimodal. *Science* (80-.). 283:1272–1273

470 Partan SR, Marler P (2005) Issues in the Classification of Multimodal. *Am Nat* 166:231–245

471 Partan SR, Marler P, Partan SR, Marler P (2013) Issues in the Classification of Multimodal.
472 166:231–245

473 Pitcher B, Harcourt R, Charrier I (2012a) Individual identity encoding and environmental
474 constraints in vocal recognition of pups by Australian sea lion mothers. *Anim Behav*
475 83:681–690

476 Pitcher BJ, Ahonen H, Charrier I, Harcourt RG (2011a) Allosuckling behavior in the Australian
477 sea lion (*Neophoca cinerea*): An updated understanding. *Mar Mammal Sci* 27:. doi:
478 10.1111/j.1748-7692.2010.00440.x

479 Pitcher BJ, Ahonen H, Harcourt RG, Charrier I (2009) Delayed onset of vocal recognition in
480 Australian sea lion pups (*Neophoca cinerea*). *Naturwissenschaften* 96:. doi:
481 10.1007/s00114-009-0546-5

482 Pitcher BJ, Harcourt RG, Charrier I (2012b) Individual identity encoding and environmental
483 constraints in vocal recognition of pups by Australian sea lion mothers. *Anim Behav* 83:.
484 doi: 10.1016/j.anbehav.2011.12.012

485 Pitcher BJ, Harcourt RG, Charrier I (2010) Rapid onset of maternal vocal recognition in a
486 colonially breeding mammal, the Australian sea lion. *PLoS One* 5:771–6. doi:
487 10.1371/journal.pone.0012195

488 Pitcher BJ, Harcourt RG, Schaal B, Charrier I (2011b) Social olfaction in marine mammals:
489 Wild female Australian sea lions can identify their pup’s scent. *Biol Lett* 7:60–62. doi:
490 10.1098/rsbl.2010.0569

491 Preininger D, Boeckle M, Freudmann A, et al (2013) Multimodal signaling in the Small
492 Torrent Frog (*Micrixalus saxicola*) in a complex acoustic environment. *Behav Ecol*
493 *Sociobiol* 67:1449–1456. doi: 10.1007/s00265-013-1489-6

494 Riedman M (1990) *The pinnipeds: seals, sea lions, and walruses*. University of California
495 Press

496 Rowe C, Halpin C (2013) Why are warning displays multimodal? *Behav Ecol Sociobiol*
497 67:1425–1439. doi: 10.1007/s00265-013-1515-8

498 Shannon C, Weaver W (1949) *The mathematical theory of communication* (Urbana, IL

499 Starnberger I, Preininger D, H??dl W (2014) The anuran vocal sac: A tool for multimodal
500 signalling. *Anim Behav* 97:281–288. doi: 10.1016/j.anbehav.2014.07.027

501 Stoffel MA, Caspers BA, Forcada J, et al (2015) Chemical fingerprints encode mother-
502 offspring similarity, colony membership, relatedness, and genetic quality in fur seals.
503 *Proc Natl Acad Sci U S A* 112:E5005–E5012. doi: 10.1073/pnas.1506076112

504 Uetz GW, Roberts JA, Clark DL, et al (2013) Multimodal signals increase active space of
505 communication by wolf spiders in a complex litter environment. *Behav Ecol Sociobiol*
506 67:1471–1482. doi: 10.1007/s00265-013-1557-y

507 Uy JAC, Safran RJ (2013) Variation in the temporal and spatial use of signals and its
508 implications for multimodal communication. *Behav Ecol Sociobiol* 67:1499–1511. doi:
509 10.1007/s00265-013-1492-y

510 Wartzok D, Ketten D (1999) Marine mammal sensory systems. In: *Biology of marine*
511 *mammals*. pp 117–175

512 Wierucka K, Barthes N, Harcourt R, et al (2019a) Chemical fingerprints suggest direct
513 familiarisation rather than phenotype matching during olfactory recognition in
514 Australian sea lions (*Neophoca cinerea*). *J Exp Mar Bio Ecol* 517:. doi:
515 10.1016/j.jembe.2019.06.001

516 Wierucka K, Barthes N, Pitcher BJ, et al (2019b) Chemical Profiles of Integumentary and
517 Glandular Substrates in Australian Sea Lion Pups (*Neophoca cinerea*). *Chem Senses* 44:.
518 doi: 10.1093/chemse/bjz008

519 Wierucka K, Charrier I, Harcourt R, Pitcher BJ (2018a) Visual cues do not enhance sea lion
520 pups' response to multimodal maternal cues. *Sci Rep* 8:. doi: 10.1038/s41598-018-
521 28171-w

522 Wierucka K, Pitcher BJ, Harcourt R, Charrier I (2017) The role of visual cues in mother–pup
523 reunions in a colonially breeding mammal. *Biol Lett* 13:20170444. doi:
524 10.1098/rsbl.2017.0444

525 Wierucka K, Pitcher BJ, Harcourt R, Charrier I (2018b) Multimodal mother–offspring
526 recognition: the relative importance of sensory cues in a colonial mammal. *Anim Behav*
527 146:135–142. doi: 10.1016/j.anbehav.2018.10.019

528