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SHORT COMMUNICATION

The memory remains: long-term vocal recognition in Australian sea lions

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Abstract The ability to recognize other individuals plays an important role in mediating social interactions. As longitudinal studies are challenging, there is only limited evidence of long-term memory of individuals and concepts in mammals. We examined the ability of six wild Australian sea lions to discriminate between the voice of their mother and another adult female, both while they were dependent on their mother and when they were independent, 2 years after weaning. Here, we show that even after a long period of independence, juveniles retain the ability to identify their mother's voice. Both when dependent and independent, animals showed stronger responses to maternal calls than to the calls of another female. This demonstration of recognition provides rare evidence of the long-term memory capabilities of wild mammals.

Keywords Long-term memory · Individual vocal recognition · *Neophoca cinerea* · Discrimination · Social communication · Pinniped

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Introduction

In social contexts where individuals work toward a common aim to obtain direct or indirect fitness benefits, recognition is essential to ensure resources are directed toward the correct recipient (Bradbury and Vehrencamp 1998). Identifiable signatures contained in communication signals of individuals or groups allow a receiver to readily interpret and classify the identity of the signaler (Boughman and Moss 2002). Experimental studies have demonstrated the ability of mammals to maintain memories of individuals or concepts for long periods of time (e.g. Trillmich 1981; Hanggi and Schusterman 1990; Hanggi 1992; Insley 2000; Kendrick et al. 2001; Reichmuth Kastak and Schusterman 2002; Charrier et al. 2003; Hanggi and Ingersoll 2009). However, there is evidence to suggest that over increasing periods of separation the ability to recognize other individuals may decline due to the reallocation of neural resources (Kendrick et al. 2001) or a gradual change in identity cues (Newberry and Swanson 2008).

The study of long-term vocal recognition in wild animals is inherently difficult. Few studies have addressed the ability of mammals to recognize previously familiar social vocalizations after a period of separation. With the exception of anecdotal observations of African elephant (*Loxodonta africana*) responses to playbacks of former group member's vocalizations (McComb et al. 2000), the only experimental evidence of long-term recognition of vocalizations in non-primate mammals comes from studies of otariids (sea lions and fur seals). Otariid species have developed strong, accurate and early vocal recognition between mother and offspring as an adaptation to high selective pressures (see Insley et al. 2003). Indeed, these species live in dense colonies where the risk of confusion between individuals is extremely high, and this is exacerbated by the fact that mothers and pups are frequently separated for short periods during lactation (i.e., mothers forage at sea for periods lasting from several hours to 3 weeks, Riedman 1991), from shortly after birth. Mother–pup recognition is thus critical for both pup's survival and female's breeding success. Such strong pressures for individual recognition may have resulted in long lasting recognition. In Northern fur seals (*Callorhinus ursinus*), Insley (2000) showed that 4-year-old females responded more to the calls of their mother than another female from the same colony 3.7–3.8 years after weaning. Similarly, 2-year-old Galapagos fur seals (*Arctocephalus galapagoensis*) only responded to playbacks of their mother's call and not to the calls of other females (Trillmich 1981). In addition, Charrier et al. (2003) demonstrated that female subantarctic fur seals (*Arctocephalus tropicalis*) maintained a memory of their pup's vocalizations recorded when the pups were 1–2 days of age during playback experiments undertaken just before weaning, 9 months after parturition, even though the pups voice had changed significantly during this time. These experimental studies demonstrate the potential for otariids to maintain memories of socially meaningful vocalizations over long periods of time.

