

RESEARCH ARTICLE

New model for gain control of signal intensity to object distance in echolocating bats

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SUMMARY

Echolocating bats emit ultrasonic calls and listen for the returning echoes to orient and localize prey in darkness. The emitted source level, SL (estimated signal intensity 10 cm from the mouth), is adjusted dynamically from call to call in response to sensory feedback as bats approach objects. A logarithmic relationship of $SL=20\log_{10}(x)$, i.e. 6 dB output reduction per halving of distance, x , has been proposed as a model for the relationship between emitted intensity and object distance, not only for bats but also for echolocating toothed whales. This logarithmic model suggests that the approaching echolocator maintains a constant intensity impinging upon the object, but it also implies ever-increasing source levels with distance, a physical and biological impossibility. We developed a new model for intensity compensation with an exponential rise to the maximum source level: $SL=SL_{\max}-ae^{-bx}$. In addition to providing a method for estimating maximum output, the new model also offers a tool for estimating a minimum detection distance where intensity compensation starts. We tested the new exponential model against the 'conventional' logarithmic model on data from five bat species. The new model performed better in 77% of the trials and as good as the conventional model in the rest (23%). We found much steeper rates of compensation when fitting the model to individual rather than pooled data, with slopes often steeper than -20 dB per halving of distance. This emphasizes the importance of analyzing individual events. The results are discussed in light of habitat constraints and the interaction between bats and their eared prey.

Key words: gain control model, echolocation, intensity compensation, bat, biosonar.

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INTRODUCTION

Sophisticated forms of echolocation have evolved in two mammalian groups, laryngeal echolocating bats and toothed whales. Echolocation (or biosonar) is an active orientation system allowing individuals to navigate and forage in the dark based on the echo returns from their own short, high-frequency sound emissions. The echo return depends on a number of factors, including the outgoing signals' intensity and time–frequency structure, the target strength of the echo-reflecting object, the distance between the echolocator and the object, and the two-way transmission loss (Madsen and Wahlberg, 2007; Moss and Surlykke, 2010; Neuweiler, 1990; Schnitzler and Kalko, 2001). The main component of the transmission loss comes from spherical spreading, which will attenuate sound by $20\log_{10}(x)$ (where x is distance) or -6 dB per doubling of distance as it travels away from the emitter. Echoes reflected off a point target are also attenuated by the spherical spreading loss. Hence, for echoes from small (point) targets there is a two-way transmission loss of $40\log_{10}(x)$ or -12 dB per doubling of distance. Thus, if an echolocating animal emits calls of constant intensity while approaching a small object, the echo intensity will increase by ca. $40\log_{10}(x)$, corresponding to a 12 dB increase per distance halved (Møhl, 1988; Pye, 1980). Thus, the spherical spreading alone would result in an echo level increasing at the animal's ears by 80 dB (four orders of magnitude) over an initial detection distance of 5 m to a capture distance of perhaps 5 cm. Such a dynamic range would challenge the sonar receiver (ears), auditory system and central acoustic processing, unless some mechanism of compensation exists to buffer the received echo level. In general, gain control seems to be crucial for sensory representation, in

particular for modalities such as vision and audition covering large dynamic ranges (Olsen et al., 2012).

Two important studies on big brown bats (*Eptesicus fuscus*) have focused on how such a compensation mechanism might work (Kick and Simmons, 1984; Hartley, 1992a; Hartley, 1992b). Vocalizations of echolocating bats are synchronized with activation of their middle-ear muscles, which attenuate the bat's vocalizations to protect its auditory system. However, the contraction–relaxation cycle is short, resulting in rapidly decreasing attenuation of returning echoes over time. As a result, echoes returning from short distances at short delays will be attenuated more than echoes returning from longer distances at longer delays because of the gradual relaxation of the bat's middle-ear muscles following each call emission (Henson, 1965; Suga and Jen, 1975). Kick and Simmons (Kick and Simmons, 1984) demonstrated a systematic increase in the echo detection threshold of *E. fuscus* of approximately 11 dB per halving of target distance, which would compensate for the 12 dB increase in echo level per halving of distance and keep the perceived echo level constant if the bat keeps the emitted intensity constant. Thus, they suggested that compensation occurs entirely on the receiver side of the bats' sonar system, owing to this 'automatic gain control' (ACG).

In contrast, Hartley (Hartley, 1992a; Hartley, 1992b) found that the hearing threshold only increased by 6 dB per halving of distance, but that the echo level the bat perceived was nonetheless kept constant because the bat also compensated by reducing its output, or source level, by an additional 6 dB per halving of distance as the distance to the obstacle decreased. Thus, Hartley suggested that the

combination of reducing receiver sensitivity (in the ear) and a reduction in source level compensates almost precisely for the 12 dB increase in echo level for each halving of distance.

The reduction in source level with decreasing distance to obstacles has been verified in a number of field and laboratory studies on echolocating bats (Boonman and Jones, 2002; Brinkløv et al., 2009; Brinkløv et al., 2010; Hiryu et al., 2007; Holderied et al., 2005; Koblitz et al., 2010; Surlykke and Kalko, 2008; Tian and Schnitzler, 1997) and toothed whales (Atem et al., 2009; Au and Benoit-Bird, 2003; Beedholm and Miller, 2007; Jensen et al., 2009; Rasmussen et al., 2002; Linnenschmidt et al., 2012a), although distance compensation may not be obligatory in whales (Madsen et al., 2005). Most studies assume a logarithmic relationship between distance, x , and source level, SL:

$$SL = C + a \log_{10}(x), \quad (1)$$

where C is a constant, and report a slope or rate of compensation, a , close to 20. A $20 \log_{10}(x)$ relationship, or -6 dB per halving of distance, would compensate for the one-way spherical spreading loss and keep the incident sound level on the target approximately constant. Although the $20 \log_{10}(x)$ relationship seems to fit most existing data fairly well (Au and Benoit-Bird, 2003; Hartley, 1992a; Hartley, 1992b; Jensen et al., 2009; Koblitz et al., 2010; Rasmussen et al., 2006; Surlykke and Kalko, 2008; Tian and Schnitzler, 1997), there are several difficulties with the logarithmic model.

Firstly, the model cannot be true for all distances. A model relating source level to $\log_{10}(x)$ implies ever-increasing emitted intensity with increasing distance. This obviously cannot be implemented *ad infinitum* by any type of echolocator. The medium (air or water) sets a limit to maximum sound pressures before energy is mostly lost as heat or cavitation, involving the formation and implosion of air bubbles known, for example, from snapping shrimp (Versluis et al., 2000). Physiological constraints such as body size and muscle power probably set even stricter limitations to the maximum possible source level any given animal can produce. Consequently, a realistic model should include a maximum source level, with particular values depending on species, individuals and the behavioural context.

Secondly, criteria for data sampling and analysis may have added to a misinterpretation of data. Some data apparently support the logarithmic model for all distances (Au and Benoit-Bird, 2003), but this may be because of a constant signal-to-noise criterion for analysing the data, which would bias the inclusion of recordings used for analysis towards higher and higher source levels with increasing distance (Jensen et al., 2009; Surlykke and Kalko, 2008).

