

# The paradox of learned song in a semi-solitary mammal

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## Abstract

Learning can occur via trial and error; however, learning from conspecifics is faster and more efficient. Social animals can easily learn from conspecifics, but how do less social species learn? In particular, birds provide astonishing examples of social learning of vocalizations, while vocal learning from conspecifics is much less understood in mammals. We present a hypothesis aimed at solving an apparent paradox: how can harbor seals (*Phoca vitulina*) learn their song when their whole lives are marked by loose conspecific social contact? Harbor seal pups are raised individually by their mostly silent mothers. Pups' first few weeks of life show developed vocal plasticity; these weeks are followed by relatively silent years until sexually mature individuals start singing. How can this rather solitary life lead to a learned song? Why do pups display vocal plasticity at a few weeks of age, when this is apparently not needed? Our hypothesis addresses these questions and tries to explain how vocal learning fits into the natural history of harbor seals, and potentially other less social mammals. We suggest that harbor seals learn during a sensitive period within puppyhood, where they are exposed to adult males singing. In particular, we hypothesize that, to make this learning possible, the following happens concurrently: (1) mothers give birth right before male singing starts, (2) pups enter a sensitive learning phase around weaning time, which (3) coincides with their foraging expeditions at sea which, (4) in turn, coincide with the peak singing activity of adult males. In other words, harbor seals show vocal learning as pups so they can acquire elements of their future song from adults, and solitary adults can sing because they have acquired these elements as pups. We review the available evidence and suggest that pups learn adult vocalizations because they are born exactly at the right time to eavesdrop on singing adults. We conclude by advancing empirical predictions and testable hypotheses for future work.

## KEYWORDS

harbor seal, oblique cultural transmission, sensitive phase, social learning, song learning, vocal production learning

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## 1 | VOCAL LEARNING: THE CASE OF PINNIPEDS

The ability to learn can enhance an individual's fitness, especially in response to rapidly changing conditions. While learning can happen in isolation via trial and error, social learning is faster and less costly (van Schaik, 2010; Zentall, 1996). Birdsong and human speech are examples of socially learned vocal behaviors (Baptista & Petrinovich, 1986). Vocal learning occurs when an animal is capable of modifying its vocal output based on experience with other individuals (Janik & Slater, 1997), and thereby is a form of social learning; a bird imitating nearby sounds or humans learning a new language are clear examples of this capacity. Vocal learning is extremely rare in mammals; only humans, pinnipeds (in particular phocid seals), cetaceans, elephants, and bats show this remarkable capacity (Crance et al., 2014; Favaro et al., 2016; Lattenkamp et al., 2020; Ralls et al., 1985; Stansbury & Janik, 2019; Stoeger et al., 2012; Torres Borda et al., 2021).

Several frameworks developed over the past decade aimed at characterizing the vocal learning phenotype: Vocal learning has been hypothesized to consist of several modules (discrete subtraits, Wirthlin et al., 2019), or multiple dimensions (Vernes et al., 2021). Petkov and Jarvis (2012) suggest to move away from the presence-absence dichotomy of this trait. Martins and Boeckx (2020) argue for a more permissive view, encompassing more aspects of vocal learning. All these different approaches see vocal learning as a non-binary trait. In particular, the modular framework decomposes vocal learning into three non-exhaustive modules: *vocal coordination*, *vocal production variability*, and *vocal versatility* (Wirthlin et al., 2019). Harbor seals (*Phoca vitulina*) seem one of the few mammals having all these three modules. They show turn-taking behavior (vocal coordination; Anichini et al., 2023; Ravignani et al., 2019), and external sound sources influence their vocal variability (vocal production variability; Ralls et al., 1985; Torres Borda et al., 2021). Harbor seal call diversity is interestingly limited compared to that of other phocids (earless seals) (Terhune, 2019) while showing an elaborate ability to modify vocalizations (vocal versatility; Duengen et al., 2023; Ralls et al., 1985). Harbor seals are vocal learning mammals that display species-specific breeding "songs" (Hanggi & Schusterman, 1994; Van Parijs, 2003). These seals are among the least social pinnipeds; their social system could be described as solitary with temporary gregariousness. While vocal learning commonly occurs among birds also in less social species (Brown & Long, 2007), this trait is only sporadically found in mammals. Interestingly, wherever mammalian vocal learning *does* appear, it usually does so in socially complex species (Janik & Knörnschild, 2021; Prat et al., 2017; Stansbury & Janik, 2019; Stoeger et al., 2012; Tyack, 2008). In this short paper, we present and try to solve an apparent paradox: that of the harbor seals, semi-solitary mammals that sing a song they have likely socially learnt but who experience very loose conspecific social contact throughout their lives. From who do they learn their song, and when?

