



A meta-analysis on the evolution of the Lombard effect reveals that amplitude adjustments are a widespread vertebrate mechanism

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Animal communication is central to many animal societies, and effective signal transmission is crucial for individuals to survive and reproduce successfully. One environmental factor that exerts selection pressure on acoustic signals is ambient noise. To maintain signal efficiency, species can adjust signals through phenotypic plasticity or microevolutionary response to natural selection. One of these signal adjustments is the increase in signal amplitude, called the Lombard effect, which has been frequently found in birds and mammals. However, the evolutionary origin of the Lombard effect is largely unresolved. Using a phylogenetically controlled meta-analysis, we show that the Lombard effect is also present in fish and amphibians, and contradictory results in the literature can be explained by differences in signal-to-noise ratios among studies. Our analysis also demonstrates that subcortical processes are sufficient to elicit the Lombard effect and that amplitude adjustments do not require vocal learning. We conclude that the Lombard effect is a widespread mechanism based on phenotypic plasticity in vertebrates for coping with changes in ambient noise levels.

animal behavior | communication | Lombard effect | phenotypic plasticity | vocalization

Adjustments to changes in the environment can occur through phenotypic plasticity or microevolutionary response to natural selection (1). Phenotypic plasticity is the ability of a single genotype to express different phenotypes, enabling individuals to adjust immediately to changes in the environment (2). One form of phenotypic plasticity is behavioral plasticity, which is crucial because a shift into a new niche or adaptive zone is “almost without exception initiated by a change in behavior” (3). An example of behavioral plasticity is signal adjustments to changes in the acoustic environment, which are central in the evolution of animal communication systems (4).

Communication is used in some form in most animal groups, for example, in sexual selection through male–male competition and mate choice, in parental care between parents and their offspring, and in predator–prey interactions. Animal communication in its simplest form involves a sender producing a signal that conveys information, and a receiver making a decision on how to respond to that signal (4). For the process of communication to be successful, the sender must transmit the signal across the environment to the receiver. Signals are often shaped by natural and sexual selection pressures (5, 6), and one of these selection pressures is ambient noise, which can reduce signal efficiency (7). A decrease in signal efficiency can have severe fitness consequences, such as an increase in aggressive interactions, missed mating opportunities, and lower foraging success (4). Thus, individuals are expected to adjust signals to maintain signal efficiency during periods of increased ambient noise. Acoustic signals are complex traits that consist of a number of different components (8, 9). A particular signal component is amplitude, and the increase in amplitude in response to increasing ambient noise is called the Lombard effect (10).

The Lombard effect has been reported in a variety of vertebrate species since its first description over 100 y ago. However, its evolutionary origin has been debated (11, 12) because the Lombard effect has been consistently found in birds, mammals, and fish, but not in reptiles, and in amphibians the evidence is mixed, as some studies found it, whereas others did not (13–16). This led to a dissent in the literature whether other taxonomic groups than mammals and birds can exhibit the Lombard effect (13). One explanation for these conflicting results is that the relative contribution of cortical and subcortical processes involved in the Lombard effect may differ among species. In fish and amphibians, amplitude adjustments seem to be controlled by subcortical processes (12). In mammals, amplitude adjustments seem to be modulated by cortical processes, while in birds, homologous brain areas such as the pallium are involved (12, 17). Another explanation for the conflicting results is that the occurrence of the Lombard effect may be

Significance

More than 100 years ago, Etienne Lombard discovered that humans increase their vocal amplitude when exposed to ambient noise. Since then, the Lombard effect has gathered a plethora of interest from various disciplines ranging from linguistics to zoology. One unresolved question is in regard to the evolutionary origin of the Lombard effect, because it has been found in birds, mammals, and fish, but not in reptiles, and in amphibians the evidence is disputed. Using a phylogenetically controlled meta-analysis, we show that the Lombard effect is a widespread mechanism in vertebrates, and that amplitude adjustments require neither complex cortical processes nor vocal learning.

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explained with differences in signal-to-noise ratios between a signal and ambient noise, because the Lombard effect is more likely to occur under low signal-to-noise ratio conditions (12, 18).

Using a phylogenetically controlled meta-analysis, we quantified the occurrence of the Lombard effect across taxonomic groups ranging from fish to mammals, analyzing the magnitude and the direction of amplitude adjustments. In addition, we compared signal-to-noise ratios of studies in those taxonomic groups in which the occurrence of the Lombard effect is debated (i.e., amphibians and reptiles). We predicted those studies that did not find the Lombard effect to have higher signal-to-noise ratios than those studies that found the Lombard effect.

