



Anecdotal Observations of Socially Learned Vocalizations in Harbor Seals

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Abstract – Harbor seals (*Phoca vitulina*) are more solitary than many other pinnipeds. Yet, they are capable of vocal learning, a form of social learning. Most extant literature examines social animals when investigating social learning, despite sociality not being a prerequisite. Here, we report two formerly silent harbor seals who initiated vocalizations, after having repeatedly observed a conspecific receiving food rewards for vocalizing. Our observations suggest both social and vocal learning in a group of captive harbor seals, a species that lives semi-solitarily in the wild. We propose that, in this case, social learning acted as a shortcut to acquiring food rewards compared to the comparatively costly asocial learning.

Keywords – *Phoca vitulina*, Marine mammal, Vocal learning, Social learning, Semi-solitary

Vocal learning, a form of social learning, is the ability to learn the form, function, or context of vocalizations through experience (Janik & Slater, 2000). While research has often focused on the form and function of vocal learning in humans and songbirds (e.g., see Petkov & Jarvis, 2012), this skill has been observed across a range of taxa (Tyack, 2020). In their seminal review, Janik and Slater (2000) established a framework to investigate how social learning might influence vocal communication (see Table 1), distinguishing between *vocal production* – learning *how* sounds should be produced – and *contextual learning* - learning *when* sounds should be produced. This distinction is important: while some animals may learn both how and when to produce a vocalization, these capacities are potentially independent. More recently, Vernes et al. (2021) expanded upon Janik and Slater’s framework by further qualifying forms of both usage and production learning. For example, when considering usage learning, Vernes et al. (2021) distinguished between the learning of a vocalization in a new context (e.g., blackbirds learning to alarm call to novel stimuli after observing conspecific behavior, Curio et al., 1978), and learning how to time vocalizations. Meanwhile, research on vocal production learning examines a range of learning criteria across species, including the accuracy, flexibility, or timing of vocal learning (Vernes et al., 2021). The framework provides an excellent basis on which to explore the range of behaviors linked to vocal learning. Open questions remain, in particular regarding the mechanisms underpinning the dimensions of vocal learning (Vernes et al., 2021).

Table 1*Relevant Terminology in the Field of Vocal Learning*

Term		Definition	Example
Vocal Production Learning		Modifying an already existing vocalization or innovating/imitating a novel one through experience with other individuals or sounds (Janik & Slater, 2000).	In a cross-fostering study, Favaro et al. (2016) found a captive Risso's dolphin (<i>Grampus griseus</i>) vocalizations more similar to its dolphin (<i>Tursiops truncatus</i>) pool mates than to that of its own species.
Vocal Contextual Learning	Vocal Usage Learning	Using an already existing vocalization in a new context as a result of experience (Janik & Slater, 2000).	In a playback study, Seyfarth and Cheney (1986) revealed that vervet monkeys (<i>Cercopithecus aethiops</i>) learn to use vocalizations in appropriate contexts.
	Vocal Comprehension Learning	Understanding a (novel) meaning of an already existing vocalization as a result of experience (Janik & Slater, 2000).	Magrath et al. (2015) showed in a playback study that superb fairy-wrens (<i>Malurus cyaneus</i>) learn to identify and respond to previously unfamiliar calls.

Learning by Observation

Species with higher sociality are more prone to social learning by increased opportunities for individuals to acquire information from another, such as when living in groups (Allen, 2019). Mounting evidence shows, however, that social learning is not restricted to social species, reflected in red-footed tortoises (*Chelonoidis carbonarius*) (Wilkinson et al., 2010), common octopi (*Octopus vulgaris*) (Fiorito & Scotto, 1992), and bearded dragons (*Pogona vitticeps*) (Kis et al., 2015). Heyes (2012) argued that social and asocial learning are mediated by the same learning mechanisms, proposing that social learning is not social by means of distinct learning mechanisms. Rather, the same associative processes underly learning, supported by a positive correlation of social and asocial learning in several species (Heyes, 2012). This seems reasonable, as social learning increases learning of more skills, at a faster rate, and avoids the need for costly innovations (Van Schaik & Burkart, 2011; Whiten & Van Schaik, 2007). In fact, social learning occurs in insects, fishes, amphibians, reptiles, and mammals (for a review see Whiten, 2017). Species also learn socially from other species, for instance, llamas (*Lama glama*) use information from both conspecifics and humans to solve a spatial problem (Pahl et al., 2023). A captive-housed walrus (*Odobenus rosmarus divergens*) spontaneously used a toy to produce sound underwater and two more walruses residing in the same pool adopted this behavior within one year of the initial observation (Reichmuth & Quihuis, 2022).

Despite lacking clear evidence of harbor seals learning by the observation of conspecifics, they seem to learn from humans: A male adult harbor seal under human care, Hoover, likely imitated human speech sounds that he heard as a pup (Duengen et al., 2023; Ralls et al., 1985). This case of vocal production learning was followed by reported instances of usage learning, where the seals learned vocal variants (Moore, 1996; Ralls et al., 1985) and to produce specific vocalizations upon presentation of a discriminative cue (Schusterman, 2008, Duengen & Ravnani, 2024, Duengen et al., 2024).