## 2 | THE PARADOX OF HARBOR SEALS' VOCAL LEARNING

Several vocal learning species, including some birds and whales, sing learned songs during the breeding season (Catchpole, 1987; Croll et al., 2002; Smith et al., 2008). Although less studied, songs are also common in phocid seals (Jones et al., 2014; Ray et al., 1969; Terhune, 2019), mediating territorial defense and female attraction (Mesnick & Ralls, 2009; Van Parijs, Lydersen, & Kovacs, 2003). Once sexually mature, harbor seals may deploy their vocal learning capacity (Ralls et al., 1985; Torres Borda et al., 2021) to sing extensively during the breeding season (Hanggi & Schusterman, 1994; Van Parijs et al., 1997). In harbor seals, only males sing, performing stereotypic vocal and visual displays, with some variability at the individual and geographic level (Van Parijs et al., 1997; Van Parijs, Hastie, & Thompson, 2000). Though other vocal types occur, the roar seems to be the only vocalization across all study sites associated with breeding (Björgesæter et al., 2004; Hanggi & Schusterman, 1994; Hayes, Kumar, et al., 2004; Van Parijs, Hastie, & Thompson, 2000), and shows geographic variation with significant inter- but little intraindividual variation (Hanggi & Schusterman, 1994; Nikolich et al., 2016; Van Parijs, Hastie, & Thompson, 2000). Björgesæter et al. (2004) suggest that geographic variation may stem from pups: they would partially learn the roar in their breeding areas, wander off, and develop this vocalization with modifications in a new "colony."

Roar series are termed "breeding vocalizations" or "breeding calls" (Matthews, Parks, et al., 2017; Nikolich et al., 2016) and occasionally songs (Fitch, 2006). Mounting evidence suggests that these breeding vocalizations are indeed a song-like display: Hanggi and Schusterman (1994) identified five underwater vocalizations with significant individual differences, where the roar was often combined with what was termed a "bubbly growl," and often occurred in succession. Indeed, harbor seals exhibit a rather complex breeding display, consisting of a combination of bubble blowing, vocalizing, and flipper slapping (Boness et al., 2006). Their song typically starts with pulsed low-frequency sequences followed by a more broadband roar "burst" and can be repeated over many hours (Björgesæter et al., 2004; Hanggi & Schusterman, 1994; Matthews, Parks, et al., 2017; Nikolich et al., 2016; Sabinsky et al., 2017). Definitions of song abound (Spector, 1994). Some require a general context of territoriality or breeding (Odom et al., 2014), whereas others ignore context but require vocalizations to be complex and learned (Fitch, 2006). The songs of harbor seals may not be as elaborate or harmonious as those of songbirds and whales but, according to the definition by Fitch (2006), where songs are a "complex, learned vocalization," they are songs.

What kind of sounds do harbor seals produce before sexual maturity? Over their first years of life, seal pups only regularly vocalize during the first weeks after birth. Mothers raise their pup alone and rarely vocalize, only in agonistic displays (Hanggi & Schusterman, 1994). Pups are extremely vocal, producing contact calls towards the mother, and already show developed vocal

plasticity at 2 weeks of age (Anichini et al., 2023; Torres Borda et al., 2021). Once weaned, a harbor seal presumably remains silent, except for occasional growling (Nicholson, 2000) or guttural threats, until sexual maturity (Bigg, 1981; Casey et al., 2021); at this time, the individual engages in singing, that is, it produces vocal displays to attract potential mating partners and defend the territory. From birth till death, harbor seals conduct a rather solitary life: during puppyhood the only social contacts are with their mostly silent mothers and later, during haul-outs (for resting, pupping and nursing, or molting). Pups never encounter their father but show species- and sex-specific breeding vocalizations once sexually mature (Hanggi & Schusterman, 1994; Van Parijs et al., 1997), which raises the question: *do* male harbor seals learn their breeding vocalizations, and if so, *how* do they learn them?