Thirdly, the procedure for analysis may have obscured the true shape, and especially slope, of the function(s). The standard in field studies has been to include all estimated source levels as a function of distance and fit the best possible logarithmic regression to this 'cloud of points'. Typically, the analysis includes data points originating from recordings of many different individuals under varying environmental conditions and at different points in time, based on the assumption that more data gives better evidence. However, such a procedure assumes a single, common relationship in all these events and does not consider behavioural flexibility caused, for example, by different distances of detection and reaction (e.g. a more rapid compensation in the event of late object detection). Fitting a single regression line to data that represent a series of individual steep curves, but initiated at different distances (because of differences in detection distance) will result in a shallower regression slope than the actual slopes from each individual event (Fig. 1). Consequently, an improved model should determinate slopes for each individual event.

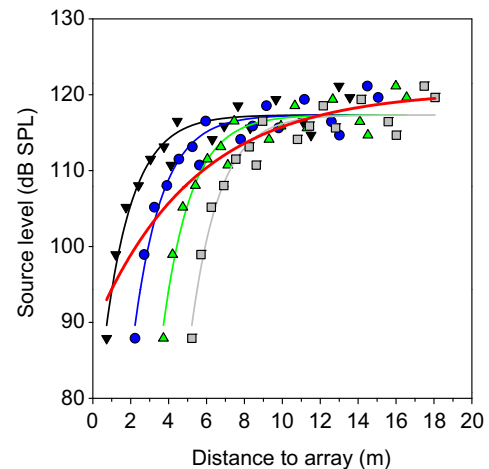


Fig. 1. Estimating the slope of the relationship between source level and distance to array. The slope estimated from a common regression through a 'cloud of points' representing pooled data from individual flights may underestimate the true slopes of the actual events. Here this is illustrated by generating four data sets from a single flight event of *Myotis daubentonii* (data from Fig. 4N). Black triangles/curve, original data; blue circles/curve, original distance to array increased by 1.5 m for each point; green triangles/curve, original distance to array increased by 3 m for each point; grey squares/curve, original distance to array increased by 4.5 m for each point; red curve, common regression through pooled data from all four events. The exponential regression model was used for both individual events and pooled data. SPL, sound pressure level.

Distance compensation or gain control – *via* the collective contributions of increased thresholds on the receiver side and reductions in source level on the emitter side – is of fundamental importance for the basic function of biosonar and more generally for the understanding of perception of sensory cues across a huge dynamic range. Understanding cognition and perception through biosonar, along with basic acoustic and biological constraints for sound communication in general, depends on realistic values for the dynamic feedback control of sound output level. Trustworthy estimates are equally important for understanding the reaction of hearing prey to echolocators and thus for understanding the constraints for the evolution of acoustic interactions between predator and prey (Goerlitz et al., 2010; Surlykke, 1988).

The present study aimed to develop an improved model for the relationship between source level and distance to objects based on field data from microphone array recordings of five echolocating bat species from the families Vespertilionidae and Phyllostomidae. We present a new exponential regression model which integrates three key features of the behavioural response: maximum source level, the minimum detection distance (inferred from the distance where intensity reduction starts) and the rate or slope of intensity reduction. Our new model shows a markedly improved fit (r^2) over the logarithmic model and facilitates comparisons of interspecific and individual variability.

Our results show much steeper rates of intensity reduction with decreasing distance than indicated by previous field studies based on pooled data, thus emphasizing the importance of logging individual flights and behaviours instead of fitting models to pooled data. Data from laboratory experiments, however, have also indicated shallow slopes even though they have been estimated for individual events, but owing to the predictability and stereotypic nature of carefully controlled laboratory experiments, such results may not be directly comparable with data from the field. It is also important to note that

in the field, bats consistently emit source levels that exceed those in the laboratory by 20 dB or more (Jakobsen and Surlykke, 2010), which may call for more steep compensation in the wild.

We predict that a more realistic and biologically relevant model will prove an important tool for understanding how echolocators and sound-producing animals in general adjust their acoustic emissions to habitat, behavioural strategies and sympatric species.

MATERIALS AND METHODS

Acquisition of sound data

We recorded four species of phyllostomid (leaf-nosed) bat and one species of vespertilionid bat in Panama, Cuba and Denmark in their natural habitats during 2008–2010. Two phyllostomid species, the Jamaican fruit bat, *Artibeus jamaicensis* Leach 1821, and the greater spear-nosed bat, *Phyllostomus hastatus* (Pallas 1767), were recorded while exiting their cave roost on Isla Colón, Bocas del Toro, Panamá. The Cuban flower bat, *Phyllonycteris poeyi* (Gundlach 1860), was recorded while flying out from a cave near Tapaste (La Habana), Cuba. *Macrophyllum macrophyllum* (Schinz 1821) and the vespertilionid *Myotis daubentonii* (Kuhl 1817) are both insectivorous bats that take prey either from closely above or by grabbing it directly from water surfaces, i.e. by trawling. The trawling bats were recorded while hunting over Lake Gatún near Barro Colorado Island, Panamá, and Skovsøen Lake, Odense, Denmark, respectively.

We used an array of four or five microphones to record the bats' echolocation signals. The array microphones were in one plane, with three on a horizontal axis 1 m apart, and either a single or two microphones displaced vertically above the horizontal axis by 1–2 m. Exact array dimensions differed between sites. The centre microphone in the horizontal part of the array was a ¼ inch G.R.A.S. microphone (40BF, G.R.A.S. Sound and Vibration, Holte, Denmark), with a preamplifier (G.R.A.S. 26AC) and amplifier (G.R.A.S. 12AA, built-in 13 kHz high-pass filters). This microphone was used for source level estimates of *P. poeyi*, *M. macrophyllum* and *M. daubentonii*. The array used to record *A. jamaicensis* and *P. hastatus* had a fifth vertically displaced ¼ inch G.R.A.S. microphone. Source levels [signal intensity estimated 10 cm from the mouth of the bat as root mean square (r.m.s.) sound pressure referenced to 20 µPa] were determined from the signals recorded on the ¼ inch calibrated microphone with the highest signal amplitude. Recorded sound levels were corrected for spherical spreading loss and atmospheric absorption calculated at the peak frequency of each call (Fig. 2) at ambient temperature and humidity. A more detailed description of this method is outlined in Brinkløv et al. (Brinkløv et al., 2009) and Surlykke and Kalko (Surlykke and Kalko, 2008). The entire recording chain had a flat frequency response (± 2 dB) up to 110 kHz. The additional microphones (Condenser ultrasound microphone CM16/CMPA,

Avisoft Bioacoustics, Berlin, Germany) provided timing information for positioning of the bats. The amplified microphone signals were digitized (250 or 300 kHz/channel, 8 or 16 bit/channel) by an Avisoft USGH (12 channels, integrated adaptive anti-aliasing filter) and stored on a Lenovo Thinkpad X60 laptop (Lenovo Denmark, Holte, Denmark).

