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Evidence for social transmission of foraging behaviour in the Australian sea lion

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ABSTRACT

In mammals, social transmission of information from mother to offspring can help young to develop specialised and complex foraging behaviours. Although this social transmission is well recognised in some marine mammals, no conclusive evidence has been reported for otariids (fur seals and sea lions). Here, using animal-borne video and movement data from an adult female Australian sea lion, we provide evidence for mother-to-pup social transmission of foraging behaviour. Social transmission of foraging behaviour may be a component of development in Australian sea lions, whereby prolonged maternal care (~18 months) could provide mothers the opportunity to demonstrate foraging behaviours to pups.

Keywords: animal-borne video, Australian sea lion, foraging behaviour, life-history, maternal strategy, pinniped, reproductive cycle, social transmission.

Introduction

In mammal species with long periods of maternal care (several years) (Mann and Sargeant 2003; Lonsdorf 2006; Weiss *et al.* 2023), mothers can demonstrate complex and specialised foraging behaviours to their young, assisting them in learning how to utilise different or difficult to exploit prey types and habitats (Estes *et al.* 2003; Ford and Ellis 2006; Kopps *et al.* 2014). Such examples include eastern chimpanzee mothers (*Pan troglodytes schweinfurthii*) demonstrating the use of sticks for 'termite fishing' to their young (Lonsdorf 2006). This mother-to-offspring transmission of foraging behaviour is well recognised in some marine mammals, including cetaceans (Ford and Ellis 2006; Sargeant and Mann 2009; Whitehead 2018) and sea otters (*Enhydra lutris*) (Estes *et al.* 2003). For example, bottlenose dolphin calves (*Tursiops* sp.) learn from mothers how to use sponges to protect their rostrums when foraging on the seabed (Kopps *et al.* 2014). In pinnipeds, pups are known to accompany mothers at sea in walruses (*Odobenus rosmarus*) (Miller and Kochnev 2021) and in phocid (true seal) species, such as Weddell seals (*Leptonychotes weddellii*) and harbor seals (*Phoca vitulina*) (Jørgensen *et al.* 2001; Sato *et al.* 2003). However, no conclusive evidence for social transmission of foraging behaviour has been reported in otariids (fur seals and sea lions). Here, we present animal-borne video and movement data from an adult female Australian sea lion (*Neophoca cinerea*) at sea with her pup, providing direct evidence for the social transmission of foraging behaviour in an otariid.

Australian sea lions have a unique life history. Breeding occurs across an ~18-month cycle that is both asynchronous (occurring at different times of the year at different colonies) and aseasonal (showing no relationship to seasonal climatic patterns), across the species' distribution (Higgins 1993; Shaughnessy *et al.* 2011; Goldsworthy *et al.* 2021). This supra-annual reproductive cycle contrasts the highly seasonal, annual and synchronised reproductive cycles conformed to by other seals (Costa 1991; Atkinson 1997). In addition to their unique reproductive cycle, adult female Australian sea lions have long-term fidelity to natal foraging habitats (Lowther *et al.* 2011, 2012), which drives the highly subdivided, fine-scale genetic structure of their populations (Campbell *et al.* 2008; Lowther *et al.* 2011). Identifying what selective factors could have shaped the unique reproductive cycle and life-history of the Australian sea lion is key to better understanding the ecological and evolutionary biology of the species.

Previous observations of Australian sea lions have identified mother–pup pairs travelling at sea together (McIntosh and Pitcher 2021). Mother–pup pairs have also been sighted at breeding/haul-out sites 20–60 km from their natal colony (Lowther and Goldsworthy 2011; Kirkwood and Goldsworthy 2013), providing preliminary evidence that Australian sea lion pups accompany their mothers at sea, as it is unlikely that pups could otherwise reunite with their mothers at such distant locations from their natal colony. However, interestingly, evidence for pups accompanying mothers to sea has not been found in previous paired tracking studies (Fowler *et al.* 2007; Lowther and Goldsworthy 2012). Additionally, mitochondrial DNA (mtDNA) analyses have not found evidence that foraging specialisation/ecotypes are maintained along matrilines (Lowther *et al.* 2012). Here, we provide direct evidence for mother-to-pup social transmission of foraging behaviour in the Australian sea lion, using video, dive and location data collected from an adult female from Seal Bay on Kangaroo Island in South Australia. In addition, we compare differences observed in the movement, diving and foraging behaviour of the mother between a pup-accompanied trip and a solo trip at sea.