Harbor seal breeding vocalizations could be innate and actively adjusted in spectral and/or temporal properties to demonstrate fitness. For instance, seals could attempt to sound bigger than they are, as other mammals do (Reby & McComb, 2003), or elongate roars to demonstrate a lung volume free of lungworm infections (Sabinsky et al., 2017). However, adults are considerably less susceptible to lungworm infections than juveniles (Measures, 2018; Ulrich et al., 2016), so the evolutionary pressure to signal health from a disease rarely occurring in adult individuals should be low. Supporting this idea, one study showed no significant female preference for any duration of broadcasted roars (Matthews et al., 2018). Duration is not used in mate choice, though highly variable among individuals and populations (Björgesæter et al., 2004; Nikolich et al., 2016; Van Parijs, Corkeron, et al., 2003), thereby arguing against the lungworm hypothesis (Sabinsky et al., 2017). Harbor seals follow acoustic allometry (de Reus et al., 2022), that is, an individual's vocalization accurately encodes their body size. Yet, these animals break allometry by vocal production learning, suggesting vocal control (de Reus et al., 2022). Harbor seals show vocal plasticity, a building block of vocal learning, extremely early in life, at 1–3 weeks of age: Seal pups lower their fundamental frequency when exposed to noise specifically overlapping with this frequency (Torres Borda et al., 2021). Moreover, a case study documented a human-raised harbor seal imitating its former caretaker's vocalizations once sexually mature (Duengen et al., 2023; Ralls et al., 1985), and wild harbor seals seem to exhibit dialects, potentially acquired by vocal learning (Van Parijs, Corkeron, et al., 2003; Van Parijs, Hastie, & Thompson, 2000). While these data do not directly show that harbor seal songs are learned, they provide important contextual information. The established presence of vocal mimicry and flexibility in harbor seals (Duengen et al., 2023; Ralls et al., 1985; Torres Borda et al., 2021) begs the question of what this capacity is used for. We suggest that vocal learning is used to learn breeding songs as the most parsimonious explanation. Vocal learning is extremely rare in mammals but appears in harbor seals, with a yet unknown ecological function; learning a song may be exactly this function.

While all these data support vocal production learning in harbor seals, no controlled experiment to date has examined this capacity in adults, raising three key questions: How can this solitary marine

