A mathematical model for the impact of noise on population dynamics of a single species experiencing Lombard effect

C. Ramirez-Carrasco [a],[*], F. Córdova-Lepe [a], F.N. Moreno-Gómez [b], N.A. Velásquez [b]

[a] *Departamento de Matemática, Física y Estadística, Facultad de Ciencias Básicas, Universidad Católica del Maule, Chile*
[b] *Departamento de Biología y Química, Facultad de Ciencias Básicas, Universidad Católica del Maule, Chile*

A B S T R A C T

Noise is a form of pollution resulting from the undeniable increase in industrialization worldwide. Consequently, it is becoming increasingly important to understand the underlying mechanisms and potential effects of noise on ecosystems. In this study, we propose a deterministic mathematical model that uses a system of nonlinear, non-autonomous differential equations to describe the population dynamics of a single species exposed to noise. The Lombard effect is a phenomenon that involves increasing the intensity of acoustic signals in response to noise, which can mask and degrade acoustic signals and prevent them from being recognized or discriminated by their target receivers. However, when the anthropogenic noise is chronic and critical (*i.e.*, that by its long duration and high intensity positively affects the mortality rate), the increase in the intensity of acoustic signals (due to the Lombard effect) only increases the chronic critical anthropogenic noise and also increase energetic, behavioral and predation costs. Therefore, the critical noise generated by the use of higher intensity acoustic signals (due to the Lombard effect) together with the chronic critical anthropogenic noise, negatively affect population survival. We analyzed the persistence of the population and found that our results are consistent with the observed ecological data as they suggest that, the maximum intensity level of critical chronic anthropogenic noise, consequently, by the Lombard effect, the maximum intensity of self generated acoustic signals, must decrease to ensure population persistence. However, when the maximum intensity level of critical chronic anthropogenic noise is uncontrollable, it is sufficient to reduce its mean intensity level to ensure persistence in the population mean. Furthermore, decreasing the degree to which noise affects the population favors the survival of the species. Finally, to validate our results, we performed numerical simulations.

1. Introduction

The soundscape is all the sounds existing in our environment and is composed of three types of sounds produced by three different sources: Anthropogenic, Biological and geophysical (Krause, 2008; Farina, 2014). For instance, sounds produced by anthropogenic sources, such as cars, airplanes, and factories, are called anthropophony (McGregor et al., 2013). Those produced by biological sources, such as animal songs, are called biophony (Pijanowski et al., 2011a). The sounds produced by any geophysical source, such as sounds caused by rain or wind, are called geophony (Pijanowski et al., 2011b).

Sounds that exceed acceptable thresholds so as not to interfere with communication between individuals or their activities relevant to their survival (permissible sound intensity limit) are called noises (Algers et al., 1978). However, although the permissible sound intensity limit is generally considered to be 90 dB (Pienkowski and Eggermont, 2010), susceptibility to noise hearing depends on the species and has been

shown to be genetically determined (Henry, 1992; Lanier et al., 2000). For example, annoyance thresholds for cattle have been observed between 90 and 100 dB, with physical damage to hearing at 110 dB and above (Phillips, 2009), and in birds, annoyance thresholds have been observed between 95 and 100 dB (Algers et al., 1978).

In particular, noises produced by anthropogenic sources are considered to be anthropogenic noises (Moudon, 2009). The World Health Organization, the European Commission Marine Strategy Framework Directive, and international legislation such as the U.S. National Environmental Policy Act state that anthropogenic noise is one of the most dangerous forms of pollution, becoming omnipresent in terrestrial, aerial and aquatic ecosystems (Simpson et al., 2016; Kunc and Schmidt, 2019; World Health Organization, Copenhagen, 2011). Thus, anthropogenic noise acts as a sound that masks the acoustic signals of animals, negatively affecting communication, distribution and foraging (Slabbekoorn et al., 2018; Dooling et al., 2009; Erbe et al.,

---

2016; Römer, 2013; Sueur and Farina, 2015; De Vincenzi et al., 2021; Goldbogen et al., 2013; Goodwin and Shriver, 2011; Hildebrand, 2009; Parris and Schneider, 2009; Slabbekoorn and Peet, 2003; Popper and Hawkins, 2016). However, at the population level, direct evidence of its effect on survival is rare. This is because, for example, as animals move away from anthropogenic noise sources and their distance from the emitting source increases, exposure levels lower, and their effects are less severe (Richardson et al., 2013; Hawkins and Popper, 2017). However, although these effects are less severe at the individual level, the potential effects at the population or community level may increase because the number of exposed individuals also increases (Babisch, 2002). The permissible sound intensity limit is critical when the effects of chronic anthropogenic noise (now critical) on mortality are negative. Correlating evidence suggests that naval sonar causes the stranding of beaked whales, thus increasing their mortality (Filadelfo et al., 2009). Noise above 100 dB from ships negatively affects predator avoidance behavior in damsel fish, thus increasing their predation-induced mortality (Simpson et al., 2016) and negatively affecting the early survival of marine invertebrates by increasing the mortality of newly hatched larvae (Nedelec et al., 2014). Chronic noise above 65 dB from traffic affects growth rates and embryo mortality in zebra finches (Potvin and MacDougall-Shackleton, 2015). Therefore, the effects of chronic anthropogenic noise on ecosystems are increasing as they tend to cause a decrease in species richness and population size (Kunc et al., 2016; Kight and Swaddle, 2011).

On the other hand, in response to increased ambient noise, animals increase the intensity of their acoustic signals. This phenomenon is known as the Lombard effect (Lombard, 1911; Sinnott et al., 1975; Katti and Warren, 2004). The Lombard effect in animals such as mammals, fish, and birds has been mostly limited to short-term studies and suggests a positive effect on population survival. This is because acoustic communication is often limited by the effects of noise, which masks and degrades the acoustic signals; thus, by increasing the intensity of these signals, the animals continue to be recognized or discriminated by their target receivers (Luo et al., 2018; Holt and Johnston, 2014; Holt et al., 2009; Helble et al., 2020). However, when chronic anthropogenic noise is critical, the use of higher intensity self-generated acoustic signals not only increases the noise, but also the energy costs of signaling (Brackenbury, 1979; Calder III, 1990; Oberweger and Goller, 2001; Warren et al., 2006; Barber et al., 2010; Read et al., 2014; Brown et al., 2021). Such increases in intensity are also linked to behavioral costs (Swaddle et al., 2015; Farina and Gage, 2017). Moreover, other factors, such as detection by unwanted receptors (e.g., predators), also contribute to the cost of intensity increase (Zollinger and Brumm, 2015; Brumm and Todt, 2002; Brumm, 2004; Luczkovich et al., 2016). Therefore, in the exposure to critical chronic anthropogenic noise, the increase in the intensity of acoustic signals, as a result of the Lombard effect could negatively influence survival rates of animals (Sementili-Cardoso and Donatelli, 2021).

