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Acoustically advertising male harbour seals in southeast Alaska do not make biologically relevant acoustic adjustments in the presence of vessel noise

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Aquatically breeding harbour seal (*Phoca vitulina*) males use underwater vocalizations during the breeding season to establish underwater territories, defend territories against intruder males, and possibly to attract females. Vessel noise overlaps in frequency with these vocalizations and could negatively impact breeding success by limiting communication space. In this study, we investigated whether harbour seals employed anti-masking strategies to maintain communication in the presence of vessel noise in Glacier Bay National Park and Preserve, Alaska. Harbour seals in this location did not sufficiently adjust source levels or acoustic parameters of vocalizations to compensate for acoustic masking. Instead, for every 1 dB increase in ambient noise, signal excess decreased by 0.84 dB, indicating a reduction in communication space when vessels passed. We suggest that harbour seals may already be acoustically advertising at or near a biologically maximal sound level and therefore lack the ability to increase call amplitude to adjust to changes in their acoustic environment. This may have significant implications for this aquatically breeding pinniped, particularly for populations in high noise regions.

1. Background

The marine environment is dominated by noise from shipping in many parts of the world. Shipping noise is low-frequency, primarily ranging from 10 Hz to 5 kHz [1], though there are high-frequency components at close range [2,3]. Low-frequency components overlap with many marine mammal vocalizations [4] and can drastically decrease the detection range of acoustic signals. Noise has been shown to reduce communication space by 50–70% in some whale and dolphin species [5–7], and there is likely a potential for even greater amounts of masking.

To compensate for elevated noise and maintain detection space, individuals must increase signal amplitude or shift vocalizations temporally or spectrally [8,9]. Temporal shifts can include adjusting duration, increasing call rate or postponing vocalizations until noise decreases. Spectral shifts involve adjusting vocalization frequency so there is less overlap with ambient noise. However, these shifts may not be physically possible or biologically beneficial for all species [10]; for example, increasing loudness is only possible if an animal is not already calling at maximal volume. A recent study showed that signature whistles in bottlenose dolphins (*Tursiops truncatus*) are produced at higher amplitudes compared to other vocalizations, leaving little room for adjustments in the presence of

noise and thereby impacting conspecific communication [11]. Increases in ambient noise may be detrimental for breeding animals who are communicating near their physiological maximum and rely on acoustic signalling to facilitate mating.

Few studies have addressed the impact of noise on aquatically mating pinnipeds (seals, sea lions and walruses) [12], despite the fact that over 80% of seal species mate underwater [13], and most rely on underwater sound to facilitate breeding [14]. This study addresses this gap by investigating the impacts of vessel noise on male advertisement behaviours of aquatically breeding harbour seals (*Phoca vitulina*). Harbour seals are a widespread pinniped, with mate choice and copulation occurring underwater [15–17]. During the breeding season, some males produce acoustic signals, known as roars, that are low frequency (primarily 100 Hz–1.1 kHz) and range in duration from 2–10 s [18,19]. Roars are thought to function both for male–male, helping establish and defend underwater territories, and male–female interactions, possibly playing a role in mate preference [20,21]. Roars directly overlap in frequency with vessel noise, highlighting that these coastally breeding seals likely experience acoustic masking in the presence of vessel traffic.

2. Material and methods

A bottom-mounted hydrophone array was deployed near a terrestrial pupping site in Glacier Bay National Park and Preserve, Alaska. Glacier Bay, a glacial fjord system in southeastern Alaska, is home to a large seasonal aggregation of harbour seals [22,23]. In Glacier Bay, tourism-related vessel traffic (cruise ships, fishing boats and personal-use vessels such as skiffs) peaks during the harbour seal breeding season (June–July) [24], introducing significant acoustic energy into the environment that overlaps in frequency with harbour seal roars [25,26].

