MIXED-MODE OSCILLATIONS AND CHAOTIC DYNAMICS NEAR SINGULAR HOPF BIFURCATION IN A TWO TIME-SCALE ECOSYSTEM

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Abstract. A two-trophic ecosystem comprising of two species of predators competing for their common prey with explicit interference competition is considered. With a proper rescaling, the model is portrayed as a system of singularly perturbed equations with one-fast (prey dynamics) and two-slow variables (dynamics of the predators). The model exhibits variety of rich and complex dynamics including mixed-mode oscillations (MMOs) featuring concatenation of small and large amplitude oscillations, depending on the value of a control parameter. In a parameter regime near the so-called “folded saddle-node of type II” (FSN II) bifurcation point or the “singular-Hopf point” (such points generically occur in one parameter families of singularly perturbed systems with two slow variables), the system exhibits a bistable behavior. In this regime, chaotic MMOs in the form of a strange attractor coexists with a periodic attractor born out of a supercritical Hopf bifurcation. The bistable regime is analyzed by computing basins of attraction of the two attractors and studying a suitable Poincaré map. The emergence of MMOs in this regime is attributed to the “generalized canard phenomenon”. To elucidate our findings, the model is reduced to a normal form near the FSN II point, which is an organizing center for the MMOs. The normal form possess a “Shil’nikov-type equilibrium” and exhibits MMOs that have unbounded number of small amplitude oscillations in their signatures, suggesting that it realizes a “suitably modified” Shil’nikov mechanism.

Key Words. Mixed-mode oscillations, singular Hopf bifurcation, canard phenomenon, Shil’nikov homoclinic bifurcation, bistability, basins of attraction, chaotic dynamics.

AMS subject classifications. 34D15, 37G10, 37D45, 37L10, 37G05, 34E17, 92D40.

1. Introduction

Complex oscillatory dynamics are ubiquitous in ecology. These dynamics typically involve disparate timescales as they govern endogenous dynamics of an ecological system. Understanding population cycles of natural populations still remains a challenging problem as it inherently involves complex multi-trophic interaction of species in a continuously changing environment. Using singular perturbation theory, regular cycles of population outbreaks and collapses are modeled by relaxation oscillation cycles, commonly known as
boom and bust cycles [34, 37, 30]. However, since events of population outbreaks are not regular and generally not periodic in time, they are not best represented by relaxation oscillations. A more realistic representation of these cycles will be temporal patterns of small fluctuations interspersed with large amplitude oscillations as observed in population cycles of small mammals such as rodents and mice [22], forest insects such as larch bud moth, gypsy moth and cankerworms [1, 14], agricultural pests such as desert locusts [11, 50] and so forth. Such cycles are best modeled by mixed-mode oscillations which are complex oscillatory patterns consisting of one or more small amplitude oscillations (SAOs) followed by large excursions of relaxation type, commonly known as large amplitude oscillations (LAOs) [12]. MMOs have been widely studied in various physical systems, including but not limited to computational neuroscience models, autocatalytic and electrochemical reactions (see [5, 8, 21, 23, 29, 31, 38] and the references therein for examples of mathematical models exhibiting MMOs). In ecology, there have been few studies on such oscillatory patterns [6, 27, 41, 42], but this area needs to be explored more.

In this paper, we study the dynamics between three interacting species, namely two predators competing for their common prey with explicit interference competition between the predators. Taking the ratio between the birth rates of the predators to the prey extremely small, separation of time scales is introduced into the system as a singular parameter. This then brings the model in the framework of singular perturbed system of equations with one-fast and two-slow variables, whereby the prey exhibits fast dynamics and the predators have slow dynamics. Similar studies have been done in forest pest models involving slow dynamics of trees and fast dynamics of pests [6], tri-trophic food chain models [9, 10] and age-structured predator-prey models with dormancy of predators [27].

The model studied in this paper is an extension of the Rosenzweig-MacArthur predator-prey model [37] with Lotka-Volterra type competition between the predators. The presence of density-dependent nonlinear interactions terms in the form of intraspecific and interspecific competition make the system analytically challenging, while giving rise to complex and rich dynamics. The competition among individuals of the same class is treated as the main control parameter and the predation efficiency of one of the predators as the secondary parameter. The main findings of this paper are existence of periodic and aperiodic MMOs, as the main input parameter is varied. Of special importance are MMOs with very long epochs of small amplitude oscillations near the so called singular-Hopf point, and the existence of a bistable regime - where a small amplitude limit cycle and chaotic MMOs coexist as stable attractors. Another observation is that the geometrical structure of the MMO orbits changes as the secondary parameter is varied.

In systems with one-fast and two-slow variables, there are several studies providing local mechanisms that organize the SAOs in MMOs, including passage near special points in phase space such as folded node singularities [7, 12, 48] and singular Hopf bifurcation [8, 10]. A global return mechanism allows for repeated reinjection into regions in phase space where the local mechanisms occur. The interplay between these mechanisms produces sequences of small and large amplitude oscillations in MMOs, which is studied in this paper. Moreover, immediately near the singular-Hopf point, which is also referred to
as folded saddle-node of type II (FSN II) point, the dynamics get more complicated as
the equilibrium lies in a vicinity of the folded node. In this regime, a stable periodic
attractor born out of a supercritical Hopf bifurcation, which lies very close to the FSN II
bifurcation in parameter space, possess a large basin of attraction, and gives rise to non-
relaxation types of dynamics. Besides, more interestingly, sudden appearance of aperiodic
MMOs with unbounded number of SAOs in their signatures are noted. These SAOs can be
related to the existence of infinitely many secondary canards [26]. The sudden emergence
of MMOs is a reminiscent of a canard explosion [25] customarily seen in two-dimensional
fast-slow systems. A normal form reduction near the singular-Hopf point/FSN II point is
performed. An analysis of the normal form reveals that the MMOs are organized by the
generalized canard mechanism [24, 26], i.e. a combination of the local passage through a
canard point with a global return mechanism that resets the dynamics after the passage
has been past. To the best of our knowledge, this is the first ecological model involving
two timescales where an analysis near an FSN II point and its associated features, such as
canard-induced MMOs is performed.

The parameter regime where the complex dynamics are observed is not only mathemati-
cally interesting, but also has an ecological significance. In this model, the singular Hopf
bifurcation/FSN II bifurcation acts as a tipping point, past which, abrupt shifts in popula-
tion dynamics occur. In fact if the system is near this critical threshold, a tiny increment in
the intraspecific interference rate of one of the species (which may be influenced by exter-
nal environmental factors) can trigger a dramatic transition in the population dynamics,
where the population density can switch from a stable coexistence state to a chaotic state
accompanied by large density fluctuations. Moreover, the bistability between the aperi-
odic MMOs and the periodic attractor in the FSN II regime can provide useful insights in
terms of assessing strategies to control outbreaks. It turns out that in this regime, a small
perturbation in phase space can lead to a transition from an aperiodic attractor inter-
mittently exhibiting large oscillations to a periodic attractor exhibiting small oscillations
(which are more robust ecologically), and thus can act as a control mechanism to prevent
large fluctuations in population densities. Furthermore, the underlying geometric structure
of the model can carry useful ecological information. For instance, the dynamics near the
cold can provide useful information in terms of management options. This is particularly
elucidated by aperiodic MMOs generated due to a slow passage near a canard point, where
the local dynamics near the equilibrium can act as a precursor to a large fluctuation in the
population density that follows soon after.

We note that Shil’nikov-type equilibria [28], i.e. equilibria of saddle-types with one di-
ensional stable manifold and two-dimensional unstable manifold typically exist in canard-
\n
based systems that involve FSN II. The existence of such an equilibrium along with the
observed characteristic features of MMOs that pass close to the equilibrium in our model
does not rule out the possibility of a Shil’nikov attractor lying in a nearby parameter

\n
regime. In fact, a first return map associated with the normal form on a suitable Poincaré
section suggests existence of an almost periodic “Shil’nikov-type” attractor that is “thin”.\n
\n
Hence our normal form realizes a “suitably modified” Shil’nikov mechanism [24].
The paper is organized as follows. In Section 2, we introduce and properly scale the model. The assumptions and physical significance of each parameter is also discussed. Preliminary analysis and background review is given in Section 3, which provides us a framework of local and global mechanisms that are responsible for MMOs. Section 4 focusses on geometrical analysis of the system in a parameter regime where a certain special point termed as folded saddle-node singularity of type II exists. Existence of bistability near this parameter regime is also studied. In Sections 5 and 6, a normal form reduction of the full system near the folded-node singularity of type II is performed and the normal form is numerically analyzed for different set of parameter values. In particular, we find a slow passage through a canard point that serves as an organizing center of the MMOs in our model. Finally we discuss our results and summarize our conclusions in the last section of the paper.

2. The Model

The ecological model that we consider is a system of three nonlinear differential equations:

\[
\begin{align*}
\frac{dX}{dT} &= rX \left(1 - \frac{X}{K}\right) - \frac{p_1 XY}{H_1 + X} - \frac{p_2 XZ}{H_2 + X} \\
\frac{dY}{dT} &= \frac{b_1 p_1 XY}{H_1 + X} - d_1 Y - a_{12} Y Z \\
\frac{dZ}{dT} &= \frac{b_2 p_2 XZ}{H_2 + X} - d_2 Z - a_{21} Y Z - mZ^2
\end{align*}
\]

under the initial conditions

\[
X(0) = \tilde{X} \geq 0, \quad Y(0) = \tilde{Y} \geq 0, \quad Z(0) = \tilde{Z} \geq 0,
\]

where \(X\) represents the population density of the prey and \(Y, Z\) represent the densities of the two species of predators. The parameters \(r\) and \(K\) represent the intrinsic growth rate and the carrying capacity of the prey, \(p_1\) is the maximum per-capita predation rate of \(Y\), \(H_1\) is the semi-saturation constant which represents the prey density at which \(Y\) reaches half of its maximum predation rate \((p_1/2)\), \(b_1\) and \(d_1\) are the birth-to-consumption ratio and per-capita natural death rate of \(Y\) respectively. The parameter \(a_{12}\) is the rate of adverse effect of \(Z\) on \(Y\), which we will refer to as the interspecific competition rate. The other parameters \(p_2, b_2, d_2, H_2, a_{21}, m_2\) are defined analogously for \(Z\). We assume that the species \(Z\) is territorial, and therefore experiences more competition for space and resources in comparison to \(Y\) (which is assumed to be non-territorial). The term \(mZ\) in the \(Z\) equation accounts for this intraspecific competition, which may include lethal fighting and cannibalism, and measures the density dependent mortality rate in the class of \(Z\). Examples of species governed by (1) may include small mammals such as rabbits/rodents preyed upon by raptors such as hawks/eagles (\(Y\)) and larger mammals such as wolves/bobcats (\(Z\)).

The density dependent mortality term in system (1) is the defining term that distinguishes the possibility of existence of a positive equilibrium state from competitive exclusion of species. In case of two competitors competing for a common species, the stronger competitor can outcompete the other; a phenomenon commonly referred to as the principle of competitive exclusion [19]. Such dynamics are known to occur in Rosenzweig-MacArthur
and Armstrong and McGhee predator-prey models \[20, 32, 34\]. In these models, the only coexistence state that the systems admit are in the form of large oscillation cycles \[30\]. However, a density dependent mortality term can prevent competitive exclusion and ensure long-term survival of the species besides guaranteeing the existence of its competitor \[39\]. Thus, the term $mZ$ is ecologically significant and we will treat the coefficient of intraspecific competition as the key parameter in this work.