Sound analysis

The planar configuration of the array allows for 3-D positioning of bats at the time of each sound emission by determining its time-of-arrival difference at the four or five array microphones. We used the positions from call to call to estimate flight paths (Brinkløv et al., 2009; Surlykke and Kalko, 2008). We selected individual flights for further analysis based on the following two criteria: (1) the approach had to be consistent and straight on, i.e. flight paths had to deviate less than 30 deg from a line perpendicular to the array and distance to the array had to decrease throughout the flight, in order to exclude aborted approaches, and (2) the number of data points had to be sufficient to allow a comparison of different regression models. For this reason we only used flights including a minimum of seven data points. No prey capture or terminal buzz calls were included in the data analyses.

Spectrograms were created in BatSound Pro (v. 4.0, Pettersson Elektronik, Uppsala, Sweden).

Statistical data analysis

General approach

In the majority of previous experiments all estimated source level (SL) data have been pooled and logarithmic models have been fitted to the resulting 'cloud of points'. The fitted regressions were statistically significant, but for field data often had modest coefficients of determination (e.g. r^2 in the range of 0.2–0.7, often below 0.5) (Au and Benoit-Bird, 2003; Jensen et al., 2009; Surlykke and Kalko, 2008). Low r^2 -values may indicate that the pooled data sets include several distinct relationships between the explanatory (distance) and the response (SL) variable. Thus, our strategy was instead to fit regression curves to the calls emitted during a single flight from an individual bat and test the fit of those regressions (see below) before pooling the data for comparison with previous experiments.

Choice of regression models

The conventional logarithmic model includes two parameters, distance and source level. We screened a number of possible regression models for non-linear curve fitting, which would take into account the constraint of a third parameter, maximum source level (SL_{max}). Models with an exponential rise to a maximum, i.e. negative exponential growth functions, fulfilled this criterion. We

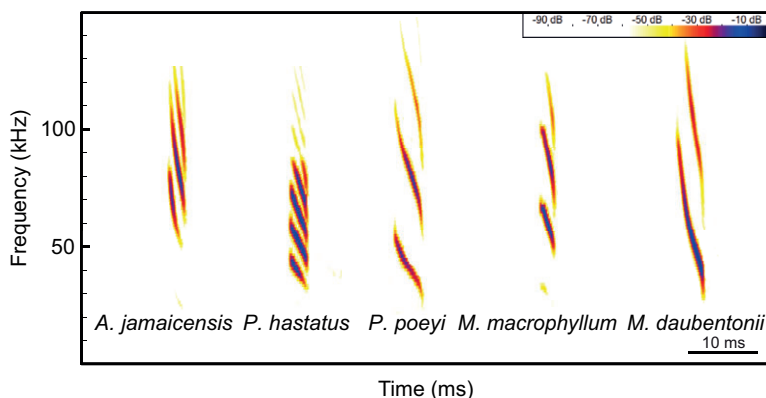


Fig. 2. Spectrograms of representative calls from each of the five bat species: *Artibeus jamaicensis*, *Phyllostomus hastatus*, *Phyllonycteris poeyi*, *Macrophyllum macrophyllum* and *Myotis daubentonii* (Hann Window, fast Fourier transform size 256, 98% overlap). The four phyllostomids typically had the most energy in the second or third harmonic of their calls, whereas the vespertilionid *M. daubentonii* had the most energy in the fundamental. Colour scale indicates the relative call energy.

also tested a number of more complex models that included more parameters, but these did not lead to significant improvements, i.e. better r^2 values compared with the exponential model. Consequently, we decided to compare the performance of the conventional two-parameter logarithmic model (Eqn 1) with that of a three-parameter exponential model (Eqn 2), with y represented by SL, distance represented by x , and constants C , SL_{\max} , a and b :

$$SL = SL_{\max} - ae^{-bx}. \quad (2)$$

Comparison of models

We attempted to use the regression P -values for comparison of models. However, out of all the logarithmic and exponential regressions, only two logarithmic regressions were not significant. For all other individual flights in our study, both regression models were significant and had comparable P -values in the range of <0.0001 to 0.005 . Thus, P -values were not useful for evaluating the relative performance of the two models. Therefore, we used two regression fit statistics to compare the logarithmic and the exponential models: (1) the adjusted coefficient of determination, i.e. the adjusted r^2 , which measures the proportion of the total variation in y explained by the regression on x , and (2) the Durbin–Watson statistic, d , which is a measure of the degree of serial correlation in the residuals of the regression (Durbin and Watson, 1951; Savin and White, 1977), as explained below.

For the adjusted r^2 -values, a minimum increase in adjusted r^2 of at least 0.05 was decided *a priori* as one criterion for improved performance of one regression model over the other. However, r^2 is a general and not always informative measure. Two different regression curves may have similar P - and r^2 -values, but one curve may pass through the middle of the data points at all x -values, whereas the other may have some regions where successive points are predominantly above the fitted curve and some regions where the data points are mostly below the fitted curve. The Durbin–Watson statistic discriminates between these situations; d always lies between 0 and 4, with 2 indicating no serial correlation of residuals, where residuals of consecutive points are uncorrelated and the points are scattered randomly around the regression curve. A value of d close to 0 indicates positive serial correlation, such that successive points have the same sign, i.e. are on the same side (above or below) of the fitted curve. A value of d close to 4 indicates negative serial correlation, where consecutive residuals consistently have opposite signs. Negative serial correlation is rarely observed and was not a problem in our data, but we observed many examples of positive serial correlation when fitting the models to pooled data as well as data from individual flights. Thus, we used an improvement in d towards 2, no serial correlation, as the second criterion for judging one regression model better than the other. The change in the two parameters, adjusted r^2 and d , were considered simultaneously, and one model was judged to have an overall better fit if either both parameters were improved or if one of the parameters was improved while the other remained unchanged.

Data for individual flights fulfilled assumptions of normality and constant variance for both the logarithmic (Eqn 1) and the exponential (Eqn 2) regression model. Statistical analysis was performed using SigmaPlot (Version 11.0 for Windows, Systat Software, Chicago, IL, USA). In all statistical tests a significance level of $\alpha=0.05$ was used.

RESULTS

The four phyllostomid species emitted short (5 ms or less) multiharmonic calls (steep, downward-modulated frequency sweeps).

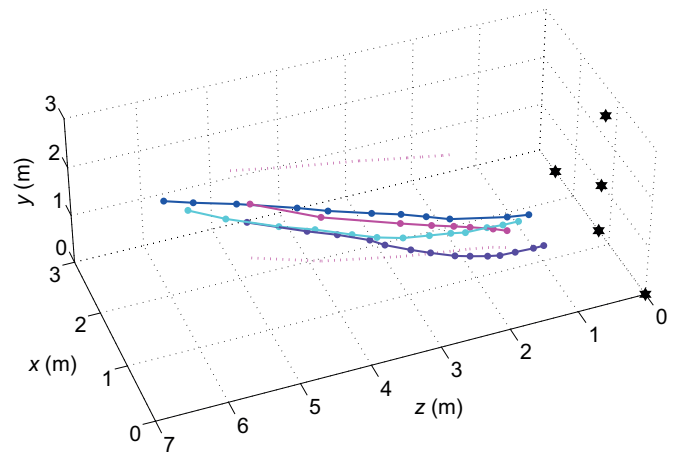


Fig. 3. Examples of flight paths from *Artibeus jamaicensis* (pink and purple traces) and *Phyllostomus hastatus* (light and dark blue traces). Both species were recorded with the same array with five microphones. Microphone positions are indicated by stars. $y=0$ corresponds to the horizontal part of the array, which was approximately 1.5 m above ground level. The pink flight path from *A. jamaicensis* is projected onto the x - z and y - z planes (dashed pink lines) and corresponds to the source level versus distance plot in Fig. 5B.