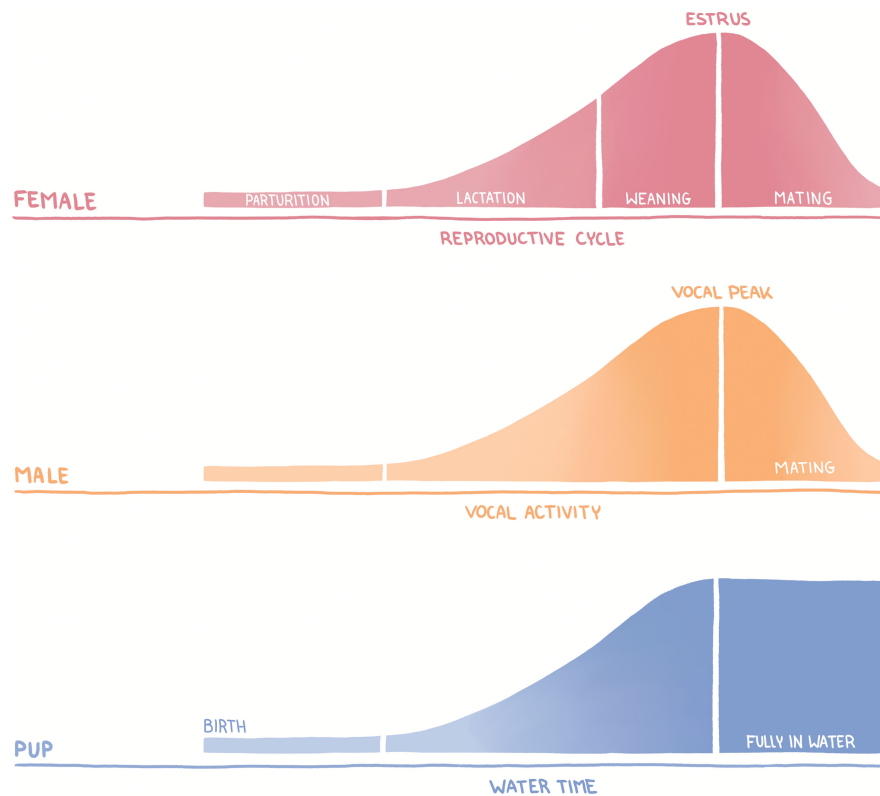
mammal learn its song? How can adult males display complex songs if their lives are marked by loose conspecific social contact? And why should pups already display enhanced vocal learning skills for no apparent purpose? The answers to these three questions may be linked. Here we present a hypothesis of vocal transmission which, while potentially obvious for some avian species, could help answer these questions for seals and some other mammals. We also propose concrete steps to investigate the conundrum of vocal learning in this semi-solitary mammal.

### 3 | THE VOCAL LEARNING–OBLIQUE CULTURAL TRANSMISSION HYPOTHESIS

Our hypothesis tries to explain vocal learning over the life span in harbor seals while addressing the questions above. From a functional and developmental perspective, we suggest that pups have vocal learning capacities so that already in puppyhood they can acquire elements of their adult song from adult conspecifics. From a mechanistic and phylogenetic perspective, we suggest that pups are born at an ideal time of the year to hear adult males and hence learn their sounds by eavesdropping.

Cultural transmission can be horizontal, that is, between individuals of the same age, vertical, that is, from individuals who are genetic or social parents, or oblique (Cavalli-Sforza et al., 1982). Our hypothesized dynamics dovetail with the “oblique cultural transmission” framework, described by Cavalli-Sforza et al. (1982) as “transmission from nonparental individuals of the parental generation to members of the filial generation” (p. 20). In fact, this type of learning is quite common among *social* species with overlapping generations and long parent-offspring associations, such as some birds, nonhuman primates, and bats (Beecher et al., 2007; Prat et al., 2017; Tagliatalata et al., 2012; van Schaik, 2010). Forms of oblique cultural transmission are well established in some avian species, where juveniles learn songs from non-kin adults (Beecher, 2017; Kroodsma, 1974; Williams, 1990). Harbor seals do not sing during adolescence, and there is no evidence for other forms of horizontal transmission. In addition, harbor seals are not a socially complex species where a pup associates with its social/genetic father, and no general evidence of vertical transmission exists. Ruling out horizontal or vertical transmission, we suggest that oblique cultural transmission is the most parsimonious explanation in harbor seals.

Building on Björgesæter et al. (2004) and Cavalli-Sforza et al. (1982), we hypothesize that adult vocalizations in seals are socially learned by a seasonal overlap of behaviors from pups, adult males, and adult females. First, pups may enter a sensitive learning phase (similar to that of some open-ended learning birds; Cornez et al., 2020; Orije et al., 2021) a few weeks before and after weaning (Figure 1, “female” timeline). Second, pups' sensitive learning phase coincides with their intense foraging expeditions at sea (Figure 1, “pup” timeline; Skinner, 2006). Third, pups' sea explorations coincide, in turn, with the time of the year in which adult male harbor



**FIGURE 1** Infographic (exemplifying probability-like estimates on the y axis and time and the x axis) of harbor seals' female reproductive cycle (red), vocal activity of males (orange), and pup water time (blue) (Atkinson, 1997; Boness et al., 2006; Fisher, 1954; Galatius et al., 2020; Hayes, Costa, et al., 2004; Matthews, Gabriele, & Parks, 2017; Reijnders, 1990; Skinner, 2006). Female estrus, peak of male vocal activity, and pup's increased water time - on the right side of the graph - coincide. We hypothesize oblique cultural transmission to occur during this latter period. If the circannual timing of any of these cycles were considerably shifted, oblique learning could not occur as easily.

seals peak in their singing activity (Figure 1, "male" timeline; Hayes, Costa, et al., 2004; Matthews, Gabriele, & Parks, 2017).