The array was deployed and recorded continuously from May to October 2015, fully encompassing the breeding season when males are acoustically active [27]. Four hydrophones were arranged in a diamond planar array (approx. 1 km separation) near a known cruise ship route (for map, see [26]); hydrophone depths ranged from 65 to 81 m. The array recorded from 15 Hz to 4 kHz (hydrophone model ITC 1032, analogue sensitivity of -192 dB re 1 V μPa^{-1} , ADC input voltage ± 1.25 V, flat frequency response of ± 1 dB over the 15 Hz–4 kHz frequency band, 10 kHz sampling rate, low-pass filter at 4 kHz to eliminate aliasing, 16 bit resolution). Recordings encompassed the entire frequency range of harbour seal breeding vocalizations in Glacier Bay [27]. Hydrophones were equipped with a precise real-time clock (Q-Tech QT2010 MCXO, error of approximately 1 s yr^{-1}) for time synchronization to facilitate acoustic localization. The clock on the eastern-most hydrophone malfunctioned and those data were excluded from analysis; data presented here represent a three-element array.

Stratified random sampling was used to generate a subset of 36 h of acoustic data from 9 days during peak breeding season. This subset accounted for time of day and hours were equally spaced throughout the peak breeding season. In this study, there was a range of ambient noise conditions. Visual confirmation of acoustic data indicated that higher noise periods corresponded to vessel passages and lower noise periods were associated with vessel absence or distant vessels. The arrival and departure time of cruise ships in this region is known [26].

Vocalizations were visually annotated in Raven Pro v. 1.5 [28] (Hann window, discrete Fourier transform size = 1024, 50% overlap, analysis resolution = 9.7 Hz, 0.05 s). Calls were localized using the near-beamforming method in Raven Pro v. 2.0 [29]

and source levels (dB_{RMS} re 1 μPa @ 1 m, 40–500 Hz) were estimated. Localization and source level estimates followed the methods detailed in Matthews *et al.* [27].

Four additional parameters were manually selected and measured using Raven Pro v. 2.0: total duration, pulse duration, minimum start frequency and peak frequency. Total duration refers to the length of time between the start and end of the roar; pulse duration refers to the length of the broadband component of the vocalization, which occurs towards the end of the roar. The minimum start frequency is the lowest frequency at the onset of the call and the peak frequency is the frequency with the greatest amplitude. These parameters have been previously shown to be important for comparative analyses of roars [30,31].

Ambient noise values (dB_{RMS} re 1 μPa , 40–500 Hz) were extracted for the 2 s preceding each call using Raven Pro's inband power feature for the hydrophone closest to the localized call. For each roar, signal excess was calculated by logarithmically subtracting the ambient noise from the source level. Signal excess describes how much louder an individual roar is than the concurrent soundscape.

Each call was assigned a 'seal ID' corresponding to a distinct individual, in order to ensure that acoustic data were collected from multiple animals and to account for individual variation. Previous work on harbour seal territoriality has indicated that individual males can hold discrete acoustic territories for multiple years [32]. Therefore, male harbour seals can be classified as individuals by mapping the locations of vocalizations to visualize acoustic territories. In this study, the number of acoustic hotspots—areas of high roar density—were counted as an estimated proxy for the number of callers. It should be noted that not all males hold territories during the breeding season, as some use alternative strategies. Our estimate does not account for these individuals.

Linear mixed effects models with a Gaussian link function [33] were used to fit source level, signal excess and call parameters as a function of ambient noise, adding individual ID as a random effect to avoid dependence issues. Q–Q plots, histograms and Levene's tests indicated that the assumptions of linearity, normality and equal variance were met. Features were extracted with the same analysis resolution as the acoustic analysis (9.7 Hz, 0.05 s). AIC model selection was used to assess variable relevance (see electronic supplementary material). To avoid statistical artefacts, biological significance was set at the 0.05 level and required a measurable change in call parameters that exceeded spectrogram resolution.