In otariids, the ability to recognize and reunite with their mother is critical to the survival of pups. Allosuckling is rare in Australian sea lions (*Neophoca cinerea*) and pups face aggression from other females and starvation if they cannot reunite with their mother (Marlow 1972, 1975). In the Australian sea lion, maternal care usually lasts between 15 and 18 months (Higgins and Gass 1993). The mother stays with the pup for the first 10 days after birth and then alternates between foraging trips and time ashore nursing the pup (approximately 2 days each) until weaning (Higgins and Gass 1993). Upon each return to the colony, and after separations within the colony, the mother and pup must locate and reunite with each other. Like other pinnipeds (Insley et al. 2003), the Australian sea lion uses a combination of vocal and olfactory (Pitcher et al. 2009; B. J. Pitcher et al. unpublished data) and potentially visual and spatial cues (Stirling 1972; Marlow 1975; Pitcher et al. 2009) to facilitate these reunions. Analysis of vocalizations has shown that both mothers and pups possess individual vocal signatures (Charrier and Harcourt 2006) and that pups use the amplitude and frequency modulations as well as the exact frequency components of the mothers voice when identifying her (Charrier et al. 2009). We have previously shown that Australian sea lion pups are slower than other otariids to learn their mother's voice (Pitcher et al. 2009), albeit, mothers learn their pup's voice within days of birth (B. J. Pitcher et al. unpublished data). With very low colony densities and high levels of female philopatry (Campbell et al. 2008), Australian sea lions are likely at the ecological extreme compared to other otariid species, subject to less selective pressures for individual recognition compared to northern, subantarctic and Galapagos fur seals (Charrier and Harcourt 2006).

In this study, we used playback presentations of pup attraction calls to investigate the long-term recognition capabilities of a group of Australian sea lions. These wild individuals were initially tested for their ability to discriminate between the calls of their mother and another adult female during their first year while they were still dependent on their mother. The same group of individuals were tested a second time 2 years after weaning to determine if any discrimination ability remained in independent animals. In so doing, we experimentally investigate if long-term vocal recognition is present in the Australian sea lion.

Methods

Study location and animals

This study was carried out at Seal Bay Conservation Park (35°41′S, 136°53′E) and Cape Gantheaume National Park (36°1′S, 137°32′E), Kangaroo Island, South Australia. Australian sea lion pups born between January and February 2006 at Seal Bay were double-tagged in the web of the fore flippers with an individually numbered two-part plastic tag (Rototags, Dalton Supplies, UK) and injected with unique passive integrated transponder tag (Allflex, Brisbane, QLD, Australia) for individual identification (Charrier et al. 2009; Pitcher et al. 2009). During their first year, while dependent on their mother for survival, six pups (four males and two females) were tested for the ability to differentiate between their mother's pup attraction call and another female's pup attraction call using a playback experiment at Seal Bay. In June and July 2009 the individuals, at approximately 3.5 years of age, were tested a second time (four at Seal Bay and two at Cape Gantheaume, approximately 20 km away) to again determine their ability to differentiate their mother's call from that of another female. The animals used in this experiment were part of the study population used by Charrier et al. (2009) and Pitcher et al. (2009). The responses of animals to playbacks during their first year are included in the analysis of Charrier et al. (2009) and stimulus preparation and presentation follows the procedure of Charrier et al. (2009) and Pitcher et al. (2009).

Stimulus preparation

Pup attraction calls were recorded from mothers who were searching for their pup, either after returning from foraging or after being separated in the colony. All calls were recorded using a BeyerDynamic M69 TG microphone (frequency response 50 Hz–16 kHz, ±2.5 dB, BeyerDynamic, Heilbronn, Germany) mounted on a 3-m boom connected to a Marantz PMD 660 digital recorder (frequency response 16 kHz (−0.5 dB), dynamic range 80 dB, Marantz Europe, Eindhoven, The Netherlands). The distance between the animal and the microphone was kept at approximately 2 m. Calls were recorded at a 44.1-kHz sampling frequency, with 16-bit resolution. All mothers' recordings were made during 2006, since it was not possible to find again the mothers in 2009, as females were not flipper tagged nor easily identifiable with natural marks.

Playback stimuli were prepared using Avisoft SAS Lab Pro (R. Specht, Avisoft Bioacoustics, Berlin, Germany) and GoldWave (GoldWave Incorporated, St. John's, NL, Canada). Calls were resampled to 22.05 kHz sampling frequency, and high-pass filtered at 200 Hz to remove wind and ocean noise. Filtering did not affect the playback of the vocalizations, as there is no energy below 450 Hz (Charrier and Harcourt 2006).