With the following change of variables and parameters:

$$
\begin{align*}
t &= rT, \\
x &= \frac{X}{K}, \\
y &= \frac{p_1 Y}{rK}, \\
z &= \frac{p_2 Z}{rK}, \\
\zeta_1 &= \frac{b_1 p_1}{r}, \\
\zeta_2 &= \frac{b_2 p_2}{r}, \\
\beta_1 &= \frac{H_1}{K}, \\
\beta_2 &= \frac{H_2}{K}, \\
c &= \frac{d_1}{b_1 p_1}, \\
d &= \frac{d_2}{b_2 p_2}, \\
h &= \frac{mZ}{b_2 p_2}, \\
\alpha_{12} &= \frac{a_{12} Z}{b_1 p_1}, \\
\alpha_{21} &= \frac{a_{21} Y}{b_2 p_2},
\end{align*}
$$

system (1) takes the following dimensionless form:

$$
\begin{align*}
x' &= x \left(1 - x - \frac{y}{\beta_1 + x} - \frac{z}{\beta_2 + x}\right) \\
y' &= \zeta_1 y \left(\frac{x}{\beta_1 + x} - c - \alpha_{12} z\right) \\
z' &= \zeta_2 z \left(\frac{x}{\beta_2 + x} - d - \alpha_{21} y - h z\right),
\end{align*}
$$

where the primes denote differentiation with respect to the time variable $t$. Similar scaling variables were considered in a three-trophic food chain model by Deng \[9\]. We will assume the following conditions on the parameters:

(A) The maximum per capita growth rate of the prey is much larger than the per capita growth rates of the predators, i.e. $b_1 p_1 << r$ and $b_2 p_2 << r$, thus yielding $0 < \zeta_1, \zeta_2 << 1$. This is usually observed in many ecosystems where the prey has a higher birth rate than its predators \[36\]. Examples include insects and their avian predators, rodents and their aerial or ground-based predators and so forth. For simplicity, we will assume in our model that $\zeta_1 = \zeta_2 = \zeta$ (say). Similar dynamics are obtained when $\zeta_1 \neq \zeta_2$, but have the same order.

(B) The parameters $c$ and $d$ satisfy the inequality $0 < c, d < 1$, which implies that the growth rates of the predators are greater than their death rates. This is a default assumption otherwise the predators would die out faster than they could reproduce even at their maximum reproduction rate.

(C) The parameters $\beta_1$ and $\beta_2$ are dimensionless semi-saturation constants measured against the prey’s carrying capacity. We will assume that both predators are efficient, and hence they will reach the half of their maximum predation rates before the prey population reaches its carrying capacity, thus yielding $0 < \beta_1, \beta_2 < 1$.

(D) The parameters $\alpha_{12}$ and $\alpha_{21}$ are dimensionless interspecific competition coefficients measuring the interference effect of $Z$ on $Y$ and of $Y$ on $Z$ respectively. We will assume that the effect of interference on the growth rate does not exceed the intrinsic growth rate of the species, yielding $0 < \alpha_{12}, \alpha_{21} < 1$.

Under the assumptions (A)-(D), system (3) transforms to a singular perturbed system of equations with two time scales, where the prey exhibits fast dynamics and the predators exhibit slow dynamics.
3. THE GEOMETRIC SINGULAR PERTURBATION APPROACH

In this section, we provide a preliminary analysis of system (3) which reads as

\[
\begin{aligned}
    x' &= x\left(1 - x - \frac{y}{\beta_1 + x} - \frac{z}{\beta_2 + x}\right) := xu(x, y, z) \\
y' &= \zeta y\left(\frac{x}{\beta_1 + x} - c - \alpha_{12}z\right) := \zeta yv(x, y, z) \\
z' &= \zeta z\left(\frac{x}{\beta_2 + x} - d - \alpha_{21}y - hz\right) := \zeta zw(x, y, z),
\end{aligned}
\]

(4)

where \(u = 0\), \(v = 0\), and \(w = 0\) are the nontrivial \(x\), \(y\), and \(z\)-nullclines respectively. On rescaling \(t\) by \(\zeta\) and letting \(s = \zeta t\), system (4) can be reformulated as

\[
\begin{aligned}
    \dot{x} &= xu(x, y, z) \\
    \dot{y} &= yv(x, y, z) \\
    \dot{z} &= zw(x, y, z),
\end{aligned}
\]

(5)

where the overdot denotes differentiation with respect to the variable \(s\). The variables \(t\) and \(s\) are referred to as the fast and slow time variables respectively. The parameter \(\zeta\) can be regarded as the separation of time scales. We will use geometrical singular perturbation theory to analyze system (5) (or equivalently system (4)). The foundation of such geometric approach to analyze systems with a clear separation in time scales was given by Fenichel [15].

As \(\zeta \to 0\) the trajectories of (4) during fast epochs approach to the solutions of the “layer equations” given by

\[
\begin{aligned}
x' &= xu(x, y, z) \\
y' &= 0 \\
z' &= 0.
\end{aligned}
\]

(6)

On the other hand, during slow epochs trajectories of (5) converge to the solutions of the “reduced problem” given by

\[
\begin{aligned}
0 &= xu(x, y, z) \\
\dot{y} &= yv(x, y, z) \\
\dot{z} &= zw(x, y, z).
\end{aligned}
\]

(7)

The subsystems (6) and (7) can be used to understand and study the dynamics of the full system (3) or (4) (see [42] for details). The algebraic equation in (7) defines the critical manifold

\[
\mathcal{M} = \{(x, y, z) : x = 0 \text{ or } u(x, y, z) = 0\} := T \cup S,
\]

where \(T = \{(y, z) : y, z \geq 0\}\) and \(S = \{(x, y, z) : u(x, y, z) = 0\}\). The critical manifold \(\mathcal{M}\) is the nullsurface of the layer system (6). It consists of two normally attracting sheets \(S^a\) and \(T^a\), and two repelling sheets \(S^r\) and \(T^r\), separated by fold curves \(F^+\) and \(F^-\) (see figure 1(A)). The fold curve \(F^+ = S \cap \{u(x, y, z) = 0\}\) is the set of all points on \(S\) where the normal hyperbolicity is lost. It is along this curve where saddle-node bifurcations of equilibria of the fast subsystem (6) occur. More precisely, \(S^a\) and \(S^r\) meet along \(F^+\). The
curve $\mathcal{F}^- = T \cap S$ is the set of transcritical points of the fast flow and divides the plane $T$ into two sheets, $T^a$ and $T^r$. By Fenichel’s theory [15], the normally hyperbolic segments of the critical manifold $\mathcal{M}$ perturb to locally invariant attracting and repelling slow manifolds $T^a_\zeta \cup S^a_\zeta$ and $T^r_\zeta \cup S^r_\zeta$ respectively for $\zeta > 0$, and the slow flow restricted to these manifolds is an $O(\zeta)$ perturbation of the reduced flow on $\mathcal{M}$. However, the theory breaks down in neighborhoods of $\mathcal{F}^\pm$ and interesting dynamics such as relaxation oscillations and MMOs can occur.

Note that the reduced flow is restricted to the plane $x = 0$ or to the surface $S := \{(x, y, z) : u(x, y, z) = 0\}$. On the plane $T$, the reduced dynamics solves the system

$$
\begin{aligned}
    x &= 0 \\
    \dot{y} &= yv(0, y, z) \\
    \dot{z} &= zw(0, y, z).
\end{aligned}
$$

(8)

Since $\dot{y} < -cy$ and $\dot{z} < -dz$ on $T$ with $(0, 0, 0)$ being the global attractor of (8), the reduced flow descends along this plane and eventually reaches the curve $\mathcal{F}^-$, below which $T$ is repelling. Due to the loss of normal hyperbolicity, the flow after reaching $\mathcal{F}^-$, should get connected to $S^a$ by a fast fiber of (6). However, the reduced flow crosses $\mathcal{F}^-$ and stays on $T$ for a while, until it reaches a point $(0, y_m, z_m) \in T^r$, where a fast orbit concatenates with
The phenomenon of delay is referred to as the Pontryagin’s delay of stability loss [36, 35, 45]. The delay map $P^0: T^a \rightarrow T^r$ is defined by $P^0(y_0, z_0) = \left( y(\tau_0(y_0, z_0)), z(\tau_0(y_0, z_0)) \right)$, where the delay $\tau_0$ is expressed by the integral

$$\int_0^{\tau_0} u(0, y(s), z(s)) \, ds = 0,$$

where $(y(s), z(s))$ solves [8] with initial value $(y_0, z_0) \in T^a$.

Typically, a singular periodic orbit for fast-slow systems with “S-shaped” critical manifolds is constructed by concatenating the reduced flow, occurring along the attractive branches of $M$, with fast fibers, along which transitions between the branches occur when certain points known as “jump points” on the fold curves $F^\pm$ are reached. However, the existence of the Pontryagin’s delay of stability loss point on $T^r$ makes the construction of the singular orbit more subtle for system (5). In this case, the slow piece of the singular orbit besides containing the reduced flow along $T^a$ and $T^r$ also contains the flow along $T^r$ until the delay of stability loss point is reached.

Note that since $u_z \neq 0$, by the implicit function theorem, the surface $S$ can be locally written as a graph of $z = \phi(x, y)$, i.e. $u(x, y, \phi(x, y)) = 0$. Hence we can project the dynamics of (7) onto the $(x, y)$ coordinate chart. Differentiating $u(x, y, z) = 0$ implicitly with respect to time gives us the relationship $u_x \dot{x} + u_y \dot{y} + u_z \dot{z} = 0$. Thus, the reduced flow (7) restricted to $S$, where $S$ is considered as the graph of $z = \phi(x, y)$ reads as

$$\left( \begin{array}{c} \dot{x} \\ \dot{y} \end{array} \right) = \left( \begin{array}{c} u_y yv + u_z zw \\ u_x yv \end{array} \right) \bigg|_{z=\phi(x,y)}.$$  

System (9) has singularities when $u_x = 0$ and its solutions blow-up in finite time at $F^+$. Hence standard existence and uniqueness results do not hold. Points on $F^+$ for which $u_y yv + u_z zw \neq 0$ are called “jump points” and they satisfy the “normal switching condition” [7]. At these points, a solution of (5) exits into relaxation after reaching $F^+$ giving rise to relaxation dynamics or more commonly, referred to as boom and bust cycles in ecology. During these cycles, the up and down states of a trajectory correspond to slow movement along the attractive branches $S^a_\xi$ and $T^a_\xi$ of the slow manifold and fast transitions between these states occur once a neighborhood of a jump point on $F^+$ or the Pontryagin’s delay of stability loss point on $T^r_\xi$ are reached. On the other hand, points of $F^+$ where the normal switching condition is violated can give rise to canards as discussed below.

To analyze the solutions where the normal switching condition fails, we rescale the time $s$ by a phase-space-dependent time transformation factor $-u_x$, i.e. $ds = -u_x dt_s$ [12]. This removes the finite-time blow up of solutions and system (9) transforms to the desingularized system

$$\left( \begin{array}{c} \dot{x} \\ \dot{y} \end{array} \right) = \left( \begin{array}{c} u_y yv + u_z zw \\ -u_x yv \end{array} \right) \bigg|_{z=\phi(x,y)},$$

where the overdot denotes $t_s$ derivatives. System (10) is topologically equivalent to system (9) on $S^a$. However, the phase-space-dependent time transformation reverses the orientation of the orbits on $S^r$, therefore, the flow of (9) on $S^r$ is obtained by reversing the
direction of orbits of (10). Hence the reduced flow is either directed towards the fold or away from it.