3. Results

(a) Source levels

A total of 545 calls corresponding to a minimum of four male harbour seals were included in the analysis. All localized roars were within 1.06 km of the array (average = 0.31 km, range = 0.17–1.06 km). AIC model selection indicated the random effect of seal should be dropped from the source level and excess models ($\Delta\text{AIC} \geq 3$). Average roar source level (153 dB_{RMS} re 1 μPa @ 1 m, 40–500 Hz) fell within previously estimated ranges (139 – 159 dB_{RMS} re 1 μPa @ 1 m, 40–500 Hz) [27], and a small, but statistically significant, increase in source level was observed in response to ambient noise. Source levels increased by 0.16 dB for every 1 dB increase in ambient noise ($F_{1,543} = 89.17$, $p < 2 \times 10^{-16}$, figure 1). However, this level of change falls within the resolution of this system; it is below the threshold for instrument error. When extrapolated across the range of ambient noise conditions observed in this study (82–107 dB), the predicted change in source level for an individual harbour seal between the highest and

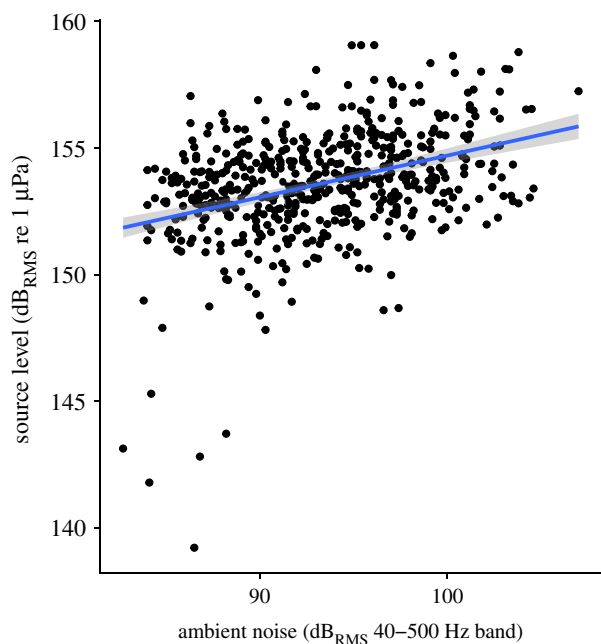


Figure 1. Harbour seal source levels plotted against ambient noise. Raw data are indicated by dots. Model output and 95% CIs are indicated by the blue line and shaded ribbon.

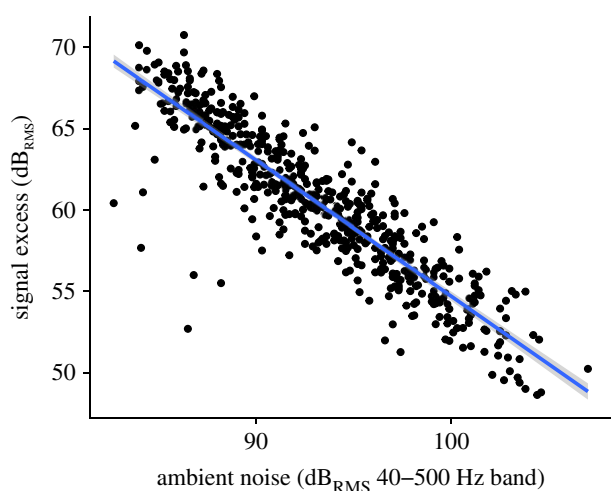


Figure 2. Signal excess for harbour seal roars plotted against ambient noise. Raw data are indicated by dots. Model output and 95% CIs are indicated with the blue line and shaded ribbon.

lowest noise conditions would be 4 dB, which is within the natural range of individual variability observed here and elsewhere [27]. Therefore, despite the statistical significance, it is likely that these adjustments are not effective in the context of harbour seal communication.

(b) Signal excess

For every 1 dB increase in ambient noise, harbour seal signal excess decreased by 0.84 dB (95% CI 0.8–0.9 dB, min = 48 dB, max = 71 dB; figure 2).

(c) Call parameters

There was no biologically relevant relationship between peak frequency, minimum frequency, total duration or pulse duration and ambient noise (see electronic supplementary material). In each case, shifts in call parameters fell below the

spectrogram resolution by an order of magnitude; visual plot inspection supported a lack of relationship between call parameters and ambient noise.