During each test in 2006 as well as in 2009, each individual received two stimuli. A stimulus consisted of three repetitions of the same pup attraction call given at a rate of one every 3 s (Charrier et al. 2001, 2003, 2009; Pitcher et al. 2009). One stimulus consisted of a pup attraction call recorded from the individual's mother and the other was a pup attraction call of another female from the Seal Bay colony that sired a pup during the same breeding season as the target individual's birth. The same 'mother' stimulus was used during both trials (2006 and 2009), since new recordings of mothers' calls could not be made; however, the other female stimulus was different and randomly chosen from those available. Pseudo-replication is very unlikely as animals were only tested twice and even though it was the same series there was a 3.5-year interval.

Playback presentation

Each animal was tested twice during this study, once while dependent (i.e. suckling) on their mother during their first year (dependent) and once post-weaning at approximately 3.5 years of age (independent). For the initial trial (i.e., on dependent pups), pups were located in the colony on the day following the mother's departure for a foraging trip, and for the second trial (i.e., on independent pups) animals were tested while resting in the colony between their own foraging trips. The location of the target animal's mother was unknown during the second test as mothers were not marked at this time. However, no tested individual was resting in close proximity to another during the trials. Playbacks were performed when animals were resting in the colony, and all animals responded to at least one of the calls presented to them. Calls were broadcast using a Marantz PMD 670 or an Edirol R-09 (Roland Corporation, Los Angeles, CA, USA) connected to an Anchor Explorer Pro loudspeaker (30 W, frequency response 80 Hz–16 kHz ±3 dB, Anchor Audio, Torrance, CA, USA) placed from 4 to 6 m from the pup. Calls were played back at approximately natural amplitudes (83 ± 3 dB SPL measured 1 m from the source; Charrier et al. 2009). Presentation of playback stimuli was separated by at least 2 min, and the presentation order was randomized.

Playback analysis

We recorded the latency of the animal to first look toward the playback speaker, the latency to begin approaching the speaker, the latency to the first vocalization and the number of vocalizations. All measurements commenced at the beginning of the playback stimulus and continued for 60 s. Responses were scored in situ by an observer blind to the stimulus type. Because of the small sample size, two methods of analysis were used to ensure the validity of the results: ethological scale and a principal components analysis (PCA) on raw behavioral data.

For analysis using the ethological scale, each individual was scored as one of four categories; 0—no observable response to the playback from the speaker, 1—individual only looks toward the speaker, 2—individual looks and vocalizes *or* approaches the speaker, 4—individual looks, vocalizes *and* approaches the speaker. Ethological scores obtained with the maternal calls and the other female calls were compared using a Wilcoxon matched pair tests. Data were also analyzed using a PCA of the raw behavioral data (after McGregor 1992). The PCA included the three measures of latency (look, call and approach) and the count of vocalizations and was used to construct a composite score. The scores of the principal components with eigenvalues greater than 1 were compared using two-tailed Wilcoxon matched pair tests. Statistical comparisons were made using SPSS 10 for Windows (SPSS Incorporated, 2000) and Statistica 6.0 (StatSoft, 2001).

Results

Ethological scale

Young Australian sea lions, both when dependent on their mother and independent from them, responded more to their mother's vocalizations than to the vocalizations of another female (dependant: $n = 6$, $Z = -2.23$, $P = 0.026$; independent: $n = 6$, $Z = -2.07$, $P = 0.038$; Fig. 1). Moreover, if we compare the differences in responses to the calls of the mother and another female between the two trials (2006 and 2009), there was not a significant change in the magnitude of responses between the dependent and