Results

We analyzed the magnitude and the direction of signal amplitude adjustments in response to experimentally manipulated noise levels in two overall models, including the effect sizes of all species. In addition, we ran separate models for amphibians, birds, and mammals, but not for fish and reptiles due to the limited number of species available. Adjustments were considered statistically significant if the 95% CI did not cross zero (19). We calculated the total amount of heterogeneity (I^2_{total}), which provides the statistical basis for exploring causes of variation among effect sizes (20). We also calculated the individual contributions of the variation between effect sizes ($I^2_{effect\ sizes}$), studies ($I^2_{studies}$), and species ($I^2_{phylogeny}$) to total heterogeneity (I^2_{total}).

Our final dataset included 79 effect sizes from 28 experimental studies on 27 species (Fig. 1). In both overall models, we found evidence for the Lombard effect as the magnitude and direction of amplitude adjustments deviated from zero. The total heterogeneity (I^2_{total}) was high, with most of the variation attributed to effect sizes ($I^2_{effect\ sizes}$), and some variation attributed to studies ($I^2_{studies}$) and phylogeny ($I^2_{phylogeny}$), indicating that most species exhibited amplitude adjustments (Table 1 and Fig. 2).

Both birds and mammals increased their signal amplitude in response to increasing ambient noise levels, and there was no variation among species ($I^2_{phylogeny}$), demonstrating that species respond consistently in both the magnitude and the direction of response (Table 1). In contrast, amplitude adjustments of amphibians deviated from zero in the magnitude but not in the direction of response (Table 1). Variation among amphibian species ($I^2_{phylogeny}$) was high, suggesting that species show different responses when ambient noise levels change (Fig. 2). To test whether the absence of the Lombard effect could be explained by differences in signal-to-noise ratios between experiments, we compared signal-to-noise ratios of taxonomic groups that contained species that did not exhibit the Lombard effect (i.e., amphibians and reptiles) (SI Appendix, Table S3). The studies that were not able to establish the presence of the Lombard effect had higher signal-to-noise ratios (Fig. 3, black bars) than those studies that did find the Lombard effect (Fig. 3, blue bars, $W = 42$, $P = 0.0011$).