Existing mathematical models that study noise as an important factor in population dynamics consider noise a stochastic factor (Vilar and Solé, 1998; Spagnolo et al., 2003; Upadhyay et al., 2007; Das and Samanta, 2018). However, these models do not consider the thought that when noise exceeds a permissible limit, the use of higher intensity of acoustic signals, due to the Lombard effect, increases energetic, behavioral, and predation costs, which could negatively influence the persistence of animals in noisy environments. To our knowledge, there is no literature on deterministic mathematical models describing the negative effects of anthropogenic noise and the Lombard effect on the population dynamics of a species.

This paper presents a new deterministic mathematical model consisting of a system of nonlinear, non-autonomous differential equations to describe the population dynamics of a single species exposed to chronic noise. We assume, that the chronic noise is critical, that is, it exceeds a critical permissible sound intensity limit, the limit up to which the noise does not affect the population mortality rate. In

the model, noise is generated by a chronic and critical anthropogenic noise source and in response, due to the Lombard effect, a biological source that emits acoustic signals of increased intensity by conspecifics, thus increasing energetic, behavioral and predation costs that in the long-term negatively affect population survival. Population density is negative related to the noise intensity to which the population is exposed through a mortality rate response equation with respect to noise (Filadelfo et al., 2009; Simpson et al., 2016; Nedelec et al., 2014; Potvin and MacDougall-Shackleton, 2015; Sinnott et al., 1975; Katti and Warren, 2004; Oberweger and Goller, 2001). Therefore, this study aimed to analyze the effects of noise on the population persistence of a single species experiencing the Lombard effect. More specifically, we tried to answer the following question: What are the sufficient conditions for the model parameters to guarantee the persistence of the population when exposed to noise?

Our results are discussed together with ecological data, suggesting that the maximum intensity level of critical chronic anthropogenic noise, consequently, by the Lombard effect, the maximum intensity of self-generated acoustic signals, must decrease to ensure population persistence. However, when the maximum intensity level of critical chronic anthropogenic noise is uncontrollable, it is sufficient to reduce its mean intensity level to ensure persistence in the population mean. Furthermore, decreasing the degree to which noise affects the population favors the survival of the species. Finally, to validate our results, we performed numerical simulations.

2. Model formulation

We considered a population of biological species in which the mortality rate is positively affected by noise. Individual organisms in the population were assumed to be identical and uniformly distributed in their habitats. The state variables of the model are non-negative functions of time $N(t)$ and $I(t)$, denoting the population size and chronic noise intensity to which the population is exposed at time t, respectively.

2.1. Population growth

Considering the positive constants b_0, b_1, d_0, and d_1 ($b_0 > d_0$), $B(N) = b_0 - b_1 N$ and $D(N) = d_0 + d_1 N$ are thought to be the linear representations (for abundance) of the respective population birth and death rates. Then, in the absence of noise or when the noise has not reached or has still not reached a certain threshold, $N(\cdot)$ follows the classical logistic equation $N' = (r_0 - \lambda N)N$ for $t \geq 0$, where $r_0 = b_0 - d_0 > 0$ is the intrinsic growth rate, and $\lambda = b_1 + d_1$ represents the per capita loss of growth due to intraspecific competition.

We assume that the critical limit of permissible noise intensity is I_μ, a limit up to which the noise does not affect the mortality rate of the population. Thus, when $I \leq I_\mu$, the population follows classical logistic growth. Implicitly, this is explained by the positive effect of the Lombard effect, that is, the population increases the intensity of its songs to maintain a constant signal to noise ratio. Otherwise, when $I > I_\mu$ (called critical noise, which from now on we will simply call now noise). Implicitly, this is, the noise has a positive effect on mortality rate. Thus, increase in the intensity of acoustic signals (due to the Lombard effect) only increases the chronic critical anthropogenic noise and also increase energetic, behavioral and predation costs. Therefore, the noise generated by the use of higher intensity acoustic signals (due to the Lombard effect) together with the chronic critical anthropogenic noise, negatively affect population survival. Thus, the noise intensity experienced by the population increases the per capita mortality rate proportionally to the noise by an amount $d > 0$ for each unit of noise; *i.e.*, $\tilde{D}(N, I) = D(N) + dI$. Thus, the new per capita growth rate, as a function of noise and population size, is $r(N, I) = B(N) - \tilde{D}(N, I) = r_0 - dI - \lambda N$, which explicitly depends linearly on I. Therefore, the

population dynamics of this phenomenon can be described by the following equation of logistic type:

$$N'(t) = r(N, I) N = (r_0 - d\chi(I - I_\mu)I - \lambda N)N \tag{1}$$

where the function $\chi : \mathbb{R} \longrightarrow \{0, 1\}$, is defined as $\chi(I - I_\mu) = 0$ when $I \leq I_\mu$ and $\chi(I - I_\mu) = 1$ when $I > I_\mu$, with the new intrinsic growth rate given by $r_0 - dI$.

2.2. Noise intensity

Sound intensity can be classified into physical (or exposed) and auditory (or perceived) intensities. The physical intensity, measured in watts per square meter (w/m^2), is given by the equation $I = P/A$, where P denotes the transmitted power per unit area A perpendicular to the direction of propagation of the acoustic wave at a point in the acoustic field. Auditory intensity, measured in dimensionless decibels (dB), is given by the equation $L = 10\log(I/I_*)$, where I_* denotes the minimum physical intensity audible to an individual. This last equation is based on the Weber–Fechner psychophysical law (Dehaene, 2003), which establishes a logarithmic relationship between the physical intensity of sound I and the minimum physical intensity audible to individual I_*.

Auditory intensity is the most common method to measure sound. However, unlike physical intensity, the sum of the decibels does not occur in a linear manner. For example, the sum $\oplus$ of decibels L_1 and L_2, is given by $L_1 \oplus L_2 = 10\log(10^{L_1/10} + 10^{L_2/10})$. For this reason, in this article, we considered our state variable I as the measured physical intensity, and called it intensity.

2.3. The Lombard effect

Previous research has shown that in several species of birds, mammals, and fish, the intensity of their acoustic signals may increase in response to increased ambient noise to compensate for the masking of acoustic signals by this noise (Brackenbury, 1979; Calder III, 1990; Oberweger and Goller, 2001; Warren et al., 2006; Barber et al., 2010; Read et al., 2014; Brown et al., 2021). Thus, according to the Lombard effect, the intensity of an individual's song increases as the intensity of noise increases. However, owing to physiological limitations, the song intensity is limited. Therefore, the function intensity of the song emitted by a conspecific per unit time in response to an environmental intensity I, denoted by $\beta(I)$, must be positive, increasing, and bounded. In mathematical terms:

$$\beta(I) > 0, \quad \partial\beta/\partial I \geq 0, \quad \forall I > 0 \quad \text{and} \quad \beta^* := \sup_{I>0} \beta > 0. \tag{2}$$

2.4. Noise intensity variation

Given an instant t and a time variation of Δt, to calculate the variation in the noise intensity $\Delta I = I(t + \Delta t) - I(t)$ at the extremes of the time interval $[t, t + \Delta t]$, it should be noted that the noise intensity

(a) Increases with:

    (a.1) The noise intensity $\alpha F(t)$ emitted by an anthropogenic source: The function $F(t)$ represents the noise intensity measured *in situ* per unit time and is assumed to be bounded by $\sup_{t \in [0+\infty)} F(t) = f^*$. The adimensional parameter $\alpha > 0$ is negatively correlated with the distance (average) of the population to the source.