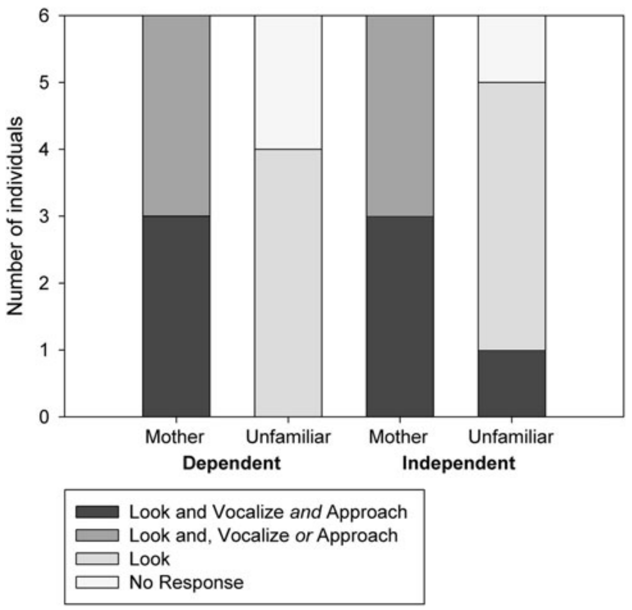

Fig. 1 Ethological scale scores for the six individuals. At both ages (dependent and independent), all six individuals responded to the playback of their mother's calls by looking and calling and/or approaching the playback speaker. By contrast, most individuals simply looked or did nothing in response to the playback of an unfamiliar female's vocalization

independent age groups ($n = 6$, Z = −1.00, $P = 0.32$), indicating that animals responded with the same strength at 3.5 years of age as they did while dependent on their mother.

Principal components analysis of all behavioral measures

The PCA extracted four factors, but only the first principal component had an eigenvalue greater than 1 (eigenvalue = 2.32) and explained 58% of the variance in the response of individuals. The second principal component (eigenvalue = 0.79) only explained a further 19.8% of the variance. All behavioral measures were highly correlated with the first principal component ($>|0.5|$). Greater negative values of latency scores and higher positive values of the number of vocalizations corresponded to a stronger response through shorter response times. Both dependent and independent animals showed significantly stronger responses to the maternal calls than to the other female calls (dependent: $n = 6$, Z = 2.20, $P = 0.027$; independent: $n = 6$, Z = 2.20, $P = 0.027$; Fig. 2).

Discussion

Long-term vocal recognition between mothers and offspring has been previously demonstrated in northern fur seals 3.7–3.8 years after weaning (Insley 2000, $n = 4$ mother–pup pairs) and Galapagos sea lions at 2 years of age (Trillmich 1981, $n = 2$ pups), both species that show strong selective pressures for individual recognition. In the present study, six Australian sea lions showed the ability to differentiate between playbacks of their mother's call and that of another female both while dependent on their mother and when they had been weaned for approximately 2 years. The strength of this recognition does not appear to be diminished after this long time. This demonstrates that long-term vocal recognition occurs in Australian sea lions and that at least some individuals can identify their mother's vocalizations for at least 2 years after weaning. The two most likely explanations for the maintenance of vocal recognition over many years are that (1) it is a by-product of the importance of strong recognition early in life, or (2) the continued ability to identify mothers plays a role in social interactions (see Insley 2000; Charrier et al. 2003).

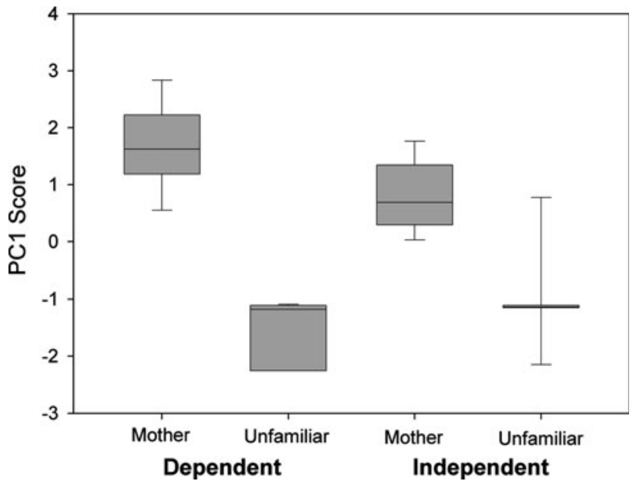

Fig. 2 Principal components analysis of the four behavioral measures of response (latency to look, call and approach, and number of vocalizations). In both age classes (dependent and independent), individuals responded more strongly to the playback of their mother's call than to the playback of calls of another adult female. $N = 6$ line = median, box = inter-quartile range and whiskers = 10–90% range