More specifically, we hypothesize multiple co-occurring dynamics. Harbor seals may have a lek-type mating system, where females select males (Boness et al., 2006), potentially based on vocal parameters, as in some fish, frog, and bird species (Gerhardt, 1991; Myrberg Jr et al., 1986; Ritschard et al., 2010). Adult males perform extensive underwater vocal displays spatially close to females in estrus (Hayes, Kumar, et al., 2004; Sullivan, 1981; Van Parijs et al., 1999). During female estrus, male acoustic activity peaks (Figure 1, "female" and "male" timelines; Boness et al., 2006; Hanggi & Schusterman, 1994; Hayes, Kumar, et al., 2004; Van Parijs et al., 1997). Females roam male territories freely accompanied by their pups (Hayes, Costa, et al., 2004), during which pups are likely exposed to male calls, which may enhance learning. Females without pups enter estrus 2 weeks later than females with pups (Atkinson, 1997; Reijnders, 1990). In other words, having a pup alters the mothers' reproductive biology so that their pups have 2 extra weeks of male singing exposure. Right after a pup is weaned, its mother enters estrus and mates, therefore, pups spend most time in the water as they now must forage independently (Figure 1, "female" and "pup" timelines; Fisher, 1954; Reijnders, 1990). Pups swim and dive at birth (Bowen et al., 1999; Greaves et al., 2005; Jørgensen et al., 2001) and are nursed for a period of maximum 6 weeks (Bigg, 1981; Skinner, 2006). Pups spend up to 60% of their time in the water (Bowen et al., 1999; Jørgensen et al., 2001; Skinner, 2006); pups' time in water increases with age, in synchrony with males increasingly singing at sea (Figure 1, "male" and "pup" timelines). As a result, both before and after weaning,

pups are substantially exposed to male breeding vocalizations. This period may start during the last weeks of lactation (~3–4 weeks of age) and end a few weeks after weaning (~6–7 weeks of age). All this shows that seals' chronobiology is consistent with the hypothesis that harbor seals may learn song via oblique cultural transmission during puppyhood.

#### 4 | CONVERGING EVIDENCE FROM BIRDS AND PINNIPEDS

The cultural transmission of vocalizations we hypothesize in the semi-solitary harbor seal is quite rare in *non-social mammals* but may occur in a few social ones, such as the naked-mole rat (*Heterocephalus glaber*) (Barker et al., 2021), grey seal (*Halichoerus grypus*) (Stansbury & Janik, 2021), and some cetaceans (for a review, see Garland & McGregor, 2020). This rarity may stem from a lack of evidence rather than negative evidence because vocal learning in mammals is much less studied than in birds. This leads to a knowledge gap: what are the dynamics of vocal learning in less social mammals?

Research on bird song learning suggests similar learning dynamics to those we hypothesize for mammals. Two concepts easily carry over to our framework: open-ended vs. closed-ended learning and sensitive phases (Beecher & Brenowitz, 2005; Johnson & Clark, 2022; Todt & Geberzahn, 2003). Closed-ended learners such as zebra finches (*Taeniopygia castanotis*) or white-crowned sparrows (*Zonotrichia leucophrys*) exclusively learn song as juveniles during a sensitive period (Nelson et al., 1997). In contrast, open-ended

learners such as canaries or parrots learn throughout their lifetime. In addition, seasonality modulates vocal learning strategies: some closed-ended learning species have a second sensitive period in the following spring, e.g., nightingales (*Luscinia megarhynchos*), and some open-ended learners show a seasonal sensitive phase, e.g., canaries (Brainard & Doupe, 2002; Nottebohm et al., 1987; Voigt & Leitner, 2008). Within this framework, and based on the evidence reviewed above, we suggest harbor seals to learn their breeding songs during a sensitive phase of ~3–7 weeks of age.

