Modelling, Dynamics and Analysis of Multi-Species Systems with Prey Refuge

By

Shireen Jawad

A Thesis Submitted in Partial Fulfilment of the Requirements

for the Degree of Doctor of Philosophy

Supervised By: Dr. Matthias Winter

Department of Mathematics

College of Engineering, Design and Physical Sciences

Brunel University London

May 2018

Dedication

I dedicate this thesis to:

- ♡ **God, who has given me the power to believe in myself and thus, to pursue my dreams. Without faith I have in you and your blessings, this work would never have been done;**
- ♡ **All who have helped to make me the strong person that I have become.**

ACKNOWLEDGMENTS

Dr Matthias Winter, I cannot thank you enough for your unlimited support, helpful advice, continuous guidance and useful comments. For, without your valuable suggestions, this work has not been completed in such a timely manner. Also, my profound gratitude goes to, the Iraqi Ministry of Higher Education and Scientific Research and the Iraqi Cultural Attaché in London, for being the sponsors of this study. Finally, my warm thanks go to all my family and friends in Iraq and the UK, who have provided moral support during my study journey. To all of you, thank you for everything.

TABLE OF CONTENTS

Page

LIST OF FIGURES x

SYMBOLS xiv

1 Introduction 1

- 1.1 Background 1
- 1.2 Problem statement and motivations 4
- 1.3 Thesis aim and objectives 5
- 1.4 Thesis overview 6

2 Background 9

- 2.1 Introduction 9
- 2.2 Qualitative behaviour in the nonlinear dynamical system 9
- 2.3 Mathematical tools 10
  - 2.3.1 Local stability analysis 10
  - 2.3.2 Routh-Hurwitz criterion 12
  - 2.3.3 Local stable and unstable manifold 14
  - 2.3.4 Hartman-Grobman criterion 15
  - 2.3.5 Lyapunov method 15
  - 2.3.6 Two-dimensional flow 16
  - 2.3.7 Bendixson-Dulic's criterion 17
  - 2.3.8 Persistence and extinction 17
  - 2.3.9 Local bifurcation 19
  - 2.3.10 Hopf bifurcation 20