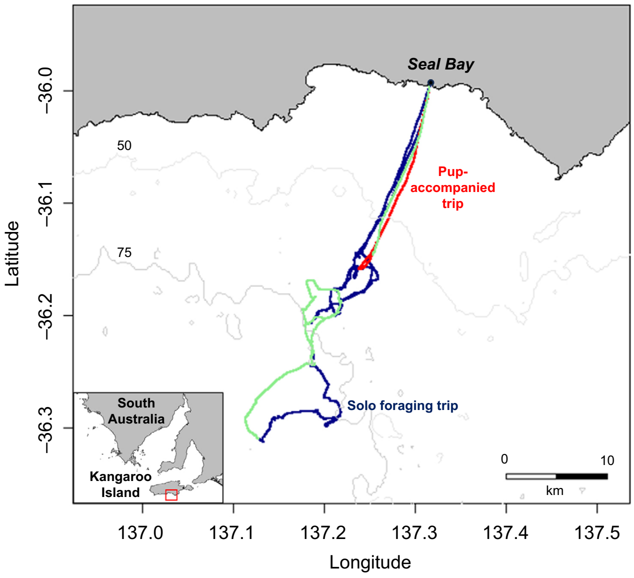

Fig. 1. Dead-reckoned foraging path of an adult female Australian sea lion from Seal Bay, for an 8-h pup-accompanied trip (red) and a ~3-day solo foraging trip (dark blue). Green segments indicate where video data were available. Isobaths represent depth contours at 50 (light grey) and 75 m (dark grey).

Materials and methods

In June 2023, data were collected from an 8-year-old Australian sea lion female that had an 11-month-old pup (Supplementary Material Table S1) from Seal Bay Conservation Park (35.994°S, 137.317°E) on Kangaroo Island in South Australia (Fig. 1). The female was fitted with an archival underwater camera (CATS Cam, 135 × 96 × 40 mm, 400 g), positioned at the base of the scapula and an Argos-linked GPS logger with an integrated time–depth recorder (SPLASH-10, Wildlife Computers, 100 × 65 × 32 mm, 200 g), positioned posterior to the camera. In addition, a triaxial accelerometer and magnetometer (Axy-5 XS, TechnoSmArt, 28 × 12 × 9 mm, 4 g) was positioned at the crown of the head. To attach the instruments, the adult female was initially sedated with Zoletil® (~1.3 mg/kg, Virbac), administered intramuscularly via a syringe dart (3.0 mL syringe body with a 14-gauge 25-mm barbed needle, Paxarms), delivered remotely by a dart gun (MK24c Projector, Paxarms). The female was then anaesthetised using Isoflurane® (5% induction, 2.0–3.0% maintenance with medical-grade oxygen) for ~20 min while instruments were attached. Isoflurane was delivered via a purpose-built gas anaesthetic machine, using a Cyprane Tec III vapouriser (The Stinger™ Backpack anaesthetic machine, Advance Anaesthetic Specialists). Throughout anaesthesia, vital signs (e.g. respiratory rate, capillary refill and palpebral reflex) were continuously monitored and a pulse oximeter was clipped to the tongue to monitor heart rate and blood oxygen levels. All bio-logging instruments were preadhered to neoprene patches that were then glued to the pelage on the dorsal midline of the female, using a two-part quick-setting epoxy (Selleys Araldite® 5 Minute Epoxy Adhesive).

The satellite-linked GPS logger collected Fastloc® locations when the animal surfaced and the time–depth recorder measured depth every second. These depth data were analysed in *R* using the *diveMove* package (Luque 2007), which identified descent, ascent, bottom and surface phases for each dive. Triaxial accelerometer and magnetometer data were used to dead-reckon at-sea movement from the GPS data, using the methods outlined in Angelakis *et al.* (2023). High-definition video (forward-facing) was collected while the female was at sea at depths greater than 5 m during daylight hours (from 0800 to 1700 hours local time).

Analysis of the video was conducted using the open-source Behavioral Observation Research Interactive Software (BORIS, ver. 7.12.2). The duration of time spent in different benthic habitats and the duration of predation events were recorded. The at-sea behaviour of the pup was also recorded. Benthic habitats were classified using the methods in Angelakis *et al.* (2024). The proportion of time allocated to different benthic habitats for the pup-accompanied trip and the solo trip was compared using a permutational multivariate analysis of variance (PERMANOVA). Firstly, a distance matrix was calculated, using Bray–Curtis distance. A PERMANOVA (permutations = 999) was then run, using the *vegan* package in *R* (Dixon 2003), to assess statistical differences in the allocation of time across benthic habitats between the two trips. Dive performance was compared between the two trips, based on the durations of dive phases. As Australian sea lions are benthic predators (Peters *et al.* 2015; Berry *et al.* 2017; Goldsworthy *et al.* 2019) that maximise bottom time when foraging (Costa and Gales 2003; Fowler *et al.* 2007), statistical differences between bottom duration, dive duration and bottom depth were assessed. These variables exhibited non-normal distributions for both trips, therefore non-parametric Wilcoxon rank-sum tests were conducted to assess significant differences between the pup-accompanied trip and the solo foraging trip.

