# On two families of stochastic predation models with Allee effect

## Pablo Aguirre

ABSTRACT. Two classes of stochastic models of predator-prey interaction with Allee effect on prey are presented in this paper. Both families are introduced as generalizations of Leslie type predation models with Holling type functional response. The stochastic perturbations are considered of polynomial kind in order to model environmental random noise affecting both species. The only difference between both families of models is the way the Allee effect is modeled, namely, by means of a generic term whose conveniently chosen properties give rise to a behavior that is representative of either additive or multiplicative Allee effect, respectively.

We show that both classes of models are well-posed in the sense that any positive solution starting in the open first quadrant remains in that region and, hence, it never becomes negative. In the particular case when the random noise is absent, we find that all the solutions are bounded for both sets of models. We also prove that the stochastic solutions exist, are unique in pathwise sense and have bounded moments. Moreover, we find that, as a consequence of our modeling approach, for sufficiently low population densities, the solutions of the random systems behave like the associated deterministic trajectories and, in doing so, the overall dynamics is determined by the features of the Allee effect.

## 1. Introduction

Population models are a key tool to understand the interactions of one or more species in time [**4, 24, 25**]. Of special interest is the situation of a low density population that faces difficulties to grow and avoid extinction. This is commonly known as the Allee effect [**6, 35**]. This phenomenon is reportedly generated by the difficulty of finding mates, social interaction or predation [**12, 19, 31**], among other mechanisms. Typically, the Allee effect induces a population growth rate to decrease under some minimum critical level [**11**], and sometimes even to become negative, creating an extinction threshold —commonly known as the Allee threshold— that

the population has to overcome in order to survive [**11**, **14**, **18**, **42**]. In this paper, we are interested in the presence of a species subjected to a predation-driven Allee effect [**15**, **16**, **26**, **32**]. Indeed, if the prey population is of a sufficiently small size, it tends to have difficulties to show an antipredator behavior, that is, to better defend or disguise themselves from the predator [**21**, **40**, **45**, **46**]. See also Table 2 in [**22**] for a wide range of Allee effects generated by predation.

The Allee effect may also interact with random environmental conditions such as alien species invasions [**33**] or other catastrophic events [**10**]; see also [**1**, **5**] and the references therein for more details. As a consequence, the amplitude of population fluctuations may increase and even drive a population to extinction [**7**, **18**, **39**].

In this paper, two classes of stochastic predator-prey models are proposed in which the prey population is subjected to an Allee effect. The only difference between both families is the way the Allee effect is modeled. We first consider the approach of modeling the Allee effect by means of adding a suitable (negative) term —called an Allee function throughout— in the prey growth rate in what is traditionally known as an additive Allee effect [**3**, **4**, **17**, **42**]. This type of model is the subject of section **3**. The second approach is to multiply an Allee function to the classic logistic growth rate in the prey equation; we have called this form a multiplicative Allee effect [**4**] as opposed to the additive case; see also [**23**]. The family of models with multiplicative Allee effect is treated in section **4**. In both additive and multiplicative families, the corresponding Allee function is not stated explicitly but given a few suitably chosen basic generic properties that agree with, and generalise, a number of concrete realistic models studied recently [**5**, **23**, **44**]. This is the main reason why we speak of *families* of models.

Both classes of models show some common ingredients as well. In the same spirit of modeling the Allee effect, the predator rate consumption is conveniently modeled by a generic predation function that aims to reproduce (and generalise) the common properties of the well-known class of (smooth) Holling type functional responses [**34**, **37**, **40**, **43**]; see also [**3**, **4**] and the references therein for further discussion. On the other hand, we assume that both families of models are of Leslie type [**30**, **44**], i.e., one considers that the typical environmental carrying capacity of the predator is proportional to prey abundance as in the May-Holling-Tanner model [**9**] and other models recently analyzed [**3**, **4**, **24**, **37**]. Finally, a random noise —associated to the environment of the populations [**5**, **39**]— affects independently the growth rates of both preys and predators and its intensity is of polynomial type in the population sizes.

The deterministic scenario of the multiplicative case has been recently studied in [**2**] in terms of sufficient conditions for the occurrence of different bifurcations. In turn, in this work, for each family of stochastic predation models, we show that the model is well-posed in the sense that there can not be populations with negative number of individuals; we also show that the deterministic solutions are always bounded. Even though each system does not satisfy a globally Lipschitz condition, we prove that a weaker one-sided Lipschitz condition holds which allows us to show that the stochastic solutions have sample pathwise uniqueness and bounded moments. In addition, we find that for sufficiently low populations, the trajectories of the stochastic

systems behave like the ones from the associated deterministic models, that is, the variability of the solution process dies down as the populations decreases.

This paper is structured as follows: The basic notation, definitions and general setting are presented in section 2. In section 3 we study the case of an additive Allee effect. Section 4 treats the multiplicative Allee effect. Finally, in section 5 we sumarize and discuss the main results in this paper, as well as explore possible future challenges of research.

## 2. Problem set-up

We work with a system of Ito's stochastic differential equations of the form

$$(2.1) \qquad d\mathbf{X}(t) = \mathbf{F}\left(x(t), y(t)\right) \, dt + \mathbf{G}(x(t), y(t)) \, d\mathbf{W}(t),$$

where $\mathbf{X}(t) = (x(t), y(t))^T$ represents the vector of population densities of prey $(x)$ and predator $(y)$ species at time $t > 0$. The vector field $\mathbf{F}$ induces a flow that governs the deterministic dynamics. The matrix

$$\mathbf{G}(x, y) = \left( \begin{array}{cc} x \, \sigma_{11}(x, y) & x \, \sigma_{12}(x, y) \\ y \, \sigma_{21}(x, y) & y \, \sigma_{22}(x, y) \end{array} \right)$$

models the intensity of the random perturbations, where the coefficients $\sigma_{ij}(x, y)$ are polynomials of degree $l_{ij} \geqslant 0$. Finally, $\mathbf{W}(t) = (W_1(t), W_2(t))^T$ is a two-dimensional Brownian motion.