Page

2.3.11 Gronwall lemma 22

2.3.12 Descartes rule of signs 23

2.4 Summary 23

3 Background and literature review 24

3.1 Introduction 24

3.2 Prey predator model 24

3.3 Logistic growth 29

3.4 The behaviour of multi-species interactions 30

3.5 The refuge in population dynamics 33

3.6 Summary 36

4 The effect of the reserve zone on the behaviour of a food chain model . . 37

4.1 Introduction 37

4.2 Mathematical model 38

4.3 Boundedness 39

4.4 Positive invariance 40

4.5 Existence of equilibria 41

4.5.1 The existence of the planar equilibrium point 41

4.5.2 The existence of the top predator-free equilibrium point . . . 43

4.5.3 The existence of the positive equilibrium point 43

4.6 Local stability of the equilibrium points 45

4.6.1 Local stability behaviour of F_0 45

4.6.2 Local stability behaviour of F_1 46

4.6.3 Local stability behaviour of F_2 47

4.6.4 Local stability behaviour of F_3 49

4.7 Global dynamical behaviour 50

4.8 Persistence analysis 54

4.9 Local bifurcation analysis 56

4.10 Numerical analysis 63

4.10.1 The effect of varying the migration rate of the prey to the reserved area . . . 64

4.10.2 The effect of varying the natural death rate of the predator . 65

4.10.3 The effect of varying the natural death rate of the top predator 66

4.10.4 The effect of varying the attack rate of the top predator on the predator . . . 67

4.10.5 The effect of varying the conversion rate of the predator to the top predator . . . 68

4.10.6 The effect of varying the unreserved area rate on the species 69

4.10.7 The effect of varying the conversion rate of the prey in the unreserved zone to the predator . . . 70

4.10.8 The effect of varying the attack rate of the predator on the prey in the unreserve zone . . . 71

4.11 Conclusion . . . 72

5 The effect of the reserve zone on the partially dependent predator-prey model 74

5.1 Introduction . . . 74

5.2 Mathematical model . . . 75

5.3 Boundedness . . . 76

5.4 Positive invariance . . . 77

5.5 Existence of equilibria . . . 77

5.5.1 The existence of the axial equilibrium point . . . 77

5.5.2 The existence of the $zw-$ planar equilibrium point . . . 78

5.5.3 The existence of the top predator-free equilibrium point . . . 78

5.5.4 The existence of the positive equilibrium point . . . 80

5.6 Local stability of the equilibrium points . . . 81

5.6.1 Local stability behaviour of F_0 . . . 81

5.6.2 Local stability behaviour of F_1 . . . 82

5.6.3 Local stability behaviour of F_2 . . . 83

5.6.4 Local stability behaviour of F_3 . . . 84

5.6.5 Local stability behaviour of F_4 . . . 85

Page

5.6.6 Local stability behaviour of F_5 87

5.7 Global dynamical behaviour 88

5.8 Persistence analysis 92

5.9 Local bifurcation analysis 92

5.10 Numerical analysis 99

5.10.1 The effect of varying the migration rate of the prey to the reserved area 101

5.10.2 The effect of varying the natural death rate of the predator . 102

5.10.3 The effect of varying the natural death rate of the top predator 103

5.10.4 The effect of varying the attack rate of the top predator on the predator 104

5.10.5 The effect of varying the conversion rate of the predator to the top predator 105

5.10.6 The effect of varying the unreserved area rate on the species 106

5.10.7 The effect of varying the conversion rate of the prey in the unreserved zone to the predator 107

5.10.8 The effect of varying the attack rate of the predator on the prey in the unreserve zone 108

5.11 Conclusion 109

6 The effect of the reserve zone on the behaviour of a food web model . . . 110

6.1 Introduction 110

6.2 Mathematical model 111

6.3 Boundedness 112

6.4 Positive invariance 113

6.5 Existence of equilibria 113

6.5.1 The existence of the specialist predator-free equilibrium point 113

6.5.2 The existence of the positive equilibrium point 114

6.6 Local stability of the equilibrium points 115

6.6.1 Local stability behaviour of F_0 116

6.6.2 Local stability behaviour of F_1 116

Page

6.6.3 Local stability behaviour of F_2 117

6.6.4 Local stability behaviour of F_3 118

6.6.5 Local stability behaviour of F_4 120

6.7 Global dynamical behaviour 122

6.8 Persistence analysis 127

6.9 Local bifurcation analysis 128

6.10 The Hopf bifurcation analysis 136

6.10.1 The Hopf bifurcation analysis near $F_i (i = 0, 1, 2, 3)$ 136

6.10.2 The Hopf bifurcation analysis near the positive equilibrium point 137

6.11 Numerical analysis 138

6.11.1 The effect of varying the migration rate of the prey to the reserved area 141

6.11.2 The effect of varying the natural death rate of the specialist predator 142

6.11.3 The effect of varying the natural death rate of the generalist predator 143

6.11.4 The effect of varying the attack rate of the generalist predator on the specialist predator 144

6.11.5 The effect of varying the conversion rate of the specialist predator to the generalist predator 145

6.11.6 The effect of varying the unreserved area rate on the species 146

6.11.7 The effect of varying the attack rate of the specialist predator on the prey in the unreserve zone 147

6.11.8 The effect of varying the conversion rate of the prey in unreserve area to the specialist predator 148

6.11.9 The effect of varying the attack rate of the generalist predator on the specialist predator 149

6.11.10 The effect of varying the conversion rate of the prey in unreserve area to the generalist predator 150

6.12 Conclusion 151

Page

7 Conclusions and future works 152

7.1 Summary of the thesis and conclusions 152

7.2 Suggestions and recommendations for future work 154

LIST OF REFERENCES 156

list of Publications 162

LIST OF FIGURES

Figure Page

4.1 Convergence of the solution of the system (4.1) to the positive equilibrium point with the data given by Eq.(4.40). 63

4.2 Convergence of the solution of the system (4.1) for the data given by Eq.(4.40) with (a) $\sigma_1 = 0.001$ to the stable point(17.17, 20.02, 2.00, 25.74) in the interior of $\mathbb{R}^4_+$. (b) $\sigma_1 = 1$ to the stable point (13.14, 31.8, 2.00, 19.69) in the interior of $\mathbb{R}^4_+$. 64

4.3 Convergence of the solution of the system (4.1) for the data given by Eq.(4.40) with (a) $\beta_0 = 1$ to the stable point (15.46, 27.91,2.00, 21.19) in the interior of $\mathbb{R}^4_+$. (b) $\beta_0 = 0.001$ to the stable point (15.46, 27.91,2.00, 23.18) in the interior of $\mathbb{R}^4_+$. 65

4.4 Convergence of the solution of the system (4.1) for the data given by Eq.(4.40) with (a) $\alpha = 1$ to the stable point (4.38, 22.75, 5.00, 6.55) in the interior of $\mathbb{R}^4_+$. (b) $\alpha = 0.1$ to the stable point (39.47, 35.76, 0.5, 59.19) in the interior of $\mathbb{R}^4_+$. (c) $\alpha = 0.01$ to the stable point (44.85, 38.49, 0.05, 74.75) in the interior of $\mathbb{R}^4_+$. (d) $\alpha = 0.001$ to the stable point (50.94, 38.77, 0.005, 76.39) in the interior of $\mathbb{R}^4_+$. 66

4.5 Convergence of the solution of the system (4.1) for the data given by Eq.(4.40) with (a) $\gamma_1 = 0.001$ to the stable point (15.46, 27.91, 2.00, 11.58) in the interior of $\mathbb{R}^4_+$. (b) $\gamma_1 = 1$ to the stable point (15.46, 27.91, 2.00, 1158.1) in the interior of $\mathbb{R}^4_+$. 67