4. Discussion

This study demonstrates that, when faced with noise from passing vessels, these four male harbour seals did not sufficiently adjust amplitude, duration or frequency of roars. While male harbour seals did show a statistical increase in amplitude in response to noise, the increase was within the natural range of amplitude and was not biologically relevant. For harbour seals to detect a roar, signal loudness must substantially exceed background noise [34]. Thus, the lack of evidence for shifts in source levels as noise increases may have negative implications for the reproductive success of males who rely on roars to defend territories and attract potential mates [20,21]. This pattern is consistent with findings in other species, such as the Pacific chorus frog (*Pseudacris regilla*), that do not adjust breeding call amplitude to compensate for anthropogenic noise, and as a result, potential communication with mates is decreased [35].

Acoustic displays made during the breeding season are costly in that males roar in Glacier Bay at all hours [36]. This redundant production of signals is common for vocalizations associated with breeding [37]. Males also forgo foraging in order to advertise; previous work has indicated that males can lose 0.47% of their body weight each day of the breeding season as a result of these behaviours [38–40]. Our results suggest males are already advertising at or near biologically maximum loudness and may be incapable of compensating for masking by increasing signal amplitude, but future research should aim to investigate whether signal redundancy is compromised.

Further, as ambient noise increased, harbour seal signal excess decreased. This indicates that when vessel noise is present, harbour seal communication space is reduced and continues to decrease as vessels approach and background noise increases. This behavioural response confirms models that predict that vessel noise masks roars in Glacier Bay [41].

Male harbour seals similarly failed to adjust duration or pitch in the presence of elevated noise. In many species, acoustic parameters vary between individuals as a form of honest advertisement [42,43]. These honest signals can function in mate choice—for example, female red deer (*Cervus elaphus*) and tungara frogs (*Physalaemus pustulosus*) prefer lower frequency calls corresponding to larger males [44,45], and female grey treefrogs (*Hyla versicolor*) prefer longer duration calls, indicating a larger energetic expenditure [46]. There is some evidence to suggest that female harbour seals prefer lower frequency and longer duration signals, corresponding to more dominant males [20]. Longer duration vocalizations may also indicate healthier males [31]. It is plausible that increasing pitch would negatively impact a male's probability of mating, while providing only minimal release from masking. Maintaining consistent pitch may be the best strategy, regardless of ambient noise conditions, particularly if natural releases from masking (quiet periods) exist within the acoustic habitat.

It should be noted that the results presented here only reflect an estimated four individuals. While these appear to be the only harbour seal males in this location with territories, this study does not account for individuals that employ

alternative mating strategies, as it is not possible to acoustically identify these males. It would be of interest for future work to investigate noise impacts on roaming individuals.

The highest levels of vessel noise in Glacier Bay overlap directly with the harbour seal breeding season [24,36]. Currently, vessel noise in Glacier Bay is periodic and concentrated at two times of day [24]; thus, the probability of a roar being detected by a potential mate is still high for much of the day and night. Harbour seal acoustic activity has been shown to increase at night in this area, which is a notably quieter time of day [26,36]. This may be to increase the likelihood of encountering a female [36], but could also serve to reduce the risk of acoustic masking.

Glacier Bay has enacted various measures to mitigate underwater noise, such as vessel quotas, speed restrictions, and the designation of biologically important areas as non-motorized [24]. These measures have been effective in regulating underwater noise [24,47]. However, vessel noise is still apparent in biologically important areas, such as those used by male harbour seals during the breeding season and is altering the behaviour of other species on short timescales, despite mitigation efforts [26]. Future work should investigate

the cumulative effects of repeated vessel noise exposure on the reproductive success of harbour seal males.

Data accessibility. Data can be found in the electronic supplementary material.