The polynomial random noise in (2.1) is a generalization of multiplicative-type stochastic perturbations as used in [5, 37] and in previous works for Lotka-Volterra type models in [8, 13, 29, 34, 41].

We distinguish two types of models of the form (2.1) which depend on the way the Allee effect is modeled in the vector field $\mathbf{F}$.

**2.1. Additive Allee effect.** By adding a suitable term $-A(x)$ in the well-known logistic equation [18], we obtain a model with the so-called additive Allee effect [3, 4, 5, 42]; we will say that $A(x)$ is an *Allee function*. We also denote the predator rate consumption as $\phi(x)$. In this setting, our model with additive Allee effect is given by the system

(2.2)
$$\begin{cases} dx &=& \left[r\left(1 - \frac{x}{k} - A(x)\right)x - \phi(x)\, y\right] \, dt + x\left[\sigma_{11}(x, y) + \sigma_{12}(x, y)\right] dW_1(t); \\ \\ dy &=& \left[s\left(1 - \frac{y}{nx}\right)y\right] \, dt + y\left[\sigma_{21}(x, y) + \sigma_{22}(x, y)\right] dW_2(t); \end{cases}$$

where $(x(t), y(t)) \in \mathcal{D} := \{(x, y) \in \mathbb{R}^2 \mid x > 0, y \geqslant 0\}$. Model parameters have the following meanings: $r > 0$ (resp. $s > 0$) is the intrinsic growth rate or biotic potential of the population $x$ (resp. $y$), and $k > 0$ is the environment carrying capacity of $x$ [38]. Moreover, the conventional environmental carrying capacity $K_y$ of the predator is proportional to prey abundance $x$ [38], that is, $K_y = nx$, where $n > 0$.

We assume that the Allee function $A(x)$ is of class $\mathcal{C}^\infty$ in $\mathcal{D}$ and satisfies the following conditions:

**(A.1)** $A(x) > 0$, for all $x > 0$.
**(A.2)** $\lim_{x \to 0^+} A(x) = M < \infty$, with $M > 0$.

**(A.3)** $\lim_{x \to \infty} A(x) = 0$.

Note that the conditions **(A.1)**–**(A.3)** are in agreement with the features found in concrete realistic models with additive Allee effect; see [**4, 42**] for instance.

In addition, the functional response $\phi(x)$ is also smooth enough in $\mathcal{D}$ and is assumed to satisfy the following conditions:

**(B.1)** $\lim_{x \to 0^+} \phi(x) = 0$.

**(B.2)** $\phi'(x) > 0$, for all $x > 0$.

**(B.3)** $\lim_{x \to \infty} \phi(x) = N < \infty$.

A predation rate function $\phi(x)$ that satisfies conditions **(B.1)**–**(B.3)** is a generalisation of a Holling-type functional response II–IV [**40, 43, 45, 46**]. In particular, conditions **(B.1)** and **(B.2)** imply that $\phi(x) \geqslant 0$, for all $x > 0$.

Model (2.2) is the subject of section 3.

**2.2. Multiplicative Allee effect.** The second class of models that we consider in this paper is given by the so-called multiplicative Allee effect in the following system:

$$(2.3) \quad \begin{cases} dx & = & \left[ r\,x \left( 1 - \frac{x}{k} \right) A(x) - \phi(x)\,y \right]\, dt + x \left[ \sigma_{11}(x,y) + \sigma_{12}(x,y) \right] dW_1(t); \\[2mm] dy & = & \left[ s\,y \left( 1 - \frac{y}{nx} \right) \right]\, dt + y \left[ \sigma_{21}(x,y) + \sigma_{22}(x,y) \right] dW_2(t); \end{cases}$$

where $(x(t), y(t)) \in \mathcal{D}$. Note that the domain $\mathcal{D}$ and the parameters in (2.3) have the same definitions as those of (2.2). The term $A(x)$ —also called an Allee function— is now multiplying the classic logistic expression; hence the name of this modeling approach. Moreover, it is assumed that the function $\phi$ satisfies conditions **(B.1)**–**(B.3)** as well, so that the only modification in (2.3) is due to the inclusion of the multiplicative Allee effect.

More concretely, we assume that $A(x)$ is a $\mathcal{C}^\infty$ function in $\mathcal{D}$ and satisfies the following conditions:

**(C.1)** There exists a value $m \in \mathbb{R}$ with $|m| < k$, such that $A(m) = 0$.

**(C.2)** $A'(x) > 0$, for all $x > 0$.

**(C.3)** $\lim_{x \to 0^+} A(x) = M < \infty$.

With these properties, equation (2.3) emerges as a generalization of a number of proposed models with multiplicative Allee effect; see [**4, 23, 25**] for instance. Model (2.3) is the subject of section 4.

## 3. Model with additive Allee effect

We refer to model (2.2) using the vector notation in (2.1) whenever useful.

Our first result deals with the issue of the well-posedness of model (2.2) in the sense that for any given initial condition in $\mathcal{D}$, the corresponding solution remains in $\mathcal{D}$.