4.6 Convergence of the solution of the system (4.1) for the data given by Eq.(4.40) with (a) $\gamma_2 = 1$ to the stable point (41.69, 36.37, 0.40, 62.51) in the interior of $\mathbb{R}^4_+$, (b) $\gamma_2 = 0.01$ to the stable point (0.44, 20.28, 40.00, 0.58) in the interior of $\mathbb{R}^4_+$, (c) $\gamma_2 = 0.0004$ to the stable point (0.01, 20.01, 999.38, 0.003) in the interior of $\mathbb{R}^4_+$, (d) $\gamma_2 = 0.00039$ to the stable point (0.01, 20, 1025.8, 0) in the interior of $\mathbb{R}^3_+$. 68

Figure Page

4.7 Convergence of the solution of the system (4.1) for the data given by Eq.(4.40) with (a) $\sigma_2 = 1$ to the stable point (15.6, 27.58, 2.00, 23.38) in the interior of $\mathbb{R}^4_+$. (b) $\sigma_2 = 0.001$ to the stable point (0.04, 39.98, 2.00, 0.05) in the interior of $\mathbb{R}^4_+$. (c) $\sigma_2 = 0.0003$ to the stable point (0.01, 39.99, 2.00, 0.002) in the interior of $\mathbb{R}^4_+$, (d) $\sigma_2 = 0.00029$ to the stable point (0.01, 39.99, 1.82, 0) in the interior of $\mathbb{R}^3_+$. 69

4.8 Convergence of the solution of the system (4.1) for the data given by Eq.(4.40) with (a) $\beta_2 = 1$, to the stable point (15.6, 27.91, 2.00, 30.9) in the interior of $\mathbb{R}^4_+$. (b) $\beta_2 = 0.01$, to the stable point (15.46, 27.91, 2.00, 0.28) in the interior of $\mathbb{R}^4_+$. (c) $\beta_2 = 0.0002$, to the stable point (15.46, 27.91, 2.00, 0.04) in the interior of $\mathbb{R}^4_+$. (d) $\beta_2 = 0.00019$ to the stable point (51.05, 38.79, 0, 0) in the interior of $\mathbb{R}^2_+$. 70

4.9 Convergence of the solution of the system (4.1) for the data given by Eq.(4.40) with (a) $\beta_1 = 0.1$ to the stable point (45.76, 37.45, 2.00, 68.62) in the interior of $\mathbb{R}^4_+$. (b) $\beta_1 = 0.01$ to the stable point (50.52, 38.66, 2.00, 75.76) in the interior of $\mathbb{R}^4_+$. (c) $\beta_1 = 0.0001$ to the stable point (51.05, 38.79, 2.01, 76.58) in the interior of $\mathbb{R}^4_+$. (d) $\beta_1 = 0.00001$ to the stable point (51.05, 38.79, 1.99, 76.59) in the interior of $\mathbb{R}^4_+$. 72

5.1 Convergence of the solution of the system (5.1) to the positive equilibrium point with the data given by Eq.(5.56). 100

5.2 Convergence of the solution of the system (5.1) for the data given by Eq.(5.56) with (a) $\sigma_1 = 0.001$ to the stable point(6.12, 20.00, 4.00, 11.90) in the interior of $\mathbb{R}^4_+$. (b) $\sigma_1 = 1$ to the stable point (5.59, 26.12, 4.00, 11.10) in the interior of $\mathbb{R}^4_+$. 101

5.3 Convergence of the solution of the system (5.1) for the data given by Eq.(5.56) with (a) $\beta_0 = 1$ to the stable point (5.94, 23.59, 4.00, 9.65) in the interior of $\mathbb{R}^4_+$. (b) $\beta_0 = 0.001$ to the stable point (5.94, 23.59, 4.00, 11.64) in the interior of $\mathbb{R}^4_+$. 102

5.4 Convergence of the solution of the system (5.1) for the data given by Eq.(5.56) with (a) $\alpha = 1$ to the stable point (1.84, 21.24, 10.00, 5.08) in the interior of $\mathbb{R}^4_+$. (b) $\alpha = 0.0001$ to the stable point (50.82, 38.74, 0.01, 79.20) in the interior of $\mathbb{R}^4_+$. 103

5.5 Convergence of the solution of the system (5.1) for the data given by Eq.(5.56) with (a) $\gamma_1 = 0.01$ to the stable point (5.94, 23.59, 4.00, 581.59) in the interior of $\mathbb{R}^4_+$. (b) $\gamma_1 = 1$ to the stable point (5.94, 23.59, 4.00, 5.81) in the interior of $\mathbb{R}^4_+$. 104

Figure Page

5.6 Convergence of the solution of the system (5.1) for the data given by Eq.(5.56) with (a) $\gamma_2 = 1$ to the stable point (39.47, 35.76, 0.50, 62.589) in the interior of $\mathbb{R}^4_+$, (b) $\gamma_2 = 0.0001$ to the stable point (0.30, 20.21, 51.69, 0.41) in the interior of $\mathbb{R}^4_+$. 105

5.7 Convergence of the solution of the system (5.1) for the data given by Eq.(5.56) with (a) $\sigma_2 = 1$ to the stable point (5.96, 16.56, 4.00, 11.65) in the interior of $\mathbb{R}^4_+$. (b) $\sigma_2 = 0.0001$ to the stable point (0.01, 39.99, 4.00, 2.70) in the interior of $\mathbb{R}^4_+$. 106