Competing interests. We declare we have no competing interests

Authors' contributions. L.M. carried out fieldwork, led data processing and analysis, participated in the design of the study and co-drafted the manuscript; M.E.H.F. carried out fieldwork, carried out the statistical analyses, participated in the design of the study and co-drafted the manuscript; C.G. carried out fieldwork, participated in the design of the study and critically revised the manuscript; H.K. participated in study design and offered technical/engineering support, and critically revised the manuscript; S.P. coordinated the study, participated in study design and critically revised the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

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References

- Hildebrand JA. 2009 Anthropogenic and natural sources of ambient noise in the ocean. *Mar. Ecol. Prog. Ser.* **395**, 5–20. (doi:10.3354/meps08353)
- Arveson PT, Vendittis DJ. 2000 Radiated noise characteristics of a modern cargo ship. *J. Acoust. Soc. Am.* **107**, 118–129. (doi:10.1121/1.428344)
- Hermannsen L, Beedholm K, Tougaard J, Madsen PT. 2014 High frequency components of ship noise in shallow water: implications for harbor porpoises (*Phocoena phocoena*). *J. Acoust. Soc. Am.* **136**, 1640–1653. (doi:10.1121/1.4893908)
- Tyack PL. 2008 Implications for marine mammals of large-scale changes in the marine acoustic environment. *J. Mammal.* **89**, 549–558. (doi:10.1644/07-mamm-s-307r.1)
- Jensen FH, Bejder L, Wahlberg M, de Soto NA, Johnson MP, Madsen PT. 2009 Vessel noise effects on delphinid communication. *Mar. Ecol. Prog. Ser.* **395**, 161–175. (doi:10.3354/meps08204)
- Hatch LT, Clark CW, Van Parijs SM, Frankel AS, Ponirakis DW. 2012 Quantifying loss of acoustic communication space for right whales in and around a U.S. National Marine Sanctuary. *Conserv. Biol.* **26**, 983–994. (doi:10.1111/j.1523-1739.2012.01908.x)
- Cholewiak D *et al.* 2018 Communicating amidst the noise: modeling the aggregate influence of ambient and vessel noise on baleen whale communication space in a national marine sanctuary. *Endanger Species Res.* **36**, 59–75. (doi:10.3354/esr00875)
- Brumm H, Slabbekoorn H. 2005 Acoustic communication in noise. *Adv. Stud. Behav.* **35**, 151–209. (doi:10.1016/S0065-3454(05)35004-2)
- Hotchkiss C, Parks S. 2013 The Lombard effect and other noise-induced vocal modifications: insight from mammalian communication systems. *Biol. Rev.* **88**, 809–824. (doi:10.1111/brv.12026)
- Slabbekoorn H. 2013 Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. *Anim. Behav.* **85**, 1089–1099. (doi:10.1016/j.anbehav.2013.01.021)
- Kragh IM, McHugh K, Wells RS, Sayigh LS, Janik VM, Tyack PL, Jensen FH. 2019 Signal-specific amplitude adjustment to noise in common bottlenose dolphins (*Tursiops truncatus*). *J. Exp. Biol.* **222**, jeb216606. (doi:10.1242/jeb.216606)