LEMMA 3.1. *The domain $\mathcal{D}$ is invariant under system (2.2).*

**Proof Lemma 3.1.** Our aim is to show that no trajectory of (2.2) crosses the positive axes of $\mathbb{R}^2$.

Let $\mathbf{F} = (F_1, F_2)^T$ denote the components of the deterministic vector field $\mathbf{F}$. Along the axis $\{y = 0\}$, the stochastic system (2.2) has the form $d\mathbf{X} = (dx, 0)^T$;

hence, the $x$-axis is invariant under the system (2.2). On the other hand, the $y$-axis is not part of the domain $\mathcal{D}$ since $F_2$ is not defined along the axis $\{x = 0\}$. To deal with this, we extend the vector field $\mathbf{F}$ to the $y$-axis by means of the transformation

$$(3.1) \qquad (x, y, t) \mapsto \left(x, ny, \frac{xt}{ns}\right)$$

and the change of parameters

$$(3.2) \qquad (r, k, s, n) \mapsto \left(r, k, \frac{1}{\beta}, \frac{r\beta}{\alpha k}\right).$$

In this way, the new vector field, denoted as $\widetilde{\mathbf{F}}$ is given as

$$(3.3) \qquad \widetilde{\mathbf{F}} : \begin{cases} \dot{x} &= \alpha\,(k - x - A(x))\,x^2 - \beta\,\phi(x)\,x\,y; \\ \dot{y} &= y\,(x - y). \end{cases}$$

From conditions **(A.2)** and **(B.1)**, the vector field $\widetilde{\mathbf{F}}$ is well defined in the axis $\{x = 0\}$ and is a qualitatively equivalent extension of $\mathbf{F}$ to the closure of $\mathcal{D}$, i.e., the change of coordinates (3.1) and reparameterization (3.2) define a biunique diffeomorphism between orbits of $\mathbf{F}$ in $\mathcal{D}$ and orbits of $\widetilde{\mathbf{F}}$ in the same domain; we refer to [20, 27] for details on topological equivalency of vector fields. Since $\widetilde{\mathbf{F}}(0, y) = (0, -y^2)^T$, $\widetilde{\mathbf{F}}$ is invariant along the axis $\{x = 0\}$. Hence, no orbit of $\widetilde{\mathbf{F}}$ crosses the $y$-axis. It follows that every orbit of $\mathbf{F}$ in the interior of the first quadrant remains inside that region.

Finally,

$$\mathbf{G}(0, y) = \begin{pmatrix} 0 & 0 \\ y\,\sigma_{21}(x, y) & y\,\sigma_{22}(x, y) \end{pmatrix}.$$

Hence, every solution in $\mathcal{D}$ of the stochastic system (2.2) remains in $\mathcal{D}$. $\square$

**3.1. Boundedness.** Next we want to verify that all the solutions of the associated deterministic system remain bounded.

From the proof of Lemma 3.1, we consider the topologically equivalent dynamics induced by the extended vector field (3.3).

Let $\omega > k$ be arbitrary but fixed. The task is to prove that the set

$$(3.4) \qquad \mathcal{D}_\omega := \{(x, y) \in \mathbb{R}^2 : 0 \leqslant x < \omega, 0 \leqslant y < \omega\}$$

is invariant by examining the dynamics in its boundary $\partial\mathcal{D}_\omega$, which is the square of vertices $(0, 0), (\omega, 0), (\omega, \omega)$ and $(0, \omega)$; see Fig. 1.

Let us define the function $f_\omega : \mathcal{D} \longrightarrow \mathbb{R}$, given by $f_\omega(x, y) = x - \omega$ and consider the vertical line segment

$$V_\omega = f_\omega^{-1}(0) \cap \{0 \leqslant y \leqslant \omega\}$$

in the $(x, y)$-plane. Geometrically, the set $f_\omega^{-1}(-\infty, 0)$ is a vertical stripe that extends in the $y$-direction. Now we prove that every trajectory of the vector field $\widetilde{\mathbf{F}}$ that crosses the line $f_\omega^{-1}(0)$ —and in particular the segment $V_\omega$— enters the region $f_\omega^{-1}(-\infty, 0)$ transversally; see Fig. 1. Since $\widetilde{\mathbf{F}}$ is tangent to every solution, this is equivalent to
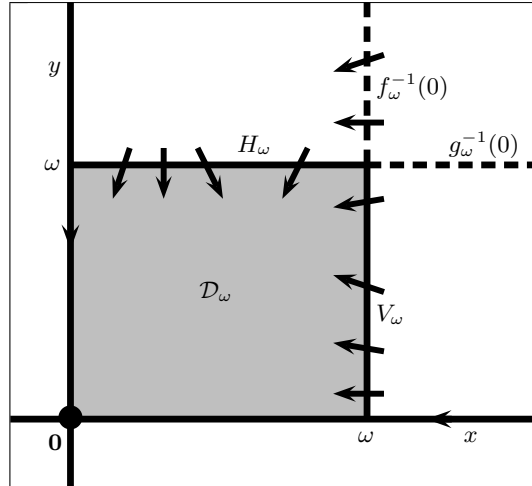
FIGURE 1. The invariant set $\mathcal{D}_\omega$ and the lines $f_\omega^{-1}(0)$ and $g_\omega^{-1}(0)$ defined for an arbitrary but fixed $\omega > k$.

prove that the vector field satisfies $\widetilde{\mathbf{F}} \cdot \nabla f_\omega < 0$ in every point on the line $f_\omega^{-1}(0)$ for a suitable choice of $\omega$. We have that for every $(x,y) = (\omega, y) \in f_\omega^{-1}(0)$:

$$\varphi_\omega(y) := \widetilde{\mathbf{F}} \cdot \nabla f_\omega = -\beta \, \phi(\omega)\omega y + \alpha \, \omega^2 \left( k - \omega - A(\omega) \right),$$

From conditions **(B.1)** and **(B.2)**, geometrically, the graph of $\varphi_\omega(y)$ is a straight line with negative slope $-\beta \, \phi(\omega)\omega < 0$ and intercept $\alpha \, \omega^2 \left( k - \omega - A(\omega) \right)$. Since $A(\omega) > 0$ for every $\omega > 0$ —from condition **(A.1)**—, then for every $\omega > k$ the following inequalities hold:

$$(3.5) \qquad\qquad\qquad k - \omega < 0 < A(\omega).$$

Hence, for every $\omega > k$, $\varphi_\omega(y) < 0$ as desired.