The ability to recognize and reunite mother and offspring is crucial for offspring survival in Australian sea lions prior to weaning. Learning and memory of these identity cues by pups is potentially mediated by the 'filial imprinting phenomenon' (see Chalmers 1983). Such filial imprinting is likely to be resistant to extinction and has been suggested to occur in a number of pinniped species (see Trillmich 1981; Hanggi and Schusterman 1990; Schusterman et al. 1992; Charrier et al. 2003). Selection is likely to favor individuals that have a strong memory for their mother's voice during the period of dependence and as a consequence this memory may persist until later in life even if this persistence is non-adaptive. Similar evidence for the persistence of long-term memory in pinnipeds was demonstrated by a California sea lion which reliably performed a conceptual test 10 years after training (Reichmuth Kastak and Schusterman 2002). While long-term recognition of maternal calls may be a by-product of the strong and permanent learning during nursing, the general long-term memory abilities of pinnipeds may be used in a variety of social and ecological contexts.

Evidence from other species suggests that long-term recognition may play a role in the mediation of social interactions. In pinnipeds, these social interactions may include inbreeding avoidance and associations between related animals in the colony. Inbred animals have been shown to be less healthy (Acevedo-Whitehouse et al. 2003), and females avoid breeding with related males and seek out males with high heterozygosity and low relatedness, presumably to increase the fitness of their offspring (Hoffman et al. 2007). Considering the sexual maturity and breeding longevity of Australian sea lion, there is potentially opportunity for mothers and their male offspring to breed together (Shaughnessy 1999; McIntosh 2007). Vocal cues may be used in conjunction with visual and olfactory cues associated with the major histocompatibility complex to assess mate relatedness and avoid inbreeding (Hoffman et al. 2007).

Grouping of closely related individuals in a breeding colony may provide opportunities for behaviors that increase inclusive fitness (Ross 2001). A number of studies have investigated the potential for kin clustering to influence the groupings of pinnipeds in breeding colonies (see Poland et al. 2008). Insley (2000) suggested that long-term vocal recognition as has been seen in the northern fur seal and now in this study with the Australian sea lion could facilitate such associations between mothers and mature offspring. Observations of grouping behavior has provided some evidence for kin associations in Galapagos sea lions (Wolf et al. 2007; Wolf and Trillmich 2008) and grey seals (Pomeroy et al. 2000). However, while kin associations may occur in some parts of a breeding colony in grey seals (Pomeroy et al. 2000; Poland et al. 2008) or in some harems in southern elephant seals (Fabiani et al. 2006) these associations do not occur more often than unrelated associations at least in ecologically similar phocids (Fabiani et al. 2006; Poland et al. 2008). In contrast, individuals within Galapagos sea lion communities are more likely to be related than individuals between communities (Wolf and Trillmich 2008). Thus, although long-term vocal recognition would allow associations between mothers and offspring, the low prevalence of this behavior suggests that it is not the cause of the maintenance of such recognition.

As in many otariid species, vocal recognition during the period of maternal care is crucial for the survival of Australian sea lion pups. It is likely that selection for a strong, unalterable memory of a mother's voice has resulted in the by-product of a long-term memory of these calls. We suggest that while social interactions such as inbreeding avoidance and preferential relationships within colonies are potentially important for the fitness of offspring, it is unlikely that these interactions solely have resulted in selection for long-term memory of maternal voice. Our study demonstrates that some Australian sea lions can identify their mother's voice 2 years after weaning, and in combination with previous studies on northern fur seals (Insley 2000) and Galapagos fur seals (Trillmich 1981) provides the only experimental evidence for long-term memory of social vocalizations in otariids and in wild mammals. We suggest that long-term recognition capability may be a trait common across otariids.

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Conflict of interest statement The authors declare that they have no conflict of interest.

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