5.8 Convergence of the solution of the system (5.1) for the data given by Eq.(5.56) with (a) $\beta_2 = 1$, to the stable point (5.94, 23.59, 4.00, 14.60) in the interior of $\mathbb{R}^4_+$. (b) $\beta_2 = 0.0001$, to the stable point (5.94, 23.59, 4, 2.70) in the interior of $\mathbb{R}^4_+$. 107

5.9 Convergence of the solution of the system (5.1) for the data given by Eq.(5.56) with (a) $\beta_1 = 1$ to the stable point (5.14, 23.17, 4.00, 10.42) in the interior of $\mathbb{R}^4_+$. (b) $\beta_1 = 0.001$ to the stable point (50.95, 38.77, 4.00, 79.14) in the interior of $\mathbb{R}^4_+$. (c) $\beta_1 = 0.0001$ to the stable point (51.05, 38.79, 4.00, 79.29) in the interior of $\mathbb{R}^4_+$. 108

6.1 Convergence of the solution of the system (6.1) to the positive equilibrium point with the data given by Eq.(6.39). 140

6.2 Convergence of the solution of the system (6.1) for the data given by Eq.(6.39) with (a) $\sigma_1 = 1$ to the stable point (2.08,22.62,14.58,12.29) in the interior of $\mathbb{R}^4_+$, (b) $\sigma_1 = 0.001$ to the stable point (2.17,20,14.11,12.86) in the interior of $\mathbb{R}^4_+$. 141

6.3 Convergence of the solution of the system (6.1) for the data given by Eq.(6.39) with (a) $\beta_0 = 0.001$ to the stable point (2.14, 21.55, 14.28, 12.83) in the interior of $\mathbb{R}^4_+$, (b) $\beta_0 = 0.0001$ to the stable point (2.14, 21.15, 14.29, 12.84) in the interior of $\mathbb{R}^4_+$, (c) $\beta_0 = 0.16$ to the stable point (2.7, 21.44, 11.47, 13) in the interior of $\mathbb{R}^4_+$, (d) $\beta_0 = 0.161$ to the stable point (5, 22.53, 0, 45.54) in the interior of $\mathbb{R}^3_+$. 142

6.4 Convergence of the solution of the system (6.1) for the data given by Eq.(6.39) with (a) $\alpha = 1$ to the stable point (0.29, 20.16, 98.52, 1.57) in the interior of $\mathbb{R}^4_+$, (b) $\alpha = 0.24$ to the stable point (4.8, 22.44, 0, 56.81) in the interior of $\mathbb{R}^3_+$. 143

Figure Page

6.5 Convergence of the solution of the system (6.1) for the data given by Eq.(6.39) with (a) $\gamma_1 = 0.061$ to the stable point (2.54, 21.36, 12.25, 12.37) in the interior of $\mathbb{R}^4_+$, (b) $\gamma_1 = 0.062$ to the stable point (5, 22.53, 0, 45.54) in the interior of $\mathbb{R}^3_+$, (c) $\gamma_1 = 0.001$ to the stable point (0.56, 20.31, 22.19, 158.29) in the interior of $\mathbb{R}^4_+$, (d) $\gamma_1 = 0.0001$ to the stable point (0.23, 20.1, 23.78, 530.24) in the interior of $\mathbb{R}^4_+$. 144

6.6 Convergence of the solution of the system (6.1) for the data given by Eq.(6.39) with (a) $\gamma_2 = 0.1$ to the stable point (2.15, 21.16, 14.21, 12.74) in the interior of $\mathbb{R}^4_+$, (b) $\gamma_2 = 0.011$ to the stable point (5, 22.53, 0, 45.54) in the interior of $\mathbb{R}^3_+$, (c) $\gamma_2 = 0.0099$ to the stable point (2.09, 21.13, 14.65, 12.39) in the interior of $\mathbb{R}^4_+$. (d) $\gamma_2 = 0.0001$ to the stable point (0.03, 20.02, 825.28, 0) in the interior of $\mathbb{R}^3_+$. 145

6.7 Convergence of the solution of the system (6.1) for the data given by Eq.(6.39) with (a) $\sigma_2 = 0.09$ to the stable point (0.36, 37.25, 23.17, 1.9) in the interior of $\mathbb{R}^4_+$, (b) $\sigma_2 = 0.08$ to the stable point (0.03, 39.72, 26.59, 0) in the interior of $\mathbb{R}^3_+$, (c) $\sigma_2 = 1$ to the stable point (1.6, 12.89, 16.74, 9.7) in the interior of $\mathbb{R}^4_+$. 146

6.8 Convergence of the solution of the system (6.1) for the data given by Eq.(6.39) with (a) $\beta_1 = 0.48$ to the stable point (2.48, 21.33, 12.55, 14.73) in the interior of $\mathbb{R}^4_+$, (b) $\beta_1 = 0.47$ to the stable point (5, 22.53, 0, 45.54) in the interior of $\mathbb{R}^3_+$, (c) $\beta_1 = 1$ to the stable point (0.7, 20.39, 21.48, 4.01) in the interior of $\mathbb{R}^4_+$. 147