    (a.2) The higher intensity acoustic signals $\beta(I)N$ emitted by the biological source, that is, by the total song or population song, that is, the sum of the songs of conspecifics.

(b) Decreases with the different atmospheric attenuation mechanisms γI, where $\gamma > 0$ is the attenuation coefficient per unit time.

Thus, the following noise intensity balance equation is obtained:

$$I(t + \Delta t) = I(t) + \alpha F(t)\Delta t + \beta(I)N(t)\Delta t - \gamma I(t)\Delta t. \tag{3}$$

Considering $\Delta I/\Delta t$, when $\Delta t \to 0$, we obtain:

$$I'(t) = \alpha F(t) + \beta(I(t))N(t) - \gamma I(t). \tag{4}$$

2.5. Differential model

Therefore, a mathematical model describing the dynamics of the abundance of a species exposed to noise emitted by an anthropogenic source and the self-generated (biological) species is formulated by the following system of differential equations:

$$\begin{cases} N' &= (r_0 - d\chi(I - I_\mu)I - \lambda N) N \\ I' &= \alpha F(t) + \beta(I) N - \gamma I, \end{cases} \tag{5}$$

defined in the time interval $[0, \infty)$, with positive initial conditions given by $N(0) = N_0 > 0$ and $I(0) = I_0 > 0$. The definitions and units of the variables and parameters of model (5) are summarized in Table 1.

3. Model analysis and results

This section introduces some of the necessary notations and definitions. We then show that model (5) behaves well; namely, given an initial state, it determines a unique, positive, and bounded trajectory. Finally, we present the main results of this research, which characterize the dynamic behavior of the population size by parametric conditions.

Note that the right-hand side of model (5) is discontinuous, thus admitting a solution analysis in a Carathéodory sense. In the intervals where $I \leq I_\mu$, the first equation of model (5) becomes the well-known logistic equation. The logistic equation has a unique positive and bounded solution and the population persists if $r_0 > 0$. Then, interesting dynamics occur in the intervals where the population experiences noise, that is, when $I > I_\mu$. In this study, we focused only on the case in which the population always experiences noise. For this, we set $I_\mu = \inf I$, so that $\chi = 1$ for all $t > 0$.

3.1. Notations and definitions

Given a real-valued function $x(\cdot)$, defined over a domain $[0, \infty)$, we denoted simplicity $\langle x(t) \rangle$ as its average over the interval $[0, t]$. In other words:

$$\langle x(t) \rangle = (1/t) \int_0^t x(s)\,ds, \quad t > 0. \tag{6}$$

Definition. Given a population and a corresponding abundance function $N(\cdot)$ defined in $[0, \infty)$, we say that the population is

- *Persistent*, if there exist constants $\alpha_1 > 0$ y $\alpha_2 > 0$ such that $0 < \alpha_1 \leq \liminf_{t \to +\infty} N(t) \leq \limsup_{t \to +\infty} N(t) \leq \alpha_2 < +\infty$.
- *Mean Persistent*, if there is a constant $M > 0$ such that $0 < \limsup_{t \to +\infty} \langle N(t) \rangle \leq M < +\infty$.
- *Moving towards extinction*, if $\lim_{t \to +\infty} N(t) = 0$.

Note that it follows from these definitions and rule of L'Hospital's that, for a given population, persistence implies persistence at the mean.

3.2. Uniqueness, positivity and boundedness

As we are concerned about a biological phenomenon, we must consider certain regularities in the solution of the ODE system given by (5), such as uniqueness, positivity, and boundedness. In the following theorem, we prove the existence of a solution that satisfies these regularity parameters.

Table 1
Biological meaning of variables and parameters.

Symbol	Definition	Unit
N	Population abundance	n
I	Noise intensity to which an individual is exposed	w/m^2
$F(t)$	Anthropogenic noise intensity at time t	$t^{-1}(w/m^2)$
$\beta(I)$	Intensity of the song emitted by a conspecific with Lombard effect	$t^{-1}n^{-1}(w/m^2)$
r_0	Intrinsic growth rate	t^{-1}
d	Degree to which noise affects the population	$t^{-1}(w/m^2)^{-1}$
λ	Intraspecific competition coefficient	$t^{-1}n^{-1}$
γ	Noise attenuation coefficient for different atmospheric mechanisms	t^{-1}

Theorem 3.1. *Given the constants $N_0 > 0$ and $I_0 > 0$, for the ODE system given by* (5)*, there exists a solution $(N(\cdot), I(\cdot))$ such that $(N(0), I(0)) = (N_0, I_0)$, which is (a) unique, (b) positive, and (c) bounded.*

Proof.

(a) As for $\chi = 1$, with $t > 0$, the right-hand side of model (5) is completely continuous and locally Lipschitzian; there is a unique solution $(N(\cdot), I(\cdot))$ defined on $[0, a)$, where $0 < a \leq +\infty$ (see Hale and Lunel, 2013).

(b) For $N_0 > 0$, from the first equation of model (5), we have:

$$N(t) = N_0 \exp\left\{ \int_0^t \{r_0 - d\,I(s) - \lambda N(s)\}\,ds \right\} > 0,\ t \geq 0. \tag{7}$$

Below, we show that $I(t) > 0$ for $t \geq 0$. By contradiction, suppose there exists a first instant $\tau \in [0, a)$ in which $I(\tau) = 0$, and the differentiability forces $I'(\tau) \leq 0$. However, the existence of such a case is contradicted by the second equation of model (5), as $I'(\tau) = \alpha F(\tau) + \beta(0)N(\tau) > 0$. Therefore, $I(t) > 0$ for $t \geq 0$.

(c) From the first equation of model (5), we have $N'(t) < (r_0 - \lambda N(t))N(t)$. Subsequently, using the comparison principle, we obtain $\limsup_{t \to +\infty} N(t) < r_0/\lambda$. However, from the second equation of the model, $I'(t) \leq \alpha f^* + \beta^* N - \gamma I$. Then, by the principle of comparison, we obtain

$$\limsup_{t \to +\infty} I(t) < \Lambda_F + \Lambda_\beta, \tag{8}$$

where $\Lambda_F = \alpha f^*/\gamma$ represents the equilibrium at which the anthropogenic noise intensity stabilizes if there is a source emitting at the top (f^*) and no population is present. Similarly, $\Lambda_\beta = \beta^*(r_0/\lambda)/\gamma$ is the equilibrium biological sound intensity resulting from population singing in the absence of an anthropogenic noise source but with the population at its carrying capacity permanently singing at maximum capacity (β^*). $\quad\square$

3.3. Persistence and extinction

We now present the most important results of this research. Sufficient conditions were provided to test the model parameters for population survival.