Harbor Seals: Solitary Mammals with Temporary Gregariousness

Harbor seals (*Phoca vitulina*) are socially less complex than other pinniped species (Bigg, 1981; following the framework by Kappeler, 2019): Their social organization fluctuates between solitary and group living –swimming and foraging solitarily, but temporarily aggregating in unstable, large groups on sandbanks, rocks, or beaches to rest, thermoregulate, molt and pup (Hamilton et al., 2014). The social structure of harbor seals is not entirely understood; they might have a size, male and/or age-based dominance hierarchy, potentially driven by space availability (Neumann, 1999; Sullivan, 1982). Yet, harbor seals prefer a well-spaced distance to their conspecifics (Davis & Renouf, 1987), do not interact much within their extensive haul-outs and lack stable social units (Godsell, 1988). In their lek-type mating system, males aggregate and display near females, with some variability in mating tactics (Boness et al., 2006).

Despite pupping in aggregations, no cooperative breeding occurs in the harbor seals' care system: females raise their offspring solitarily, with a short nursing period of 3-6 weeks (Cottrell et al., 2002; Muelbert & Bowen, 1993; Skinner, 2006).

Interestingly, most social – and vocal – behavior seems to occur during breeding: Harbor seal pups call during the nursing period (Renouf, 1984) and become primarily silent until sexual maturity at 5 - 7 years of age (Bjørge et al., 1995; Casey et al., 2021). Adult females rarely vocalize (Insley et al., 2003), except during agonistic interactions (Van Parijs & Kovacs, 2002). Adult males sing during breeding season and perform extensive visual and vocal displays (Bjørge et al., 1995; Nicholson, 2000). These consist of pulsed low frequency sounds, a 'roar' vocalization, bubble blowing, and flipper slapping (Boness et al., 2006; Hanggi & Schusterman, 1994; Van Parijs et al., 2000) and are thought to serve female attraction, and territory defense (Hayes et al., 2004; Nikolich et al., 2018).

Vocal flexibility occurs in harbor seals and closely related phocids as early as a few weeks after birth (de Reus et al., 2022; Stansbury & Janik, 2021; Torres Borda et al., 2021), and converging evidence suggests both vocal production and contextual learning in adults (Duengen et al., 2024; Garcia & Ravignani, 2020; Ralls et al., 1985; Ravignani & Garcia, 2022; Schusterman, 2008; Stansbury & Janik, 2019). Can this species acquire vocalizations via social learning? Here, we present anecdotal evidence of socially learned vocal behavior, and argue for framing this behavior within vocal and social learning. We discuss potentially underlying learning mechanisms, and suggest more research in diverse animal taxa. Although far from a controlled experiment, we hope our report encourages future experimental work under controlled conditions.

Methods

Ethical Approval

All behavioral experiments were conducted according to the requirements of the Landesamt für Natur, Umwelt und Verbraucherschutz NRW, Germany, section animal experiment affairs (file Az. 81-04.78).

Observation

The reported observations occurred in a group of four adult harbor seals (females L and E, males J and R) residing with three juveniles (males M, S, and R) in a 230,000-liter freshwater pool of a 300 m² enclosure. All animals were housed at Zoo Cleves, Germany, and were born in human care (see Table 2). The seals were trained twice per day (see below) on six days/week, with sessions ranging from 30 to 60 minutes. The zoo staff conducted one training session per day, which involved medical training and enrichment. A second session, research training, was conducted by an experimenter. Research training was conducted for a different study (Duengen et al., 2024; Duengen & Ravignani, 2024) on the vocal behavior of the adult female 'L'. Seal L was frequently observed vocalizing, usually before, during or shortly after feeding. This vocal behavior developed at the zoo of origin (Table 2); how this behavior was acquired is unknown (pers. communication, Zoo Cleves personnel). Both zoo personnel and the authors hypothesize the behavior had attention-getting and/or begging aims. Prior to this report, seal L was the only vocalizing female from the group. Among males, only male J had been observed singing the typical breeding 'roar' during breeding season.

Table 2*Animal's Date of Birth, Zoo of Origin, and Arrival at Zoo Cleves, if Applicable*

Seal	Sex	Age at the Start of the Study	Date of Birth	Arrival at Zoo Cleves	Zoo of Origin
Lisa (L)	Female	23 years	07.06.1997	29.04.2002	Zoo Duisburg
Robbie (R)	Male	19 years	24.07.2001	30.04.2002	Zoo Heidelberg
Jannik (J)	Male	15 years	10.06.2005	06.09.2005	Zoo Duisburg
Elektra (E)	Female	5 years	06.07.2015	28.07.2016	Zoo Osnabrück
Mogli (M)	Male	9 ¼ months	02.07.2020	x	x
Schnappi (S)	Male	9 ½ months	22.06.2020	x	x
Robert (R)	Male	unborn	10.07.2021	x	x

Note. x indicates birth at Zoo Cleves. Up to three juveniles resided in the tank during part of the training, until two moved in early September 2021.