The set of equilibrium points of (10) that do not lie on the fold curve \( F^+ \) (i.e. for which \( u_x \neq 0 \)) are known as *ordinary singularities*. On the other hand, equilibrium points of (10) that lie on \( F^+ \) are termed as *folded singularities* or canard points. The set of folded singularities form isolated points of \( F^+ \). The trajectories of the reduced system (7) may pass through the canard points and can thus cross from \( S^a \) to \( S^r \) with finite speed. Such a solution is called a singular canard. The classification of a folded singularity as a folded node or a folded saddle or a folded focus or a degenerate folded node is based on the linearization of the folded singularity when considered as an equilibrium of (10). More precisely, if \( \lambda_1, \lambda_2 \) are eigenvalues of the linearization (10) at a folded singularity \( p \), then \( p \) is a folded focus if \( \lambda_1, \lambda_2 \in \mathbb{C} \). If \( \lambda_1, \lambda_2 \in \mathbb{R} \) such that \( \lambda_1\lambda_2 < 0 \), then \( p \) is a folded saddle, while if \( \lambda_1, \lambda_2 < 0 \), then \( p \) is a folded node. Further degeneracies may occur if one of the eigenvalues pass through 0 and can give rise to folded saddle node (FSN) bifurcation of types I and II [12].

The folded node possesses strong and weak eigenvalues \( \lambda_s \) and \( \lambda_w \), respectively. The singular strong canard \( \gamma_s \) is the unique trajectory to (10) tangent to the strong eigendirection \( v_s \), at \( p \), while the singular weak canard \( \gamma_w \) is tangential to the weak eigendirection, \( v_w \). The fold curve \( F^+ \) and the strong singular canard \( \gamma_s \) form a trapping region (singular funnel) on \( S^a \), such that all solutions in the funnel converge to the folded node \( p \) (see figure 1 (B)). In fact, the folded node allows a sector of singular canards to flow from \( S^a \) to \( S^r \) and can give rise to local oscillations for \( 0 < \zeta << 1 \). The extension of \( S^a_\zeta \) and \( S^r_\zeta \) into a neighborhood of \( F^+ \) results in local twisting of the slow manifolds giving rise to maximal canard solutions, including extensions of \( \gamma_s \) and \( \gamma_w \).

The eigenvalue ratio \( \mu = \lambda_w / \lambda_s \) determines the maximal number of rotations that occur in an \( O(\sqrt{\zeta}) \) neighborhood of a folded node singularity. For sufficiently small \( \zeta > 0 \), the strong singular canard \( \gamma_s \) perturbs to a maximal canard denoted by \( \gamma^\zeta_s \) and if \( \mu^{-1} \notin \mathbb{N} \), the singular weak canard \( \gamma_w \) perturbs to a maximal canard \( \gamma^\zeta_w \) for \( \zeta > 0 \). Moreover, if \( k \in \mathbb{N} \) be such that

\[
2k + 1 < \mu^{-1} < 2k + 3 \quad \text{and} \quad \mu^{-1} \neq 2(k + 1),
\]

there exists \( k \) other additional canards referred to as secondary canards. For \( 1 \leq j \leq k \), the \( j \)-th secondary canard \( \gamma^\zeta_j \) twists \( 2j + 1 \) times around \( \gamma^\zeta_w \). A trajectory trapped inside the singular funnel experiences small rotations around the weak canard \( \gamma^\zeta_w \) until it jumps to the other attracting sheet \( T^a_\zeta \). A global return mechanism can re-inject trajectories to the folded-node funnel to induce mixed-mode oscillations. The singular funnel acts as a separatrix in the phase-space, locally dividing between those trajectories that twist around \( \gamma^\zeta_w \) and those that do not [7] [18].

The secondary canards \( \gamma^\zeta_j, j = 1, 2, \ldots k \) divide the singular funnel near the folded node into \( k \) distinct subsectors with different rotational properties, where each subsector is associated with a rotation number. The first subsector is formed by the maximal strong canard \( \gamma^\zeta_s \) and the first secondary canard \( \gamma^\zeta_1 \). The trajectories make one rotation if they lie within
this subsector. The second subsector is formed by the second and third secondary canards \(\gamma_2^\zeta\) and \(\gamma_3^\zeta\), respectively; trajectories that enter this subsector make two rotations. The last subsector is bounded by the \(k\)th secondary canard and the fold curve \(F^+\). Trajectories in this subsector make \(k\) rotations \([7, 12]\).

Another mechanism that may generate small amplitude oscillations in two-slow and one-fast system is the occurrence of FSN II bifurcation in system \([10]\) \([26]\). The bifurcation occurs when an ordinary singularity (for instance, an equilibrium \(p_e\) of the full system \([4]\)) and a folded singularity of the desingularized system \([10]\) merge together and then split again, interchanging their type and stability. The change in the stability occurs at a transcritical bifurcation in system \([10]\), where \(p_e\) crosses the fold curve \(F^+\). The corresponding point is called an FSN of type II and has its center manifold transverse to \(F^+\). Importantly when \(\zeta > 0\), a singular Hopf bifurcation occurs in system \([4]\) at a distance \(O(\zeta)\) in parameter space. In this situation the SAOs are induced by dynamics near an equilibrium point of system \([4]\) which is a saddle-focus with a pair of unstable complex eigenvalues. Trajectories can get closer to a small neighborhood of this equilibrium point along the one-dimensional stable manifold, \(W^s(p_e)\) of the equilibrium. SAOs occur as the trajectory spirals away from the equilibrium along the two-dimensional unstable manifold \(W^u(p_e)\) of the equilibrium. If the Hopf bifurcation is supercritical, then for parameter values close enough to the Hopf bifurcation, stable periodic orbits \(\Gamma_\nu\) of small amplitude are created for some bifurcating parameter \(\nu\). A new type of bifurcation, namely a tangent bifurcation of the two-dimensional global invariant manifold \(W^u(p_e)\) with the two-dimensional repelling Fenichel manifold \(S^\zeta_r\) has been identified in \([16]\), where \(S^\zeta_r\) wraps around \(W^s(p_e)\) in backward time, while \(W^u(p_e)\) accumulates in forward time on, and is bounded by the attracting periodic orbit \(\Gamma_\nu\). The interaction between \(S^\zeta_r\) and \(W^u(p_e)\) generates the large amplitude oscillations, consequently giving rise to a global return mechanism which then allows the possibility of a trajectory leaving a neighborhood of the equilibrium point to return and perform MMOs.

Complex, chaotic MMOs could also suddenly rise from a homoclinic bifurcation, known as Shil’nikov homoclinic bifurcation, where the homoclinic orbit can a serve as an organizing center for MMOs \([21]\). The presence of a saddle-focus equilibrium \(p_e\) with two-dimensional unstable manifold \(W^u(p_e)\) and one-dimensional stable manifold \(W^s(p_e)\) along with a global return mechanism allows orbits to be reinjected to a neighborhood of \(p\) along \(W^s(p_e)\) and spiral out along \(W^u(p_e)\). Some studies have been dedicated to detect the existence of a Shilnikov homoclinic orbit \([18, 33]\). However, detecting these orbits is very challenging and requires extensive numerical computation.

4. Bistability, chaotic dynamics and the effect of intraspecific interference.

System \([4]\) has 8 free parameters which make the analysis very challenging. In the absence of interference competition, i.e. \(\alpha_{12} = \alpha_{21} = 0\), there exists a unique coexistence equilibrium in a suitable parameter regime. MMO orbits and chaotic dynamics exist as a control parameter is varied. This case has been studied in details in \([42]\). When
Figure 2. One-parameter bifurcation demonstrating a period-doubling route to chaos of $\Gamma_h$ as $h$ is varied. The $y$-axis represents the maximum of $x$. The other parameters are given by (11).

$\alpha_{12}, \alpha_{21} \neq 0$, a preliminary analysis of a similar model was performed in [41] with $\beta_2$ as the input parameter, where different MMO patterns with transition from one pattern to the other were analyzed. In this paper, the focus of the work is to investigate the dynamics analytically and numerically in a neighborhood of an FSN II point. To this end, we take all the parameter values to be nonzero such that the intersection of the non-trivial nullclines $u = 0, v = 0$ and $w = 0$ produces equilibria that lie in the positive octant. Unless otherwise stated, we fix the parameter values to $\zeta = 0.01, \beta_1 = 0.25, \beta_2 = 0.35, c = 0.4, d = 0.21$, $\alpha_{12} = 0.5, \alpha_{21} = 0.1$

and vary $h$.

The coexistence equilibrium point $p_e$ exists for $h > 0.7425$. In the singular limit of system (3), FSN II bifurcation occurs at $h \approx 0.7785$, where a folded singularity $p$ and the equilibrium $p_e$ (an ordinary singularity) exchange their stabilities. At the bifurcation, the folded singularity $p$ transforms into a folded node and thereafter, persists as a folded node. The interior equilibrium $p_e$ is still an attractor of the full system (3). A supercritical Hopf bifurcation occurs at $h \approx 0.7803$, where a family of stable periodic orbits $\Gamma_h$ is born. The equilibrium $p_e$ is now a saddle-focus with one negative and two complex (with positive real parts) eigenvalues. The periodic orbits $\Gamma_h$ grow in size and then undergo a cascade of period-doubling bifurcations for $h \in (0.797, 0.798)$, resulting into small amplitude chaotic invariant sets (see figure 2).

Past the regime of period doubling bifurcations of $\Gamma_h$, chaotic dynamics featuring small amplitude and large amplitude oscillations are observed in the interval $(0.798, 0.82)$. On further increasing $h$, a sequence of period doubling and saddle-node bifurcations of limit cycles produce periodic MMO orbits predominantly with signatures $1^s$ where $s \in \mathbb{N}$, and
other complicated signatures, which are usually a mix of $1^i$ and $1^{i+1}$ as seen in the one-parameter bifurcation diagram in figure 3 (also see figure 10). For $h > 0.98$, relaxation oscillation cycles are obtained. The details are omitted here for brevity.

Interestingly, in the parameter regime where $\Gamma_h$ is stable, i.e. for $0.7803 < h < 0.797$, MMOs are also observed as shown in figure 4(A). The MMO trajectories in this range are aperiodic as demonstrated by the non-periodicity of the time series in figure 4(C). The SAOs in MMOs in this regime are partly canard-induced, organized by the folded node singularity $p$. As a trajectory gets trapped in a singular funnel and is funneled through folded node, the primary weak canard imparts rotational properties leading to canard-induced SAOs. The other factor that generates additional rotations is the equilibrium $p_e$, whereby the SAOs are organized by $W^u(p_e)$. The unstable manifold $W^u(p_e)$ spirals out and interferes with the slow dynamics on $S^r_{\eta}$ before following the fast fibers of the system. As predicted by the canard theory, inside the funnel, a trajectory undergoes several rotations, but as the trajectory leaves the funnel, the exit point is close to $p_e$ and the dynamics are influenced by the local vector field of $p_e$ leading to additional rotations (see figure 4(B)).

However, it is not clear at this point if there are other mechanisms such as Shil’nikov homoclinic bifurcation, involved in generating the MMOs. The folded node singularity $p$ and the true equilibrium $p_e$ are very close to each other in phase space, and the global return map brings the MMO trajectory close to $W^s(p_e)$. Hence the epoch of SAOs increases in length and the oscillations get too small to be detectable (see figure 4(D)). It is possible that a homoclinic orbit to $p_e$ passes through the twisting region in the funnel.