Main call energy was usually in the second or third harmonic around 79 kHz for *A. jamaicensis*, 55 kHz for *M. macrophyllum*, 55 kHz for *P. hastatus* and 75 kHz for *P. poeyi*. The vespertilionid *M. daubentonii* emitted calls with most energy in the first harmonic and peak frequency around 45 kHz (Fig. 2). A total of 14, 7, 16, 8 and 8 individual flights for *A. jamaicensis*, *M. macrophyllum*, *M. daubentonii*, *P. hastatus* and *P. poeyi*, respectively, fulfilled our criteria for flights approaching our array straight on with at least seven positions where source level could be estimated (Fig. 3). These were selected for further analysis. Some bats reacted to the setup by increasing the call rate and decreasing call duration, but none of the selected flights included terminal buzz-like signals, that is, we only used calls emitted at repetition rates <40 Hz, typical of search or approach phases. We excluded buzz calls because source level is always reduced drastically (20 dB or more) in the buzz (Jakobsen and Surlykke 2010), which would obscure the reaction to the array. Further, the high buzz repetition rate of up to 200 s^{-1} precludes sonar signal adjustments on a call-to-call basis (Elemans et al., 2011).

Comparison of regression models

The two regression models were fitted to both the pooled data and to individual flights. Fig. 4 shows all analyzed flights of *M. daubentonii* and Fig. 5 summarizes the results for the four remaining species. For the pooled data, there were no large differences between the fits of the two models for any of the five species and the test values were quite similar with r^2 ranging from 0.26 to 0.69 for the logarithmic model and from 0.25 to 0.72 for the exponential model. The Durbin–Watson statistic, d , was low, around 0.5 for pooled data for most species, which indicates positive serial correlation (Table 1). When we used data from individual flights to model regression lines rather than pooled data, the fit of both models, logarithmic as well as exponential, was markedly improved for all species (Table 1). Fitting to individual flights gave average adjusted r^2 -values of 0.57–0.80 for the logarithmic model and 0.80–0.95 for the exponential model (Table 1). Fits based on individual flights also showed improvements in d , with values approaching 2, i.e. indicating no serial correlation (Table 1).

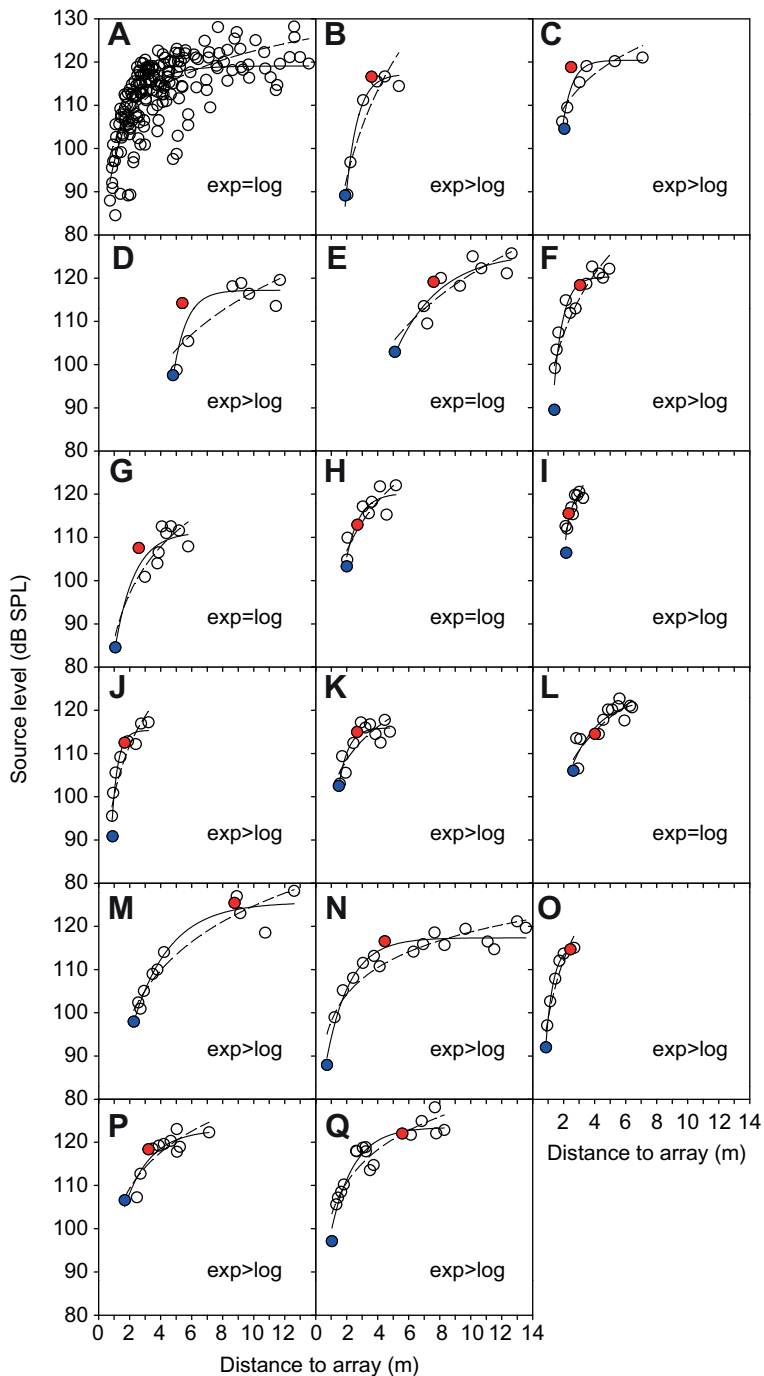


Fig. 4. Relationship between source level and distance to the array for *Myotis daubentonii*. (A) All flights ($N=16$) pooled. (B–Q) Individual flights. Solid lines, exponential regression model; dashed lines, logarithmic regression model. exp=log, no difference between the fits of the exponential and the logarithmic models; exp>log, the exponential model provides a better fit than the logarithmic model. Red circles, detection distance x_2 , which is the point at which source level compensation was initiated; blue circles, final point, x_1 , at the closest recorded distance to the array; open circles, additional data points.