Similarly, let $g_\omega : \mathcal{D} \longrightarrow \mathbb{R}$ be given by $g_\omega(x,y) = y - \omega$. Then,

$$\widetilde{\mathbf{F}} \cdot \nabla g_\omega = \omega(x - \omega) < 0,$$

for every point $(x,y) = (x, \omega)$ with $x < \omega$. Therefore, for every point $(x,y)$ in the horizontal line segment $H_\omega = g_\omega^{-1}(0) \cap \{0 \leqslant x \leqslant \omega\}$ its associated trajectory crosses this line transversally towards the region $g_\omega^{-1}(-\infty, 0)$; see Fig. 1.

Furthermore, from the proof of Lemma 3.1, the axes $x = 0$ and $y = 0$ are invariant. In particular, along the line $x = 0$, $\widetilde{\mathbf{F}}(0, y) = (0, -y^2)^T$ and, hence, trajectories converge to the origin $(x,y) = (0,0)$. On the other hand, along the line $y = 0$, $\widetilde{\mathbf{F}}(x, 0) = \left( \alpha \, x^2(k - x - A(x)), 0 \right)^T$. From (3.5), $\alpha \, x^2(k - x - A(x)) < 0$ for every $x \geqslant \omega > k$, and the solutions decay. As a consequence, no trajectory along the coordinate axes converge to infinity.

To sum up, for any arbitrary $\omega > k$ the set $\mathcal{D}_\omega$ is invariant, i.e., every solution inside $\mathcal{D}_\omega$ does not leave this region again in forward time and, in particular, these

solutions remain bounded. Since the value of $\omega > k$ is arbitrary, we have the following theorem:

THEOREM 3.1. *Let $\overline{\mathcal{D}} = \mathcal{D} \cup \{x = 0\}$ be the extension of $\mathcal{D}$ in $\mathbb{R}^2$ to the axis $x = 0$ and let $\mathcal{D}_\omega$ be as in (3.4). Then for any given initial condition $(x(0), y(0)) \in \overline{\mathcal{D}}$, there is a value $\omega^* > k$ such that the trajectory $(x(t), y(t))$ of (3.3) through the point $(x(0), y(0))$ is entirely contained, for $t > 0$, in the bounded set $\mathcal{D}_\omega$ for every $\omega \geqslant \omega^*$.*

**3.2. Main results on the stochastic model.** The effect of the random noise in system (2.2) becomes stronger in a sufficiently small neighbourhood of the curves $F_1^{-1}(0) \cup F_2^{-1}(0)$, i.e., near the nullclines of $\mathbf{F}$. Moreover, in the particular case when the matrix $\mathbf{G}$ only contains terms of degree 1, by Ito's rule, near the set $F_1^{-1}(0) \cup F_2^{-1}(0)$, system (2.2) behaves like $z(t) \approx z_0 \exp\left(\sigma W(t) - \frac{\sigma^2 t}{2}\right)$, where $z$ stands for $x$ or $y$, and $W(t)$ is the corresponding Brownian motion with (constant) intensity $\sigma$.

Furthermore, since the stochastic perturbations in (2.2) are proportional to the population sizes, the closer an orbit gets to the origin $(0,0)$ in $\mathbb{R}^2$, the smaller the random fluctuations are. Hence, in doing so, a trajectory tends to 'look like' the deterministic solutions near the origin. As a consequence, for low populations, the routes to mutual extinction of prey and predator become increasingly less dependent on the environmental noise.

In the following results, we will show that the solutions of (2.2) have sample pathwise uniqueness and bounded moments. One of the main technical details is that, by construction, the deterministic vector field $\mathbf{F}$ only satisfies a local Lipschitz-type condition in every point and, due to the term $\frac{y}{nx}$, $\mathbf{F}$ is not globally Lipschitz. To obtain our result, we first need to prove that the system (2.2) satisfies a so-called *one-sided Lipschitz condition*. In what follows, $\langle \cdot, \cdot \rangle$ denotes the euclidean inner product and $|\cdot|$ denotes both the euclidean norm or the Frobenius matrix norm.

LEMMA 3.2. *Consider the vector notation (2.1) for the system (2.2). Then for the vector field $\mathbf{F}$ and the matrix $\mathbf{G}$ there exist constants $\lambda, \mu > 0$ such that*

$$(3.6) \qquad \langle \mathbf{u} - \mathbf{v}, \mathbf{F}(\mathbf{u}) - \mathbf{F}(\mathbf{v}) \rangle \leqslant \lambda |\mathbf{u} - \mathbf{v}|^2, \qquad \forall \mathbf{u}, \mathbf{v} \in \mathcal{D},$$

$$(3.7) \qquad |\mathbf{G}(\mathbf{u}) - \mathbf{G}(\mathbf{v})|^2 \leqslant \mu |\mathbf{u} - \mathbf{v}|^2, \qquad \forall \mathbf{u}, \mathbf{v} \in \mathcal{D}.$$

**Proof Lemma 3.2.** Let $\mathbf{F} = (F_1, F_2)^T$ denote the components of the deterministic vector field $\mathbf{F}$ and let $\mathbf{u} = (u_1, u_2)$, $\mathbf{v} = (v_1, v_2) \in \mathcal{D}$.

Let us suppose initially the case $u_1 > v_1$.