Another interesting feature that occurs in a neighborhood of FSN II is a sudden transition from MMO dynamics to pure SAOs. As shown in figure 5, a trajectory was exhibiting MMOs initially, but settles down into the small periodic orbit $\Gamma_h$. Such a transition occurs
as a result of interaction between the repelling slow manifold $S^r_\xi$, the unstable manifold $W^u(p_e)$, and $W^s(\Gamma_h)$, the stable manifold of $\Gamma_h$. As discussed earlier, the MMOs occur when trajectories from the slow attracting manifold $S^a_\xi$ are funneled to the repelling slow manifold $S^r_\xi$ and a global return mechanism brings them back to the funnel. The jumps from the fold curve $F^+$ and the Pontryagin’s delay of stability loss point below $F^-$, along the fast fibers form two important components of the global return map. However, as a trajectory leaves the funnel along $W^u(p_e)$, it can get attracted towards $W^s(\Gamma_h)$. In this situation, the trajectory after exiting the funnel may follow the fast fibers initially, but rather than jumping to the other attracting branch $T^a_\xi$ of the slow manifold, it gets attracted to $W^s(\Gamma_h)$ and flows along this invariant manifold. This prevents the concatenation between the fast fibers and the slow flow on $T^a_\xi \cup T^r_\xi$, thereby not admitting a reinjection into the singular funnel to produce MMOs. To explore this further, we transform system (4) into its normal
Figure 5. (A) Time series of the $x$-coordinate of a trajectory that initially exhibits MMOs settles down to $\Gamma_h$ for $h = 0.785$. (B) Time series of $\Gamma_h$. All the other parameter values are as in \[11\].

form near FSN II bifurcation in Section 5 and numerically study the dynamics of the normal form in Section 6.

Remark 4.1. (a) System \[5\] demonstrates that a small increment in the strength of intraspecific competition among $z$, which depends on the birth/mortality rate of the species (where external environmental factors such as climate change may play a role), can have far lasting consequences, especially if the system is near a tipping point. The value of the parameter at the FSN II bifurcation in fact serves as a critical threshold for system \[5\], as the system transitions from a stable coexistence state to chaotic and oscillatory states soon after the threshold value is crossed.

(b) The regime where bistability between the two attractors is observed, occurs in an $O(\zeta)$ neighborhood of the FSN II point, is ecologically important. In this regime, depending on the initial densities of the populations, as the system evolves, we may observe population cycles with small annual fluctuations or MMO dynamics which represent episodes of outbreak and collapse separated by periods of almost constant densities. Importantly, the system allows transition from MMO dynamics to small amplitude cycles (which are more robust from the point of view of ecology) and this information can be useful for population regulations.

(c) Contrary to the obvious intuitive explanation for a sudden dramatic change in an ecosystem is the occurrence of a sudden large external impact, there exists a range of ecosystems demonstrating transition between states with radically different properties subjected to slowly varying conditions. Some examples include standing waters that can be overgrown by floating plants, the shift in the Caribbean coral reefs, and savannahs that become encroached suddenly by bushes (see \[46\] and the references therein). Our findings align with the theory that even a tiny incremental change in conditions can trigger a large shift in
dynamics. Consequently, the parameter windows over which bistability and chaotic MMOs occur, though sufficiently small, can be significantly important.

To analyze the dynamics in the bistable regime, we consider a Poincaré section by following trajectories lying in basins of attraction of each attractor. Let $\Sigma_h$ be a plane through the folded node $p$, chosen parallel to the weak eigendirection, and transverse to the critical manifold $S$ as shown in figure 6. A zoomed view of the SAOs of an MMO trajectory is also included in figure 6. During the epoch of SAOs the $y$-coordinates increase while the $z$-coordinates decrease as the trajectory moves toward to $p_e$, until the trajectory gets repelled by $W^u(p_e)$ and reaches a jump point on $F^+$ and jumps to $T^\alpha$, the other attracting sheet of the slow manifold. As the orbit performs SAOs, its intersections (first return) with $\Sigma_h$, only in the direction of decreasing $x$ are recorded to yield the Poincaré map.

Starting with initial condition $(0.4641, 0.0978, 0.3272)$, the $(x, y)$ and $(x, z)$ coordinates of the intersections of this trajectory in the direction of decreasing $x$ with the plane $\Sigma_h$ are recorded. The corresponding Poincaré sections are shown in figure 7(A)-(B). Similarly a trajectory starting at $(0.01, 0.01, 0.12)$ is integrated and its first intersection with $\Sigma_h$ is recorded as shown in figure 7(C)-(D). The trajectory with initial condition $(0.4641, 0.0978, 0.3272)$ eventually stabilizes to $\Gamma_h$, while the trajectory with initial condition $(0.01, 0.01, 0.12)$ gets attracted to an aperiodic MMO orbit. The periodic orbit $\Gamma_h$ intersects with $\Sigma_h$ at $(0.3353, 0.0968, 0.3453)$, and this is marked in figure 7(A)-(B). The Poincaré sections in figure 7(C)-(D) indicate that the trajectory repeatedly enters
the singular funnel and stays in a close neighborhood of the folded node singularity $p = (0.3383, 0.0923, 0.3474)$, while twisting along the primary weak canard and getting pushed towards the equilibrium $p_e = (0.3299, 0.1004, 0.3378)$. Moreover, a zoomed view of the sections in panels (C)-(D) show that the trajectory while moving towards $p_e$, intersects with the Poincaré section at innumerous points forming a dense array of segments as shown in figure 8(A)-(B). This indicates that the MMO orbit is indeed aperiodic. Comparing the Poincaré sections in panels (A)-(B) with (C)-(D) in figure 7, it is evident that both trajectories visited the same regions in the phase space initially, until the first trajectory gets
trapped in $W^s(\Gamma_h)$, and thereafter exhibits SAOs. This suggests the existence of a separatrix in the state space, which lies outside the singular funnel, possibly in a close proximity of $W^s(\Gamma_h)$.

Figure 8. A zoomed view of the regions $a_1$ and $a_2$ of the Poincaré sections in figure 7(C)-(D) near the folded node.

The wide gaps in the Poincaré sections in figure 7(A)-(B) indicate that the trajectory which once approached the regions nearby the funnel never returned to those neighborhoods as time elapsed. In particular, the wide gap around the point $(0.343, 0.089, 0.353)$ does not appear in panels (C)-(D). This occurs because the trajectory does not enter the funnel anymore, and therefore makes no intersection with $\Sigma_h$ in that area. Similarly, the gap in a neighborhood of the point $(0.333, 0.098, 0.343)$ suggests that the trajectory does not twist around the weak canard any longer and therefore cannot intersect $\Sigma_h$. Depending on the location of exit from the funnel, the trajectory can either connect with the global return map and re-enter the funnel or can get trapped in the invariant manifold $W^s(\Gamma_h)$.

To study the asymptotic behavior of points lying in a region close to the folded node, we consider a grid on a plane that lies outside the singular funnel and compute the basins of attraction of the two attractors restricted to each point on the grid. We choose equally spaced points on a grid of size $[0.08, 0.115] \times [0.325, 0.36]$ on the plane $x = 0.3428$ and integrate trajectories starting at each point on this grid. A trajectory $\gamma(s) = (x(s), y(s), z(s))$ is defined to be in the basin of attraction of the MMO attractor, if the maximum value of the local peaks of $x(s)$ is larger than 0.7 for all $s > 4000$, while it is in the basin of attraction of the periodic orbit $\Gamma_h$, if the maximum value of the local peaks of $x(s)$ lies between 0.35 and 0.5 for all $s > 4000$. The asymptotic behavior of the trajectories from the grid are recorded in figure 9(A) giving us the basins of attraction.

Past the cascade of period doubling bifurcations of the periodic orbit $\Gamma_h$, in the parameter regime $h \in (0.8, 0.82)$, the eigenvalue ratio at the folded node singularity, $\mu = \lambda_w/\lambda_s$ is significantly small. In fact, $\mu = O(\zeta)$ in this regime. This ratio determines the maximal
number of SAOs possible between two LAOs in an MMO orbit. The upper bound of the number of SAOs is given by $s_{\text{max}} = (\mu + 1)/(2\mu)$, where this bound is determined from a normal form for folded nodes [7]. The distance from the strong canard at which the singular orbit enters the singular funnel determines how close is the actual number of SAOs to the upper bound $s_{\text{max}}$ in an MMO orbit. Closer the global return is to the strong canard, smaller is the number of SAOs. In contrast, if the global return is closer to the fold curve $F^+$, then the number of SAOs is closer to $s_{\text{max}}$ [26]. The amplitude of the SAOs also depend on the entry point of the global return map into the funnel. It is expected that the amplitudes of the SAOs are tiny if the global return point inside the funnel is $O(1)$ distance from the strong canard. On the other hand, if the global return point is $O(\sqrt{\varepsilon})$ from the strong canard, mixed MMO signatures with larger amplitude SAOs are likely to occur [26].

Stable $1^k$ orbits are difficult to be observed in the regime $(0.8, 0.82)$. The stability interval of such orbits is relatively small and non-$1^k$ orbits are more readily seen in this parameter regime. As an illustration, we consider the Poincaré section $\Sigma_h$ (the plane through $p$ parallel to the weak eigendirection $v_w$ and transverse to $S$) at $h = 0.819$ near the folded node region and study the intersection of MMO orbits with $\Sigma_h$ in the decreasing direction of $x$. We note that the section gets prominently divided into segments as shown in figure 10(B), where each segment corresponds to intersection of the orbit with $\Sigma_h$ while performing a loop. The MMO orbit observed is aperiodic, and the number of SAOs typically vary between 10 and 11 between two LAO cycles (see figure 10(A)). The Poincaré section thus gets prominently divided into 12 distinct segments, the top segment is generated by the LAO cycles and the rest by the SAOs. Combining this with the canard theory, it seems

Figure 9. Basins of attraction of $\Gamma_h$ and the aperiodic MMO attractor for $h = 0.785$ restricted to the plane $x = 0.3428$. (B): Plotted against $h$, average number of SAOs in a time series of an MMO attractor computed over an interval of length 2000. The other parameter values are given by (11).
plausible that the global returns fall inside the singular funnel into the 10th and the 11th rotational sectors repeatedly at different points, giving rise to a chaotic MMO orbit with \(1^{10}1^{11}\) as its predominant signature. Note that at this parameter value, \(\mu \approx 0.0066\), which yields \(s_{\text{max}} = 76\).

As the input parameter \(h\) is further increased, MMOs of form \(1^k\) and \(1^k1^{k-1}\) dominate the stable dynamics. The Farey sequences observed in the transition are roughly of the form \(... \rightarrow 1^k \rightarrow 1^k1^{k-1} \rightarrow 1^{k-1}...\). On further increasing \(h\), stable MMO orbits of the form \(2^1\) are observed until the dynamics enter into relaxation regime; see figure 3. From an ecological point of view, the frequency of population outbreaks (which correspond to relaxation cycles) increases with the strength of intraspecific competition \(h\). By determining the characteristic timescale for oscillations of the SAOs and the average number of SAOs occurring between two spikes, one can therefore predict the return time between two outbreaks as a function of the input parameter. We thereby plot the average number of SAOs, denoted by \(N_{\text{avg}}\), between two LAOs over a time interval of length 2000 as a function of the bifurcating parameter \(h\) in figure 9(B), which can then be related to the average return time between the outbreaks. As predicted by the canard theory, \(N_{\text{avg}}\) decreases with \(h\), except near the FSN II region (\(h \approx 0.78\)). The discrepancy is due to the fact that the SAOs are mostly indistinguishable to be separately counted near FSN II. It will be interesting to study the effect of demographic and environmental stochasticity on the distribution of SAOs in system (4). Similar studies in [40, 43] reveal that the distribution of the number of SAOs between two spikes in presence of stochasticity is asymptotically geometric in a parameter regime near singular Hopf bifurcation.

Figure 10. (A): Time series in \(x\) of an aperiodic MMO orbit at \(h = 0.819\). (B): \((x, y)\) coordinates of intersection of the orbit with the Poincaré section \(\Sigma_h := 2.96x + 1.40y - 1.64z = 0.597\) such that \(dx/ds < 0\). The other parameter values are fixed as in [11].
In [8], the authors studied the interaction of canard and singular Hopf mechanism for generation of SAOs in a reduced neuronal competition model. In their work, they classified the SAOs in an MMO orbit as “canard-induced” or induced by the local vector field around a saddle-focus equilibrium by numerically computing the “way-in/way-out” function [26] which describes the maximal delay expected for generic solutions passing through FSN singularity. A similar analysis can be performed in system (4) as a function of the bifurcating parameter in the parameter regime away from the zero-Hopf bifurcation (see figure 11). We leave this for future work.