Although the use of individual flight data improved the fit of both models, the exponential model performed better than the logarithmic model in the majority of flights (77%). In 13 of 14 flights for *A. jamaicensis*, four of seven flights for *M. macrophyllum*, 12 of 16 flights for *M. daubentonii* and six of eight flights for both *P. hastatus* and *P. poeyi*, the exponential model provided a major improvement compared with the logarithmic model. Further, we found not a single example of a better fit for the logarithmic over the exponential model. On average, the adjusted r^2 increased by 0.08–0.23 for the five species when the exponential rather than the logarithmic model was applied to individual flights. The highest average adjusted r^2 for the logarithmic model for individual flights was 0.80, whereas for the exponential model 0.80 was the lowest average r^2 and the highest average r^2 was 0.95 (Table 1).

The exponential model also led to improvements in d , which was close to 2 (1.94–2.36) for all species, indicating no serial correlation, compared with 0.93 to 1.54 for the logarithmic model, indicating positive serial correlation and, hence, a poorer fit (Table 1).

Estimation of maximum source level, detection distance and rate of compensation

We used the exponential model (Eqn 2) to estimate three biologically important parameters: maximum source level, detection distance and slope of the decrease in emitted sound level as the bats approached the recording array.

The maximum source level, SL_{\max} , was estimated directly from the regression results. The detection distance, x_2 , was estimated as the closest distance where the approaching bat still emitted a source

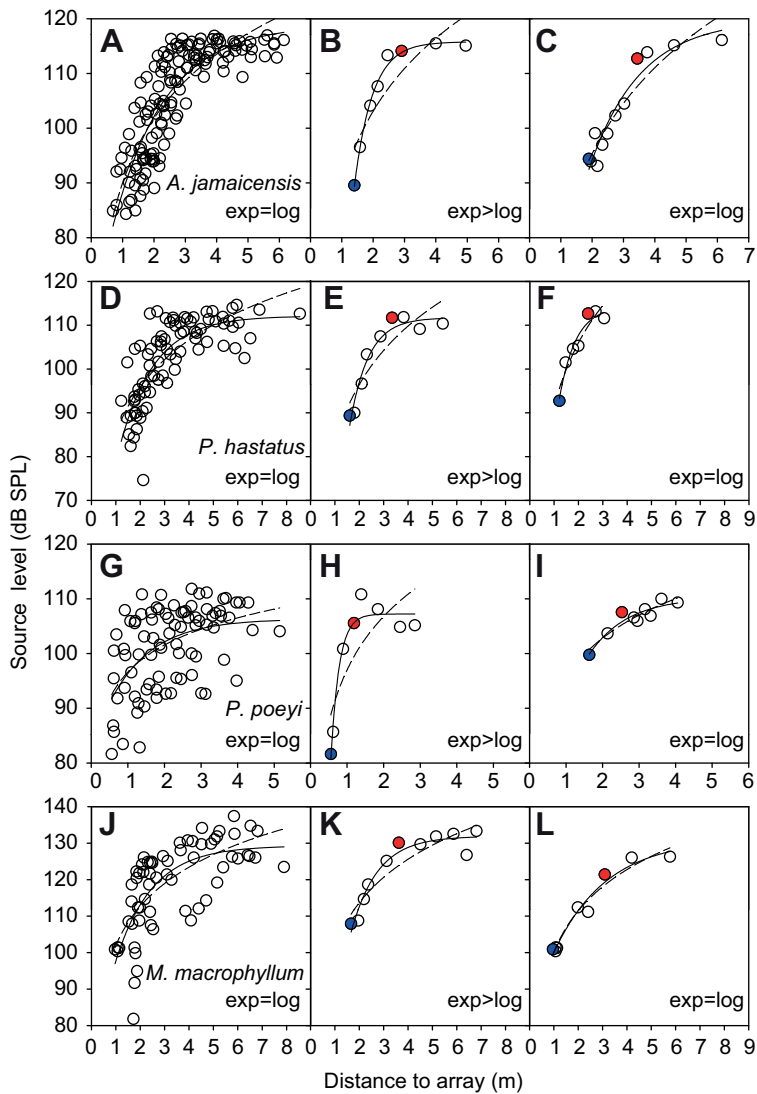


Fig. 5. Relationship between source level and distance to the array in four species of bats. *Artibeus jamaicensis*: (A) all flights ($N=14$) pooled; (B,C) examples of individual flights. *Phyllostomus hastatus*: (D) all flights ($N=8$) pooled; (E,F) examples of individual flights. *Phyllonycteris poeyi*: (G) all flights ($N=8$) pooled; (H,I) examples of individual flights. *Macrophyllum macrophyllum*: (J) all flights ($N=7$) pooled; (K,L) examples of individual flights. Solid lines, exponential regression model; dashed lines, logarithmic regression model. exp=log, no difference between the fits of the exponential and the logarithmic models; exp>log, the exponential model provides a better fit than the logarithmic model. Red circles, detection distance x_2 , which is the point at which source level compensation was initiated; blue circles, final point, at the closest recorded distance to the array, x_1 ; open circles, additional data points. Note the differences in scaling of the x- and y-axes.

level, SL_2 , that was greater than the lower 95% confidence limit of the maximum source level, $SL_{\max(LCL)}$, whereas all subsequent source levels emitted at shorter distances were below $SL_{\max(LCL)}$ (Fig. 6). Although the bat might have detected the target several calls earlier, there is no way to determine this in the absence of a detectable behavioural response. Detection distance was therefore inferred from the bat's reaction as the distance to the array at the last call just before the first clear reduction in source level. Hence, this is an estimate of minimum detection distance (Fig. 6).

In order to estimate the slope of source level compensation, we used the decrease in source level from the detection distance, i.e. the point where compensation started (x_2, SL_2), to the final point included in the flight path (x_1, SL_1), where the bat was at minimum distance from the array (Fig. 6). From the SL values at the two points we estimated the slope, a , of the intensity compensation (derived from Eqn 1):

$$a = \frac{SL_2 - SL_1}{\log_{10}(x_2/x_1)} \quad (3)$$

To facilitate comparisons with previous studies, we calculated the rate (slope) of compensation as the increase in source level per doubling of distance (dB/dd) between the two points (x_2, SL_2) and (x_1, SL_1):

$$\text{Slope} = a \log_{10}(2) \quad (4)$$

Table 2 summarizes average estimates for the maximum source level (SL_{\max}), detection distance, i.e. the point of compensation onset (x_2, SL_2), and the slope of compensation.

We determined SL_{\max} based on pooled data as well as individual flights (Table 2). SL_{\max} varied from species to species. For individual flights, *M. macrophyllum* showed the highest mean value (127.6 ± 3.6 dB), followed by *M. daubentonii* (119.5 ± 1.0 dB), *A. jamaicensis* (115.9 ± 0.6 dB), *P. hastatus* (112.3 ± 1.6 dB) and *P. poeyi* (104.8 ± 2.0 dB). SL_{\max} estimates based on pooled data did not differ by more than a few decibels from those based on individual flights (Table 2).

Our results showed that bats started compensating, i.e. decreasing their source level, ca. 2–4 m from the array, which we took as a proxy for detection distance. The general trend of the data indicated that increased detection distance coincided with higher maximum source levels (Table 2): the longest mean detection distance, x_2 , was observed for *M. daubentonii* (3.9 ± 0.5 m), followed by *M. macrophyllum* (3.4 ± 0.5 m), *P. hastatus* (3.2 ± 0.2 m), *A. jamaicensis* (3.0 ± 0.1 m) and *P. poeyi* (1.8 ± 0.2 m).