Theorem 3.2. *If $0 < f^* < r_0/\alpha\{\gamma/d - \beta^*/\lambda\}$, then $\beta^* < \gamma\lambda/d$ and the population persists.*

Proof. From In Eq. (8), we have that for any $\varepsilon > 0$, there exists $t_0 > 0$ such that $I(t) < \Lambda_F + \Lambda_\beta + \varepsilon$, for $t > t_0$. Then, from the first equation of model (5), we obtain $N' \geq \{r_0 - d(\Lambda_F + \Lambda_\beta + \varepsilon) - \lambda N\}N$, $t > t_0$. From this hypothesis, we obtain $\mathcal{L} := r_0 - d(\Lambda_F + \Lambda_\beta) > 0$. We can choose ε small enough, such that $\mathcal{L} - d\varepsilon > \mathcal{L}' > 0$, for a certain positive $\mathcal{L}'$ that exists for the density of real numbers. Thus, $N' > (\mathcal{L}' - \lambda N)N$. Then by a principle of comparison we obtain:

$$\liminf_{t \to +\infty} N(t) > \mathcal{L}'/\lambda. \quad\square \tag{9}$$

The results of Theorem 3.2 indicate that it is easier for the population to survive with a lesser degree of noise affectation d. Higher growth rates r_0 and noise attenuation γ are more useful for population survival.

When $f^* \geq r_0/\alpha\{\gamma/d - \beta^*/\lambda\}$, the conclusions of the following theorem provide sufficient conditions that guarantee persistence at the mean and, in the worst case, extinction of the population.

Theorem 3.3.

(a) *If $\liminf_{t \to +\infty} \langle F(t) \rangle < r_0\gamma/\alpha d$, the population persists at its mean.*

(b) *If $\liminf_{t \to +\infty} \langle F(t) \rangle \geq r_0\gamma/\alpha d$, the population will become extinct.*

Proof.

(a) If what is stated in Theorem 3.3 is false, that is, $\limsup_{t \to +\infty} \langle N(t) \rangle = 0$, it is concluded that $\lim_{t \to +\infty} \langle N(t) \rangle = 0$. This results in a contradiction. First, we proved that $\liminf_{t \to +\infty} \langle I(t) \rangle < r_0/d$. Integrating the second equation in model (5) over $[0, t)$, $t > 0$, we can rewrite:

$$\{I(t) - I_0\}/t = \alpha\langle F(t) \rangle + \langle \beta(I)N(t) \rangle - \gamma\langle I(t) \rangle. \tag{10}$$

As $\beta(\cdot)$ is bounded, $\lim_{t \to +\infty} \langle \beta(I)N(t) \rangle = 0$. Then, applying the lower limit to both sides in Eq. (10), we obtain:

$$\liminf_{t \to +\infty} \langle F(t) \rangle = (\gamma/\alpha)\liminf_{t \to +\infty} \langle I(t) \rangle. \tag{11}$$

Therefore, $\liminf_{t \to +\infty} \langle I(t) \rangle < r_0/d$, is an immediate consequence of the hypothesis of the theorem. Dividing the first equation in model (5) by $N(t)$ and integrating over $[0, t)$, $t > 0$, we obtain:

$$\ln\left(N(t)/N_0\right) = r_0 t - d\int_0^t I(s)\,ds - \lambda\int_0^t N(s)\,ds, \tag{12}$$

which, when rearranging and dividing by t, we have:

$$(1/t)\ln\left(N(t)/N_0\right) + \lambda \cdot \langle N(t) \rangle = r_0 - d \cdot \langle I(t) \rangle. \tag{13}$$

Then, taking the upper limit on both sides of Eq. (13) and recalling that $\langle N(t) \rangle \to 0$, we obtain:

$$\limsup_{t \to +\infty}(1/t)\ln\left(N(t)/N_0\right) = r_0 + \limsup_{t \to +\infty}\{-d\langle I(t) \rangle\}$$
$$= r_0 - d\liminf_{t \to +\infty}\langle I(t) \rangle. \tag{14}$$

Furthermore, we know that $\liminf_{t \to +\infty} \langle I(t) \rangle < r_0/d$, and thus, we have

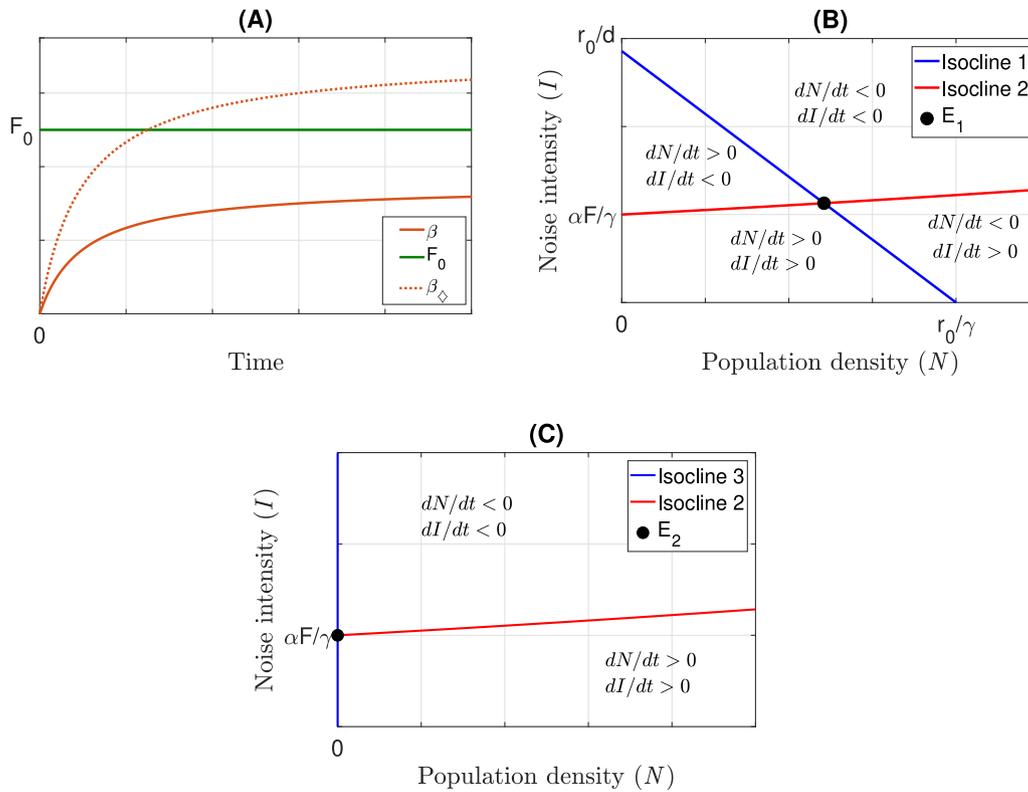$$\limsup_{t \to +\infty}(1/t)\ln\left(N(t)/N_0\right) > 0, \tag{15}$$

which is a contradiction, because $N(\cdot)$ is bounded. Therefore, the conclusion of this theorem is valid.