Due to properties **(A.1)** and **(B.2)** in section 3, we have $F_1(x, y) \leqslant rx$, for all $(x, y) \in \mathcal{D}$. Then the following inequalitites hold:

$$\begin{array}{rcl} (u_1 - v_1)F_1(\mathbf{u}) & \leqslant & (u_1 - v_1)ru_1, \\ (u_1 - v_1)F_1(\mathbf{v}) & \leqslant & (u_1 - v_1)rv_1. \end{array}$$

Subtracting both inequalities leads to:

$$(3.8) \qquad (u_1 - v_1)[F_1(\mathbf{u}) - F_1(\mathbf{v})] \leqslant r(u_1 - v_1)^2.$$

By direct computation it is clear that inequality (3.8) also holds when $u_1 \leqslant v_1$. Indeed, one only has to substract the following inequalities:

$$
\begin{aligned}
(v_1 - u_1)F_1(\mathbf{v}) &\leqslant (v_1 - u_1)rv_1, \\
(v_1 - u_1)F_1(\mathbf{u}) &\leqslant (v_1 - u_1)ru_1.
\end{aligned}
$$

In particular, if $u_1 = v_1$, (3.8) is satisfied in a trivial way.

Analogously, since $F_2(x, y) \leqslant sy$, for all $(x, y) \in \mathcal{D}$, we have:

$$
(3.9) \qquad\qquad (u_2 - v_2)[F_2(\mathbf{u}) - F_2(\mathbf{v})] \leqslant s(u_2 - v_2)^2.
$$

From (3.8) and (3.9) we obtain

$$
(u_1 - v_1)[F_1(\mathbf{u}) - F_1(\mathbf{v})] + (u_2 - v_2)[F_2(\mathbf{u}) - F_2(\mathbf{v})] \leqslant \lambda \left((u_1 - v_1)^2 + (u_2 - v_2)^2\right)
$$

with $\lambda = \max\{r, s\}$, as desired. Finally, inequality (3.7) follows directly from the fact that the entries of $\mathbf{G}$ are polynomials, and so, globally Lipschitz functions. $\square$

We say that two solutions $\mathbf{X}(t)$ and $\widetilde{\mathbf{X}}(t)$ of (2.1) are the same if they have, almost surely, the same sample trajectories for $t \in [0, T]$, i.e.,

$$
\mathbb{P}\left[\sup_{0 \leqslant t \leqslant T} |\mathbf{X}(t) - \widetilde{\mathbf{X}}(t)| > 0\right] = 0.
$$

With this definition in mind, we prove the uniqueness of solutions in system (2.2).

THEOREM 3.2. *For any initial condition* $\mathbf{X}_0 \in \mathcal{D}$, *system* (2.2) *has a unique solution* $\mathbf{X}(t)$ *such that* $\mathbf{X}(0) = \mathbf{X}_0$.

**Proof of Theorem 3.2.** Consider the translation given by

$$
(3.10) \qquad \mathcal{T} : \mathbb{R}^2 \longrightarrow \mathbb{R}^2, \quad \text{such that} \quad (x, y) \mapsto (x - x_0, y - y_0),
$$

with $(x_0, y_0) \in \mathcal{D}$. The change of coordinates $\mathcal{T}$ is a $\mathcal{C}^\infty$−conjugacy, that is, trajectories of $\mathbf{F}$ are biuniquely mapped by $\mathcal{T}$ to trajectories of the equivalent vector field, denoted as $\widetilde{\mathbf{F}}$, preserving time scale; see [**20, 27**] for further details. Moreover, $\widetilde{\mathbf{F}}(x, y) = \mathbf{F}(x + x_0, y + y_0)$, for all $(x, y) \in \widetilde{\mathcal{D}} := \mathcal{T}^{-1}(\mathcal{D})$. In particular, $\mathbf{0} := (0, 0) \in \widetilde{\mathcal{D}}$.

From Lemma 3.2, for all $\mathbf{u} \in \widetilde{\mathcal{D}}$ we have:

$$
\begin{aligned}
\langle \widetilde{\mathbf{F}}(\mathbf{u}), \mathbf{u} \rangle &= \langle \widetilde{\mathbf{F}}(\mathbf{u}) - \widetilde{\mathbf{F}}(\mathbf{0}), \mathbf{u} \rangle + \langle \widetilde{\mathbf{F}}(\mathbf{0}), \mathbf{u} \rangle \\
&\leqslant \lambda |\mathbf{u}|^2 + |\widetilde{\mathbf{F}}(\mathbf{0})||\mathbf{u}| \\
&\leqslant \tfrac{1}{2}|\widetilde{\mathbf{F}}(\mathbf{0})|^2 + \left(\lambda + \tfrac{1}{2}\right)|\mathbf{u}|^2,
\end{aligned}
$$

and

$$
|\widetilde{\mathbf{G}}(\mathbf{u})|^2 \leqslant 2|\widetilde{\mathbf{G}}(\mathbf{0})|^2 + 2|\widetilde{\mathbf{G}}(\mathbf{u}) - \widetilde{\mathbf{G}}(\mathbf{0})|^2 \leqslant 2|\widetilde{\mathbf{G}}(\mathbf{0})|^2 + 2\mu|\mathbf{u}|^2,
$$

where $\widetilde{\mathbf{G}}(x, y) := \mathbf{G}(x + x_0, y + y_0)$, with $(x, y) \in \widetilde{\mathcal{D}}$. Hence:

$$
(3.11) \qquad \max\left\{\langle \widetilde{\mathbf{F}}(\mathbf{u}), \mathbf{u} \rangle, |\widetilde{\mathbf{G}}(\mathbf{u})|^2\right\} \leqslant \alpha + \beta|\mathbf{u}|^2, \quad \forall \mathbf{u} \in \widetilde{\mathcal{D}},
$$

where $\alpha = \max\left\{\tfrac{1}{2}|\widetilde{\mathbf{F}}(\mathbf{0})|^2, 2|\widetilde{\mathbf{G}}(\mathbf{0})|^2\right\}$ and $\beta = \max\left\{\left(\lambda + \tfrac{1}{2}\right), 2\mu\right\}$. In this way, the existence and uniqueness of solutions of system (2.2) follows directly from Theorem 2.3.5 in [**36**], the $\mathcal{C}^\infty$−conjugacy (3.10) and inequality (3.11). $\square$

The following corollary on the boundedness of moments is a direct consequence of the one-sided Lipschitz condition in Lemma 3.2 and from Lemma 3.2 in [**28**].