Ethics approval

This research was reviewed and approved by The University of Adelaide Animal Ethics Committee (#S-2021-001), PIRSA Animal Ethics Committee (#16/20) and the Department for Environment and Water (Permit/Licence to Undertake Scientific Research #A24684-22/23 and Marine Parks Permit to Undertake Scientific Research #MR00071-7-R).

Results

Dead-reckoned movement data showed the adult female undertook an 8-h pup-accompanied trip (Fig. 1), followed by an ~11.5-h haul-out period (Supplementary Fig. S1), before a ~3-day solo foraging trip (Fig. 1). The pup-accompanied trip achieved a maximum distance from the colony of ~20 km, whereas the solo foraging trip achieved a maximum distance of ~40 km from the colony (Fig. 1).

A total of 12 h and 1 min of video across three days at sea was collected from the animal-borne camera. This comprised 2 h and 13 min of video from the 8-h pup-accompanied trip, with 47 dives observed and the pup visible in 35 of these (Fig. 2), and 9 h and 48 min of video from a ~3-day solo foraging trip, with 164 dives observed. The benthic habitats that were used, differed between the two trips (PERMANOVA: $P = 0.001$, $F = 39.659$, d.f. = 389). For the pup-accompanied trip, the majority of bottom time was spent on macroalgae-dominated reefs and macroalgae meadows (Fig. 3*a*), whereas on the solo foraging trip the adult female mostly spent bottom time across deeper invertebrate-dominated reefs (Fig. 3*b*). Three prey attempts were observed on the pup-accompanied trip (averaging an attempt approximately every 16 dives). Two of these were unsuccessful and one resulted in the capture of a giant cuttlefish (*Sepia apama*) by the mother. On the solo foraging trip, a total of 172 prey capture attempts were observed (averaging an attempt approximately every dive), with 44 (26%) of these attempts being successful.

Diving behaviour also differed between the two trips (Table 1). Bottom durations on the pup-accompanied trip (median = 71 s), were significantly shorter than those on the solo foraging trip (median = 112 s) (Wilcoxon rank-sum test: $U = 25468$, $P \leq 0.001$), as well as total dive durations, (median = 175 and 224 s, respectively) (Wilcoxon rank-sum test: $U = 21131$, $P \leq 0.001$). Bottom depths were also significantly shallower on the pup-accompanied trip (median = 45.0 m), compared to the solo foraging trip (median = 70.0 m) (Wilcoxon rank-sum test: $U = 12191$, $P \leq 0.001$).