6.9 Convergence of the solution of the system (6.1) for the data given by Eq.(6.39) with (a) $\beta_2 = 0.25$ to the stable point (2.48, 21.33, 12.58, 12.21) in the interior of $\mathbb{R}^4_+$, (b) $\beta_2 = 0.24$ to the stable point (5, 22.53, 0, 45.54) in the interior of $\mathbb{R}^3_+$, (c) $\beta_2 = 1$ to the stable point (1.42, 20.78, 17.88, 28.25) in the interior of $\mathbb{R}^4_+$. 148

6.10 Convergence of the solution of the system (6.1) for the data given by Eq.(6.39) with (a) $\alpha_1 = 1$ to the stable point (1, 20.56, 19.95, 5.85) in the interior of $\mathbb{R}^4_+$, (b) $\alpha_1 = 0.09$ to the stable point (5.61, 23.51, 0, 439.86) in the interior of $\mathbb{R}^3_+$. 149

6.11 Convergence of the solution of the system (6.1) for the data given by Eq.(6.39) with (a) $\alpha_2 = 0.06$ to the stable point (4.16, 22.14, 0, 51.54) in the interior of $\mathbb{R}^3_+$, (b) $\alpha_2 = 0.0001$ to the stable point (1.24, 20.68, 24.98, 7.24) in the interior of $\mathbb{R}^4_+$. 150

SYMBOLS

Symbol	**Abbreviations**
$\dot{V} = dV/dt$	A derivative taken with respect to time
$x(0) = x_0$	Initial condition
Interior of $\mathbb{R}^2_+$	$\{(x, y), x > 0, y > 0\}$
Interior of $\mathbb{R}^3_+$	$\{(x, y, z), x > 0, y > 0, z > 0\}$
Interior of $\mathbb{R}^4_+$	$\{(x, y, z, w), x > 0, y > 0, z > 0, w > 0\}$
$J^*(F_i)$	the Jacobian matrix $J(F_i)$ at the bifurcation parameter
Int.$\mathbb{R}^3_{+(\mathrm{xyz})}$	the interior of $\mathbb{R}^3_{+(\mathrm{xyz})}$
$\partial\mathbb{R}^3_{+(\mathrm{xyz})}$	the boundary axes of $\mathbb{R}^3_{+(\mathrm{xzw})}$
$\mathbb{R}^2_+$	$\{(x, y), x \geq 0, y \geq 0\}$
$\mathbb{R}^3_+$	$\{(x, y, z), x \geq 0, y \geq 0, z \geq 0\}$
$\mathbb{R}^4_+$	$\{(x, y, z, w), x \geq 0, y \geq 0, z \geq 0, w \geq 0\}$
Ω	The region of attraction
$x(t; p)$	Vector of state variables
$det(A)$	Determinate of matrix A
$\|\|$	Modulus, absolute value

Abstract

Many biological problems can be reduced to the description of a food chain model or a food web. In these systems, the biodiversity and coexistence of all species are vital issues to discuss. Three ecological models have been proposed in case of the existence of a reserved area, in order to understand multi-species interactions so as to prevent the slow extinction of some endangered species and to test the stability when the length of the food chain and size of the web models are increased. It is taken that the environment has been divided into two disjoint regions, namely, unreserved and reserved zones, where a predator is not allowed to enter the latter. The first model describes a four species food chain predator-prey model with prey refuge (prey in the reserved zone, prey in the unreserved zone, predator and top predator), with the predator being entirely dependent on the prey in the unprotected area. The second model addresses the same problem, but in addition, a third component in the chain partially depends on the prey in the unreserved zone. Finally, the last model investigates a four species food web system with a prey refuge and in this case, the fourth component can also feed directly on the prey in the unreserved zone. The boundedness, existence and uniqueness of the solutions of the proposed models are established. The local and global dynamical behaviours are investigated, with the persistence conditions of the models being elicited. The local bifurcation near each of the equilibrium points is obtained. The numerical simulations in MATLAB® are used to study the influence of the existence of the reserved zone on the dynamical behaviour of the proposed models. It has been concluded that the role of the reserved area could be beneficial for the survival and stabilising of multi-species interactions.

Chapter 1: Introduction

1.1 Background

Ecology is that part of Biology, which deals with the study of the distribution and the interactions of organisms with their environment and with one another. A group of organisms whose members have the same structural traits and who can interbreed with each other is known as a species. An ecosystem is the set of all species of a given area and the encompassing physical environment. The application of mathematical concepts to problems in ecology has resulted in a branch of biology known as mathematical ecology. Population dynamics deals with the time-dependent behaviour of modelled ecological systems. These models provide significant insights into the behaviour of nature. Usually, these systems consider many complex communities involving many species, which interact in a very complicated manner and hence, can be challenging to analyse as well as compute models and draw conclusions from them. The mathematical equations can govern the time evolution of interacting species. The evolution and growth of the species depend on many factors, such as overcrowding, age structure, past population size, sources of food supply, interactions with other species, topographical, ecological and environmental conditions in the habitat, including seasonal and climatic variations. For more detail see [1].