(b) When, by contradiction, we assume that the population will not go extinct; that is, $\liminf_{t \to +\infty} N(t) > 0$. We can rewrite second equation of the model (5) as:

$$\langle I(t) \rangle = \gamma^{-1}\left[\alpha\langle F(t) \rangle + \langle \beta(I)N(t) \rangle - (I(t) - I_0)/t\right]. \tag{16}$$

Then, replacing Eq. (16) in Eq. (13), we obtain:

$$(1/t)\ln\left(N(t)/N_0\right) + \lambda\langle N(t) \rangle$$
$$= r_0 - d\gamma^{-1}\left[\alpha\langle F(t) \rangle + \langle \beta(I)N(t) \rangle - \{I(t) - I_0\}/t\right], \tag{17}$$

Fig. 1. Survival analysis using isocline intersections. **(A)** The population experiences noise produced by two sources. The first, an anthropogenic source represented by the constant function $F(t) = F_0 > 0$ (green line). The second, the biological source, which is noise self-generated by the singing of conspecifics experiencing the Lombard effect represented by the increasing function $\beta(I) = \beta^* I/(I + 1)$ with $\beta^* < F_0$ (solid curve with horizontal axis I). The increasing function $\beta_\diamond$ shows the behavior of β, when an individual can sing at its maximum intensity over the anthropogenic noise intensity, i.e. $\beta^* > F_0$ (dashed curve with horizontal axis I). **(B)** When $F_0 < r_0\gamma/\alpha d$ there is a point E_1 of intersection between the isoclines $N_1(I) = (r_0 - dI)/\lambda$ (blue line) and $N_2(I) = (\gamma I - \alpha F_0)(I + 1)/\beta^* I$ (red line), which represents a global attractor of the model. Therefore in this case the population persists. **(C)** When $F_0 \geq r_0\gamma/\alpha$ the equilibrium point E_2 represents a global attractor of the model; therefore, in the case, the population goes to extinction.

and thus, we obtain:

$$d\alpha\langle F(t)\rangle = r_0\gamma - (\gamma/t)\ln\left(N(t)/N_0\right) - \gamma\lambda\langle N(t)\rangle \\ - d\langle\beta(I)N(t)\rangle + d\left\{I(t) - I_0\right\}/t. \tag{18}$$

Using the lower limit in Eq. (18), we obtain $\liminf_{t\to+\infty}\langle F(t)\rangle < r_0\gamma/\alpha d$, which is a contradiction. $\square$

The conclusions of Theorem 3.3 show that the lower limit of the anthropogenic noise intensity level must be lower than the $r_0\gamma/\alpha d$ value to maintain persistence at the population mean. If the attenuation of anthropogenic noise is low (i.e., α is larger) and the degree to which noise affects population d is large, the above value tends to decrease. As the intrinsic growth rate r_0 and noise attenuation γ increase, the level of anthropogenic noise that the population can withstand increases.

The following is an example of analyzing the survival of a population exposed to constant anthropogenic noise emission.

Example 1. We suppose that the anthropogenic noise intensity is represented by the constant function $F(t) = F_0 > 0$ and the biological sound intensity is represented by $\beta(I) = \beta^* I/(I + 1)$, $\beta^* > 0$. Model (5) has two equilibrium points $E_1(N_*, I_*)$ with $N_* > 0, I_* > 0$ and $E_2(0, \alpha F_0/\gamma)$, whose stability analysis leads to the persistence and extinction of the population respectively.

Note that $N_* > 0$ and $I_* > 0$ satisfy $N_* = (\gamma I_* - \alpha F_0)(I_* + 1)/\beta_* I_*$ and $I_* = (r_0 - \lambda N_*)/d$. The Jacobian matrix of model (5) in (N_*, I_*) is given by

$$J(N_*, I_*) = \begin{pmatrix} -r_0 + dI_* & -dN_* \\ \beta(I_*) & (\partial\beta/\partial I(I_*))N_* - \gamma \end{pmatrix} \tag{19}$$

and characteristic polynomial is given by:

$$p(\delta) = \delta^2 - S\delta + P, \tag{20}$$

where

$$S = [(-r_0 + dI_*) + ((\partial\beta/\partial I(I_*))N_* - \gamma)]$$
$$P = [(-r_0 + dI_*)((\partial\beta/\partial I(I_*))N_* - \gamma) + \beta(I_*)dN_*].$$

Then, the Hurwitz matrix of polynomial (20) is:

$$H(N_*, I_*) = \begin{pmatrix} -S & 0 \\ 1 & P \end{pmatrix}. \tag{21}$$

Applying the Hurwitz criterion (Barnett and Cameron, 1975), we find that polynomial (20) has roots with a negative real part only if $S < 0$ and $P > 0$; that is, equilibrium point E_1 is asymptotically stable if $I_* < r_0/d$. Analogously, we find that equilibrium point E_2 is asymptotically stable if $I_* \geq r_0/d$. These results are consistent with Theorems 3.2 and 3.3. In summary we have:

- If $F_0 < r_0\gamma/\alpha d$, then the population persists.
- If $F_0 \geq r_0\gamma/\alpha d$, then the population goes to extinct.

The previous result can be observed in Fig. 1 by analyzing the intersection between the isoclines $N_1(I) = (r_0 - dI)/\lambda$, $N_2(I) = (\gamma I - \alpha F_0)(I + 1)/\beta^* I$, $N_3(I) = 0$ and the change in the sign of the rates of change in the population density and the level of noise intensity experienced by the population.