Patchy evidence from other pinnipeds seems to support our hypothesis. The closely related grey seals may show similar vocal learning strategies: in a recent experiment, wild pups copied playback stimuli, becoming more accurate in imitations over time (Stansbury & Janik, 2021). Their fundamental frequency ( $f_0$ ) matching became especially pronounced around 2–3 weeks of age, which

may denote a sensitive period and cultural transmission of vocalizations in this phocid species (Stansbury & Janik, 2021). Further support comes from the case of Hoover, a human-raised harbor seal pup (Ralls et al., 1985). Daily, over his first few months of life, Hoover received auditory input from his caretaker and occasionally responded (Swallow, 2001). He was then transferred to an aquarium and stopped vocalizing. Crucially, once he reached sexual maturity, Hoover started to repeat the human utterances heard as a pup (Ralls et al., 1985). This clear imitation of speech was untrained and particularly pronounced during the breeding season (Duengen et al., 2023). Hoover's anecdote dovetails with key elements of our hypothesis, formulated for wild seals, namely that harbor seal breeding vocalizations are (i) learned, (ii) achieved by matching an auditory template, and (iii) acquired at a specific, early age during puppyhood.

**TABLE 1** The vocal learning-oblique cultural transmission hypothesis generates alternative predictions, namely that seals are open- or closed-ended vocal learners, pups may have a sensitive phase crucial for learning, and synchrony of life stages play a role in acquiring breeding vocalizations.

Prediction	Testing	Expected result
Harbor seal pups have a sensitive phase of vocal learning	Conduct playback experiments broadcasting altered pup calls (e.g., following Stansbury & Janik, 2021) to probe the convergence of vocalizations toward playback stimuli. Perform these experiments starting at different ages (e.g., 2, 4, 6, 8 weeks) to measure the degree of similarity between pup vocalizations and auditory input over time, and ultimately quantify vocal imitation across age groups	Pups exposed to playbacks adjust their own vocal parameters toward those of the playbacks. A comparison between different age groups shows in which age class pups learn most efficiently and pinpoint the time window of the sensitive phase
	Expose captive male pups of different ages to playbacks of male breeding vocalizations. Record pups once sexually mature to test the (spectral and/or temporal) similarity between their vocalizations and the adult models	Acoustic features in a sexually mature individual are closer to playbacks heard during the sensitive phase than to other adult vocal displays sampled from the population
	Record wild pups via passive acoustic tags until sexual maturity to track auditory input and vocal output	An individual, once sexually mature, shows a song closer to that of males heard during puppyhood than to males heard in the following years
Pups and adult males show synchrony of life stages	Record sounds from and observe populations of wild seals (e.g., from Ireland to Estonia) to test whether an earlier pupping season predicts an earlier singing activity peak in adults	If life stages are synchronized (as in Figure 1), harbor seal populations will show a correlation between male singing activity peak and pup's increased time expenditure at sea
Harbor seals are open-ended vocal learners, with a (i) seasonally reoccurring sensitive phase, (ii) decreased acquisition flexibility over time, or (iii) constant vocal learning capacity throughout all life stages	Perform active training of $f_0$ - and/or formant shifts outside an adult harbor seals' natural frequency range to provide insight into underlying vocal learning mechanisms. Alternatively, train vocal mimicry to probe whether an animal instantaneously imitates playbacks (e.g., Stansbury & Janik, 2019). Carry out training and testing at different times of the year (i) and during different life stages (ii, iii). The degree of similarity between the model and imitation might identify a seasonally reoccurring sensitive phase (i), or a decreased (ii), or constant (iii) vocal learning capacity throughout life	If harbor seals are open-ended learners, adult harbor seal calls' $f_0$ - and/or formant modulation and/or vocal mimicry capacities will (i) periodically oscillate, (ii) monotonically decrease with age, or (iii) remain constant throughout life stages
Harbor seals are closed-ended vocal learners	Carry out training and testing of vocal modification during different life stages, as described above, to test for the presence or absence of harbor seals' vocal production learning capacities	If harbor seals are closed-ended vocal learners, they will excel at vocal production learning as pups but show no evidence of this capacity beyond puppyhood

Note: Within one of the main existing frameworks, these experiments address mostly the modules of vocal production variability and vocal versatility (Wirthlin et al., 2019).