COROLLARY 3.1. *For every $p > 2$ and for any initial point $\mathbf{X}_0 \in \mathcal{D}$ there exists $C = C(p, T) > 0$ such that the solution $\mathbf{X}(t)$ of (2.2) satisfies:*

$$\mathbb{E}\left[\sup_{0 \leqslant t \leqslant T} |\mathbf{X}(t)|^p\right] \leqslant C\left(1 + \mathbb{E}[|\mathbf{X}_0|^p]\right).$$

## 4. Model with multiplicative Allee effect

In this section we explore the class of models (2.3). Once again, for the sake of simplicity, we use the vector notation in (2.1) to refer to model (2.3) whenever useful. In particular, we keep the notation $\mathbf{F} = (F_1, F_2)^T$ for the components of the deterministic vector field $\mathbf{F}$.

The results and analysis for (2.3) are similar to those for model (2.2), namely, the effect of the stochastic perturbations in the system (2.3) is stronger in a sufficiently small neighbourhood of the curves $F_1^{-1}(0) \cup F_2^{-1}(0)$. Moreover, in the particular case when $\mathbf{G}$ only contains terms of degree 1, by Ito's rule, near the set $F_1^{-1}(0) \cup F_2^{-1}(0)$, system (2.3) behaves like $z(t) \approx z_0 \exp\left(\sigma W(t) - \frac{\sigma^2 t}{2}\right)$, where $z$ stands for $x$ or $y$, and $W(t)$ is the corresponding Brownian motion with (constant) intensity $\sigma$. Furthermore, the closer a trajectory gets to the origin $(0, 0)$ in $\mathbb{R}^2$, the smaller the random fluctuations are, and as a consequence, the solution 'behaves' like the deterministic solutions near the origin.

LEMMA 4.1. *The domain $\mathcal{D}$ is invariant under system (2.3).*

**Proof of Lemma 4.2.**

We consider an extended vector field $\widetilde{\mathbf{F}}$ given as

(4.1)
$$\widetilde{\mathbf{F}}: \begin{cases} \dot{x} &= \alpha\, x^2(k - x)A(x) - \beta\, \phi(x)\, x\, y; \\ \dot{y} &= y\, (x - y); \end{cases}$$

which is obtained by means of the transformation (3.1) and the change of parameters (3.2) on $\mathbf{F}$ in (2.3). Indeed, conditions **(B.1)** and **(C.3)** ensure that (4.1) is well defined on the axis $x = 0$. The proof follows the same arguments as those of Lemma 3.2. □

THEOREM 4.1. *Every solution of the deterministic system associated to (2.3) is bounded. More precisely, let $\overline{\mathcal{D}} = \mathcal{D} \cup \{x = 0\}$ be the extension of $\mathcal{D}$ in $\mathbb{R}^2$ to the axis $x = 0$ and let $\mathcal{D}_\omega$ be as in (3.4). Then for any given initial condition $(x(0), y(0)) \in \overline{\mathcal{D}}$, there is a value $\omega^* > k$ such that the trajectory $(x(t), y(t))$ of (4.1) through the point $(x(0), y(0))$ is entirely contained, for $t > 0$, in the bounded set $\mathcal{D}_\omega$ for every $\omega \geqslant \omega^*$.*

**Proof Theorem 4.1.** From the proof of Lemma 4.2, we consider the topologically equivalent dynamics induced by the extended vector field (4.1).

Following similar arguments as those of the proof of Theorem 3.1 in Section 3.1, it is easy to prove that for any $w > k$ arbitrary but fixed, the set $\mathcal{D}_\omega$ is invariant, i.e., every solution inside $\mathcal{D}_\omega$ does not leave this region again in forward time and, as a consequence, these solutions remain bounded. □

For model (2.3) the deterministic vector field **F** satisfies a local Lipschitz-type condition in every point of $\mathcal{D}$, but it is not globally Lipschitz. Hence, in order to obtain uniqueness of solutions, in the next lemma we prove that **F** satisfies the one-sided Lipschitz condition.

LEMMA 4.2. *Consider the vector notation (2.1) for the system (2.3). If the Allee function $A(x)$ in (2.3) is bounded in $\mathcal{D}$, then there exist constants $\lambda, \mu > 0$ such that*

$$\langle \mathbf{u} - \mathbf{v}, \mathbf{F}(\mathbf{u}) - \mathbf{F}(\mathbf{v}) \rangle \leqslant \lambda \left| \mathbf{u} - \mathbf{v} \right|^2, \quad \forall \mathbf{u}, \mathbf{v} \in \mathcal{D},$$

$$\left| \mathbf{G}(\mathbf{u}) - \mathbf{G}(\mathbf{v}) \right|^2 \leqslant \mu \left| \mathbf{u} - \mathbf{v} \right|^2, \quad \forall \mathbf{u}, \mathbf{v} \in \mathcal{D}.$$

**Proof Lemma 4.2.** The entries of the matrix **G** are polynomial, hence the inequality in the statement for **G** follows.