4.1. A two-parameter bifurcation of system (5). In addition to studying the effect of intraspecific competition, we consider the effect of varying predation efficiency of the predator $y$ on the existence of MMOs. To this end, keeping all the parameter values fixed as in (11), except for $\beta_1$, we consider a two-parameter bifurcation in $(h, \beta_1)$ parameter space and study the dynamics that occur. The two-parameter bifurcation diagram is shown in figure 11. A saddle-node bifurcation of the non-trivial equilibria of (4) occurs along the SN curve (shown in red). The equilibria lying in the region to the left of the right branch of the SN curve are not biologically feasible (as they have one or more negative components). A unique stable positive equilibrium of (4) exists in the region lying in between the SN curve and the Hopf curve (shown in blue). To the right of the Hopf curve, the positive
equilibrium is unstable and oscillatory dynamics such as MMOs and relaxation oscillations appear. The PD curve, corresponding to the period-doubling bifurcation of the periodic orbit born out of the Hopf bifurcation demarcates MMOs from relaxation oscillations in the parameter space. The FSN II curve meets with the Hopf curve at the zero-Hopf bifurcation (ZH), which is a co-dimension two bifurcation (see Remark 4.2).

Figure 12. A one-parameter bifurcation diagram in $h$ with $\beta_1 = 0.35$ and the other parameter values are as in (11). The $y$-axis represents the maximum value of $x$.

We note that when $\beta_1 = 0.35$, so that $\beta_1 = \beta_2$, i.e. both species of predators have equal predation efficiencies, MMOs are observed, though not in the immediate neighborhood of the supercritical Hopf bifurcation. The MMOs obtained for this set of parameter values are organized by the folded node singularity. A one-parameter bifurcation diagram in $h$ in figure 12 illustrates the sequence of MMOs that occur. The SAOs associated with these MMOs have distinctively larger amplitudes. The time series of the $x$-coordinate in figure 13 (A) shows the SAOs are quite different from figure 10. Note that the parameter regime chosen for both figures is just past the cascade of period doubling bifurcation of the small limit cycle $\Gamma_h$. However the structure of the slow manifold $S^\zeta$ changes with $\beta_1$, and the amplitude of the SAOs are governed by the extent to which $S^\zeta_a$ and $S^\zeta_r$ twist while guiding the path of a trajectory through the folded node regime. A tight twisting of $S^\zeta_a$ and $S^\zeta_r$ forces a decrease in amplitude of the SAOs as observed in figure 10.

At higher values of $\beta_1$, i.e. for $\beta_1 > 0.39$, MMOs do not occur. As $h$ is varied, a supercritical Hopf bifurcation of the positive equilibrium gives birth to a family of stable periodic orbits which grow in size to relaxation oscillations.

Remark 4.2. A zero-Hopf bifurcation occurs at $(\beta_1, h) = (0.197019, 0.60803)$, which is a co-dimension two bifurcation. Near this parameter value, other bifurcations may occur including saddle-node bifurcations of periodic orbits, bifurcation of Shil’nikov homoclinic orbit to a saddle-focus etc. The latter type of bifurcation can serve as an organizing center for the MMOs observed in this model.
Figure 13. (A): The time series of the $x$-coordinate of a $1^5$ MMO orbit at $h = 1.63$, $\beta_1 = 0.35$ and the other parameter values are as in (11). (B): A zoomed view of the orbit near the folded node, shown by a dot in cyan. The weak eigendirection is shown in red and the equilibrium by the green dot.

5. Normal form near the singular Hopf bifurcation

In the previous section, we observed that the MMOs in system (4) occur in a close vicinity of the supercritical Hopf bifurcation which lies $O(\zeta)$ away from FSN II bifurcation in the parameter space. The FSN II point/singular-Hopf point plays an important role in governing the SAOs in the MMOs. A normal form for singular Hopf bifurcation in one-fast and two-slow variables was first constructed by Braaksma [4], Guckenheimer [16], later proposed another normal form for such systems which retains the form of the original system (namely one-fast and two slow-variables). However, to generate MMOs, a cubic term in the $x$-equation is added in [16]. By rescaling time by a factor of $\sqrt{\zeta}$ and by a sequence of coordinate transformation, the normal form in [16] can be transformed to the form in [4], and therefore the two forms are topologically equivalent.

In this article, we will adopt the transformations used in [4] to generate the normal form for system (4) near the FSN II point. The advantages of using this particular normal form are many: (i) besides covering the dynamics in a small neighborhood of FSN II, the normal form contains a cubic term which allows global returns of trajectories to the vicinity of the equilibrium point, (ii) the equations for the scaled variables contain as many $O(1)$ terms as possible, (iii) the numerical computations are much easier to perform on this form for sufficiently small $\zeta$, (iv) the time is scaled by a factor of $\sqrt{\zeta}$ to be consistent with the characteristic timescale for singular oscillations (the characteristic timescale for oscillations of the periodic orbits born due to Hopf bifurcation is $O(1/\sqrt{\zeta})$). We remark that a canonical form of the FSN II singularity was considered in [26], where a blow-up
analysis is performed to understand the evolution of trajectories in a small neighborhood of the FSN II singularity. The emergence of MMOs in [26] is attributed to the generalized canard phenomenon, which is defined as a combination of local passage through a canard point, and a global return that resets the system dynamics after the passage has been completed [24]. With the aid of our normal form we will show that the generalized canard phenomenon is responsible for the MMOs in system (4) near FSN II bifurcation.

Since we are interested in dynamics near the singular Hopf bifurcation, which is a co-dimension 1 bifurcation, we will treat \( h \) as the bifurcating parameter. The reduction of system (5) to its normal form allows us to explicitly calculate Hopf bifurcation analytically. To this end, we rewrite system (5) as

\[
\begin{align*}
\dot{\zeta} &= f_1(x, y, z, h) \\
\dot{y} &= f_2(x, y, z, h) \\
\dot{z} &= f_3(x, y, z, h)
\end{align*}
\]  

(12)

where \( f_1(x, y, z, h) = xu(x, y, z, h), \ f_2(x, y, z, h) = yv(x, y, z, h), \ f_3(x, y, z, h) = zw(x, y, z, h) \).

The overdot is with respect to the slow time variable \( s \). Throughout our work we keep all the parameters fixed, except for \( h \). Let \((\bar{x}, \bar{y}, \bar{z}, \bar{h})\) be a point where the following conditions hold:

- (P1) \( \bar{u} = 0 \), \( \bar{v} = 0 \), \( \bar{w} = 0 \).
- (P2) \( \bar{u}_x = 0 \).
- (P3) \( \det J \neq 0 \), where \( J = \begin{pmatrix} (\bar{f}_1)_x & (\bar{f}_1)_y & (\bar{f}_1)_z \\ (\bar{f}_2)_x & (\bar{f}_2)_y & (\bar{f}_2)_z \\ (\bar{f}_3)_x & (\bar{f}_3)_y & (\bar{f}_3)_z \end{pmatrix} \).
- (P4) \( (\bar{f}_1)_y (\bar{f}_1)_z - (\bar{f}_2)_x (\bar{f}_3)_x < 0 \).
- (P5) \( \bar{u}_{xx} \neq 0 \).
- (P6) \( -((\bar{f}_1)_{xx} (\bar{f}_1)_{xy} (\bar{f}_1)_{xz}) J^{-1} \begin{pmatrix} (\bar{f}_1)_h \\ (\bar{f}_2)_h \\ (\bar{f}_3)_h \end{pmatrix} + (\bar{f}_1)_{xh} \neq 0 \),

where bars denote the values of the expressions evaluated at \((\bar{x}, \bar{y}, \bar{z}, \bar{h})\). Note that conditions (P1) and (P2) indicate that a FSN II bifurcation of the reduced system corresponding to system (12) occurs at \((\bar{x}, \bar{y}, \bar{z}, \bar{h})\), where \((\bar{x}, \bar{y}, \bar{z})\) is a fold point. Condition (P3) implies the existence of a smooth family of equilibria \((x_o(h), y_o(h), z_0(h))\) in a neighborhood of \( \bar{h} \) via the implicit function theorem. Condition (P4) implies that the linearization of system (12) at equilibria \((x_o(h), y_o(h), z_0(h))\) admits a pair of eigenvalues with singular imaginary parts for sufficiently small \( \zeta \). Condition (P5) implies that the fold point is non-degenerate. Finally condition (P6) implies that \( \frac{d\sigma}{dh} \neq 0 \) at \((\bar{x}, \bar{y}, \bar{z}, \bar{h})\), where \( \sigma \) is the real part of the pair of eigenvalues with singular imaginary parts of the linearization of system (12) at the equilibrium.
Theorem 5.1. Under conditions (P1)-(P6), system (12) can be written in the normal form:

\[
\begin{aligned}
\frac{du}{dt} &= v + \frac{u^2}{2} \beta u + \delta F(u, w, \alpha) + O(\delta^2) \\
\frac{dv}{dt} &= -u + O(\delta^2) \\
\frac{dw}{dt} &= \delta H(u, w) + O(\delta^2)
\end{aligned}
\]

with \( \delta = O(\sqrt{\zeta}) \) and \( \tau = s/\delta \). The functions \( F \) and \( H \) have the structures

\[
F(u, w, \alpha) = \alpha u + F_{uw}uw + \frac{1}{6}F_{uuu}u^3, \quad H(u, w) = H_{ww} + \frac{1}{2}H_{uu}u^2,
\]

where

\[
\begin{align*}
\delta &= \frac{\sqrt{\zeta}}{\omega}, \\
F_{uw} &= \frac{\alpha_{12}\bar{y}\bar{u}}{\beta_2 + \bar{x}} + \frac{\alpha_{21}\bar{u}}{\beta_1 + \bar{x}} + \frac{\alpha_{21}\bar{u}\bar{z}(\beta_1 + \bar{x})}{(\beta_2 + \bar{x})^2} + \frac{(\beta_2 - \beta_1)\bar{u}^2}{2(\beta_1 + \bar{x})(\beta_2 + \bar{x})^2} + \frac{\beta_1\bar{u}^2}{(\beta_1 + \bar{x})^2} - \frac{\beta_2\bar{u}^2}{(\beta_2 + \bar{x})^2}, \\
F_{uuu} &= \frac{1}{\omega^2}\left(\frac{\alpha_{12}\bar{y}\bar{u}}{\beta_1 + \bar{x}}\right) + \frac{\alpha_{21}\bar{z}(\beta_1 + \bar{x})}{(\beta_2 + \bar{x})^2} + \frac{h\beta_2\bar{u}^2}{(\beta_2 + \bar{x})^2} - \frac{3w^2}{2\bar{u}^2} + \frac{\beta_1\bar{u}^2}{(\beta_1 + \bar{x})^2} - \frac{\beta_2\bar{u}^2}{(\beta_2 + \bar{x})^2}, \\
H_{ww} &= \frac{\alpha_{12}\bar{y}\bar{u}}{\omega^2(\beta_1 + \bar{x})(\beta_2 + \bar{x})} + \frac{(\beta_1\bar{z} + \bar{y})}{(\beta_1 + \bar{x})^2} + \frac{1}{\omega^2} - \frac{\beta_2\bar{u}^2}{(\beta_2 + \bar{x})^2}, \\
H_{uu} &= \frac{1}{\omega^2}\left(\frac{\beta_1\bar{y}}{\beta_1 + \bar{x}}\right) + \frac{\beta_2\bar{u}^2}{\omega^2(\beta_2 + \bar{x})^2}, \\
\alpha &= \frac{2\bar{u}(\beta_2 + \bar{x})}{\omega^3(\beta_1 + \bar{x})(\beta_2 + \bar{x})^2} - \frac{\alpha_{12}\bar{y}\bar{u}}{\beta_1 + \bar{x}} + \frac{\alpha_{21}\bar{z}(\beta_1 + \bar{x})}{(\beta_2 + \bar{x})^2} + \frac{h\beta_2\bar{u}^2}{(\beta_2 + \bar{x})^2}.
\end{align*}
\]

The quantity \( H_{ww} \) is invertible which allows a further reduction of system (13) using center manifold theory. The normal form is valid for \((x, y, z, h) = (\bar{x} + O(\sqrt{\zeta}), \bar{y} + O(\zeta), \bar{z} + O(\zeta), \bar{h} + O(\zeta))\).