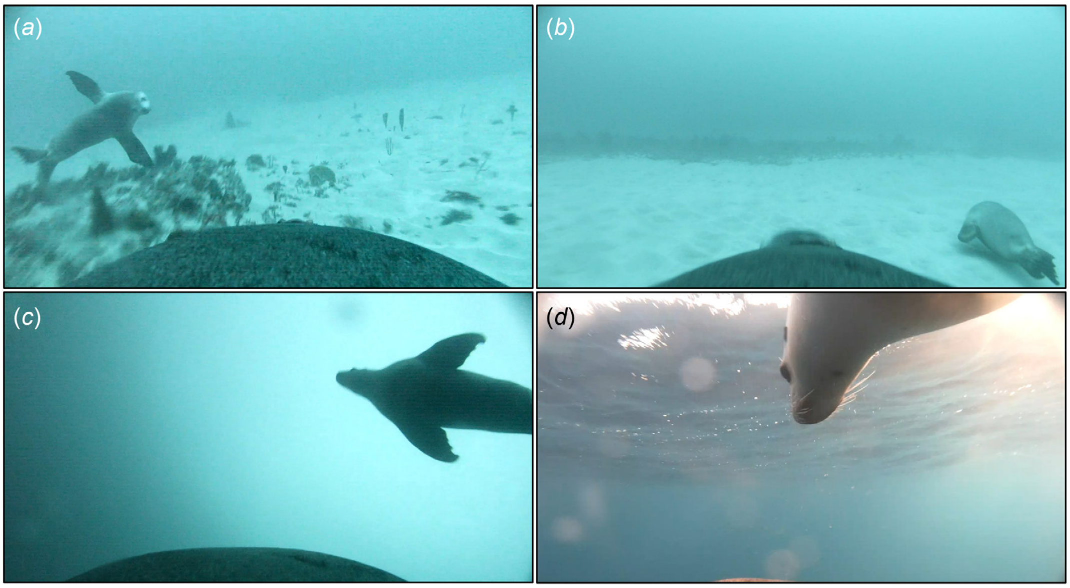

Fig. 2. Still images taken from an animal-borne video camera, attached to an adult female Australian sea lion, highlighting a pup-accompanied trip at sea: (*a*) travelling across sponge garden habitat, (*b*) swimming over bare sand habitat, (*c*) ascending, and (*d*) at the surface.

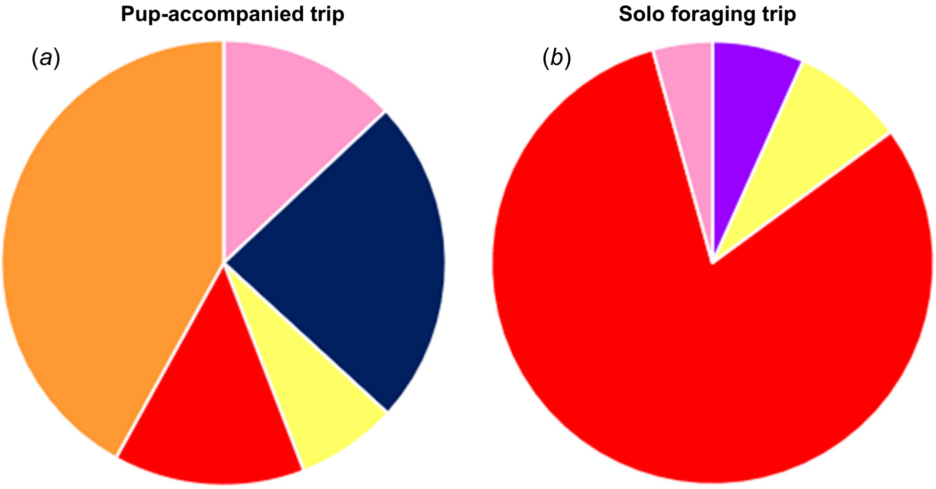

Fig. 3. Percentage of bottom time in different benthic habitats, identified from animal-borne video from an adult female Australian sea lion, on (*a*) a pup-accompanied trip, and (*b*) a solo foraging trip. Benthic habitats are highlighted for macroalgae reef (orange), macroalgae meadow (dark blue), invertebrate reef (red), sponge garden (pink), bare sand (yellow) and invertebrate boulder (purple) habitats.

Table 1. Summary of trip and dive data collected from a GPS logger and time–depth recorder from an adult female Australian sea lion, for a pup-accompanied trip and a solo foraging trip.

Trip	Trip duration (days, h, min)	Descent duration (s)	Ascent duration (s)	Bottom duration (s)	Dive duration (s)	Bottom depth (m)	Total dives	Dive frequency (h^{-1})
Pup-accompanied trip	0, 8, 3	44 (1–101)	48 (1–140)	71 (1–153)	175 (3–253)	45.0 (3.5–70.0)	152	18.9
Solo foraging trip	2, 21, 30	50 (1–172)	54 (1–258)	112 (1–283)	224 (3–378)	70.0 (3.5–92.0)	842	12.1

For descent, ascent, bottom and total dive durations and bottom depth, medians are provided with minimum and maximum values (in parentheses); all other metrics are otherwise specified.

Discussion

In this study, animal-borne video has revealed an 11-month-old Australian sea lion pup accompanying its mother on a trip to sea, providing direct evidence for mother-to-pup social transmission of foraging behaviour in an otariid species. Animal-borne video and movement data have also highlighted differences in the behaviour of the adult female between a pup-accompanied trip and a solo foraging trip at sea.