These examples have concrete implications for our hypothesis. In particular, harbor seals could be (i) closed-ended learners that exclusively learn during the sensitive phase, (ii) open-ended learners with a seasonally re-occurring sensitive period, (iii) open-ended learners, with an enhanced sensitive period followed by a decreasing potential for acquiring novel vocalizations over development, or (iv) open-ended vocal learners with a constant vocal learning capacity throughout all life stages. Testing our hypothesis in seals and disentangling these mechanisms will require a series of experiments (Table 1).

## 5 | TESTABLE PREDICTIONS AND ALTERNATIVE HYPOTHESES

Our vocal learning-oblique cultural transmission hypothesis describes the occurrence of a sensitive phase in harbor seal pups as the most parsimonious explanation for acquiring breeding vocalizations. Yet whether seals are open-ended or closed-ended learners is unclear, and each scenario generates alternative, testable predictions. Our predictions focus on two of the modules suggested by Wirthlin et al. (2019): *vocal production variability* and *vocal versatility*. The capacity for *vocal coordination* in the harbor seal has been preliminary shown and would be worth further study as well (Anichini et al., 2023; Ravignani, 2019). Testing these predictions will reveal where harbor seals lie on the gradient spanning from open-ended to closed-ended learning. Table 1 summarizes testable predictions and alternative scenarios stemming from our hypothesis.

As harbor seals are mostly silent until sexual maturity, one might wonder how they maintain their learned songs until song deployment. Harbor seals may behave like canaries, open-ended learners who show a re-occurring seasonal propensity for vocal learning. For a species with such high site fidelity (Cordes & Thompson, 2015; Dietz et al., 2013), seasonal auditory input may facilitate template construction; it is also compatible with the observed geographic variation of songs (Van Parijs et al., 1999; Van Parijs, Hastie, & Thompson, 2000, Van Parijs, Janik, & Thompson, 2000). One may argue that the most well-known case of vocal production learning in this species features a seal imitating human speech heard as a pup, but not imitating novel models, such as aquarium visitors. This instance may argue against open-ended learning, or for open-ended learning with a decreased potential for acquiring novel vocalizations over development. However, if vocal learning mediates reproductive success, this criticism is moot: Hoover was a reproductively highly successful individual at the aquarium and may not have had the need to vocally adjust.

## 6 | CONCLUSIONS

In this paper, we point to an apparent paradox in behavioral ecology: how can a semi-solitary mammal learn its song? We suggest that it does so by oblique cultural transmission: pups learn songs from

non-parental males via a fine-tuned temporal overlap among male, female, and pup life stages. We formulate our hypothesis by combining evidence from behavioral ecology, cognition, and bioacoustics in seals, drawing parallels from other species whose vocal learning and cultural transmission are better understood. The value of our hypothesis is (i) showing how a general theoretical framework for cultural evolution could be applied to mammalian vocal behavior, (ii) concurrently filling multiple gaps and open questions in pinnipeds' behavioral ecology, and (iii) providing a framework potentially applicable to other species. Although speculative, our hypothesis is consistent with all available data, and most importantly, it offers testable predictions. We hope that it will generate future empirical work to falsify or support it.

### AUTHOR CONTRIBUTIONS

**Diandra Duengen:** Conceptualization; Investigation; writing – original draft; writing – review and editing. **Andrea Ravignani:** Conceptualization; Project administration; Supervision; Resources; writing – review and editing.

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The authors declare that they have no conflict of interest.

### DATA AVAILABILITY STATEMENT

Not applicable.

### ETHICS STATEMENT

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