Regarding the result on **F**, our goal is to obtain suitable bounds for $F_1(x, y)$ such that we can follow the same steps in the proof of Lemma 3.2. For a start, due to property **(B.2)** in section 2.1, we have $F_1(x, y) \leqslant rx \left(1 - \frac{x}{k}\right) A(x)$, for all $x > 0$.

Let us first assume the case $0 < x < m$ where $m$ is as in condition **(C.1)** in section 2.2. Then, condition **(C.2)** ensures that $A(x) < 0$. Hence,

$$F_1(x, y) \leqslant \frac{rA^*}{k} x^2 \leqslant \frac{rA^* m}{k} x$$

where $A^* > 0$ is the maximum value of $|A(x)|$. Therefore, since $m < k$, one obtains $F_1(x, y) \leqslant rA^* x$.

In the case $x = m$, one has $F_1(x, y) \leqslant 0 < x$.

Finally, if $x > m$, from conditions **(C.1)** and **(C.2)**, one obtains $A(x) > 0$. Then, $F_1(x, y) \leqslant rA^* x$.

From the arguments in the proof of Lemma 3.2, it follows that the statement of Lemma 4.2 holds for $\lambda = \max\{1, rA^*, s\}$. □

Finally, Theorem 4.2 and Corollary 4.1 below follow from the one-sided Lipschitz condition in Lemma 4.2 and the same arguments given in section 3.

THEOREM 4.2. *For any initial condition $\mathbf{X}_0 \in \mathcal{D}$, system (2.3) has a unique solution $\mathbf{X}(t)$ such that $\mathbf{X}(0) = \mathbf{X}_0$.*

COROLLARY 4.1. *For every $p > 2$ and for any initial point $\mathbf{X}_0 \in \mathcal{D}$ there exists $C = C(p, T) > 0$ such that the solution $\mathbf{X}(t)$ of (2.3) satisfies:*

$$\mathbb{E}\left[\sup_{0 \leqslant t \leqslant T} |\mathbf{X}(t)|^p\right] \leqslant C\left(1 + \mathbb{E}[|\mathbf{X}_0|^p]\right).$$

## 5. Conclusions

The purpose of this paper has been to introduce two classes of models of predator-prey interaction and Allee effect on prey. Each family of models proposes a generalisation of the main mathematical characteristics of the additive Allee effect and of the multiplicative Allee effect, respectively. In both cases, the prey consumption by the predator is modeled by a generic smooth function which presents the geometric features of a Holling functional response of types II–IV. Our families of models also

assume that environmental random noise affects both species and it is modeled by means of polynomial stochastic perturbations.

For each family of stochastic models, we proved that any solution starting in the open first quadrant remains in that region. In particular, this property prevents any population to become negative. In the same spirit of model validation, we showed that, in the special case when the random noise is zero, all the realistic solutions are bounded. We also proved that, for both classes of models, the stochastic solutions exist, are unique in pathwise sense and have bounded moments. Moreover, if both populations have a low density, the trajectories of the stochastic system tend to 'look like' the solutions from the associated deterministic model and, hence, the time evolution of the species is increasingly governed by the Allee effect. On the other hand, as a consequence of our modeling approach, the effect of the environmental randomness is stronger for higher population sizes.

## References

[1] A. Ackelh, L. Allen, J. Carter, Establishing a beachhead: a stochastic population model with an Allee effect applied to species invasion, Theoretical Population Biology 71 (2007) 290–300.

[2] P. Aguirre, A general class of predation models with multiplicative Allee effect, Nonlinear Dynamics, June 2014, (Online First), DOI: 10.1007/s11071-014-1465-3

[3] P. Aguirre, E. González-Olivares, E Sáez, Two limit cycles in a Leslie-Gower predator-prey model with additive Allee effect, Nonlinear Analysis: Real World Applications 10 (2009) 1401–1416.

[4] P. Aguirre, E. González-Olivares, E Sáez, Three limit cycles in a Leslie-Gower predator-prey model with additive Allee effect, SIAM Journal on Applied Mathematics 69 (2009) 1244–1262.

[5] P. Aguirre, E. González-Olivares, S Torres, Stochastic predator-prey model with Allee effect, Nonlinear Analysis: Real World Applications 14 (2013) 768–779.

[6] W. C. Allee, Animal Aggregations, a Study in General Sociology, University of Chicago Press, Chicago, 1931.

[7] L. J. S. Allen, J. F. Fagan, G. Högnäs, H. Fagerholm, Population extinction in discrete-time stochastic population models with an Allee effect, J. Differ. Equ. Appl. 11 (2005) 273–293.

[8] M. Arató, A famous nonlinear stochastic equation (Lotka-Volterra model with diffusion), Mathematical and Computer Modelling 38 (2003) 709–726.

[9] D. K. Arrowsmith, C. M. Place, Dynamical Systems, Differential Equations, Maps and Chaotic Behaviour, Chapman & Hall, 1992.

[10] M. Assaf, A. Kamenev, B. Meerson, Population extinction risk in the aftermath of a catastrophic event, Phys. Rev. E 79 (2009) 011127.

[11] J. Bascompte, Extinction thresholds: insights from simple models, Ann. Zool. Fennici 40 (2003) 99–114.

[12] L. Berec, E. Angulo, F. Courchamp, Multiple Allee effects and population management, Trends in Ecology and Evolution 22 (2007) 185–191.

[13] G. Q. Cai, Y. K. Lin, Stochastic analysis of predator-prey type ecosystems, Ecological Complexity 4 (2007) 242–249.

[14] C. W. Clark, Mathematical Bioeconomic. The Optimal Management of Renewable Resources, John Wiley and sons, 1990.