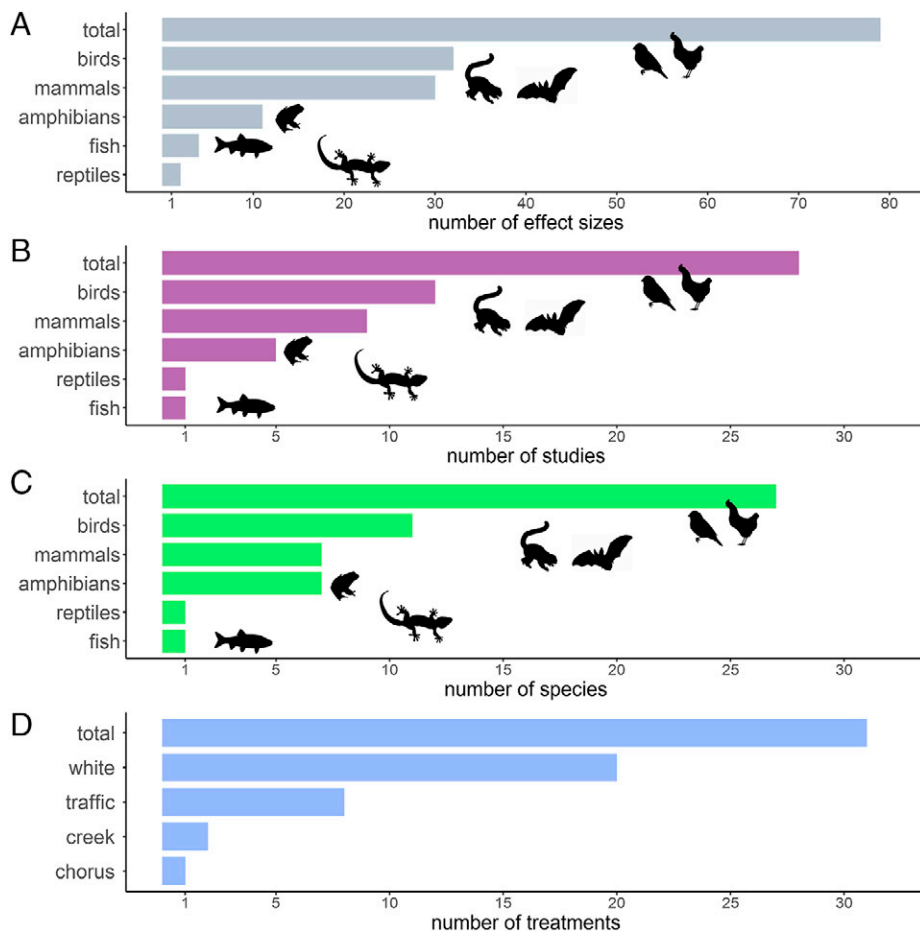


Fig. 1. Data structure for testing of the Lombard effect across vertebrates, using a phylogenetic controlled meta-analysis. (A) Effect sizes per taxonomic group, (B) studies per taxonomic group, (C) species in each taxonomic group, (D) type of ambient noise played back to increase noise levels. Note that scales of the x-axis differ.

Table 1. Quantification of the Lombard effect

	Estimate	SE	Z	95% CI		Heterogeneity I^2 , %			
				Lower	Upper	ES	Study	Phylogeny	Total
Magnitude*									
Overall model									
Amplitude	1.48	0.31	4.81	0.88	2.09	42.58	20.99	20.02	83.6
Taxon-specific models									
Amphibians	1.29	0.64	2.04	0.05	2.54	0	36.56	56.18	92.74
Birds	1.22	0.14	8.75	0.95	1.5	60.2	0.98	0	61.18
Mammals	2.48	0.38	6.46	1.73	3.23	68.51	13.92	0	82.43
Direction†									
Overall model									
Amplitude	1.27	0.48	2.67	0.34	2.2	36.33	19.9	30.54	86.76
Taxon-specific models									
Amphibians	0.51	1.11	0.46	-1.67	2.7	0	44.99	51.3	96.29
Birds	1.22	0.16	7.64	0.91	1.54	54.80	4.41	0	59.21
Mammals	2.46	0.41	6.02	1.66	3.26	65.01	15.28	0	80.29

The Lombard effect is an increase in signal amplitude with increasing background noise levels. Estimates and 95% CIs calculated from a phylogenetically controlled meta-analysis. All effect sizes (ES) are derived from experimental noise exposure studies. Heterogeneity allows us to assess how much of the inconsistencies among ES are attributable to phylogenetic relatedness. Model estimates were considered statistically significant if their 95% CIs did not cross zero. The full table is provided in [SI Appendix, Table S1](#).

*Magnitude of adjustments.

†Direction of signal adjustments.

Visual inspection of the funnel plots for signal amplitude suggested an asymmetrical distribution of effect sizes around the meta-analytic residuals ([SI Appendix, Fig. S2A](#)). Egger's regression supports the visual impression, and we found evidence for publication bias (intercept \pm SE: 5.52 ± 1.38 , lower CI: 2.8, upper CI: 8.2, $P < 0.001$). Visual inspection of time-lag plot for signal amplitude suggested no influence of year on effect sizes ([SI Appendix, Fig. S2B](#)), which was confirmed by the model (estimate \pm SE: -0.03 ± 0.04 , lower CI: -0.1 , upper CI: 0.05, $P = 0.49$). Sensitivity analyses show that our results are robust, as the removal of one effect size, one species, or one study did not affect the outcome for the overall model or the results for each taxonomic group ([SI Appendix, Table S2](#)).

Discussion

The Lombard effect was found in all included taxonomic groups apart from reptiles. In the overall models, total heterogeneity (I^2_{total}) stems mostly from variation among effect sizes ($I^2_{\text{effect sizes}}$) and some variation among studies (I^2_{studies}) due to differences in study design within taxonomic groups (see below). In the overall models, variation among species ($I^2_{\text{phylogeny}}$) can be explained by different responses among amphibians, because $I^2_{\text{phylogeny}}$ in the taxonomic models was zero for birds and mammals, but not for amphibians.