Training of Seal L

As a first training step, Seal L was trained to vocalize upon presentation of a visual cue. The experimenter presented a hand sign whenever seal L vocalized, immediately followed by a food reward. In operant conditioning, animals learn from the consequences of their behavior (Thorndike, 1911). Here, this included associative learning of a discriminative cue (hand sign) with vocalizing and positive reinforcement (food reward). During training of seal L, all animals, except for the juveniles, were stationed next to each other on the training platform (Figure 1). All other animals, between one and three juveniles (see Table 2), remained in the water during training.

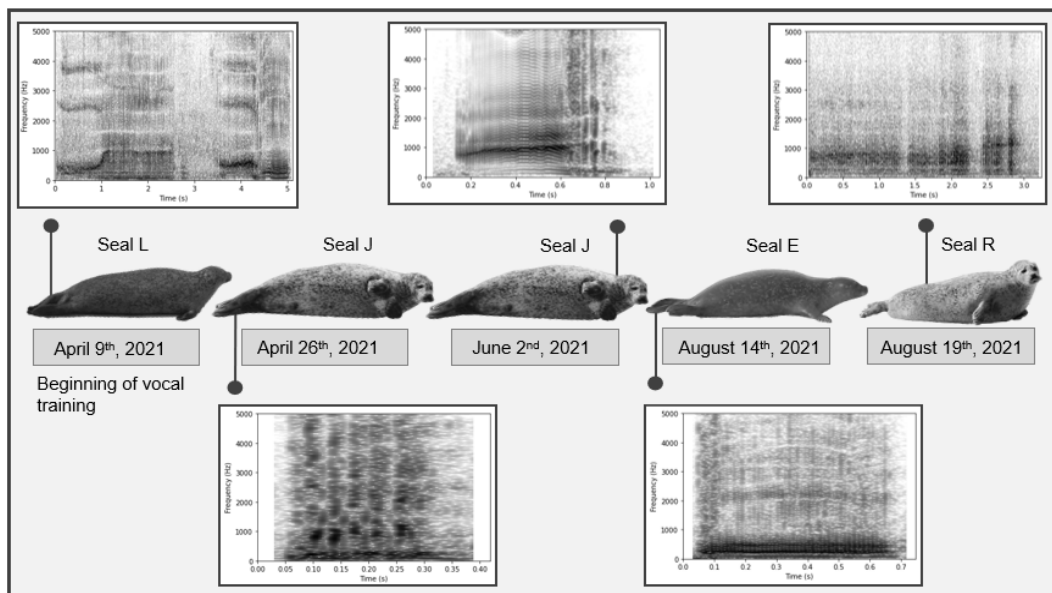
Figure 1*The Experimenter Trains Seal L to Vocalize on Cue*

Note. All seals are stationed at their target position, from left to right: seal R, seal E, seal J, and seal L. Note that all seals could always see the experimenter. Seals could also see each other, except for seal R, who had impeded vision and was stationed on the far left.

Seal L's vocalization consisted of two parts (Figure 2), which she usually produced in succession, and she rarely produced only the first part. Vocal training started when all animals were stationed at their target position. Importantly, in this position all animals could see and hear both the trainer and the other seals (Figure 1), with a potentially reduced visibility for seal R, who suffered from an eye condition. Initially, the experimenter would wait for seal L to show the attention-getting behavior (vocalizing, or flipper slapping). Once seal L showed the desired behavior (vocalizing), the trainer presented the cue (hand sign) and rewarded seal L via a whistle and immediate food reward. During training, the other seal's stationing behavior was intermittently reinforced, i.e., these seals occasionally received fish during a variable temporal interval (usually < 1 minute). Seals were free to leave their position at any point, resulting in no reward. Any undesired behavior (e.g., flipper slapping or approaching) was ignored. The experimenter regularly took notes to document training advances and behavior.

Figure 2

Timeline of Seal Vocal Behavior, Including Spectrograms of Respective Calls



Note. First vocalization of Seal L noted at the zoo of origin, not in the figure. Spectrograms were obtained with the Parselmouth package in Python (version 0.4.1, Praat 6.1.38; window length=0.03 s, dynamic range=70 dB, max. frequency=7000 Hz (Boersma & Weenink, 2022; Jadoul et al., 2023; Jadoul et al., 2018)). Vocalizations were recorded with a Zoom H6 digital recorder, and Sennheiser ME-67 unidirectional microphone (frequency response of 40–20,000 Hz \pm 2.5 dB), covered by a foam wind shield.

Three More Seals Start Vocalizing

Three formerly silent adult seals (J, E, and R) started vocalizing within a few weeks/months from reinforcement of seal L's vocal behavior (Figure 2); no other novel behaviors appeared. After less than three weeks, seal J started vocalizing during training of seal L, a few weeks later he initiated a second vocalization. Some weeks later, seal E initiated vocal behavior. Finally, seal R started to vocalize.