[15] C. W. Clark, The Worldwide Crisis In Fisheries: Economic Models And Human Behavior, Cambridge University Press, 2006.

[16] F. Courchamp, B. T. Grenfell, T. H. Clutton-Brock, Impact of natural enemies on obligately cooperative breeders, Oikos 91 (2000) 311–322.

[17] B. Dennis, Allee effects: population growth, critical density and the chance of extinction, Natural Resource Modelling 4 (1989) 481–538.

[18] B. Dennis, Allee effects in stochastic populations, Oikos 96 (2002) 389–401.

[19] A. M. de Roos, L. Persson, Size-dependent life-history traits promote catastrophic collapses of top predators, PNAS 20 (2002) 12907–12912.

[20] F. Dumortier, J. Llibre, J. C. Artès, Qualitative Theory of Planar Differential Systems, Springer, 2006.

[21] H. I. Freedman, G. S. K. Wolkowicz, Predator-prey systems with group defence: The paradox of enrichment revisted, Bulletin of Mathematical Biology 8 (1986) 493–508.

[22] J. Gascoigne, R. N. Lipcius, Allee effects driven by predation, Journal of Applied Ecology 41 (2004) 801–810.

[23] E. González-Olivares, B. González-Yáñez, J. Mena-Lorca, J. D. Flores, Uniqueness of limit cycles and multiple attractors in a Gause-type predator-prey model with nonmonotonic functional response and Allee effect on prey, Mathematical Biosciences and Engineering 10 (2013) 345–367.

[24] E. González-Olivares, J. Mena-Lorca, A. Rojas-Palma, J. D. Flores, Dynamical complexities in the Leslie-Gower predator-prey model as consequences of the Allee effect on prey, Applied Mathematical Modelling 35 (2011) 366–381.

[25] E. González-Olivares, A. Rojas-Palma, Limit cycles in a Gause-type predatorprey model with sigmoid functional response and weak Allee effect on prey, Math. Meth. Appl. Sci. 35 (2012) 963–975.

[26] S. Gregory, F. Courchamp, Safety in numbers: extinction arising from predator-driven Allee effects, Journal of Animal Ecology 79 (2010) 511–514.

[27] J. Guckenheimer, P. Holmes, Nonlinear Oscillations, Dynamical Systems, and Bifurcations of Vector Fields, Springer-Verlag, New York, 1983.

[28] D. Higham, X. Mao, A. Stuart, Strong convergence of Euler-type methods for nonlinear stochastic differential equations, SIAM Journal on Numerical Analysis 40 (2002) 1041–1063.

[29] R. Z. Khasminskii, F. C. Klebaner, Long term behavior of solutions of the Lotka-Volterra system under small random perturbations, The Annals of Applied Probability 11 (2001) 952–963.

[30] A. Korobeinikov, A Lyapunov function for Leslie-Gower predator-prey models, Applied Mathematical Letters 14 (2001) 697–699.

[31] A. M. Kramer, B. Dennis, A. M. Liebhold, J. M. Drake, The evidence for Allee effects, Popul. Ecol. 51 (2009) 341–354.

[32] A. M. Kramer, J. M. Drake, Experimental demonstration of population extinction due to a predator-driven Allee effect, Journal of Animal Ecology 79 (2010) 633–639.

[33] M. Krstić, M. Jovanović, On stochastic population model with the Allee effect, Mathematical and Computer Modelling 52 (2010) 370–379.

[34] Y. Li, H. Gao, Existence, uniqueness and global asymptotic stability of positive solutions of a predator-prey system with Holling II functional response with random perturbation, Nonlinear Analysis 68 (2008) 1694–1705.

[35] W. Z. Lidicker Jr, The Allee effect: Its history and future importance, Open Ecology Journal 3 (2010) 71–82.

[36] X. Mao, Stochastic Differential Equations and Applications, Horwood, Chichester, UK, 1997.

[37] P. S. Mandal, M. Banerjee, Stochastic persistence and stability analysis of a modified Holling-Tanner model, Math. Meth. Appl. Sci. doi:10.1002/mma.2680

[38] R. M. May, Stability and Complexity in Model Ecosystems, 2nd Edition, Princeton University Press, Princeton, NJ, 2001.

[39] O. Ovaskainen, B. Meerson, Stochastic models of population extinction, Trends Ecol. Evol. 25 (2010) 643–652.

[40] S. Ruan, D. Xiao, Global analysis in a predator-prey system with nonmonotonic functional response, SIAM Journal on Applied Mathematics 61 (2001) 1445–1472.

[41] Rudnicki R. Long-time behavior of a stochastic prey-predator model, Stochastic Processes and their Applications 108 (2003) 93–107.

[42] P. A. Stephens, W. J. Sutherland, Consequences of the Allee effect for behaviour, ecology and conservation, Trends in Ecol. 4 (1999) 401–405.

[43] R. J. Taylor, Predation, Chapman and Hall, 1984.

[44] P. Turchin, Complex population dynamics. A theoretical/empirical synthesis, Monographs in Population Biology 35, Princeton University Press, 2003.

[45] G. S. W. Wolkowicz, Bifurcation analysis of a predator-prey system involving group defense, SIAM Journal on Applied Mathematics 48 (1988) 592–606.

[46] D. Xiao, S. Ruan, Bifurcations in a predator-prey system with group defense, International Journal of Bifurcation and Chaos 11 (2001) 2123–2131.

[47] D. Xiao, K. F. Zhang, Multiple bifurcations of a predator-prey system, Discrete and Continuous Dynamical System series B 8 (2007) 417–433.

Departamento de Matemática
Universidad Técnica Federico Santa María
Casilla 110-V,
Valparaíso, Chile
    *E-mail address*: `pablo.aguirre@usm.cl`