Both birds and mammals exhibited the Lombard effect consistently, and the total heterogeneity (I^2_{total}) in the taxonomic models of birds and mammals stems mostly from variation among effect sizes ($I^2_{\text{effect sizes}}$). The variation among effect sizes within studies may result from different acoustic stimuli, causing variation in the magnitude of amplitude adjustments (e.g., by using stimuli masking specific frequencies of acoustic signals). The consistent response among species of mammals and birds is noteworthy because for both taxonomic groups, our analysis comprises several different species: In mammals, our sample consists of species of two orders, Primates and Chiroptera (Fig. 4). Some species in the order Chiroptera produce calls with very distinctive functions and frequency ranges—social calls to communicate among conspecifics and echolocation calls to gather information about the environment (4), indicating

that the Lombard effect in mammals is exhibited irrespective of call type and function. In birds, our sample consists of both passerine and nonpasserine species (Fig. 4), and the lack of variation in amplitude adjustments among birds demonstrates that species of both groups exhibit the Lombard effect consistently. The consistent increase in amplitude suggests that the Lombard effect occurs independently of vocal learning, as it is found in passerines that learn their songs as well as in nonpasserines that do not acquire songs through vocal learning. Fish exhibited the Lombard effect, which is notable, because it demonstrates that the Lombard effect is a widespread mechanism in vertebrates to cope with changing ambient noise levels.

In amphibians and reptiles, the interpretation of results is more complicated, as some species increased signal amplitude, others decreased it, and some did not change signal amplitude at all (Fig. 4). In reptiles, the Lombard effect could not be detected, but the lack of amplitude adjustments cannot be explained with a general lack of phenotypic plasticity of signal components, as other components were adjusted to changing noise levels (Fig. 4). While *Gekko gecko* did not increase amplitude within a syllable type, individuals achieved favorable signal-to-noise ratios by producing a louder syllable type more often when exposed to noise (21). For both amphibians and reptiles, we found that the studies that did not detect the Lombard effect in our dataset had higher signal-to-noise ratios than those studies that did detect amplitude adjustments (Fig. 3). Future studies must ensure that signal-to-noise ratios are sufficient to elicit signal adjustments.

Our analysis suggests that the most parsimonious explanation for the reported absence of the Lombard effect in some species are high signal-to-noise ratios. However, several other explanations have been put forward as to why some species did not express the Lombard effect and we briefly discuss them in light of our analysis:

- (1) Some species lack the brain structures needed to exhibit the Lombard effect. Our analysis shows that the occurrence of the Lombard effect is taxonomically widespread and spans from fish to mammals, suggesting that subcortical processes alone allow them to elicit the Lombard effect, as species of