Stationed next to the demonstrator, seal J initiated vocalizations as the first seal of the group; he produced broadband vocalizations in late April 2021 and more tonal vocalizations less than two months later (Figure 2), which were aurally and spectrally different from his breeding vocalizations and occurred well ahead of breeding time. All vocalization types were easily distinguishable by ear. Broadband vocalizations are non-tonal and rather noisy, where sound energy is distributed over a broad frequency range. Conversely, tonal vocalizations are rather harmonic, with more energy at lower frequencies (Figure 2).

A few weeks after seal J initiated the second vocalization, Seal E started vocalizing while being trained with the other seals (Figure 2). Once the novel vocalizations occurred, operant conditioning allowed these behaviors to be associated with a cue in both seals; after some training, these novel vocalizations were successfully produced whenever the discriminative stimulus was presented (Duengen & Ravignani, 2024).

Unlike seals E and J who both initiated their first vocalizations during training on the platform, seal R started vocalizing in water, outside of training. These vocalizations occurred rarely, and exclusively in water and could not be trained on discriminative stimulus.

All adults initiated novel vocalizations, which had not been observed or heard in these individuals at any point in time before. This was reported by the zoo staff, who were surprised by the new behavior. The vocalizations in the observers emerged between two weeks to four months after the onset of vocal training with the demonstrator (Figure 2). Seal J successively initiated two different vocalizations at two different points in time (Figure 2). None of these animals had formerly engaged in vocal behavior, covering a time span of up to 19 years, with the exception of seal J's breeding display.

Discussion

Learning can be facilitated through information acquired individually (asocial learning) or through the interaction with, or observation of, others (social learning). In our case, the observers displayed the novel vocal behavior quite rapidly. The seals were in auditory and visual proximity to each other. Therefore, we propose social learning as a parsimonious explanation for the newly established vocalizations in these harbor seals. All vocalizations occurred in close temporal proximity, and no animal had displayed this behavior in preceding years. We argue that, as the onset of untrained vocalizations was spontaneous and untrained, social learning best explains our observations. Boyd and Richerson (2013) argue that social learning may be evolutionarily preferred in some cases by saving costs of trial-and-error-learning. Similarly, we suggest that the seals used the less time-costly social learning to act as a shortcut to gaining food rewards.

Mechanisms underlying social learning are mostly distinguished based on the demonstrator's role in eliciting an observer's behavior, and are not mutually exclusive (Heyes, 1994; for a review, see Hoppitt & Laland, 2008). Several underlying social learning mechanisms may co-occur, and their relative contribution may be difficult to determine. Forms of vocal learning suffer from *incertae sedis* within the social learning literature: despite vocal learning being a form of social learning, it is not commonly nested in social learning taxonomies (Whiten & Ham, 1992; Whiten et al., 2004). Because of this, and the anecdotal nature of this report, we will not delve into potentially underlying social learning mechanisms, but rather focus on the distinguishable forms of vocal learning.

One could argue that the novel vocalizations are a product of vocal production learning, as they were never heard before. The only seals that vocalized in the past are the demonstrator and seal J. Seal J had only produced breeding vocalizations, while the two vocalization types (Figure 2) were novel. As we cannot know whether these animals had ever produced these vocalizations before in their lives, contextual learning appears as more cautious interpretation (Table 1). As Janik and Slater (1997) argued: "observational data can almost never exclude the occurrence of usage learning based on a pre-existing vocal repertoire" (p. 6). Seal E's and seal J's vocalization did neither aurally nor spectrally match those of the demonstrator, therefore vocal imitation, a clear instance of production learning, can be excluded. What we can certainly say is that the seals, during the following training, showed vocal usage learning, as seal E's and seal J's novel vocalizations were successfully trained to be associated with cues (Duengen & Ravignani, 2024; Duengen et al., 2024, Janik & Slater, 2000).

Most likely, seal R did not socially learn to vocalize, even though his vocalizations appeared to be new. This seal's novel vocal behavior occurred during breeding season, while bottling (standing upright in the water column), which is indicative of breeding behavior in this zoo. Indeed, inspecting the vocalization's spectrogram revealed the typical breeding vocalization, the 'roar' (Figure 2). Seal R continued to vocalize exclusively during breeding seasons, including bubble blowing, showing the typical breeding display. Interestingly, this seal was the seal stationed farthest away from the demonstrator and

experimenter (Figure 1) and suffered from an eye condition. Speculatively, this distance and his partial blindness may have led to missing the context necessary for social learning.

We conclude by suggesting that harbor seals socially learned to vocalize for a food reward, after which reinforcement occurred. While it remains unclear which underlying mechanisms contributed most, we argue that the animal initiated vocal behavior by means of social learning from a conspecific; learning to vocalize on cue, later actively trained by the experimenter, constitutes instead individual vocal usage learning (Duengen & Ravignani, 2024). Both seals learned to produce two different vocalizations upon presentation of two different discriminative stimuli (Duengen & Ravignani, 2024). This indeed constitutes a clear example of vocal usage learning (Janik & Slater, 2000; Vernes et al., 2021). This could occur in wild harbor seals, too: It is still not known how male harbor seals establish their breeding vocalizations (Duengen & Ravignani, 2023), but our observations could indicate that harbor seals learn by observing conspecifics.