The slopes of compensation for all individual flights were much steeper than shown previously. The highest mean slope of compensation was found in *M. daubentonii* (29.9 ± 6.7 dB/dd), followed by *P. hastatus* (24.8 ± 1.9 dB/dd), *M. macrophyllum* (24.4 ± 5.5 dB/dd), *A. jamaicensis* (24.1 ± 1.5 dB/dd) and *P. poeyi*

Table 1. Performance of the two regression models as evaluated by comparing adjusted r^2 -values and the Durbin–Watson statistic, d

Species	Regression	Logarithmic model		Exponential model		Comparison of models		
		Adj. r^2	d	Adj. r^2	d	exp>log	exp=log	exp<log
<i>Artibeus jamaicensis</i>	Pooled data	0.69	0.50	0.72	0.50	–	1	–
	Individual flights	0.80±0.02	0.93±0.11	0.95±0.01	2.11±0.13	13	1	0
<i>Macrophyllum macrophyllum</i>	Pooled data	0.48	0.42	0.50	0.43	–	1	–
	Individual flights	0.74±0.07	1.54±0.31	0.85±0.03	2.19±0.20	4	3	0
<i>Myotis daubentonii</i>	Pooled data	0.50	0.77	0.54	0.83	–	1	–
	Individual flights	0.77±0.02	1.40±0.15	0.85±0.02	2.23±0.15	12	4	0
<i>Phyllostomus hastatus</i>	Pooled data	0.58	0.62	0.62	0.62	–	1	–
	Individual flights	0.77±0.03	1.05±0.19	0.91±0.02	1.94±0.24	6	2	0
<i>Phyllonycteris poeyi</i>	Pooled data	0.26	0.44	0.25	0.46	–	1	–
	Individual flights	0.57±0.09	1.53±0.19	0.80±0.04	2.36±0.17	6	2	0

Values are given for the regressions for the pooled data for all flights, as well as for individual flights (means \pm s.e.m.). Comparison of models shows the number of flights where: exp>log (exponential model best), exp=log (no model superior) and exp<log (logarithmic model best). Total number of flights from each species: 14 for *A. jamaicensis*, 7 for *M. macrophyllum*, 16 for *M. daubentonii*, 8 for *P. hastatus* and 8 for *P. poeyi*.

(16.5±3.5 dB/dd). We ascribe these high compensation rates to using individual flight paths rather than pooled data, for which the regressions resulted in compensation rates between 5.0 and 11.8 dB/dd, hence underestimating the slope by a factor of two to five compared with the individual flights (Table 2).

We observed a high degree of inter-flight variability in the rate of source level reduction. This could indicate behavioural flexibility, such that if a bat detects an object at close range, it adjusts the source level more steeply than when detecting an object at longer range. In most flights the compensation started at a distance of 2–3 m from the array and continued over a range of 1–2 m to the last (closest) distance where source level was estimated. In some cases, however, source level reduction occurred over a range of up to 7 m, whereas in others, bats did not decrease their source level until they were less than 1 m from the microphone array. We plotted the rate of compensation for all flights from all species as a function of the distance range (distance over which compensation occurred) of the recorded compensation, x_2-x_1 , in Fig. 7. For each species, three types of regression models were compared (linear, exponential decrease and log–log). Only for *M. daubentonii* and *A. jamaicensis* were significant regressions found and an exponential decrease model, $y=y_0+ae^{-bx}$, gave the best fit between rate of compensation and distance: *M. daubentonii*: $y=13.89+105.06e^{-1.90x}$ (adjusted $r^2=0.58$, $P=0.0013$, $N=16$); *A. jamaicensis*: $y=16.22+36.43e^{-1.07x}$ (adjusted $r^2=0.35$, $P=0.0375$, $N=14$). Most rates of compensation were 10–35 dB/dd, but we observed very high rates of compensation, up to approximately 100 dB/dd for *M. daubentonii*, when compensation occurred over the shortest distance range (<1 m), while compensation rates were below 15 dB/dd for *M. daubentonii* when compensation occurred over distance ranges longer than approximately 3.5 m. Keeping in mind that we selected on-axis recordings for the analysed data set, the results indicate that very steep compensations can be achieved within a short distance, and point to a very high degree of flexibility and dynamic control of source level depending on the situation.

DISCUSSION

Our objective was to develop a new model for gain control in echolocating animals, i.e. the systematic decrease in emitted source level compensating for increasing echo levels with decreasing distance to objects. We tested the performance of our new exponential growth model on data from five species of echolocating bats. The new model shows a markedly improved performance over the ‘conventional’ logarithmic model, with a better fit in 77% (41 of 53) of flights and equally good fit for both models in the remaining

flights. We found no examples where the logarithmic model gave a better fit than the exponential model. Our results also emphasize the importance of analysing individual events, indicating much steeper slopes of compensation than analyses of pooled data.

The logarithmic versus the exponential model, and estimates of SL_{\max}

Previous studies of distance compensation in echolocators have shown decent fits of the conventional logarithmic model to data sets (Au, 2004; Jensen et al., 2009; Hartley, 1992a; Hartley, 1992b; Surlykke and Kalko, 2008). However, besides an improved fit, the new exponential model offers several advantages over the logarithmic model. Firstly, the exponential model includes the concept of an upper intensity limit, or maximum source level, SL_{\max} , which must obviously be a biological fact. Because the exponential

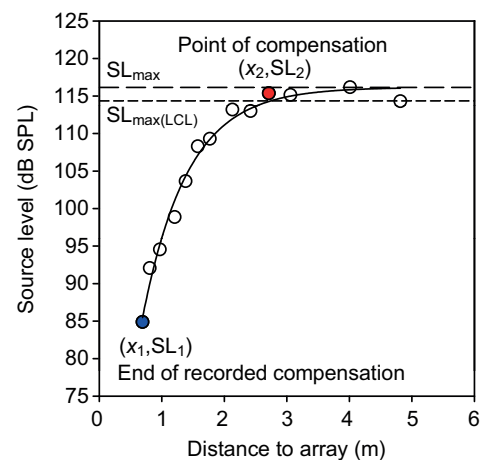


Fig. 6. Source levels as a function of distance from a flight path of *Artibeus jamaicensis*, illustrating how we estimated the parameters maximum source level, detection distance and rate of compensation using the exponential model. SL_{\max} , maximum source level; $SL_{\max(LCL)}$, lower 95% confidence limit of the maximum source level. Red circles indicate (x_2, SL_2) , the point of onset of compensation, which was estimated as the last position in the approach, where the source level was still above $SL_{\max(LCL)}$. The detection distance, x_2 , is determined by this point. Blue circles indicate (x_1, SL_1) , the end of recorded compensation, at the closest recorded distance to the array, x_1 . Open circles indicate additional data points. The rate of compensation is calculated from (x_2, SL_2) and (x_1, SL_1) , as described in the Materials and methods.