Since all living organisms in nature are interdependent, the associations existing between the different ones influence the survival of species and the performance of the entire ecosystem. Hence, to understand the comprehensive dynamics of the ecosystem, it is necessary to consider the impact of both environmental variations and multispecies interactions. The ecological interactions are positive (mutually beneficial), negative (mutually detrimental) or neutral. In an ecosystem, the populations can be very much affected by the interactions between the organisms. There are many ways that they can interact with each other and within an ecosystem, with the main types of these interactions being as follows [2].

- **Competition**

  A kind of relationship in which different organisms or populations are competing for the same limited resources at the same time, where each species is going to hurt all others. The limiting resource may be water, forest, minerals, prey, space, environment, etc., which is responsible for the growth and survival of organisms in the ecosystem. For example, in a forest different populations of plants are competing for sunlight and water nutrients in the soil. Competition can occur either within species (intraspecific), for example, resources competition or between species (interspecific). When competition occurs among the same species, they are going to harm each other.

- **Commensalism**

  A relationship between two organisms in the ecosystem in which one species benefits and the other species remain unaffected. For instance, regarding the mosquito Wyomia smithii - the larvae live inside the plant Sarracenia purpura and do not harm the plant.

- **Mutualism**

  An interspecific interaction in which both populations enhance the other. During this interaction, both communities in the presence of the other grow to survive and reproduce at a higher rate. Pollination is an excellent example for explaining mutualism, whereby the plant gets to benefit from the dispersal of pollen, and the pollinator obtains a meal of nectar from the flower.

- **Predation**

> An organism (predator) that feeds on another (prey) for its food. In this interaction, the existence of prey enhances the predator, while the latter might threaten the presence of the former. Typical examples of predation are bats eating insects and snakes eating mice.

The predator-prey interaction can be generalised to use in three species or more. A series of interrelated organisms in terms of their feeding habits is called *food chain*. It shows how resources are directly transferred from one living organism to another via food. The food chain has an essential role in maintaining the balance of the ecosystem. If one component in the food chain is missing, then the dynamics of the ecosystem will be disturbed, which will affect a population of prey or predators in the ecosystem. The following could be part of a food chain: the frog could be eaten by the snake, and the snake could be eaten by the owl. The food chain looks like this: frog → snake → owl. Let us now consider an example of a *food web*, where in addition the snake might get eaten by a fox or hawk in the forest as well as an owl and hence, in that case, one linear pathway regarding what an organism eats cannot be adequately described. For situations like this, a food web can be constructed, which consists of many connections of food chains and represents the different species that can eat and be eaten by. Since in real life each organism can eat multiple species and be eaten by multiple species, a food web is a much more practical schematic of the transfer of resources within an ecosystem [3].

To understand the ecological interaction between prey and predator, many approaches can be adopted, one of these being to develop a mathematical model. Since Lotka [4] and Volterra [5] proposed the simple model of predator-prey interaction, which is now known as the Lotka-Volterra model, many mathematical models have been introduced to understand more complex ecological interactions [6–8]. For more detail, please see Chapter 3.

1.2 Problem statement and motivations

Recently, there has been a worldwide movement aimed at enhancing the understanding of ecological stability. However, many significant problems are still unsolved. The most significant challenges to control the co-existence of the interaction between biological species can be summarised as the follows [9].

- **Resources limitation and energy conservation**

  It is well known that the resource carrying capacity of our planet is limited. All species require resources, for example, energy, light, nutrition, radiation etc. A poor understanding of ecology is leading to the destruction of resources, e.g. non-renewable sources, like oil, coal, natural gas as well as pollution and destruction of the ozone layer. Hence, effective management strategies for exploited biological resources are required. Otherwise, destruction of some organisms might happen that would mean the death of others.

- **Human activities**

  Humans continue to destroy wildlife habitats by introducing contaminants, such as pesticides and industrial waste into the environment, deforestation, climate change, mismanagement, overharvesting, ect.. This behaviour, if unchanged, could someday render the Earth uninhabitable.

- **Natural disasters**

  Every species has their environment that adapts to it, and it cannot live away from it. This environment provides all the elements of its life. The nature of the environment can be destroyed by natural disasters, such as flooding, desertification, earthquakes, volcanoes, the spread of some diseases or epidemics etc. Environmental damage might happen that breaks down communication links between species that in turn leads to the devastation of large numbers of them.

- **Resource allocation**

  All organisms need to share limited natural resources at the same time for coexistence such as air, minerals, environment and space. Lack of ecological know-how has led to deprivation and looting of these natural resources resulting in scarcity as well as competition.

The above points are aspects of an issue of increasing concern, namely, the scarcity of resources and stress on our environment, which can induce the extinction and endangerment of species. A slight change in the environment could have a profound influence on all living species. In particular, a food chain might lose one of their components. These problems will create an imbalance in the ecosystem. For species protection, some strategies and appropriate measures that will diminish interaction by species including the creation of reserved zones, restricting harvesting, etc. need to be deployed [10]. The role of reserved zones (the areas in which the prey is successfully controlled and protected from predation) in four species food chain/web predator-prey dynamics will be explored in this thesis. It will be shown how reserved zones can stabilise ecosystems.