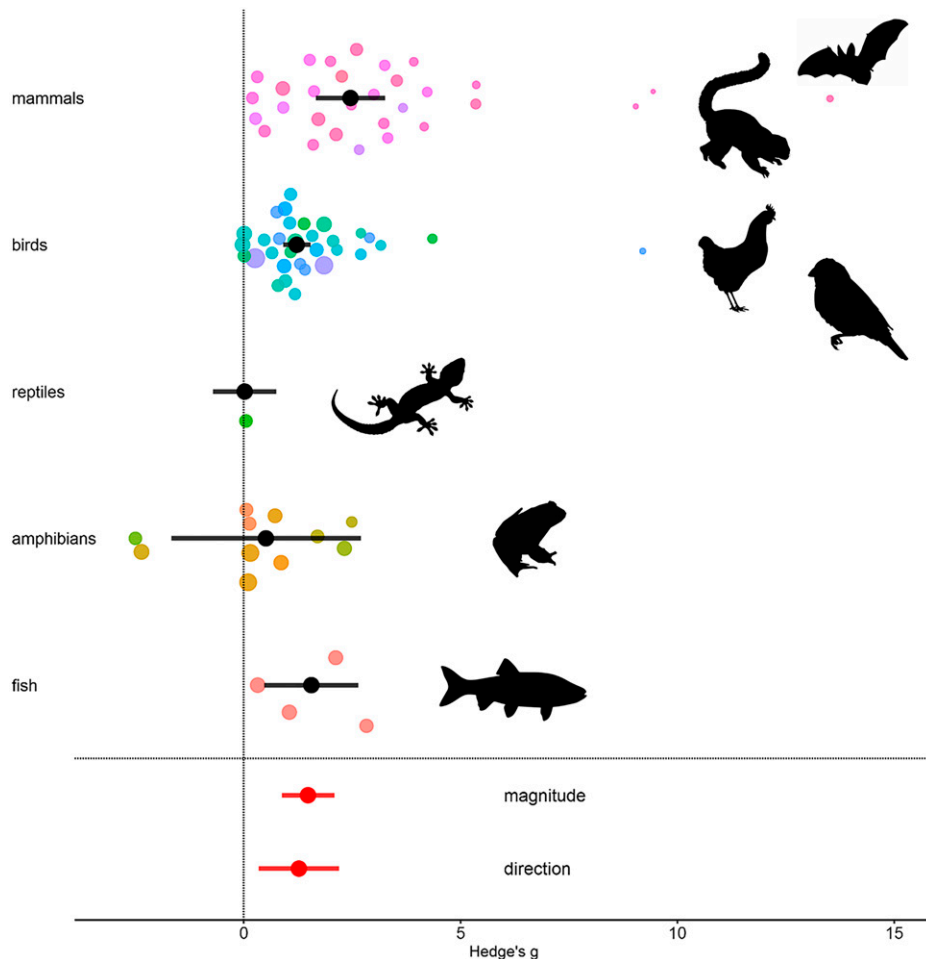


Fig. 2. Amplitude adjustments in vertebrates. Shown is Hedge's g and 95% CIs from random effect models. The vertical dashed line at zero indicates no adjustment in amplitude to changing ambient noise levels, and a statistically significant effect of noise if the 95% CI of Hedge's g does not overlap zero. The colors of the dots indicate the different species. The size of the data points is scaled by precision ($1/SE$). Sensitivity analyses show that our results are robust (see text for details).

fish and amphibians that lack cortical or homologous areas adjusted amplitude to increasing noise levels. Thus, the differences among species in the expression of the Lombard effect cannot be explained by differences in processing pathways in the brain.

- (2) Anatomy and morphology of structures involved in sound production vary among species, which may contribute to the variation in the expression of signal components (22). In this scenario, we would not expect to find differences in amplitude adjustments within a species. However, in the gray tree frog (*Dryophytes versicolor*), one study reported the Lombard effect but another one did not, suggesting that differences in signal-to-noise ratios between studies suffice to explain the conflicting results within a single species (Fig. 3).
- (3) Differences in selection pressures led to the evolution of different signal plasticities among species. For example, males of chorus-breeding species may be under strong selection pressure to produce loud calls, competing for space with other males and to attract females. In this scenario, amplitude adjustments are constrained only by limits of vocal production (23). We are not aware of any cross-species comparisons that quantifies the influence of breeding systems on amplitude adjustments formally, but within the same species amplitude did not change with assemblage density (24), suggesting that the differences found in amphibians cannot be explained with differences in breeding systems.

We found a publication bias in our dataset, which is expected because the studies were designed to test for the presence of the Lombard effect. However, for the type of analysis presented here it is not a problem as we were interested in showing the taxonomic distribution of the Lombard effect. Moreover, studies finding no amplitude adjustments should not be disadvantaged in being published, as they are crucially important to understand the evolutionary origin of the Lombard effect. We did not find any indication for a time-lag bias, which would be that an effect diminishes over time, overestimating the magnitude of a phenomenon in early studies (25). Thus, the Lombard effect can be considered a robust widespread phenotypic response to changes in the acoustic environment.

One open question concerns the signal value of amplitude: We do not imply that amplitude is not an important component of a signal, but rather its foundation, because amplitude determines the active space of a signal and its detectability (26, 27). However, signal amplitude alone may not be very effective for encoding information for several reasons. First, amplitude is not a stable signal component—in other words, during transmission, it decreases over distance. For amplitude to work as a reliable signal alone, receivers must assess the distance between themselves and the sender reliably; otherwise the receiver cannot extract information from amplitude alone. In contrast, information encoded in other signal components, such as redundancy, duration, and/or complexity, remains relatively stable over distance, which explains