We refer to the work of Braaksma in [4] for the detailed proof.

Remark 5.1. The normal form (13) can be linearly decoupled as \((u, v)\) and \(w\) subsystems as \( \delta \rightarrow 0 \), which provides a proper framework to study further bifurcations of suitable Poincaré maps. The parameter \( \alpha \) determines the linear behavior of the \((u, v)\) subsystem and the quantity \( H_{ww} \) of the \( w \)-subsystem. The nonlinear stability of the \((u, v)\) subsystem
is governed by $F_{uuu}$, which can give rise to a global return mechanism. The other two coefficients $F_{uw}$ and $H_{uu}$ represent the coupling strengths.

**Remark 5.2.** Ignoring higher order terms, the normal form (13) agrees with the rescaled canonical form of FSN II singularity as in [24, 26]. Hence, the analysis in [24, 26] can be extended to derive asymptotic formulae for the return map induced by the corresponding flow and obtain results on Farey sequences of the resulting MMO orbits. We leave this for future work.

Condition (P3) is related to proving invertibility of $H_w$. In fact, it turns out that (see [4] for details)

$$H_w = \frac{1}{\omega^2} \det J,$$

which is nonzero by assumption (P3). Expressing (P3) in terms of $(\bar{x}, \bar{y}, \bar{z}, \bar{h})$, yields

$$\frac{\bar{x}\bar{y}\bar{z}}{(\beta_1 + \bar{x})(\beta_2 + \bar{x})} \left( \frac{\alpha_{21}\beta_1}{\beta_1 + \bar{x}} + \frac{\alpha_{12}\beta_2}{\beta_2 + \bar{x}} - \frac{\beta_1\bar{h}(\beta_2 + \bar{x})}{(\beta_1 + \bar{x})^2} \right) \neq 0,$$

where $\bar{x}$ is a solution to the equation

$$\alpha_{12}(1 - \beta_1 - 2\bar{x})(\beta_1 + \bar{x})(\beta_2 + \bar{x})^2 + (\beta_2 - \beta_1)(1 - c)\bar{x} + (\beta_2 - \beta_1)c\beta_1 = 0 \quad (15)$$

with

$$\frac{1 - \max\{\beta_1, \beta_2\}}{2} < \bar{x} < \frac{1 - \min\{\beta_1, \beta_2\}}{2},$$

provided $\beta_1 \neq \beta_2$.

Furthermore, $\bar{h}$ can be expressed in terms of $\bar{x}$, namely,

$$\bar{h} = \frac{(\beta_2 - \beta_1)(\frac{\bar{x}}{\beta_2 + \bar{x}} - d) + \alpha_{21}(1 - \beta_2 - 2\bar{x})(\beta_1 + \bar{x})^2}{(1 - \beta_1 - 2\bar{x})(\beta_2 + \bar{x})^2}. \quad (16)$$

Note that for $\beta_1 \neq \beta_2$, (15) is a polynomial of 4th degree, not factorable, and so we cannot solve for $\bar{x}$ analytically, and hence computing $\bar{h}$ explicitly remains challenging. However, we can do a lot more for the special cases described below.

### 5.1. Special Cases

**Equal predation efficiencies:** When $\beta_1 = \beta_2$, one can solve for $\bar{h}$ in terms of the other parameters and can compute $(\bar{x}, \bar{y}, \bar{z})$. In this case,

$$\bar{h} = \frac{4\left[(\alpha_{12} + \alpha_{21})(1 - \beta_1) - (c\alpha_{21} + d\alpha_{12})(1 + \beta_1)\right]}{4(1 - \beta_1 - c(1 + \beta_1))},$$

where $\alpha_{12}, \alpha_{21}, c, d$ are free parameters that satisfy (17)-(18) below:

$$\alpha_{12}(1 + \beta_1)^2 > 4\left(\frac{1 - \beta_1}{1 + \beta_1} - c\right) > 0 \quad (17)$$

$$\alpha_{21}(1 + \beta_1)^2 - 4(\beta_1 - c) \neq 0. \quad (18)$$
Furthermore, 
\[ \bar{x} = \frac{1 - \beta_1}{2}, \]
\[ \bar{y} = \frac{\alpha_{12}(1 + \beta_1)^3 - 4(1 - \beta_1) + 4c(1 + \beta_1)}{4\alpha_{12}(1 + \beta_1)}, \]
\[ \bar{z} = \frac{1 - \beta_1 - c(1 + \beta_1)}{\alpha_{12}(1 + \beta_1)}. \]

For biological significance, in addition to (17)-(18) we will choose \( \alpha_{12}, \alpha_{21}, c, d \) so that the expression in the numerator of \( \bar{h} \) is positive, i.e.
\[ 4 \left[ (\alpha_{12} + \alpha_{21})(1 - \beta_1) - (c\alpha_{21} + d\alpha_{12})(1 + \beta_1) \right] > \alpha_{12}\alpha_{21}(1 + \beta_1)^3. \]

No exclusive competition: Assuming that the predators do not exhibit interference competition, i.e. \( \alpha_{12} = \alpha_{21} = 0 \), one can explicitly solve for \((\bar{x}, \bar{y}, \bar{z}, \bar{h})\), namely,
\[ \bar{x} = \frac{c\beta_1}{1 - c}, \]
\[ \bar{y} = \frac{\beta_1^2}{(1 - c)^3(\beta_1 - \beta_2)}((1 - c)(1 - \beta_2) - 2c\beta_1), \]
\[ \bar{z} = \frac{(c\beta_1 + \beta_2(1 - c))^2}{(1 - c)^3(\beta_2 - \beta_1)}((1 - c) - \beta_1(1 + c)) \]
with
\[ \bar{h} = \frac{(\beta_2 - \beta_1)((\frac{\bar{x}}{\beta_2 + \bar{x}}) - d)}{(1 - \beta_1 - 2\bar{x})(\beta_2 + \bar{x})^2}. \]

5.2. Hopf bifurcation analysis. Since system (12) has a FSN II point at \((\bar{x}, \bar{y}, \bar{z}, \bar{h})\), we expect to have a Hopf bifurcation at an \( O(\zeta) \) distance away from \( \bar{h} \) as well as from \((\bar{x}, \bar{y}, \bar{z})\). In fact, we will show that the Hopf bifurcation occurs at \( \bar{h} + \zeta + O(\zeta^3/2) \). Since \( H_w \neq 0 \), the nonhyperbolic \((u, v)\) part and the hyperbolic \( w \) part in system (13) are linearly decoupled, and hence one can further perform a center manifold reduction. The center manifold [17, 28] can be expressed as a graph
\[ w = \phi(u, v, \delta) = \frac{1}{2}\phi_{uu}u^2 + \phi_{uv}uv + \frac{1}{2}\phi_{vv}v^2 + O(3) + \delta(\frac{1}{2}\phi_{uu}u^2 + \phi_{uv}uv + \frac{1}{2}\phi_{vv}v^2 + O(3)) + O(\delta^2), \]
where \( O(3) \) represents cubic and higher-order terms in \( u \) and \( v \). The function \( \phi \) can be determined by solving the equation \( \frac{d\phi}{dv} = \delta(H_w \phi + \frac{1}{2}H_{uu}u^2) + O(\delta^2) \). Using the equation for \( w \) and the above equation and equating the coefficients of like terms, (see [1] for details) one obtains that
\[ w = \phi(u, v, \delta) = -\frac{H_{uu}}{4H_w}(u^2 + v^2) + O(3) + O(\delta). \]
The corresponding equations in the center manifold up to higher order terms are

\[
\begin{aligned}
\frac{du}{d\tau} &= v + \frac{u^2}{2} + \delta \left( \alpha u + \left( -\frac{F_{uu} H_{uu}}{4H_w} + \frac{1}{6} F_{uuu} \right) u^3 - \frac{F_{uu} H_{uu}}{4H_w} u v^2 \right) \\
\frac{dv}{d\tau} &= -u \\
\frac{dw}{d\tau} &= 0
\end{aligned}
\]  

(20)

It is clear from the governing equations of the two-dimensional center manifold that the equilibrium \((0, 0, \phi(0, 0, \delta))\) (up to higher order terms) is asymptotically stable if and only if \(\alpha < 0\), where \(\alpha\) is given by (14). A Hopf bifurcation occurs at \(\alpha = 0\) and the first Lyapunov coefficient \([17, 28]\) is

\[l_1(0) = \frac{\delta}{4} \left( \frac{1}{2} F_{uuu} - \frac{F_{uu} H_{uu}}{H_w} \right).\]

Combining the above derivation along with Theorem 1 results into the following theorem:

**Theorem 5.2.** Consider system (12) satisfying the assumptions (P1)-(P6) of Theorem 1. Then system (12) undergoes a Hopf bifurcation at \(h = \bar{h} + \zeta A + O(\zeta^{3/2})\), where \(A\) is the solution of the equation

\[
\bar{x} \bar{z} \left[ -2\alpha_{12} \left( \frac{\bar{y}}{(\bar{y} + \bar{x})^2 + \bar{z}} + \frac{\bar{z}}{(\bar{y} + \bar{x})^2 + \bar{z}} \right) + \frac{\beta_1 (\beta_1 - \beta_2)}{(\bar{y} + \bar{x})^2 (\bar{y} + \bar{x})^3} \right] A
\]

\[= \frac{1}{\omega^2} \left( \frac{\alpha_{12} \beta_2 \bar{z}^2 \bar{y}^2}{(\bar{y} + \bar{x})^2 (\bar{y} + \bar{x})^2} + \frac{\alpha_{21} \beta_1 \bar{z} \bar{y}^2}{(\bar{y} + \bar{x})^2 (\bar{y} + \bar{x})^2} + \frac{h \delta_2 \bar{z}^2}{(\bar{y} + \bar{x})^2} \right)
\]

for sufficiently small \(\zeta > 0\). The Hopf bifurcation is super(sub)critical if

\[\frac{1}{2} F_{uuu} - \frac{F_{uu} H_{uu}}{H_w} < (> 0).\]

**Remark 5.3.** (a) For \(\delta = 0\), system (13) reduces to

\[
\begin{aligned}
\frac{du}{d\tau} &= v + \frac{u^2}{2} \\
\frac{dv}{d\tau} &= -u \\
\frac{dw}{d\tau} &= 0
\end{aligned}
\]  

(21)

which is integrable. For each fixed \(w\), system (13) admits a family of closed orbits given by

\[u^2 + 2v - 2)e^v = -k,\]

for \(0 < k < 2\). The periodic orbits approach the fixed point \((0, 0)\) as \(k \to 2\) and grow in size as \(k \to 0\). The level curve \(k = 0\) separates periodic orbits surrounding \((0, 0)\) from orbits that get unbounded with \(u \to \pm \infty\) in finite time. The unbounded orbits lie above the parabola \(v = 1 - u^2/2\). For \(\delta > 0\) sufficiently small, system (13) can be viewed as a perturbation of (21) and its dynamics are typically referred to as “near-integrable” \([24]\). In context of slow-fast systems, system (21) is the two-dimensional layer problem of (13) in which \(w\) acts as a parameter.
(b) For each fixed \(w\), system (21) is a particular case of the parametrized system

\[
\begin{align*}
\frac{du}{d\tau} &= v + \frac{w^2}{2}, \\
\frac{dv}{d\tau} &= -u + \lambda,
\end{align*}
\]

(23) corresponding to the parameter \(\lambda = 0\). System (23) is a prototypical system for the occurrence of a canard explosion [25] at \(\lambda = 0\).