Alternative Explanations for the Novel Vocal Behavior

Some pinnipeds vocalize when anticipating a food reward, or in frustration (Schusterman, 2008). Here, seals were accustomed to training, and correct behavior was intermittently reinforced to prevent frustration. However, an increased proportion of stationing for research training may have theoretically caused impatience or arousal, and hence sound production. However, our experience with these individuals shows that impatience or arousal is expressed via other attention-getting behaviors, such as flipper slapping, approaching, or scratching. Crucially, none of these more established strategies occurred, suggesting that the vocal behavior is more parsimoniously explained by social learning rather than arousal.

Could it be that the seals initiated the vocalizations by means of emotional contagion? Emotional contagion is the tendency to alter an observers behavioral and affective state in response to the emotional expressions of others, e.g., as in yawn contagion (Campbell & de Waal, 2011). If seals initiated vocal behavior due to emotional contagion, one would expect this species to also show a similar behavior in the wild. However, to the best of our knowledge, adult harbor seals do not show contagious vocalizing. Even in mother-pup pairs, as opposed to many other pinnipeds (for a review, see Charrier, 2020), only pups call to their mothers, not vice versa (Renouf, 1984). Instead, recent research has shown anti-synchronous calling among pups (Anichini et al., 2023; Ravignani, 2019). Crucially, if vocal contagion played a role, the observers should have started vocalizing years before, as the demonstrator has vocalized ever since she arrived at the zoo (Table 2).

An alternative explanation considers the seasonal onset of the seals' calls, which is late spring, early summer. Male harbor seal vocalizations occur seasonally around breeding time, both in human care and in the wild (Casey et al., 2021; Sabinsky et al., 2017). Yet, the first vocalizations occurred outside breeding time, and are different from the species-typical breeding vocalization, both aurally and spectrally, in all seals, except seal R. Taking together the short temporal succession of the individuals' vocal onset, and the fact that most of the seals never vocalized before, observational learning rather than a seasonally occurring vocalizations seems reasonable, for both seal E and seal J.

Conclusions

Here, we anecdotally report semi-solitary marine mammals under human care engaging in social learning to acquire food rewards. Ours may be the first observation of two harbor seals socially learning from conspecifics. We suggest this to be a profitable strategy in this semi-solitary, yet seasonally gregarious, pinniped species. Recent converging evidence shows that sociality is not needed for social learning (Allen, 2019; Kis et al., 2015; Webster & Laland, 2017); it may even, and simply, reflect a more general ability to learn (Pouca et al., 2020). Our observations dovetail with this: the rather non-social lifestyle of seals still enables social learning, and Heyes (2012) importantly points out how social and asocial learning rely on the same underlying learning mechanisms. The animals in our study were constantly exposed to conspecifics (see also Kocsis et al., 2023); unlike wild harbor seals, which only temporarily

aggregate. How this affects our conclusion and if a certain plasticity in sociality and/or social learning is prevalent e.g., under human care, remains to be understood.

We anecdotally report social and vocal learning capacities in harbor seals; further controlled experiments should validate this. Future studies should test whether observational learning is more commonly found, e.g., in other (harbor) seal groups at zoological institutions and investigate under controlled conditions which specific social learning mechanism(s) underlie their behavior. Social learning seems to be more widespread across species than previously thought, potentially due to its many benefits, and one new challenge for the field is connecting behavioral evidence with ultimate evolutionary benefits.

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References

- Allen, J. A. (2019). Community through culture: From insects to whales: How social learning and culture manifest across diverse animal communities. *BioEssays*, 41(11), e1900060. <https://doi.org/10.1002/bies.201900060>
- Anichini, M., De Reus, K., Hersh, T. A., Valente, D., Salazar-Casals, A., Berry, C., Keller, P. E., & Ravignani, A. (2023). Measuring rhythms of vocal interactions: a proof of principle in harbour seal pups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 378(1875), 20210477. <https://doi.org/10.1098/rstb.2021.0477>
- Bigg, M. A. (1981). Harbour seal *Phoca vitulina* Linnaeus, 1758 and *Phoca largha* Pallas, 1811. In R. J. Harrison & S. H. Ridgway (Eds.), *Handbook of marine mammals* (pp. 1–28). London: Academic Press.
- Bjerge, A., Thompson, D., Hammond, P., Fedak, M., Bryant, E., Aarefjord, H., Roen, R., & Olsen, M. (1995). Habitat use and diving behaviour of harbour seals in a coastal archipelago in Norway. In *Developments in Marine Biology* Vol. 4 (pp. 211–223). Elsevier. [https://doi.org/10.1016/S0163-6995\(06\)80025-9](https://doi.org/10.1016/S0163-6995(06)80025-9)
- Boersma, P., & Weenink, D. (2022). *Praat: doing phonetics by computer* In *Glott International* (Version 6.2.12) retrieved 17 April 2022 from <http://www.praat.org/>
- Boness, D. J., Bowen, W. D., Buhleier, B. M., & Marshall, G. J. (2006). Mating tactics and mating system of an aquatic-mating pinniped: the harbor seal, *Phoca vitulina*. *Behavioral Ecology and Sociobiology*, 61(1), 119–130. <https://doi.org/10.1007/s00265-006-0242-9>
- Boyd, R., & Richerson, P. J. (2013). An evolutionary model of social learning: The effects of spatial and temporal variation. In *Social learning* (pp. 41–60). Psychology Press.
- Campbell, M. W., & de Waal, F. B. (2011). Ingroup-outgroup bias in contagious yawning by chimpanzees supports link to empathy. *PloS ONE*, 6(4), e18283. <https://doi.org/10.1371/journal.pone.0018283>
- Casey, C., Sills, J. M., Knaub, S., Sotolotto, K., & Reichmuth, C. (2021). Lifelong patterns of sound production in two seals. *Aquatic Mammals*, 47(5), 499–514. <https://doi.org/10.1578/AM.47.5.2021.499>