4. Numerical simulations

In this section, we present numerical simulations to corroborate the results obtained in Theorems 3.2 and 3.3. The results can be illustrated as follows: if the population growth rate and noise attenuation can increase or the degree to which the population is affected by noise is smaller, the population will persist, otherwise, the population will die out.
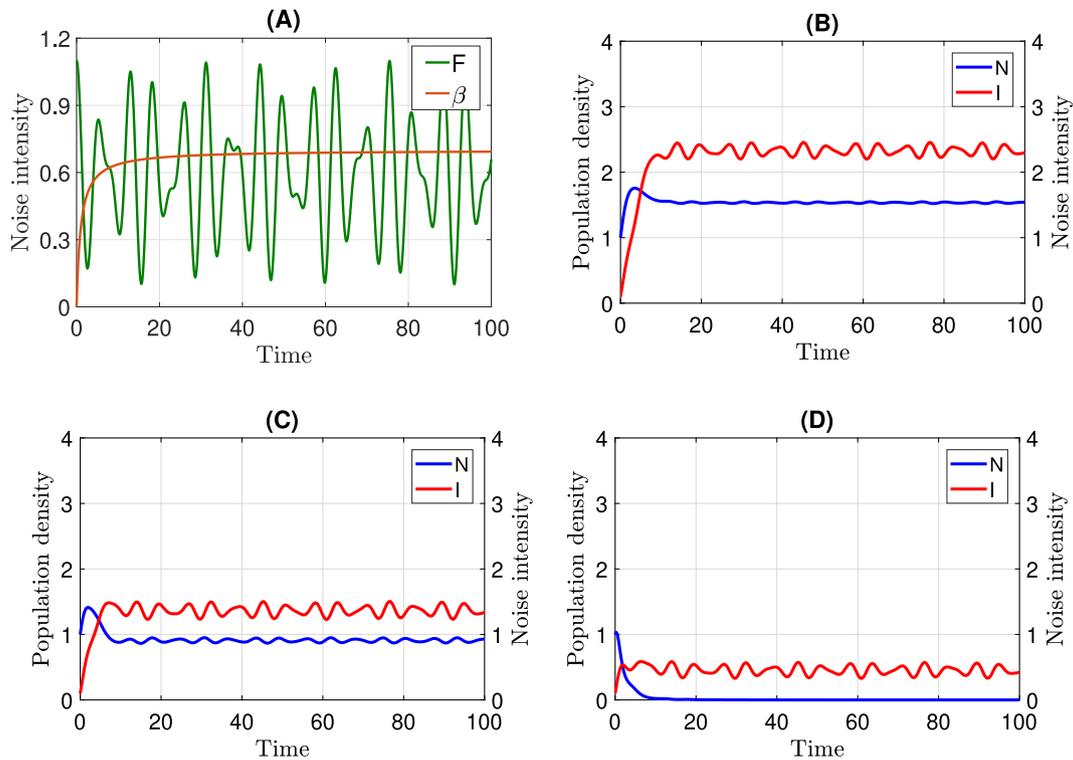
Fig. 2. Numerical simulations for population survival or extinction with different degrees at which noise affects the population. **(A)** The noise experienced by the population arises from two sources. The first, an anthropogenic source represented by the quasi-periodic function $F(t) = 0.3\cos(t) + 0.2\cos(\sqrt{2}t) + 0.6$ with $f^* = 1.1$. Second, biological sources, which is noise self-generated by the singing of conspecifics undergoing the Lombard effect, represented by the increasing function $\beta(I) = 0.7I/(1 + I)$ with $\beta^* = 0.7$ (horizontal axis I). **(B)** When the degree to which noise affects the population is $d = 0.1$, the conditions of Theorem 3.2 are satisfied; therefore, we observe that the population persists. **(C)** When the degree to which noise affects the population is $d = 0.4$, the first condition of Theorem 3.3 is satisfied; therefore, we observe that the population persists at its mean. **(D)** When the degree to which noise affects the population increases to a level of $d = 2$, the second condition of Theorem 3.3 is satisfied; therefore, we observe that the population moves towards extinction.

When the values of the following parameters are $r_0 = 1$, $\lambda = 0.5$, $\alpha = 0.3$ and $\gamma = 0.4$, then model (5) will be considered with initial conditions $N(0) = 1$ and $I(0) = 0.1$, so that it becomes

$$\begin{cases} N' = (1 - d\,I - 0.5\,N)\,N \\ I' = 0.3F(t) + \beta(I)N - 0.4I. \end{cases}$$

Fig. 2 shows the evolution of the dynamics of population density and the level of noise intensity experienced by the population over time.

5. Discussion

There is evidence that chronic exposure to noise can cause changes in the mortality rates of a population, causing that the effects of noise over time can negatively affect the persistence and extinction of a population (Sementili-Cardoso and Donatelli, 2021; Babisch, 2002; Filadelfo et al., 2009; Nedelec et al., 2014; Potvin and MacDougall-Shackleton, 2015; Jaeger et al., 2005; Reijnen et al., 1996). In the current research, we modeled these changes by considering the population mortality rate to be a function of the population size and the intensity of the noise to which the population is exposed.

Our results are consistent with observations that a lower level of anthropogenic noise intensity is favorable for population survival (Farina, 2014; Pijanowski et al., 2011a; Slabbekoorn et al., 2018; Kunc et al., 2016; Kight and Swaddle, 2011; De Vincenzi et al., 2021; Goldbogen et al., 2013; Hildebrand, 2009). Likewise, although the Lombard effect is known to be beneficial in that important acoustic signals are not masked by noise, when noise exceeds the permissible limit, a limit up to which noise has no effect on the population, observations indicate that the use of higher intensity acoustic signals increases energetic, behavioral, and predation costs, which could result in lower ecological fitness, influencing animal survival rates in noisy

environments (Brackenbury, 1979; Calder III, 1990; Oberweger and Goller, 2001; Warren et al., 2006; Barber et al., 2010; Read et al., 2014; Brown et al., 2021; Swaddle et al., 2015; Farina and Gage, 2017; Zollinger and Brumm, 2015; Brumm and Todt, 2002; Brumm, 2004; Luczkovich et al., 2016; Sementili-Cardoso and Donatelli, 2021). In other words, from Theorem 3.2, if an effort is made to reduce the intensity level of anthropogenic noise F, and the maximum intensity level of acoustic signals emitted by conspecifics β^*, which otherwise increases with respect to noise due to the Lombard effect, then the population will persist. However, according to Theorem 3.3-a, for the persistence of the population to remain at the mean, it is sufficient to reduce the anthropogenic noise intensity level, because the maximum intensity level of the acoustic signals generated by the population does not have a significant impact on the mean population persistence. In particular, when the degree to which noise affects the population, d, is lower, persistence and mean persistence are benefitted (see Figs. 2-B and 2-C). Conversely, Theorem 3.3-b indicates that when intensity of anthropogenic noise is high or the degree to which noise affects the population is greater, the population goes to extinction (see Fig. 2-D). Population extinction can also be understood as the displacement or migration of a population away from an anthropogenic noise source.

Parameter d, which indicates the degree to which noise affects the population can be understood to have a negative correlation with the degree of noise adaptation. Therefore, some species show a considerable degree of adaptation to noisy environments. For example, invertebrates show evidence that they are capable of evolutionary adaptation and behavioral plasticity in response to noise sources (Morley et al., 2014). In addition, animal song plasticity facilitates vocal adjustments that contribute to reduced noise masking (Fernandez-Juricic, 2001; Brumm, 2004; Rheindt, 2003). These adjustments may be the outcome of physiological adaptations, such as those present in some

fish that exhibit adaptations, that convey sensitivity to sound pressure. In fish, these adaptations include having a gas bubble or swim bladder that is close to or connected to the ear (Schulz-Mirbach et al., 2012). For instance, the swim bladder of the Atlantic cod (*Gadus morhua*) is located near the ear and, when filled with gas, the organism's sensitivity to sound pressure is reduced (Sand et al., 1973). However, as the mechanisms of adaptation to noise are unique for each species, the manipulation of the parameter d is uncontrollable. Therefore, the best way to mitigate the effects of noise on a population is to control the level of noise intensity of the anthropogenic source.