- Cummings WC, Holliday DV, Lee BJ. 1984 Potential impacts of man-made noise on ringed seals: vocalizations and reactions. U.S. Dep. Commer., NOAA, OCSEAP Final Rep. 37: pp. 95–230. See <https://www.arlis.org/docs/vol1/OCSEAP2/Final/OCSEAP-Final-v37.pdf>.
- Van Parijs SM. 2003 Aquatic mating in pinnipeds: a review. *Aquat. Mamm.* **29**, 214–226. (doi:10.1578/016754203101024167)
- Stirling I, Thomas JA. 2003 Relationships between underwater vocalizations and mating systems in phocid seals. *Aquat. Mamm.* **29**, 227–246. (doi:10.1578/016754203101024176)
- Coltman DW, Bowen WD, Wright JM. 1998 Male mating success in an aquatically mating pinniped, the harbour seal (*Phoca vitulina*), assessed by microsatellite DNA markers. *Mol. Ecol.* **7**, 627–638. (doi:10.1046/j.1365-294x.1998.00373.x)
- Lowry L. 2016 Harbor seal. *Phoca vitulina*. *The IUCN Red List of Threatened Species* **2016**, e.T17013A45229114. (doi:10.2305/IUCN.UK.2016-1.RLTS.T17013A45229114.en)
- LeBoeuf BJ. 1991 Pinniped mating systems on land, ice, and in the water: emphasis on the Phocidae. In *The behaviour of pinnipeds* (ed. D Renouf), Dordrecht, The Netherlands: Springer.
- Hanggi EB, Schusterman RJ. 1994 Underwater acoustic displays and individual variation in male harbour seals, *Phoca vitulina*. *Anim. Behav.* **48**, 1275–1283. (doi:10.1006/anbe.1994.1363)
- Van Parijs SM, Thompson PM, Tollit DJ, Mackay A. 1997 Distribution and activity of male harbor seals during the mating season. *Anim. Behav.* **54**, 35–43. (doi:10.1006/anbe.1996.0426)
- Matthews LP, Blades B, Parks SE. 2018 Female harbor seal (*Phoca vitulina*) behavioral response to playbacks of underwater male acoustic advertisement displays. *PeerJ.* **6**, e4547. (doi:10.7717/peerj.4547)
- Hayes SA, Kumar A, Costa DP, Mellinger DK, Harvey JT, Southall BL, Le Boeuf BJ. 2004 Evaluating the function of the male harbour seal, *Phoca vitulina*, roar through playback experiments. *Anim. Behav.* **67**, 1133–1139. (doi:10.1016/j.anbehav.2003.06.019)
- Calambokidis J, Taylor B, Carter S, Steiger GH, Dawson PK, Antrim LD. 1987 Distribution and haul-out behavior of harbor seals in Glacier Bay, Alaska. *Can. J. Zool.* **65**, 1391–1396. (doi:10.1139/z87-219)
- Womble JN, Pendleton GW, Mathews EA, Blundell GM, Bool NM, Gende SM. 2010 Harbor seal (*Phoca vitulina richardii*) decline continues in the rapidly changing landscape of Glacier Bay National Park, Alaska 1992–2008. *Mar. Mamm. Sci.* **26**, 686–697.
- McKenna MF, Gabriele C, Kipple B. 2017 Effects of marine vessel management on the underwater acoustic environment of Glacier Bay National Park. *AK. Ocean Coast Manage.* **139**, 102–112. (doi:10.1016/j.ocecoaman.2017.01.015)
- Kipple BM, Gabriele CM. 2003 Glacier Bay underwater noise—August 2000 through August 2002. Naval Surface Warfare Center—Carderock