1.3 Thesis aim and objectives

In this thesis, we show how the mathematical models play an essential role in describing and understanding the dynamical behaviour of ecosystems by using the principles of biology. However, the aim of this study to keep the prey in food chain/web from extinction. Accordingly, the main objectives of this thesis are listed as follows.

1. Proposing four species food chain/web prey-predator models with prey refuge. Analysis and understanding the dynamical behaviour of the models, by which it will become known what might happen in a system over time. Hence, it will be more possible to forecast threats to extinction and then act to prevent potentially adverse effects that might occur.

2. Mathematical analysis of the proposed models is used to establish the conditions that influence the existence, uniqueness, positivity, stability and boundedness of the solutions of the models.
3. Investigating how parameters such as birth rate, death rate, predator handling time of the prey, competition among prey and the attack rate of the predator affect the dynamics of the population densities of the proposed systems.
4. Find out how the reserved zone impacts on the long-term survival of each species subject to ecological stability.

1.4 Thesis overview

Having provided an introduction, the motivations as well as the contributions in this chapter, the rest of the thesis is organised as follows.

- **Chapter two**: some principles, theorems, tools and methods that are used in this study are explained.
- **Chapter three**: in this chapter, the historical background and a literature review regarding the dynamics of multi-component models, such as predator-prey models, food chain models, food web models as well as models with a reserved zone in ecological systems, are provided.
- **Chapter four**: in this chapter, the modelling of the four species food chain prey-predator model with a prey refuge is proposed. A variety of analytical methods and tools are used to study the existence, uniqueness, boundedness, local stability, local bifurcation, and persistence of the solutions of the model. The global dynamics of this model is investigated analytically as well as numerically. The model shows a rich dynamic in the space of nonnegative solutions. In particular, the dynamics around the different equilibrium points are studied in detail, including the strictly positive equilibrium, the equilibrium for which only

the top predator vanishing and the remaining components are strictly positive, the equilibrium with two vanishing components and the trivial equilibrium. The long-term behaviour of the system is investigated, and conditions for persistence derived.

- **Chapter five**: In this chapter, the model in Chapter four is modified by proposing that the predator (the third component) has its logistic growth term. Thus, the latter has two supply resources. A variety of analytical methods and tools are used to study the existence, uniqueness, boundedness, local stability, local bifurcation, and persistence of the solutions of the proposed model. The global dynamics of this model are investigated analytically as well as numerically. All the equilibrium points are obtained, which correspond to those in Chapter four plus two new equilibrium points. The first one, in which only the third component is strictly positive and the remaining are vanishing. The second one only the last two component are strictly positive and the other two are zero. The simulations of this model show that for larg-time the solutions approach the strictly positive steady state.

- **Chapter six**: this chapter presents and analyses the modelling of a four species food web prey-predator model in the case of the existence of a prey refuge. It is a modification of the model in Chapter four, but now the last predator can feed directly on the first prey, in addition to all the other connections in the previous model. The boundedness, existence and uniqueness of the solution of the model under consideration are studied. The local stability analysis of this four-dimensional system is discussed analytically, and the conditions for the persistence of all species are established. The global dynamics of the model is studied using analytical and numerical tools. The dynamical behaviour is found to be very sensitive to parameter values and initial data, in particular, the stability of equilibrium points. Now, all the equilibrium points are obtained, which correspond to those in Chapter four plus a new equilibrium point, for which only the third component vanishes and the remaining components are strictly positive.

- **Chapter Seven**: provides a summary of the thesis, makes conclusions and some suggestions are put forward for future research avenues.

Chapter 2: Preliminaries

2.1 Introduction

Through mathematical differential equations, scientific problems can be formulated and studied. To analyse these differential equations, various mathematical tools are required. In this chapter, they are reviewed together with some of the definitions, basic concepts, and theorems that are used throughout this thesis.

2.2 Qualitative behaviour in the nonlinear dynamical system

Deterministic nonlinear dynamics is classified according to the qualitative behaviour of its attractors. An attractor is a geometrical object in the state space, which attracts all trajectories starting within its domain. The most straightforward kind of dynamics is stability around the equilibrium point. A stable equilibrium is a point in phase space, to which the trajectory returns after a small perturbation. The approach to the stable point can be either exponential or oscillatory [11].

A more complex dynamical behaviour is a stable limit cycle. In continuous models, the limit cycle attractor is a closed curve in phase space towards which all trajectories approach. In order for a differential model to be able to exhibit a stable cycle, it should be of order two or higher. A limit cycle is a periodic attractor in the strict mathematical sense, because its trajectory repeats itself precisely after some time. In situations when these two simple attractors govern the asymptotic dynamics, then the system is said to be in an ordered state. If a system is so, its future state at any point can be predicted with an arbitrary degree of accuracy. Quasi-periodicity has very similar behaviour to limit cycles. It occurs in two-or higher-dimensional discrete models and three-or higher-dimensional continuous ones. It resembles limit cycles, but the periods of the oscillations vary and the system never precisely repeats itself. Neighbouring points remain near one another in quasi-cycles. Quasi-periodicity often occurs when periodic subsystems are coupled [12].