In conclusion, our model responds to growing concerns about the possible effects of noise at the population level. We believe that our research will motivate other researchers to consider the effects of biological sounds and the Lombard effect on population persistence. Note that we only analyzed the long-term effects of noise on population density. However, even in the short-term, the population is exposed to noise, which can have behavioral or physiological effects on the individuals of a population. To evaluate this, controlled experiments are required to measure the parameters that appear during noise exposure.

CRediT authorship contribution statement

C. Ramirez-Carrasco: Investigation, Formal analysis, Writing – original draft, Software. **F. Córdova-Lepe:** Supervision, Validation. **F.N. Moreno-Gómez:** Conceptualization, Supervision. **N.A. Velásquez:** Conceptualization, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

References

Algers, B., Ekesbo, I., Strömberg, S., 1978. The impact of continuous noise on animal health. Acta Vet. Scand. Suppl. (68), 1–26.

Babisch, W., 2002. The noise/stress concept, risk assessment and research needs. Noise Health 4 (16), 1.

Barber, J.R., Crooks, K.R., Fristrup, K.M., 2010. The costs of chronic noise exposure for terrestrial organisms. Trends Ecol. Evol. 25 (3), 180–189.

Barnett, S., Cameron, R.G., 1975. Introduction to Mathematical Control Theory. vol. 5, Clarendon Press, Oxford, pp. 33–42.

Brackenbury, J.H., 1979. Power capabilities of the avian sound-producing system. J. Exp. Biol. 78 (1), 163–166.

Brown, N.A., Halliday, W.D., Balshine, S., Juanes, F., 2021. Low-amplitude noise elicits the lombard effect in plainfin midshipman mating vocalizations in the wild. Anim. Behav. 181, 29–39.

Brumm, H., 2004. The impact of environmental noise on song amplitude in a territorial bird. J. Anim. Ecol. 73 (3), 434–440.

Brumm, H., Todt, D., 2002. Noise-dependent song amplitude regulation in a territorial songbird. Anim. Behav. 63, 891–897.

Calder III, W.A., 1990. The scaling of sound output and territory size: Are they matched? Ecology 71 (5), 1810–1816.

Das, A., Samanta, G.P., 2018. Stochastic prey–predator model with additional food for predator. Physica A 512, 121–141.

De Vincenzi, G., Micarelli, P., Viola, S., Buffa, G., Sciacca, V., Maccarrone, V., Corrias, V., Reinero, F.R., Giacoma, C., Filiciotto, F., 2021. Biological sound vs. Anthropogenic noise: Assessment of behavioural changes in scyliorhinus canicular exposed to boats noise. Animals 11 (1), 174.

Dehaene, S., 2003. The neural basis of the Weber–Fechner law: A logarithmic mentalnumber line. Trends Cogn. Sci. 7 (4), 145–147.

Dooling, R.J., Leek, M., West, E., 2009. Predicting the effects of masking noise on communication distance in birds. J. Acoust. Soc. Am. 125 (4), 2517.

Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K., Dooling, R., 2016. Communication masking in marine mammals: A review and research strategy. Mar. Pollut. Bull. 103 (1–2), 15–38.

Farina, A., 2014. Soundscape Ecology: Principles, Patterns, Methods and Applications. Springer Science & Business Media, New York.

Farina, A., Gage, S.H., 2017. The ecological effects of noise on species and communities. In: Eco Acoustics: The Ecological Role of Sounds. Wiley, Oxford, pp. 95–108.

Fernandez-Juricic, E., 2001. Avian spatial segregation at edges and interiors of urban parks in Madrid, Spain. Biodivers. Conserv. 10 (8), 1303–1316.

Filadelfo, R., Mintz, J., Michlovich, E., D'Amico, A., Tyack, P.L., Ketten, D.R., 2009. Correlating military sonar use with beaked whale mass strandings: What do the historical data show? Aquatic Mammals 35 (4).

Goldbogen, J.A., Southall, B.L., DeRuiter, S.L., Calambokidis, J., Friedlaender, A.S., Hazen, E.L., et al., 2013. Blue whales respond to simulated mid-frequency military sonar. Proc. R. Soc. B 280 (1765), 20130657.

Goodwin, S.E., Shriver, W.G., 2011. Effects of traffic noise on occupancy patterns of forest birds. Conserv. Biol. 25 (2), 406–411.

Hale, J.K., Lunel, S.M.V., 2013. Introduction to Functional Differential Equations, vol. 99. Springer Science & Business Media, New York.

Hawkins, A.D., Popper, A.N., 2017. A sound approach to assessing the impact of underwater noise on marine fishes and invertebrates. ICES J. Mar. Sci. 74 (3), 635–651.

Helble, T.A., Guazzo, R.A., Martin, C.R., Durbach, I.N., Alongi, G.C., Martin, S.W., et al., 2020. Lombard effect: Minke whale boing call source levels vary with natural variations in ocean noise. J. Acoust. Soc. Am. 147 (2), 698–712.

Henry, J.P., 1992. Biological basis of the stress response. Integr. Physiol. Behav. Sci. 27 (1), 66–83.

Hildebrand, J.A., 2009. Anthropogenic and natural sources of ambient noise in the ocean. Mar. Ecol. Prog. Ser. 395, 5–20.

Holt, D.E., Johnston, C.E., 2014. Evidence of the lombard effect in fishes. Behav. Ecol. 25 (4), 819–826.

Holt, M.M., Noren, D.P., Veirs, V., Emmons, C.K., Veirs, S., 2009. Speaking up: Killer whales (*orcinus orca*) increase their call amplitude in response to vessel noise. J. Acoust. Soc. Am. 125 (1), EL27–EL32.

Jaeger, J.A., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., et al., 2005. Predicting when animal populations are at risk from roads: An interactive model of road avoidance behavior. Ecol. Model. 185 (2–4), 329–348.

Katti, M., Warren, P.S., 2004. Tits, noise and urban bioacoustics. Trends Ecol. Evol. 19 (3), 109–110.

Kight, C.R., Swaddle, J.P., 2011. How and why environmental noise impacts animals: An integrative, mechanistic review. Ecol. Lett. 14 (10), 1052–1061.

Krause, B., 2008. Anatomy of the soundscape: Evolving perspectives. J. Audio Eng. Soc. 56 (1/2), 73–80.

Kunc, H.P., McLaughlin, K.E., Schmidt, R., 2016. Aquatic noise pollution: Implications for individuals, populations, and ecosystems. Proc. R. Soc. B 283 (1836), 20160839.

Kunc, H.P., Schmidt, R., 2019. The effects of anthropogenic noise on animals: A metaanalysis. Biol. Lett. 15 (11), 20190649.

Lanier, J.L., Grandin, T., Green, R.D., Avery, D., McGee, K., 2000. The relationship between reaction to sudden, intermittent movements and sounds and temperament. J. Anim. Sci. 78 (6), 1467–1474.

Lombard, E., 1911. The signs of increasing the voice. Ann. Malad. l'Oreille Larynx, 37, 101-119. Biosemiotics 8 (3), 493–502.