- Division. Technical Report NSWCCD-71-TR-2004/521. pp. 1–78.
26. Fournet M, Matthews LP, Gabriele CM, Haver S, Mellinger DK, Klinck H. 2018 Humpback whales *Megaptera novaeangliae* alter calling behavior in response to natural sounds and vessel noise. *Mar. Ecol. Prog. Ser.* **607**, 251–268. (doi:10.3354/meps12784)
 27. Matthews LP, Parks SE, Fournet MEH, Gabriele CM, Womble JN, Klinck H. 2017 Source levels and call parameters of harbor seal breeding vocalizations near a terrestrial haulout site in Glacier Bay National Park and Preserve. *J. Acoust. Soc. Am.* **141**, EL274–EL280. (doi:10.1121/1.4978299)
 28. Center for Conservation Bioacoustics. 2014 Raven Pro: Interactive Sound Analysis Software (Version 1.5) [computer software]. Ithaca, NY: The Cornell Lab of Ornithology. See <http://ravensoundsoftware.com/>.
 29. Center for Conservation Bioacoustics. 2016 Raven Pro: Interactive Sound Analysis Software (Version 2.0) [computer software]. Ithaca, NY: The Cornell Lab of Ornithology. See <http://ravensoundsoftware.com/>.
 30. Van Parijs SM, Hastie GD, Thompson PM. 2000 Individual and geographical variation in display behaviour of male harbour seals in Scotland. *Anim. Behav.* **59**, 559–568. (doi:10.1006/anbe.1999.1307)
 31. Sabinsky PF, Larsen ON, Wahlberg M, Tougaard J. 2017 Temporal and spatial variation in harbor seal (*Phoca vitulina* L.) roar calls from southern Scandinavia. *J. Acoust. Soc. Am.* **141**, 1824–1834. (doi:10.1121/1.4977999)
 32. Hayes SA, Costa DP, Harvey JT, Le Boeuf BJ. 2004 Aquatic mating strategies of the male Pacific harbor seal (*Phoca vitulina richardii*): are males defending the hotspot? *Mar. Mamm. Sci.* **20**, 639–656. (doi:10.1111/j.1748-7692.2004.tb01184.x)
 33. R Core Team. 2017 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <https://www.R-project.org/>.
 34. Southall BL, Schusterman RJ, Kastak D. 2000 Masking in three pinnipeds: underwater, low-frequency critical ratios. *J. Acous. Soc. Am.* **108**, 1322–1326. (doi:10.1121/1.1288409)
 35. Nelson DV, Klinck H, Carbaugh-Rutland A, Mathis CL, Morzillo AT, Garcia TS. 2017 Calling at the highway: the spatiotemporal constraint of road noise on Pacific chorus frog communication. *Ecol. Evol.* **7**, 429–440. (doi:10.1002/ece3.2622)
 36. Matthews LP, Gabriele CM, Parks SE. 2017 The role of season, tide, and diel period in the presence of harbor seal (*Phoca vitulina*) breeding vocalizations in Glacier Bay National Park and Preserve, Alaska. *Aquat. Mamm.* **43**, 537–546. (doi:10.1578/am.43.5.2017.537)
 37. Bradbury JW, Vehrencamp SL. 2011 *Principles of animal communication*. Sinauer Associates. Oxford, UK: Oxford University Press.
 38. Coltman DW, Bowen WD, Boness DJ, Iverson SJ. 1997 Balancing foraging and reproduction in the male harbour seal, an aquatically mating pinniped. *Anim. Behav.* **54**, 663–678. (doi:10.1006/anbe.1997.0470)
 39. Coltman DW, Bowen WD, Iverson SJ, Boness DJ. 1998 The energetics of male reproduction in an aquatically mating pinniped, the harbour seal. *Physiol. Zool.* **71**, 387–399. (doi:10.1086/515418)
 40. Baechler J, Beck CA, Bowen WD. 2002 Dive shapes reveal temporal changes in the foraging behaviour of different age and sex classes of harbour seals (*Phoca vitulina*). *Can. J. Zool.* **80**, 1569–1577. (doi:10.1139/z02-150)
 41. Gabriele CM, Ponirakis DW, Clark CW, Womble JN, Vanselow PBS. 2018 Underwater acoustic ecology metrics in an Alaska marine protected area reveal marine mammal communication masking and management alternatives. *Front. Mar. Sci.* **5**, 65–17. (doi:10.3389/fmars.2018.00270)
 42. Clutton-Brock TH, Albon SD. 1979 The roaring of red deer and the evolution of honest advertisement. *Behaviour.* **69**, 145–170. (doi:10.1163/156853979x00449)
 43. Fitch WT, Hauser MD. 2003 Unpacking ‘honesty’: vertebrate vocal production and the evolution of acoustic signals. In *Acoustic communication*. pp. 65–137. New York, NY: Springer.
 44. Charlton BD, Reby D, McComb K. 2007 Female red deer prefer the roars of larger males. *Biol. Lett.* **3**, 382–385. (doi:10.1098/rsbl.2007.0244)
 45. Ryan MJ. 1980 Female mate choice in a neotropical frog. *Science.* **209**, 523–525. (doi:10.1126/science.209.4455.523)
 46. Gerhardt HC, Tanner SD, Corrigan CM, Walton HC. 2000 Female preference functions based on call duration in the gray tree frog (*Hyla versicolor*). *Behav. Ecol.* **11**, 663–669. (doi:10.1093/beheco/11.6.663)
 47. Frankel AS, Gabriele CM. 2007 Predicting the acoustic exposure of humpback whales from cruise and tour vessel noise in Glacier Bay, Alaska, under different management strategies. *End. Spec. Res.* **34**, 397–415. (doi:10.3354/esr00857)