Table 2. Maximum source levels (SL_{\max}), detection distances (x_2) and rates of compensation for five species of bats

Species	Regression	SL_{\max} (dB)	x_2 (m)	Rate of compensation (dB/dd)
<i>A. jamaicensis</i>	Pooled data	118.9±1.9	–	11.8±0.7
	Individual flights	115.9±0.6	3.0±0.1	24.1±1.5
<i>M. macrophyllum</i>	Pooled data	129.3±2.8	–	10.7±1.4
	Individual flights	127.6±3.6	3.4±0.5	24.4±5.5
<i>M. daubentonii</i>	Pooled data	119.1±0.9	–	6.4±0.5
	Individual flights	119.5±1.0	3.9±0.5	29.9±6.7
<i>P. hastatus</i>	Pooled data	112.1±1.9	–	10.7±1.0
	Individual flights	112.3±1.6	3.2±0.2	24.8±1.9
<i>P. poeyi</i>	Pooled data	106.3±2.5	–	5.0±0.9
	Individual flights	104.8±2.0	1.8±0.2	16.5±3.5

Values are given for the exponential regression through the pooled data for all flights (parameter ± s.e.), as well as for individual flights (means ± s.e.m.).

model includes SL_{\max} , all data points contribute to the fit, whereas the logarithmic model requires fitting to only a selection of data points, because values at long range do not fit the model. Secondly, it allows for estimation of the detection distance, the distance at which intensity compensation starts to occur. Thirdly, the slope or rate of compensation can be deduced from the model. Thus, the model should be a tool for future data-driven studies of how acoustic output is dynamically adapted to a behavioural context in echolocating animals. Further, an important result of our study is the dramatic improvement when fitting to individual flights instead of pooled data. This emphasizes the importance of monitoring and analysing individual events to obtain biologically relevant values, thus providing a better basis for understanding the basic constraints for echolocation. Because the exponential model includes SL_{\max} , all data points contribute to the estimate of SL_{\max} in a given flight. Earlier estimates of SL_{\max} based on the logarithmic model have used an ‘eyeball’ approach to determine when compensation stopped, i.e. at which distance the model no longer fitted (Atem et al., 2009; Brinkløv et al., 2009; Holderied et al., 2005; Jensen et al., 2009; Rasmussen et al., 2002; Surlykke and Kalko, 2008). Subsequently, estimates of SL_{\max} have been based only on data points above this distance, essentially points that do not support the logarithmic model.

Maximum source level estimates based upon enough data points from distances beyond the compensation range will approach estimates from the exponential model, and thus it is not surprising that the data we present here corroborate earlier estimates of maximum source levels reported for bats (Brinkløv et al., 2009; Holderied and von Helversen, 2003; Surlykke and Kalko, 2008).

The exponential model approaches a constant value ($SL_{\max}-a$) at very short distances. Although it is very likely that there is a lower limit to the source levels bats produce, we have not been able to collect data to test this because at such short distances the situation would be complicated by several facts, e.g. difficulties in manoeuvring to avoid colliding with the array. Bats will probably only fly so close to objects if it is either prey or a landing platform, and in both scenarios bats emit buzzes, with very different physiological constraints because of the high call repetition rate (Elemans et al., 2011).

Slope of source level reduction

In contrast to estimates of maximum source levels, the slopes of compensation we report here are very different from earlier estimates. In particular, fitting our exponential model to individual flights instead of pooled data provided estimates of compensation rates that were much steeper than previously reported. Rates estimated from pooled data were between 5.0 and 11.8 dB per doubling of distance (Table 2), which is within the range of previously reported values (Au and Benoit-Bird, 2003; Brinkløv et al., 2009; Brinkløv et al., 2010; Hartley, 1992a; Hartley, 1992b; Jensen et al., 2009; Koblitz et al., 2010; Rasmussen et al., 2006; Surlykke and Kalko, 2008). This supports the hypothesis that slopes based on pooled data are too shallow, because they average over a series of steeper individual functions (Fig. 1). Thus, our results lend no support to a general slope of $20\log_{10}(x)$, which would keep the incident level on the object constant. A slight individual variation of slope has been reported for horseshoe bats (Tian and Schnitzler, 1997) compensating within 60 cm of a target, but our data suggest an even higher level of dynamic control than hitherto assumed, such that echolocators can reduce the output very rapidly when needed, i.e. when they detect an object at close range. At longer detection ranges, source level is reduced more gradually, which is in line with the $20\log_{10}(x)$ relationship, i.e. a slope of -5 to -6 dB per halving of distance, shown in single flights for *Noctilio* sp. starting at long detection distances of approximately 8 m (Surlykke and Kalko, 2008).

A meticulous experiment by Hartley resulted in a $20\log_{10}(x)$ correlation between source level and object distance at close range, 10–100 cm, but in a highly artificial situation where the bat was sitting on a platform echolocating at an object moving towards it at constant

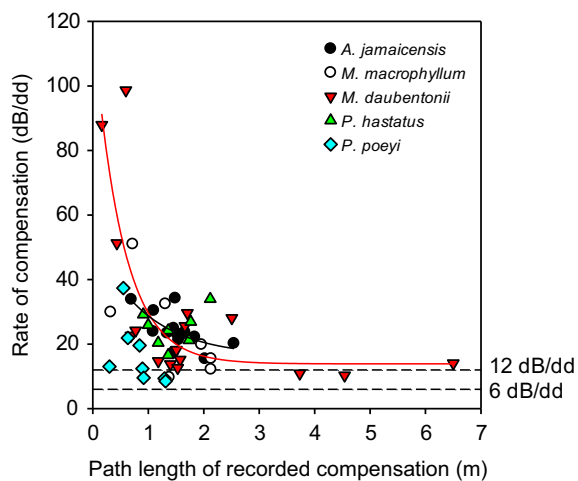


Fig. 7. Relationship between the rate of compensation (dB per doubling of distance) and the path length of the recorded compensation, x_2-x_1 , for five bat species. Data for *Myotis daubentonii* and *Artibeus jamaicensis* resulted in significant regressions. An exponential decrease model, $y=y_0+ae^{-bx}$, gave the best fit: *Myotis daubentonii* (red curve): $y=13.89+105.06e^{-1.90x}$, adjusted $r^2=0.58$, $P=0.0013$, $N=16$. *Artibeus jamaicensis* (black curve): $y=16.22+36.43e^{-1.07x}$, adjusted $r^2=0.35$, $P=0.0375$, $N=14$.

velocity by a pulley system (Hartley, 1992b). Hiryu et al. found similar slopes very close to $20\log_{10}(x)$ for individual bats (Hiryu et al., 2007; Hiryu et al., 2008), but the common denominator of those experiments is that the bats were in a laboratory in familiar surroundings and had precise expectations about the target (wall or object on pulley) and closing speed. This would explain the stereotyped reactions across both bats and individual events compared with our data. Recent data on harbour porpoises corroborate this explanation, showing an initial compensation much steeper than $20\log_{10}(x)$ upon first detection of a target revealed to the porpoise after removal of an acoustical shield (Linnenschmidt et al., 2012b). It is possible that part of the variation we see in our data is caused by variation in flight direction, as our recordings were made in the field under much more variable and unpredictable conditions. The estimated source level might also decrease because the bat turns its head in preparation to veer away from the array. It does, however, seem unlikely that such effects should fully explain the observed variation, keeping in mind that we selected only recordings with bats approaching the array on a straight line over at least seven calls (Fig. 3), and it is unlikely that our estimate of direction to the approaching bats should deviate systematically over such a long path by more than a few degrees. Earlier laboratory data with enough microphones to determine the sonar beam axis independent of bat flight also showed a reduction in on-axis source levels (Jakobsen and Surlykke, 2010; Brinklöv et al., 2011). Notably, a few other field studies have also reported very steep slopes for both dolphins (Atem et al., 2009) and bats [(Holderied et al., 2005) their fig. 6A]. Also, the emitted intensities are much higher in the field than in the laboratory (Surlykke and Kalko, 2008), which suggests that a drastic compensation is not necessary in the laboratory, because the level is already much reduced relative to SL_{\max} .