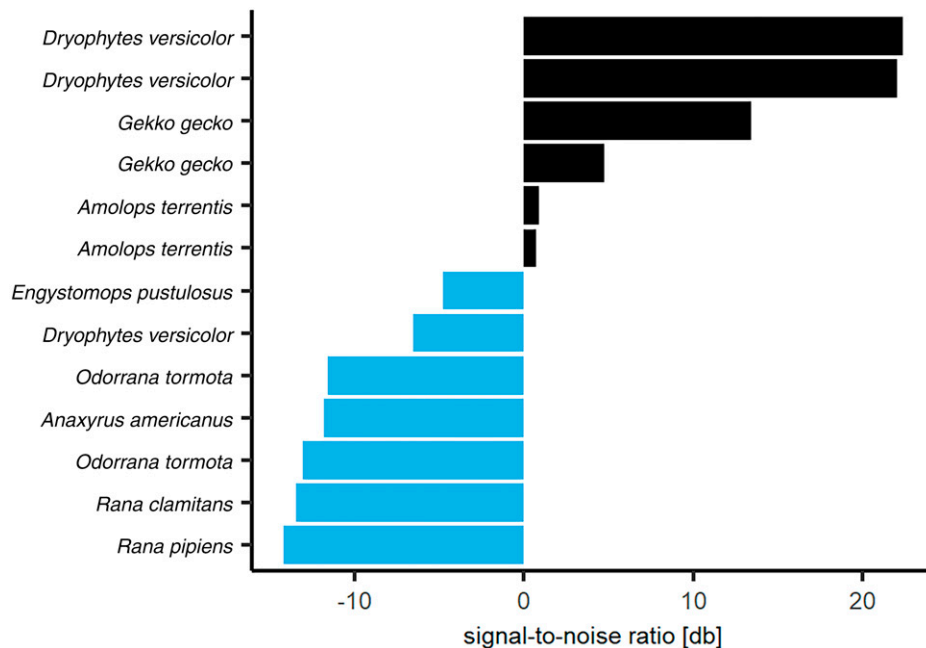


Fig. 3. The effect of signal-to-noise ratios on eliciting amplitude adjustments in amphibians and reptiles. Black bars indicate exposures in which the Lombard effect was absent; blue bars are those in which amplitude adjustments were found. Note that the two amphibian species that showed a decrease in signal amplitude have very low signal-to-noise ratios (*Rana clamitans* and *Rana pipiens*).

why many species code information in these components (6, 28). Second, even small changes in the sender position can affect signal amplitude by a factor of three (29). Hence, receivers need to assess not only the distance but also the exact emergence point of the sound source to extract reliable information from amplitude alone. Third, the directionality and context in which a signal is emitted also influences amplitude. The most omnidirectional vocalizations are those used to alert to danger, and the most directional vocalizations are those used during courtship and solicitation of copulation (30). Thus, the sender has not only to process the signal characteristics but also account for the context. All of these factors explain why an empirical link between amplitude and fitness is still missing.

In conclusion, our analysis provides several insights into the evolution of the Lombard effect. (i) There is a causal relationship between phenotypic adjustments in signal amplitude plasticity and ambient noise across species. (ii) The Lombard effect is a widespread mechanism for communicating in both aquatic and terrestrial vertebrate species, and the most parsimonious explanation is that it is a generic vertebrate response to cope with noise levels. (iii) Signal amplitude adjustments occur irrespective of the function of the signal. (iv) The presence of the Lombard effect in fish and amphibians suggests that the subcortical network is sufficient to elicit the Lombard effect and does not require vocal learning. (v) The need to study invertebrates, because our search did not return any experimental studies testing for the Lombard effect, although signal amplitudes in crickets can vary between quiet and noisy sites (31). (vi) Signal-to-noise ratios may explain variation in amphibians and reptile effect sizes. Thus, our study calls for experimental studies testing a wide range of species taking signal-to-noise ratios and signal overlap into account.

Materials and Methods

Literature Search and Study Selection Criteria. We conducted a systematic literature search in the Web of Science Core Collection and Scopus on 2020 11 June, for peer-reviewed studies that investigated potential amplitude adjustments in response to changing ambient noise levels. The search in Web of

Science was carried out on titles, abstracts, author keywords, and keywords plus. In Scopus, our search was carried out on titles, abstracts, keywords, and limited to the document type article. The search was conducted using the following combination of keywords in three independent searches: (i) "vocal plasticity AND noise," (ii) "animal communication AND noise AND amplitude," and (iii) "animal communication AND noise AND Lombard effect," returning 558 studies across both search tools. Records were downloaded as BibTeX database files (*.bib) and then merged in R (32) using the package REVTOOLS (33), resulting in a data frame with 558 studies. In REVTOOLS, we identified and removed the duplicates, which left 362 records. For each of these records, we checked the title and abstract to determine whether the research was indeed investigating amplitude adjustments (for details, see *SI Appendix, Fig. S1*). Where we could not clarify this from the title and abstract, we read the paper to find the relevant information. In addition, we found nine eligible studies by checking the bibliographies of articles.