(c) The invariant curve \(k = 0\) in (22) is a special solution of (21), which is also referred to as a “singular canard solution” in [24].

The eigenvalues of the variational matrix of (13) at the equilibrium \(p_e = (0, 0, 0)\) up to higher order terms are

\[
\lambda_1 = \delta H_w, \quad \lambda_{2,3} = \frac{1}{2} \left[ \alpha \delta \pm \sqrt{\alpha^2 \delta^2 - 4} \right].
\]

If \(H_w < 0\), then the equilibrium is a stable node or a stable spiral for \(\alpha < 0\), while it is a saddle-focus for \(0 < \alpha < 2/\delta\). For \(0 < \alpha < 2/\delta\), the flow generated by (13) linearized about the origin is given by

\[
\begin{align*}
u(\tau) &= e^{\frac{\alpha \delta}{2} \tau} \left[ u_0 \cos(\omega \tau) + \left( \frac{v_0}{\omega} + \frac{\alpha \delta u_0}{2 \omega} \right) \sin(\omega \tau) \right], \\
v(\tau) &= -\frac{\alpha \delta}{2} u(\tau) + e^{\frac{\alpha \delta}{2} \tau} \left[ \left( \frac{v_0}{\omega} + \frac{\alpha \delta u_0}{2 \omega} \right) \cos(\omega \tau) - \omega u_0 \sin(\omega \tau) \right], \\
w(\tau) &= w_0 e^{\delta H_w \tau},
\end{align*}
\]

(25) where \(\omega = \sqrt{1 - \frac{\alpha^2 \delta^2}{4}}\) and \((u(0), v(0), w(0)) = (u_0, v_0, w_0)\). When the equilibrium is a saddle-focus, the \(w\)-axis forms the one-dimensional stable manifold of the equilibrium, which we denote by \(W^s(p_e)\), and the two-dimensional unstable manifold \(W^u(p_e)\) is tangential to the \(w\)-plane. A trajectory that approaches \(p_e\) must spiral along the \(w\)-axis with the flow approximated by (25). A trajectory that leaves a neighborhood of \(p_e\) spirals out along the two-dimensional unstable manifold \(W^u(p_e)\), where the flow is roughly estimated by

\[
\begin{align*}
u(\tau) &= e^{\frac{\alpha \delta}{2} (\tau - \tau_1)} \left[ \tilde{u}_0 \cos(\omega (\tau - \tau_1)) + \left( \frac{\tilde{v}_0}{\omega} + \frac{\alpha \delta \tilde{u}_0}{2 \omega} \right) \sin(\omega (\tau - \tau_1)) \right], \\
v(\tau) &= -\frac{\alpha \delta}{2} u(\tau) + e^{\frac{\alpha \delta}{2} (\tau - \tau_1)} \left[ \left( \frac{\tilde{v}_0}{\omega} + \frac{\alpha \delta \tilde{u}_0}{2 \omega} \right) \cos(\omega (\tau - \tau_1)) - \omega \tilde{u}_0 \sin(\omega (\tau - \tau_1)) \right], \\
w(\tau) &= w_0 e^{\delta H_w \tau} + \frac{\delta H_{uw} e^{\delta H_w \tau}}{2(\alpha \delta - \delta H_w)} \left[ c(\alpha \delta - \delta H_w) \tau - c(\alpha \delta - \delta H_w) \tau_1 \right],
\end{align*}
\]

(26) for \(\tau \geq \tau_1\) with \((u(\tau_1), v(\tau_1), w(\tau_1)) = (\tilde{u}_0, \tilde{v}_0, w_0 e^{\delta H_w \tau_1})\).

Note that \(W^s(p_e)\) also forms the critical manifold of (13) and the reduced flow is governed by the equation \(dw/d\tau = \delta H_u w\). Hence for \(\delta\) sufficiently small, the slow flow occurs in a thin tubular neighborhood around the \(w\)-axis. The fast flow is governed by the layer problem (21) which is integrable, and has a continuous family of periodic solutions (22). A concatenation of the slow and the fast flow along with a global return mechanism can give rise to MMOs in system (13). As stated in Remark 5.3, the invariant curve corresponding to \(k = 0\) in (22) also referred to as a “singular canard solution”, separates the closed curves.
obtained for \( k > 0 \) from the open ones that correspond to \( k < 0 \). The SAOs in an MMO orbit observed in (13) is due to the fact that the system passes slowly through a canard point located about the origin in \((u, v, w)\) phase space. The LAO components of the MMO dynamics are generated by the global return mechanism, which takes trajectories back to the \( w \)-axis after the passage past the origin is completed. As \( \delta \to 0 \), the small-amplitude oscillations of the MMO dynamics turn out to be close to the closed curves of (21). If \( k > 0 \), the corresponding trajectory of (13) will remain in the small-oscillation regime and undergo another loop. However, if \( k < 0 \), the trajectory will exit the small-oscillation regime and undergo relaxation. Combining the local aspects of the dynamics along with the global return mechanism, we obtain MMOs in system (13).

Remark 5.4. The loss of stability of a Shil’nikov orbit can give rise to MMOs in slow-fast systems. We note that system (13) possess a Shil’nikov type equilibrium, i.e. an equilibrium of saddle-type with one dimensional stable manifold and two-dimensional unstable manifold of a spiral-focus type. For some value of \( \alpha \), it is possible that there exists a connection to the saddle-focus equilibrium (Shil’nikov orbit). A homoclinic bifurcation of a Shil’nikov orbit can give rise to complicated, chaotic dynamics. Since the Shil’nikov type equilibra are naturally present in canard-based systems that involve FSN II, we propose that the normal form (13) realizes a “suitably modified” Shil’nikov mechanism.

6. Numerical analysis of the normal form for varying predation efficiencies.

In this section, we numerically study the dynamics of system (13) in a parameter regime close to the Hopf bifurcation. The characteristic features of the MMOs are also studied as the predation efficiency of \( y \) is varied.

6.1. Analysis of (13) with \( \beta_1 < \beta_2 \). This corresponds to the situation when \( z \) is more efficient than \( y \) as a predator. We will use the normal form (13) to study the dynamics of system (4) near the singular Hopf bifurcation. To this end, we fix the parameter values to \( \beta_1 = 0.25, \beta_2 = 0.35, \ c = 0.4, \ d = 0.21, \alpha_{12} = 0.5, \alpha_{21} = 0.1 \) and treat \( h \) (and hence \( \alpha \)) as our varying parameter. In the singular limit of system (4), the singular Hopf point \((\bar{x}, \bar{y}, \bar{z})\) has coordinates \( \approx (0.3381, 0.0903, 0.3497) \) and FSN II bifurcation occurs at \( \bar{h} \approx 0.7785 \). The quantity \( \delta \) and the functions \( F(u, w) \) and \( H(u, w) \) in the normal form (13) can be explicitly written by using (14). Consequently,

\[
\delta \approx 2.4649\sqrt{\zeta}, \quad F_{uw} \approx 0.16454, \quad F_{uuu} \approx -0.6833, \quad H_w \approx -0.0145, \quad H_{uu} \approx -0.065068.
\]

The relation between \( \alpha \) and \( h \) is given by

\[
\alpha = \frac{1.5996(h - \bar{h})}{\zeta} - 0.25779.
\]

To study the dynamics near the singular Hopf bifurcation, \( \zeta \) must be chosen sufficiently small. In the original model (4), the analysis was performed for \( \zeta = 0.01 \). Here we choose
\(\zeta = 0.001\) to obtain a better approximation to the singular limit. However, all the findings that we obtain for smaller values of \(\zeta\) also hold for \(\zeta = 0.01\).

Choosing \(\zeta = 0.001\) yields \(\delta \approx 0.078\) and \(\alpha = 1599.63h - 1245.62\). For the set of parameter values in (27), we note from (24) that the eigenvalues of the variational matrix of system (13) at the equilibrium \(p_e = (0,0,0)\) (which corresponds to the positive equilibrium of system (4)) are \(\lambda_1 \approx -0.0011\) and that \(\text{Re}(\lambda_{2,3}) < 0\) if \(\alpha < 0\) and \(\text{Re}(\lambda_{2,3}) > 0\) if \(0 < \alpha < 25.65\). System (13) undergoes a Hopf bifurcation at \(\alpha = \alpha_H = 0\) (which corresponds to \(h_H \approx 0.7787\) in system (4)). By Theorem 5.2, the Hopf bifurcation is supercritical since the first Lyapunov coefficient \(l_1(0) \approx -0.0211 < 0\). Consequently, a family of stable periodic orbits \(\Gamma_\alpha\) is born at \(\alpha_H\). The periodic orbits exhibit SAOs and persist for \(\alpha > \alpha_H\), provided that \(\alpha\) lies in a small neighborhood of \(\alpha_H\).

For parameter values just past the Hopf bifurcation, \(\Gamma_\alpha\) lies in a vicinity of the unstable manifold \(W^u(p_e)\) and therefore most trajectories on \(W^u(p_e)\) converge to \(\Gamma_\alpha\) as \(\tau \to \infty\). The stable periodic orbit \(\Gamma_\alpha\) forms a boundary of \(W^u(p_e)\) (see figure 14(A)). Figure 14(B) shows a zoomed view of the trajectory that lies in the basin of attraction of \(\Gamma_\alpha\) near \(p_e\). We observe that the trajectory approaches \(p_e\) along \(W^s(p_e)\) and gets repelled along \(W^u(p_e)\), where it spirals out in the downward direction until it gets trapped in the stable manifold \(W^s(\Gamma_\alpha)\) as shown in figure 14(C). The phase portrait of \(\Gamma_\alpha\) is shown in figure 14(D).

As \(\alpha\) increases, the distance between \(W^s(p_e)\) and \(p_e\) increases, allowing the possibility of more complex dynamics. Indeed, at \(\alpha = 0.46126\) \((h = 0.77898)\), a trajectory displaying MMOs that passes close to the equilibrium \(p_e\) is observed. It approaches \(p_e\) along \(W^s(p_e)\) (in the slow direction) and spirals away from \(p_e\) along the unstable manifold \(W^u(p_e)\), where the flows are respectively given by (25)-(26). A global return mechanism, which occurs along the fast direction, then brings back the trajectory to a small neighborhood of \(W^s(p_e)\) as shown in figure 15(A). We note that the stable periodic orbit \(\Gamma_\alpha\) still exists as an attractor at this parameter value. Indeed, the two attractors are shown in figure 15(A)-(B), demonstrating bistability in system (12). The basin of attraction of \(\Gamma_\alpha\) dominates a significant portion of the phase space. Also, we note that \(W^s(\Gamma_\alpha)\) lies very close to \(W^s(p_e)\) as shown in figure 15(D). The SAOs associated with the MMO attractor are too small to be detectable and grow arbitrarily slowly as the trajectory approaches \(p_e\) (see figure 16), which causes extraordinary long epochs. The eigenvalue \(\lambda_1 \approx \delta_{H_w}\) measures the rate of contraction as the trajectory approaches the equilibrium along the slow direction \(w\) such that \(|w| \sim e^{\delta_{H_w} \tau}\) for \(\tau > 0\). The long epochs are due to the exponential contraction towards the fixed point as seen in the time-series of \(w\) in figure 16. After approaching \(p_e\), the trajectory slowly spirals away with oscillations of increasing magnitude, which roughly occur along the closed curves of (21) with decreasing \(w\). If for a certain value of \(w\), the trajectory while spiraling out crosses the level curve \(k = 0\) of (21), then it leaves the small oscillation regime and undergoes relaxation dynamics (see figure 15(B)).