- Charrier, I. (2020). Mother–offspring vocal recognition and social system in pinnipeds. *Coding Strategies in Vertebrate Acoustic Communication* (pp. 31–246). Springer
- Cottrell, P. E., Jeffries, S., Beck, B., & Ross, P. S. (2002). Growth and development in free-ranging harbor seal (*Phoca vitulina*) pups from southern British Columbia, Canada. *Marine Mammal Science*, 18(3), 721–733. <https://doi.org/10.1111/j.1748-7692.2002.tb01069.x>
- Curio, E., Ernst, U., & Vieth, W. (1978). The adaptive significance of avian mobbing. *Zeitschrift für Tierpsychologie*, 48(2), 184–202. <https://doi.org/10.1111/j.1439-0310.1978.tb00255.x>
- Davis, M., & Renouf, D. (1987). Social behavior of harbor seals, *Phoca vitulina*, on haulout grounds at Miquelon. *Canadian Field-Naturalist*, 101(1), 1-5.
- de Reus, K., Carlson, D., Lowry, A., Gross, S., Garcia, M., Rubio-Garcia, A., Salazar-Casals, A., & Ravignani, A. (2022). Vocal tract allometry in a mammalian vocal learner. *Journal of Experimental Biology*, 225(8). <https://doi.org/10.1242/jeb.243766>
- Duengen, D., Fitch, W. T., & Ravignani, A. (2023). Hoover the talking seal. *Current Biology*, 33(2), R50-R52. <https://doi.org/10.1016/j.cub.2022.12.023>
- Duengen, D., Jadoul, Y., & Ravignani, A. (2024). Vocal usage learning and vocal comprehension learning in harbor seals. *BMC Neuroscience*, 25, 48. <https://doi.org/10.1186/s12868-024-00899-4>
- Duengen, D., & Ravignani, A. (2023). The paradox of learned song in a semi-solitary mammal. *Ethology*. <https://doi.org/10.1111/eth.13385>
- Duengen, D., & Ravignani, A. (2024). Training harbor seals to participate in vocal learning experiments in a zoo. *bioRxiv* <https://doi.org/10.1101/2024/08.27.609954>
- Favaro, L., Neves, S., Furlati, S., Pessani, D., Martin, V., & Janik, V. M. (2016). Evidence suggests vocal production learning in a cross-fostered Risso's dolphin (*Grampus griseus*). *Animal cognition*, 19(4), 847–853. <https://doi.org/10.1007/s10071-016-0961-x>
- Fiorito, G., & Scotto, P. (1992). Observational learning in *Octopus vulgaris*. *Science*, 256(5056), 545–547. <https://doi.org/10.1126/science.256.5056.545>
- Garcia, M., & Ravignani, A. (2020). Acoustic allometry and vocal learning in mammals. *Biology letters*, 16(7), 20200081. <https://doi.org/10.1098/rsbl.2020.0081>
- Godsell, J. (1988). Herd formation and haul-out behaviour in harbour seals (*Phoca vitulina*). *Journal of Zoology*, 215(1), 83–98.
- Hamilton, C. D., Lydersen, C., Ims, R. A., & Kovacs, K. M. (2014). Haul-out behaviour of the world's northernmost population of harbour seals (*Phoca vitulina*) throughout the year. *PLoS ONE*, 9(1), e86055. <https://doi.org/10.1371/journal.pone.0086055>
- Hanggi, E. B., & Schusterman, R. J. (1994). Underwater acoustic displays and individual variation in male harbour seals, *Phoca vitulina*. *Animal Behaviour*, 48(6), 1275–1283. <https://doi.org/10.1006/anbe.1994.1363>
- Hayes, S. A., Kumar, A., Costa, D. P., Mellinger, D. K., Harvey, J. T., Southall, B. L., & Le Boeuf, B. J. (2004). Evaluating the function of the male harbour seal, *Phoca vitulina*, roar through playback experiments. *Animal Behaviour*, 67(6), 1133–1139. <https://doi.org/10.1016/j.anbehav.2003.06.019>
- Heyes, C. (2012). What's social about social learning? *Journal of Comparative Psychology*, 126(2), 193. <https://doi.org/10.1037/a0025180>
- Heyes, C. M. (1994). Social learning in animals: categories and mechanisms. *Biological reviews of the Cambridge Philosophical Society*, 69(2), 207–231. <https://doi.org/10.1111/j.1469-185x.1994.tb01506.x>
- Hoppitt, W., & Laland, K. N. (2008). Social processes influencing learning in animals: a review of the evidence. *Advances in the Study of Behavior*, 38, 105–165. [https://doi.org/10.1016/S0065-3454\(08\)00003-X](https://doi.org/10.1016/S0065-3454(08)00003-X)
- Insley, S., Phillips, A. V., & Charrier, I. (2003). A review of social recognition in pinnipeds. *Aquatic Mammals*, 29(2), 181–201.
- Jadoul, Y., De Boer, B., & Ravignani, A. (2023). Parselmouth for bioacoustics: automated acoustic analysis in Python. *Bioacoustics*, 1–17. <https://doi.org/10.1080/09524622.2023.2259327>
- Jadoul, Y., Thompson, B., & De Boer, B. (2018). Introducing parselmouth: A python interface to praat. *Journal of Phonetics*, 71, 1–15. <https://doi.org/10.1016/j.wocn.2018.07.001>
- Janik, V. M., & Slater, P. J. (2000). The different roles of social learning in vocal communication. *Animal Behaviour*, 60(1), 1–11. <https://doi.org/10.1006/anbe.2000.1410>
- Janik, V. M., & Slater, P. J. B. (1997). Vocal learning in mammals. In P. J. B. Slater, J. S. Rosenblatt, C. T. Snowdon, & M. Milinski (Eds.), *Advances in the Study of Behavior, Vol 26* (pp. 59-99). Elsevier Academic Press Inc. [https://doi.org/10.1016/s0065-3454\(08\)60377-0](https://doi.org/10.1016/s0065-3454(08)60377-0)
- Kappeler, P. M. (2019). A framework for studying social complexity. *Behavioral Ecology and Sociobiology*, 73(1), 13. <https://doi.org/10.1007/s00265-018-2601-8>