Source level and received echo level

The steep compensation slopes provoke the question of biological relevance. A point target will reflect an echo decreasing by 12 dB per distance doubled (dB/dd). More extended target types will reflect echoes that attenuate more slowly, i.e. by 9 dB/dd for a line target and 6 dB/dd for a planar target (e.g. a wall). Thus, if the bat decreases the output level by more than 12 dB per halving of distance, the received echo level will decrease for all target types. For example, a slope of 27 dB/dd will reduce the received echo level by 15 dB for each halving of distance for a point target and by 18 dB for a line target. Hence, the perceived level decreases rapidly as the echolocator approaches an object. However, as long as the echo level exceeds the hearing threshold, reducing the source level may be a strategy to optimize the echo-to-clutter ratio. Keeping the emitted level as low as possible will attenuate clutter echoes from objects further away relative to the target echo and improve the echo-to-clutter ratio because the relative distance to clutter objects behind the target will not decrease as rapidly as the target distance. The acoustic behaviour of *M. daubentonii* lends support to this idea (Fig. 4N). The source level is reduced by 30 dB from an SL_{\max} of 115 dB at 4 m down to 85 dB at 1 m. We assume that the bat is reacting to a point target (i.e. the on-axis $\frac{1}{4}$ inch microphone) and a planar clutter object is present at some distance, e.g. at 2 m, behind the target. This means that when the bat has reduced the distance to the target from 4 m to 1 m, i.e. by one-quarter, then the distance to the clutter has only decreased to one-half (from 6 to 3 m). The point target echo increases by 12 dB/dd, i.e. +24 dB over the distance range from 4 to 1 m. The planar clutter reflects an echo that only changes by 6 dB/dd. Thus, the target echo will decrease by 6 dB but the clutter echo will decrease by 24 dB and the echo-to-clutter ratio will improve by 18 dB.

We can also estimate the target and clutter echo level at the bat's ears if we use the simple form of the sonar equation:

$$EL = SL - 2TL + TS, \quad (5)$$

where EL is the echo level, TL is the transmission loss and TS is the target strength (Møhl, 1988; Madsen and Wahlberg, 2007). Again assuming that part of the array (one microphone) resembles a point target with a target strength close to a medium-sized moth of -20 dB (re. 0.1 m) (Surlykke et al., 1999) and using an atmospheric attenuation of 1.2 dB m^{-1} at 40 kHz (15°C), then the echo level at 1 m target distance would be ca. 23 dB at the bat's ear, which is probably above but close to the bat's hearing threshold, whereas the echo level from a similar sized clutter object 2 m behind the microphone would be approximately -1 dB, and hence below the threshold for hearing under noisy conditions as in flight. Obviously, this is only a rough estimate and should be tested in future studies.

Detection distance

The mathematical relationship in the exponential model we propose is simple, but provides improved fits with higher adjusted r^2 -values than those obtained from the logarithmic model. The exponentially based model uses all the data to fit the curve. As discussed above, this did not change estimates of maximum source level much compared with previous studies, but it resulted in slopes of the compensation function that were dramatically different from earlier estimates. In addition, the new model facilitates determination of the 95% confidence limits for SL_{\max} . By combining these two parameters, slope and the lower 95% confidence limit, we can use all data to estimate the distance at which the approaching echolocator starts compensating in each individual flight, and we propose this as a proxy for the detection distance. Detection distance is a key biological parameter that has been discussed intensely over many years (Griffin, 1958; Roeder, 1966; Jung et al., 2007; Schaub and Schnitzler, 2007; Siemers and Schnitzler, 2000) because it is crucial for understanding the range of biosonar, the reaction and adaptation to different types of habitat, as well as the relative detection distances when interacting with eared and non-eared prey (Goerlitz et al., 2010; Miller and Surlykke, 2001). The five bat species included in this study emitted signals with source levels that differed by a factor of 10 (20 dB) in intensity and showed average detection distances that differed by a factor of 2 (4–2 m) (Table 2). Both *M. daubentonii* and *A. jamaicensis* reduced the source level more steeply if the object was first detected at close range, and although not statistically significant both *M. macrophyllum* and *P. poeyi* showed the same trend, although no such trend was observed for *P. hastatus* (Fig. 7). The data show considerable scatter even though we only analysed calls from bats flying towards our recording array. This is likely because of the many sources of variation inherent to field studies, such as differences in the distances at which individual bats detected and reacted to the array. The majority of individual events recorded in the field are likely to represent a novel experience for each bat, as we recorded in situations where the bats could not familiarize themselves with the object (array), i.e. emergence from roosts (*A. jamaicensis*, *P. hastatus* and *P. poeyi*) or open field situations for the two trawling bats. Detection distance could reflect variations in source level, direction and directionality of the echolocation beam. Also, even though the flight directions were comparable, the bats may have paid attention to different objects. However, although there are many sources of variation that cannot be controlled for in field studies, the results clearly demonstrate the bats' ability to modify and even drastically alter source levels, resulting in slopes that are highly variable and often very steep. This provides a clear

demonstration of the dynamic flexibility of sonar in all five bat species studied here. We predict that the new exponential model will prove to be particularly useful in the wild for identifying species-specific reactions to prey, and thus reveal more reliably the shift from the 'search' to the 'approach' phase. This may provide a means of quantifying reactions to habitat conditions and hence using the bats' reactions to define the degree of 'clutter' instead of relying on human visual inspections. Thus, the model provides a tool with which to facilitate comparisons across species and habitats, across prey types and even across media, i.e. air and water for bats and whales, respectively, and hopefully increases the amount of data available that can help us understand the evolutionary constraints for evolving echolocation, a mode of orientation employed by more than a fifth of all mammalian species.

In conclusion, the relationship between the output intensity of sound signals and distance is not an issue restricted to echolocators, but applies to all animals communicating with sound. Animals having a 'private' conversation with a conspecific close by emit very silent signals (Nakano et al., 2008), whereas animals communicating over large distances in general emit loud signals (e.g. Naguib and Wiley, 2001). Thus, models for adjustments of emitted sound levels based on data collection from individuals of a variety of sound-producing animal species, regardless of whether they are echolocators, will be of great value in the future for understanding perception and cognition through sound.

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