To analyze the nature of the MMO orbit, a section transverse to the trajectory is considered at \(\{(u,v,w) : u = 15\}\). The intersection of the trajectory with this plane in the increasing direction of \(u\) is recorded for 5000 times. The resulting Poincaré section and the first return map is shown in figure 17. The Poincaré section indicates that the MMO orbit
is mildly chaotic. The occurrence of this characteristic pattern of the orbit, namely spiraling around the saddle-focus with long epochs of SAOs does not rule out the possibility of a Shil’nikov saddle-focus homoclinic bifurcation in a nearby parameter regime. Bifurcations of a homoclinic loop of the Shil’nikov saddle-focus can lead to birth of stable periodic orbits and other hyperbolic sets. The ratio $\nu_0 = |Re(\lambda_{2,3})/\lambda_1|$ determines whether the homoclinic bifurcation yields a unique stable MMO periodic orbit or infinitely many saddle periodic orbits which may lead to existence of chaotic invariant sets [17, 28, 44]. These stable orbits are hardly indistinguishable within chaotic attractors because they have long periods and thin attraction basins [2]. The Shil’nikov condition is satisfied if $\nu_0 < 1$. In system (13),
Figure 15. (A): Phase portrait of the two attractors: an aperiodic MMO (orange) which is very “thin” and the periodic orbit $\Gamma_\alpha$ (blue) for $\alpha = 0.4613$ ($h = 0.77898$), $\zeta = 0.001$ and the other parameter values as in [27], indicating presence of bistability in system [13]. (B): A zoomed view of the attractors near the origin projected on the $uv$-plane. (c) A trajectory (green) approaching $\Gamma_\alpha$ (blue) asymptotically. (D): The green trajectory lies in the basin of attraction of $\Gamma_\alpha$, and the cyan trajectory lies in the basin of attraction of the MMO attractor. Note a similarity in the dynamics of the two trajectories.

$p_e$ satisfies the Shil’nikov condition if $0 < \alpha < -2H_w \approx 0.029$. For $\alpha$ in this regime, the periodic orbit $\Gamma_\alpha$ lies in a vicinity of the origin, and its basin of attraction dominates a large portion of the phase space, which makes it challenging to locate any other attractors.
Figure 16. Time series of $u$ and $w$ in system \([12]\) corresponding to the MMO trajectory of figure \([15]\). (b1) is a zoomed view of the time series of $u$ preceding and proceeding a spike, and (b2) is a further zoomed view of the time series of $u$ preceding a spike.

Figure 17. (A): Intersection of the MMO trajectory of figure \([15]\) with the plane $u = 15$ with $\frac{du}{d\tau} > 0$. (B) The first return map of $v$ plotted against its initial value suggesting chaotic dynamics. The plots also suggest that the MMO attractor is “thin”.

that may pass close to the origin (cf figure 14(A)-(C)). To exactly determine whether a homoclinic orbit to the saddle-focus equilibrium \( p_e \) exists, remains for future work.

6.2. Analysis of (13) with \( \beta_1 > \beta_2 \). We next let \( \beta_1 = 0.4 \) and adhere to the other parameter values as in (27). The singular Hopf point \((\bar{x}, \bar{y}, \bar{z})\) has coordinates approximately given by \((0.30369, 0.42201, 0.06314)\) and occurs at \( \bar{h} \approx 3.36351 \). Using (14), we obtain that

\[
\delta \approx 2.4172 \sqrt{\zeta}, \quad F_{uw} \approx 0.17667, \quad F_{uuu} \approx -1.22696, \quad H_w \approx -0.1492, \quad H_{uu} \approx -0.0466,
\]

\[
\alpha = \frac{0.01125(h - \bar{h})}{\zeta} - 0.06318.
\]

We first choose \( \zeta = 0.01 \). In this case, a supercritical Hopf bifurcation of the equilibrium \( p_e \) occurs at \( \alpha_H = 0 \). Periodic orbits \( \Gamma_\alpha \) with SAOs are born and these orbits grow in size to LAOs with increasing values of \( \alpha \). MMOs are not observed here, and this is consistent with our findings in Section 4.1. Though, for \( \alpha > \alpha_H \), the equilibrium is saddle-focus with one dimensional stable manifold and two-dimensional unstable manifold, there does not exist a return mechanism that brings a trajectory back to the neighborhood of \( p_e \) along \( W^s(p_e) \).

**Figure 18.** (A): Phase portrait of an MMO orbit of signature \( 1^{14} \) of system (13) for \( \alpha \approx 1.022 \ (h = 3.46), \delta \approx 0.0764 \ (\zeta = 0.001), \beta_1 = 0.4 \) and the other parameter values as in (27). (B): Corresponding time series in \( u \). The inner panel is a zoomed view between two spikes.

Next, we let \( \zeta = 0.001 \). In this case, MMOs are not observed immediately after the Hopf bifurcation, but they are observed as \( \alpha \) gets larger. Figure 18 shows an MMO orbit of signature \( 1^{14} \) at \( \alpha \approx 1.022 \ (h = 3.46) \). The time series shows that the period between the LAOs is roughly \( k/\delta \), where \( k \) is the number of SAOs between two LAOs. The amplitude of the SAOs remain observably large. In context of systems with at least two fast variables, a local mechanism termed tourbillon [49] is used to describe the SAOs whose amplitudes
remain above an observable threshold as the trajectory passes through a dynamic Hopf bifurcation [12]. The SAOs obtained here can possibly be associated with the tourbillon mechanism, but we leave this for future work.

6.3. Analysis of (13) with $\beta_1 = \beta_2$. We finally let $\beta_1 = \beta_2 = 0.35$ and adhere to the other parameter values as in (27). The singular Hopf point $(\bar{x}, \bar{y}, \bar{z})$ has coordinates approximately given by $(0.325, 0.29266, 0.16296)$. Using (14), we obtain that

$$\delta \approx 2.43599 \sqrt{\zeta}, \quad F_{uw} \approx 0.1792, \quad F_{uuu} \approx -0.9275, \quad H_w \approx -0.09278,$$

$$H_{uu} \approx -0.09066, \quad \alpha = \frac{0.115244(h - \bar{h})}{\zeta} - 0.14944$$

where $\bar{h} \approx 1.48632$. The system admits MMOs for $\zeta = 0.01$, though the MMOs are not observed immediately after Hopf bifurcation.

7. Discussion

In this paper, we used singular perturbation theory, normal form reduction, theory of canards and numerical simulations to study the mechanism for the formation of MMOs in a predator-prey model with intraspecific and interspecific competition between the predators. The model studied involves interaction between three species in a constant environment with two time-scales and has the potential to mimic natural population fluctuations. The presence of nonlinear interaction terms in the form of intraspecific competition and the nonlinear functional responses of the predators are keys to the observed complex dynamics. The formation of MMOs in slow-fast systems in three or higher dimensions is a robust phenomenon. In three dimensions, these complex oscillatory dynamics exist in a wide parameter regime, however in this paper, we focused our analysis near an FSN II singularity, equivalent to a singular-Hopf point.

The dynamics near the FSN II singularity are complex and rich. The presence of a folded node singularity in vicinity of an unstable equilibrium of saddle-focus type gives rise to complexities. The folded node allows certain trajectories on the attracting slow manifold to cross into the repelling slow manifold by creating a funnel. The passage through the funnel induces SAOs in MMOs. Moreover, the proximity of the stable manifold of the saddle-focus equilibrium to the primary weak canard brings a trajectory close to a neighborhood of the equilibrium. As a result, trajectories follow the unstable manifold of the equilibrium leading to additional small rotations before jumping to the other attracting branch of the slow manifold. Similar dynamics were observed in [3], where the interaction between canard-induced dynamics and dynamics induced by a saddle-focus equilibrium was performed. In the model studied in this article, the time series of a typical MMO trajectory in the FSN II regime is aperiodic and have long epochs of SAOs. The prolonged quiescence between the spikes represents the adaptability of a species to the environment as their population density mildly fluctuates around the equilibrium. The aperiodicity in the time series reflects the uncertainty of occurrence of a large fluctuation.

In addition to existence of aperiodic MMO orbits, periodic attractors with small amplitude oscillations are also observed near the FSN II singularity. This occurs because the
system undergoes a supercritical Hopf bifurcation in an $O(\zeta)$ neighborhood of the FSN II point. Indeed, the system exhibits bistability in a parameter regime adjacent to the Hopf bifurcation, where the small amplitude periodic orbit and an aperiodic MMO orbit coexist as stable attractors. The interaction between the stable manifold of the limit cycle with the unstable manifold of the saddle-focus equilibrium and the repelling slow manifold governs the dynamics in this regime. The basins of attraction of the two attractors form complicated structures in phase space, and a small perturbation can lead to transition from one attractor to the other. Ecologically, this may be helpful to control population outbreaks, as an external intervention can shift the dynamics from an excited state to a more stable state.

Reducing the model to normal form near FSN II bifurcation sheds light on the generalized canard phenomenon as a mechanism responsible for MMOs in our model. The SAOs in the MMO dynamics arise due to passage through a canard point while the LAOs in the corresponding MMO time series are generated by a global return mechanism. The normal form obtained also realizes a “suitably modified” Shil'nikov mechanism. The detection of trajectories with extraordinarily large number of small oscillations between large amplitude oscillations and a chaotic return map suggests that the trajectory possibly lies in a small neighborhood of a Shil'nikov homoclinic orbit. Loss of stability (homoclinic bifurcation) of a Shil'nikov orbit can give rise to MMOs. Such a generic bifurcation requires no special properties of the system and often appears in slow-fast systems [12, 47]. Shil'nikov homoclinic orbits are limits of families of MMOs with an unbounded number of small oscillations in their signatures. The dynamics of the derived normal form is consistent with the dynamics of the full system near the singular Hopf bifurcation. For example, the existence of bistability, the long epochs of SAOs with unbounded number of oscillations in their MMO signatures have been observed in system (4) as well as in system (13) adjacent to the Hopf point.

The Koper model [21] and a reduced form of the Hodgkin-Huxley model [12] are amongst the few examples of one-fast and two-slow systems where a detailed analysis has been carried out near the FSN II points. Further analysis has been done on the Koper model to study the existence of a homoclinic orbit. However, the model in this paper is much more complicated to work because of several nonlinear interaction terms. Reducing the model to a normal form near the FSN II point involved several technicalities with long calculations. Explicitly detecting a homoclinic orbit to the saddle-focus equilibrium using the normal form remains for future study.

Though the main analysis in this work has been carried out by treating the strength of intraspecific competition between the second species of the predators as the input parameter, it is clear that the singular parameter measuring the ratios of the birth rates of the predators to the prey, the predation efficiencies and the strengths of interference competition between the predators played significant roles in governing the dynamics. As a demonstration, we studied the effect of varying predation efficiency of one of the species of predators in the system. It turns out that the structure of the slow manifold, which can organize the behavior of a dynamical system, varies with the predation efficiencies and the singular parameter. In fact, the occurrence (or absence) of MMOs and hence formation
of canards depends on the twisting properties of the attracting and repelling branches of the slow manifold. Furthermore, co-dimension 2 bifurcations such as zero-Hopf also occurs, which in turn can serve as an organizing center for Shil’nikov homoclinic bifurcation. Hence in an ecological setting, one may observe a variety of dynamics as a function of these parameters. It will be interesting to study the zero-Hopf regime in details, and we leave this for future work.

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Remark 8.1. Most of the numerical simulations in this paper were done in MATLAB. We used the predefined routine ODE45 with relative and absolute error tolerances $10^{-11}$ and $10^{-12}$ respectively.

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