- Kis, A., Huber, L., & Wilkinson, A. (2015). Social learning by imitation in a reptile (*Pogona vitticeps*). *Animal cognition*, 18(1), 325–331. <https://doi.org/10.1007/s10071-014-0803-7>
- Kocsis, K., Duengen, D., Jadoul, Y., & Ravignani, A. (2023). Harbour seals use rhythmic percussive signaling in interaction and display. *Animal Behaviour*. <https://doi.org/10.1016/j.anbehav.2023.09.014>
- Magrath, R. D., Haff, T. M., McLachlan, J. R., & Iqic, B. (2015). Wild birds learn to eavesdrop on heterospecific alarm calls. *Current Biology*, 25(15), 2047–2050. <https://doi.org/10.1016/j.cub.2015.06.028>
- Moore, B. R. (1996). The evolution of imitative learning. In C. Heyes & B. Galef Jr (Eds.), *Social learning in animals: The roots of culture*. Academic Press.
- Muelbert, M., & Bowen, W. (1993). Duration of lactation and postweaning changes in mass and body composition of harbour seal, *Phoca vitulina*, pups. *Canadian Journal of Zoology*, 71(7), 1405–1414.
- Neumann, D. R. (1999). Agonistic behavior in harbor seals (*Phoca vitulina*) in relation to the availability of haul-out space. *Marine Mammal Science*, 15(2), 507–525.
- Nicholson, T. E. (2000). *Social structure and underwater behavior of harbor seals in southern Monterey Bay, California* [Master's Thesis, San Francisco State University, San Francisco].
- Nikolich, K., Frouin-Mouy, H., & Acevedo-Gutiérrez, A. (2018). Clear diel patterns in breeding calls of harbor seals (*Phoca vitulina*) at Hornby Island, British Columbia, Canada. *Canadian Journal of Zoology*, 96(11), 1236–1243. <https://doi.org/10.1139/cjz-2018-0018>
- Pahl, A., König von Borstel, U., & Brucks, D. (2023). Llamas use social information from conspecifics and humans to solve a spatial detour task. *Animal cognition*, 1–11. <https://doi.org/10.1007/s10071-023-01808-8>
- Petkov, C. I., & Jarvis, E. D. (2012). Birds, primates, and spoken language origins: behavioral phenotypes and neurobiological substrates. *Frontiers in evolutionary neuroscience*, 4, 12. <https://doi.org/10.3389/fnevo.2012.00012>
- Pouca, C. V., Heinrich, D., Huvencers, C., & Brown, C. (2020). Social learning in solitary juvenile sharks. *Animal Behaviour*, 159, 21–27. <https://doi.org/10.1016/j.anbehav.2019.10.017>
- Ralls, K., Fiorelli, P., & Gish, S. (1985). Vocalizations and vocal mimicry in captive harbor seals, *Phoca vitulina*. *Canadian Journal of Zoology*, 63(5), 1050–1056. <https://doi.org/10.1139/z85-157>
- Ravignani, A. (2019). Timing of antisynchronous calling: A case study in a harbor seal pup (*Phoca vitulina*). *Journal of Comparative Psychology*, 133(2), 272. <https://doi.org/10.1037/com0000160>
- Ravignani, A., & Garcia, M. (2022). A cross-species framework to identify vocal learning abilities in mammals. *Philosophical Transactions of the Royal Society B*, 377(1841), 20200394. <https://doi.org/10.1098/rstb.2020.0394>
- Reichmuth, C., & Quihuis, D. (2022). Social Transmission of innovative sound production in walrus (*Odobenus rosmarus*). *Aquatic Mammals*, 48(6), 720–723. <https://doi.org/10.1578/AM.48.6.2022.720>
- Renouf, D. (1984). The vocalization of the harbour seal pup (*Phoca vitulina*) and its role in the maintenance of contact with the mother. *Journal of Zoology*, 202(4), 583–590. <https://doi.org/10.1111/j.1469-7998.1984.tb05055.x>
- Sabinsky, P. F., Larsen, O. N., Wahlberg, M., & Tougaard, J. (2017). Temporal and spatial variation in harbor seal (*Phoca vitulina* L.) roar calls from southern Scandinavia. *Journal of the Acoustical Society of America*, 141(3), 1824–1834. <https://doi.org/10.1121/1.4977999>
- Schusterman, R. J. (2008). Vocal learning in mammals with special emphasis on pinnipeds. *The evolution of communicative flexibility: Complexity, creativity, and adaptability in human and animal communication*, 41v 70.
- Seyfarth, R. M., & Cheney, D. L. (1986). Vocal development in vervet monkeys. *Animal Behaviour*, 34(6), 1640–1658.
- Skinner, J. P. (2006). *Physical and behavioral development of nursing harbor seal (*Phoca vitulina*) pups in Maine* [Master's Thesis, University of Maine].
- Stansbury, A. L., & Janik, V. M. (2019). Formant modification through vocal production learning in gray seals. *Current Biology*, 29(13), 2244–2249 e2244. <https://doi.org/10.1016/j.cub.2019.05.071>
- Stansbury, A. L., & Janik, V. M. (2021). The role of vocal learning in call acquisition of wild grey seal pups. *Philosophical Transactions of the Royal Society B*, 376(1836), 20200251. <https://doi.org/10.1098/rstb.2020.0251>
- Sullivan, R. M. (1982). Agonistic behavior and dominance relationships in the harbor seal, *Phoca vitulina*. *Journal of Mammalogy*, 63(4), 554–569.
- Thorndike, E. L. (1911). *Animal Intelligence; Experimental Studies*.
- Torres Borda, L., Jadoul, Y., Rasilo, H., Salazar Casals, A., & Ravignani, A. (2021). Vocal plasticity in harbour seal pups. *Philosophical Transactions of the Royal Society B*, 376(1840), 20200456. <https://doi.org/10.1098/rstb.2020.0456>