During the pup-accompanied trip, the pup was visible in 35 (~75%) of the 47 observed dives from the video data and may have been present but not observed in the remaining 12 dives. This indicates that while at sea, the pair were in close proximity and were diving together frequently, as observed in the video data. One successful predation of a giant cuttlefish (*S. apama*) was observed in the video data from the pup-accompanied trip; the cuttlefish was captured and brought to the surface for processing by the mother. Throughout this prey capture, the pup was swimming alongside the mother and attempting to consume part of the cuttlefish. Therefore, it is possible that the mother was demonstrating the location, capture and processing of prey to the pup. Although this observation of a joint foraging trip represents data from just one mother–pup pair (Supplementary Fig. S2), it raises fundamental questions around how common social transmission of foraging behaviour is in Australian sea lion populations, the role this behaviour may play in pup development and the period of nursing it may occur in.

The idea of social transmission of foraging behaviour has been postulated before in otariids (Franco-Trecu *et al.* 2016). For Australian sea lions, the notion was first put forward by Goldsworthy *et al.* (2009), to explain their unique 18-month reproductive cycle (Higgins 1993; Shaughnessy *et al.* 2011). Goldsworthy *et al.* (2009) suggest that as Australian sea lions target patchily distributed, cryptic benthic prey (McIntosh *et al.* 2006; Peters *et al.* 2015; Berry *et al.* 2017), pups require extensive experience and knowledge of foraging areas to hunt successfully. This hypothesis therefore proposes that the additional ~6+ months of maternal care, compared with other otariids (Costa 1991; Atkinson 1997), may provide the time and opportunity for pups to accompany mothers at sea to help develop their foraging skills. Other mammals that exhibit social transmission of foraging behaviour to young also typically share prolonged maternal investment in their offspring, such as orcas (*Orcinus orca*), chimpanzees (*P. troglodytes*) and bottlenose dolphins (*Tursiops* sp.) (Mann and Sargeant 2003; Lonsdorf 2006; Weiss *et al.* 2023). In these species, social transmission of information is thought to be crucial to the development of young (Estes *et al.* 2003; Lonsdorf 2006; Sargeant and Mann 2009). In bottlenose dolphins (*Tursiops* sp.) and orcas (*O. orca*), for example, strong specialisation to foraging behaviours and dietary preferences is even thought to change the selection pressures on genes (Ford and Ellis 2006; Kopps *et al.* 2014), thus driving the structure of populations (Morin *et al.* 2010; Riesch *et al.* 2012).

The exact role and importance of social transmission on the development of foraging behaviour in Australian sea lions is unclear. It is not known how prevalent this behaviour is across their distribution, and how frequently or from what age pups join mothers at sea. Australian sea lion pups likely begin undertaking foraging trips at 4–6 months old and gradually gain nutritional independence from 12 to 15 months old (Fowler *et al.* 2007; Lowther and Goldsworthy 2012, 2016). Although pups begin exploring the habitats utilised by adult females from 10 months old (Lowther and Goldsworthy 2012), data suggest that juveniles at 23 months old do not have the movement or diving capabilities of adult females (Fowler *et al.* 2006, 2007). As the pup in this study was 11 months old, over the final ~7 months of the nursing period the pup may have progressed its foraging abilities, both on trips with its mother and independently. Following weaning (at ~18 months old), the pup would therefore have continued to develop its foraging skills, building on the experience gained during the nursing period.

Future deployments of animal-borne cameras and biologging technology on adult females with known-age pups could improve our knowledge on the timing and importance of social transmission on the development of foraging behaviour in Australian sea lions. The presence of a social component to foraging in Australian sea lions could also have important conservation implications, such as whether mother–pup foraging trips increase or decrease predation risk, for example, to white sharks (*Carcharodon carcharias*) (Shaughnessy *et al.* 2007), as well as the risk of interactions with fisheries (Hamer *et al.* 2013; Goldsworthy *et al.* 2022). Presumably, taking pups to sea is also physiologically costly for mothers, as predation events and foraging gains are likely reduced on joint mother–pup foraging trips. Therefore, investigating the trade-offs of joint foraging trips to mothers, specifically the potential benefits imparted to pups in increasing their foraging/diving abilities, relative to the energetic costs to mothers, could be important for understanding pup survival, broader population dynamics and the conservation and management implications of these. These insights would help to deepen our understanding of the factors that may have shaped the unique 18-month reproductive cycle and life-history of Australian sea lions. The use of animal-borne cameras is continuing to provide novel and fundamental information on the foraging behaviour of Australian sea lions, highlighting their utility in contributing unique insights into the foraging behaviours of many pinniped species.

Supplementary material

Supplementary material is available online.

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Data availability. The datasets presented in this study are available in the online repository at: https://metadata.imas.utas.edu.au/geonetwork/srv/eng/catalog.search#/metadata/84cb1709-a6694f2c-b97b-5eceb7929349.

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