To be included in our analysis, the studies had to fulfill the following criteria (34, 35): (i) The effect sizes must be obtained from experimental studies, as only carefully controlled experiments allow the establishment of cause-and-effect relationships (36). In cases in which different amplitudes of noise were played back, we chose the values of those exposures with the highest noise amplitude. (ii) The reported details on sample size, measure of central tendency, and measure of spread had to be accessible in the text, figures, or supplementary material. To extract data from figures, we used the software Web plot digitizer (37). (iii) The response to the treatment had to be unambiguously elicited by changes in ambient noise *cf* (34). (iv) The exposure had to be carried out on at least two individuals. (v) The noise used to elicit the Lombard effect had to spectrally mask at least some of the signal. Initially, we planned to include the degree of signal overlap by noise (i.e., signal masking) as the moderator in our analysis. Unfortunately, the number of effect sizes that tested the influence of signal masking was too low to be included in a formal quantitative analysis. The details of the studies included in the analysis can be accessed in the data file ([Dataset S2](#)).

Choice of Effect Size and Phylogeny. We calculated Hedges' *g* using the function "escalc" in the package METAFOR (38) and the package "compute.es" (39). To control for phylogeny, we created a phylogenetic matrix of species in the dataset using the Open Tree of Life (40). We used the ROTL package (41) to access the Open Tree of Life in R. ROTL does not calculate branch lengths for trees, and thus we calculated these using the compute.brLen function in the APE package (42). A correlation matrix of phylogenetic relatedness among species

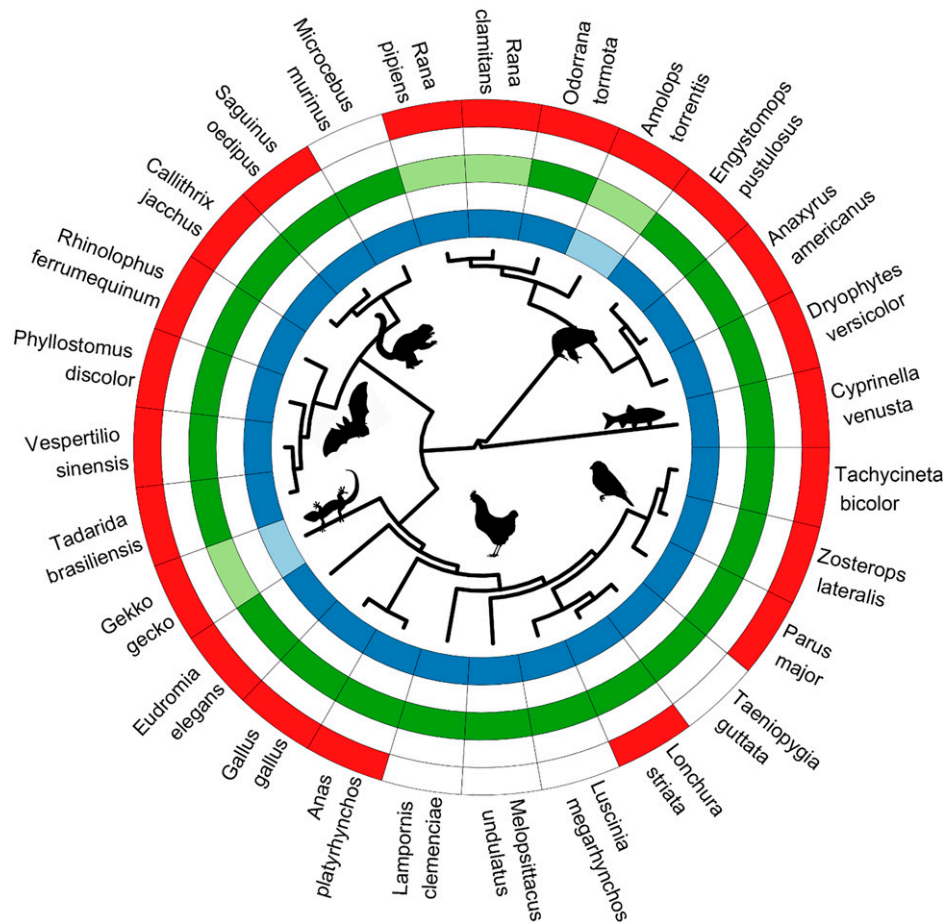


Fig. 4. Phylogenetic reconstruction of the Lombard effect. The phylogenetic tree shows the species included in our analysis (*SI Appendix, Table S4*). The blue ring shows whether a species showed amplitude plasticity (i.e., a decrease or increase in amplitude), the green ring shows the occurrence of the Lombard effect, and the red ring shows whether other signal components demonstrated plastic adjustments to noise (dark color: yes; bright color: no; white: no data available).

was then built using APE's `vcv` function. This correlation matrix was incorporated in all models in METAFOR, so that phylogenetic relatedness among effect sizes could be accounted for as a random effect (43). Silhouette drawings are from phylopic.org.