- Van Parijs, S. M., Hastie, G. D., & Thompson, P. M. (2000). Individual and geographical variation in display behaviour of male harbour seals in Scotland. *Animal Behaviour*, 59, 559–568. <https://doi.org/10.1006/anbe.1999.1307>
- Van Parijs, S. M., & Kovacs, K. M. (2002). In-air and underwater vocalizations of eastern Canadian harbour seals, *Phoca vitulina*. *Canadian Journal of Zoology*, 80(7), 1173–1179. <https://doi.org/10.1139/z02-088>
- Van Schaik, C. P., & Burkart, J. M. (2011). Social learning and evolution: the cultural intelligence hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1567), 1008–1016. <https://doi.org/10.1098/rstb.2010.0304>
- Vernes, S. C., Kriengwatana, B. P., Beeck, V. C., Fischer, J., Tyack, P. L., Ten Cate, C., & Janik, V. M. (2021). The multi-dimensional nature of vocal learning. *Philosophical Transactions of the Royal Society B*, 376(1836), 20200236. <https://doi.org/10.1098/rstb.2020.0236>
- Webster, M. M., & Laland, K. N. (2017). Social information use and social learning in non-grouping fishes. *Behavioral Ecology*, 28(6), 1547–1552. <https://doi.org/10.1093/beheco/axx121>
- Whiten, A. (2017). A second inheritance system: the extension of biology through culture. *Interface Focus*, 7(5), 20160142. <https://doi.org/10.1098/rsfs.2016.0142>
- Whiten, A., & Ham, R. (1992). Kingdom: reappraisal of a century of research. *Advances in the Study of Behavior*, 21, 239.
- Whiten, A., Horner, V., Litchfield, C. A., & Marshall-Pescini, S. (2004). How do apes ape? *Animal Learning & Behavior*, 32, 36–52.
- Whiten, A., & Van Schaik, C. P. (2007). The evolution of animal ‘cultures’ and social intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1480), 603–620. <https://doi.org/10.1098/rstb.2006.1998>
- Wilkinson, A., Kuenstner, K., Mueller, J., & Huber, L. (2010). Social learning in a non-social reptile (*Geochelone carbonaria*). *Biology letters*, 6(5), 614–616. <https://doi.org/10.1098/rsbl.2010.0092>