Luczkovich, J.J., Krahforst, C.S., Kelly, K.E., Sprague, M.W., 2016. The lombard effect in fishes: How boat noise impacts oyster toadfish vocalization amplitudes in natural experiments. In: Proceedings of Meetings on Acoustics 4ENAL, Vol. 27. (1), Acoustical Society of America, 010035.

Luo, J., Hage, S.R., Moss, C.F., 2018. The lombard effect: From acoustics to neural mechanisms. Trends Neurosci. 41 (12), 938–949.

McGregor, P.K., Horn, A.G., Leonard, M.L., Thomsen, F., 2013. Anthropogenic noise and conservation. In: Animal Communication and Noise. Springer, Berlin, Heidelberg, pp. 409–444.

Morley, E.L., Jones, G., Radford, A.N., 2014. The importance of invertebrates when considering the impacts of anthropogenic noise. Proc. R. Soc. B 281 (1776), 20132683.

Moudon, A.V., 2009. Real noise from the urban environment: How ambient community noise affects health and what can be done about it. Am. J. Prev. Med. 37 (2), 167–171.

Nedelec, S.L., Radford, A.N., Simpson, S.D., Nedelec, B., Lecchini, D., Mills, S.C., 2014. Anthropogenic noise playback impairs embryonic development and increases mortality in a marine invertebrate. Sci. Rep. 4 (1), 1–4.

Oberweger, K., Goller, F., 2001. The metabolic cost of birdsong production. J. Exp. Biol. 204 (19), 3379–3388.

Parris, K.M., Schneider, A., 2009. Impacts of traffic noise and traffic volume on birds of roadside habitats. Ecol. Soc. 14 (1), 29.

Phillips, C.J.C., 2009. Housing, handling and the environment for cattle. In: Principles of Cattle Production, second ed. pp. 95–128.

Pienkowski, M., Eggermont, J.J., 2010. Intermittent exposure with moderate-level sound impairs central auditory function of mature animals without concomitant hearing loss. Hear. Res. 261 (1–2), 30–35.

Pijanowski, B.C., Farina, A., Gage, S.H., Dumyahn, S.L., Krause, B.L., 2011a. What is soundscape ecology? An introduction and overview of an emerging new science. Landsc. Ecol. 26 (9), 1213–1232.

Pijanowski, B.C., Villanueva-Rivera, L.J., Dumyahn, S.L., Farina, A., Krause, B.L., Napoletano, B.M., Gage, S.H., Pieretti, N., 2011b. Soundscape ecology: The science of sound in the landscape. Bioscience 61 (3), 203–216.

Popper, A.N., Hawkins, A., 2016. The Effects of Noise on Aquatic Life II. Springer, New York, p. 1292.

Potvin, D.A., MacDougall-Shackleton, S.A., 2015. Traffic noise affects embryo mortality and nestling growth rates in captive zebra finches. J. Exp. Zool. A 323 (10), 722–730.

Read, J., Jones, G., Radford, A.N., 2014. Fitness costs as well as benefits are important when considering responses to anthropogenic noise. Behav. Ecol. 25 (1), 4–7.

Reijnen, R., Foppen, R., Meeuwsen, H., 1996. The effects of traffic on the density of breeding birds in Dutch agricultural grasslands. Biol. Cons. 75 (3), 255–260.

Rheindt, F.E., 2003. The impact of roads on birds: Does song frequency play a role in determining susceptibility to noise pollution? J. Ornithol. 144 (3), 295–306.

Richardson, W.J., Greene, Jr., C.R., Malme, C.I., Thomson, D.H., 2013. Marine Mammals and Noise. Academic Press, San Diego.

Römer, H., 2013. Masking by noise in acoustic insects: Problems and solutions. In: Animal Communication and Noise. Springer, Berlin, Heidelberg, pp. 33–63.

Sand, O., Enger, P.S., Møller, A.R., 1973. Function of the swimbladder in fish hearing. In: Basic Mechanisms in Hearing. pp. 893–910.

Schulz-Mirbach, T., Metscher, B., Ladich, F., 2012. Relationship between swim bladder morphology and hearing abilities–a case study on Asian and African cichlids. 7 (8), e42292.

Sementili-Cardoso, G., Donatelli, R.J., 2021. Anthropogenic noise and atmospheric absorption of sound induce amplitude shifts in the songs of Southern house Wren (Troglodytes aedon musculus). Urban Ecosyst. 1–9.

Simpson, S.D., Radford, A.N., Nedelec, S.L., Ferrari, M.C., Chivers, D.P., Mc-Cormick, M.I., Meekan, M.G., 2016. Anthropogenic noise increases fish mortality by predation. Nature Commun. 7 (1), 1–7.

Sinnott, J.M., Stebbins, W.C., Moody, D.B., 1975. Regulation of voice amplitude by the monkey. J. Acoust. Soc. Am. 58 (2), 412–414.

Slabbekoorn, H., Dooling, R.J., Popper, A.N., Fay, R.R., 2018. Effects of Anthropogenic Noise on Animals. Springer, New York.

Slabbekoorn, H., Peet, M., 2003. Birds sing at a higher pitch in urban noise. Nature 424 (6946), 267.

Spagnolo, B., Fiasconaro, A., Valenti, D., 2003. Noise induced phenomena in LotkaVolterra systems. Fluct. Noise Lett. 3 (02), L177–L185.

Sueur, J., Farina, A., 2015. Ecoacoustics: The ecological investigation and interpretation of environmental sound. Biosemiotics 8 (3), 493–502.

Swaddle, J.P., Francis, C.D., Barber, J.R., Cooper, C.B., Kyba, C.C., Dominoni, D.M., Shannon, G., Aschehoug, E., Goodwin, S.E., Kawahara, A.Y., Luther, D., Spoelstra, K., Voss, M., Longcore, T., 2015. A framework to assess evolutionary responses to anthropogenic light and sound. Trends Ecol. Evol. 30 (9), 550–560.

Upadhyay, R.K., Mukhopadhyay, A., Iyengar, S.R.K., 2007. Influence of environmental noise on the dynamics of a realistic ecological model. Fluct. Noise Lett. 7 (01), L61–L77.

Vilar, J.M., Solé, R.V., 1998. Effects of noise in symmetric two-species competition. Phys. Rev. Lett. 80 (18), 4099.

Warren, P.S., Katti, M., Ermann, M., Brazel, A., 2006. Urban bioacoustics: It's not just noise. Anim. Behav. 71 (3), 491–502.

World Health Organization, Copenhagen, 2011. Burden of disease from environmental noise: Quantification of healthy life years lost in Europe. http://www.euro.who.int/en/what-we-publish/information-for-the-media/sections/latest-press-releases/new-evidence-fromwho-on-health-effects-of-traffic-related-noise-in-europe. (Accessed 10 December 2020).

Zollinger, S.A., Brumm, H., 2015. Why birds sing loud songs and why they sometimes don't. Anim. Behav. 105, 289–295.