Statistical Analysis. All of the statistical analyses were performed in R studio (32); details for version numbers for software and packages is provided in the session information of the code (*Dataset S3*). To account for the nonindependence of effect sizes we used phylogenetically controlled meta-analytical multilevel random-effects models (38, 44). Metamodels were built using the `rma.mv` function in the package METAFOR (38). To quantify the magnitude of response to changes in ambient noise levels we ran a model on the effect sizes of amplitude, including effect size, study, and phylogeny as random factors. As Hedges' *g* does not correct for differences in the direction of response variables (45), we applied the folded normal distribution to the mean estimate (46–49). To quantify the direction of response to noise, we ran models on the raw values of the effect sizes, including study, effect size, and phylogeny as random factors. Then, we analyzed the magnitude and direction of responses separately for mammals, birds, and amphibians (for fish and reptiles, the sample sizes were not sufficient).

To test whether the lack of response could be explained by differences in signal-to-noise ratios, we compared the signal-to-noise ratios in those groups in which the Lombard effect was not found, or not consistently found (i.e., amphibians and reptiles). As the Lombard effect is best explained by the signal-to-noise ratio between vocalizations and ambient noise (see above), we calculated the signal-to-noise ratio from the ambient noise during the control treatment and the amplitude for the vocalization during the noise exposure. This allows us to test whether the signal-to-noise ratio can explain contrasting results in the literature.

Heterogeneity. Meta-analysis allows us to quantify heterogeneity I^2_{total} , which is the variance that is not due to sampling error or, in other words, the variance in true effects in contrast to the sampling variance (50). To test whether there was more heterogeneity in effect sizes among studies than could be explained by sampling error alone, we used Cochran's Q statistic. This formally tests whether variation in effect sizes is greater among studies than expected if the true effect is identical for all of the studies (51). However, the ratio assumes a constant within-study variance, which is not the case as sampling error varies due to studies having different sample sizes (50); thus, heterogeneity I^2 should be treated as a measure of "inconsistency" in effect sizes among studies (50). Therefore, total heterogeneity I^2 indicates how much of the total variance can be attributed to the total amount of heterogeneity, which is the sum of between- and within-cluster heterogeneity (38, 52). To quantify heterogeneity I^2 for the multilevel meta-analytic models, we calculated heterogeneity following the method of Nakagawa and Santos (44). These modified heterogeneity I^2 's partition the proportion of unknown variance that is not attributable to sampling variance into the contribution of random factors. In our analyses, this is the variance in effect sizes due to phylogenetic relatedness, differences among studies, and differences in within-study variation. Here, $I^2_{effect\ size}$ reflects inconsistencies within studies, I^2_{study} reflects inconsistencies among studies, $I^2_{phylogeny}$ is inconsistencies due to phylogenetic relatedness, and I^2_{total} is the sum of all of these values combined. The sum of the percentages of total variation due to these sources equals the traditional I^2 (53). High heterogeneity suggests that there may be differences in responses between studies, which can have ecologically important implications (51, 54).

Publication Bias, Time-Lag Bias, and Sensitivity Analysis. Publication bias may arise when statistically significant results are more likely than statistically nonsignificant results to be published (55). The resulting bias may lead to

unfounded conclusions that can affect the assessment of the factor under investigation (56–58). We checked for publication bias using two widely used approaches: funnel plots and Egger's regression (59–61). For the Egger's regression, we modified the multilevel random-effects models by including the precision of the effect sizes as a moderator (see, for example, Sánchez-Tójar et al. [62]). When the intercept of this regression significantly deviates from zero, the overall relationship between the precision and size of studies included in a dataset is considered asymmetrical, and therefore biased (61). We considered datasets to be biased if the intercept differed from zero at $P = 0.1$ (59). To quantify whether time-lag bias in the magnitude of effects sizes occurs in our dataset we

used graphical inspection and modified the multilevel random-effects models by including year as a moderator (25). To determine the robustness of our results, we performed a leave-one out analyses excluding either one study, one species, or one effect size at a time.

Data Availability. All study data are included in the article and/or supporting information.

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