Moreover, a chaotic or strange attractor is one whose variables do not have regular amplitudes or periods, and it is always found within a restricted range of state space. The unpredictable and irregular time evolution of many nonlinear systems has been dubbed as chaos. The critical feature of chaotic dynamics is its sensitive dependence on the initial conditions, for even a minimal change in these can lead to different results in chaotic systems. Indeed, the divergence between results grows exponentially in time for virtually all pairs of starting conditions. So, we deduced that long-term predictions of chaotic systems are futile. Also, in continuous autonomous systems, chaos cannot arise unless the dimensionality of the system is three or higher [13].

2.3 Mathematical tools

In the following, a number of mathematical tools that are used in this thesis are rviewed.

2.3.1 Local stability analysis

Consider the nonlinear autonomous system:

$$\frac{dx_i}{dt} = F_i(x_1, x_2, ..., x_n,), i = 1, 2, ..., n, \tag{2.1}$$

where, $x \in R^n$. In the following, some basic definitions are presented, which are needed to study the stability of the system (2.1).

- A system of differential equations (2.1) is said to be *dissipative*, if there is a bounded subset D of R^n such that for any $x_0 \in R^n$ there is a time t_0, which depends on x_0 and D so that the solution $\phi(t, x_0) \in D$ for $t \geq t_0$ [14].

- A point $x^* = (x_1^*, x_2^*, ..., x_n^*)$ is supposed to be an *equilibrium point* (or steady state point) of the system (2.1) if it satisfies the following equation $Fi(x^*) = 0; \forall i = 1, 2, ..., n$ [11].

- A point $p \in R^n$ is called an *ω-limit point* of $x \in R^n$, which is denoted by $\omega(x)$, if there is a sequence $\{t_i\}$ with $t_i \to \infty$ as $i \to \infty$, such that the solution of Eq. (2.1) with initial condition $x(0) = x$ satisfies that $\phi(t_i, x) \to p$ as $i \to \infty$. On the other hand, *α-limit points* are defined similarly by taking a sequence $\{t_i\}$, where $t_i \to -\infty$ as $i \to \infty$. The set of all ω-limit points is called the *ω-limit set*. The *α-limit set* is similarly defined [15].

Now, to determine the local stability of x^* we should understand the nature of the solutions of system (2.1) near the equilibrium point x^*.

Let $x(t) = x^*(t)+\xi(t)$, where $x(t)$ be any other solution and $\xi(t) = (\xi_1, \xi_2, ..., \xi_n)(t)$ represents small perturbation of the original solution. Then the linear approximation for small perturbation can be written as

$$\frac{d\xi}{dt} \cong V(t)\xi,$$

where the matrix $V(t) = (\partial F_i/\partial x_j)_{x^*}$ is the variational matrix at the equilibrium point. The eigenvalues of this matrix decide whether the equilibrium point is linearly stable or unstable. The characteristic equation for the variational matrix is computed:

$$\det(V - \lambda I) = \lambda^n + A_1\lambda^{n-1} + A_2\lambda^{n-2} + ... + A_n = 0. \tag{2.2}$$

Then, the Routh-Hurwitz criterion [16] is applied to obtain constraints on the coefficients $A_1, A_2, ..., A_n$, which are the necessary and sufficient to ensure all eigenvalues lie in the left half complex plane. If the choice of parametric values is such that all the constraints are simultaneously satisfied, then the system will be *locally asymptotically* *stable* at x^*. On the other hand, violation of any one of these conditions implies that x^* is *an unstable equilibrium point.* As a result, an equilibrium point x^* of the system (2.1) is said to be *globally asymptotically stable* if x^* is asymptotically stable for any initial point $x(0) \in R^n$. This definition means that the basin of attraction of an equilibrium point x^* that is denoted by $B(x^*)$. Here $B(x^*) = \{x(0) : \phi(t, x(0)) \xrightarrow[t\to\infty]{} x^*\}$ is equal to R^n if and only if it is globally asymptotically stable. Therefore, it should be clear that if the equilibrium point x^* is so, then it is locally asymptotically stable, but not vice versa. Moreover, An equilibrium point x^* of the system (2.1) is called a *hyperbolic equilibrium point* if none of the eigenvalues have a zero-real part. Otherwise, it is a *non-hyperbolic equilibrium point.*

2.3.2 Routh-Hurwitz criterion

Consider the following polynomial of degree n, which is defined by:

$$P_n(\lambda) = \lambda^n + a_1\lambda^{n-1} + a_2\lambda^{n-2} + ... + a_n = 0.$$

let $D_1 = a_1$, $D_2 = \det \begin{bmatrix} a_1 & a_3 \\ 1 & a_2 \end{bmatrix}$, $D_k = \det \begin{bmatrix} a_1 & a_3 & a_5 & \dots & a_{2k-1} \\ 1 & a_2 & a_4 & \dots & a_{2k-2} \\ 0 & a_1 & a_3 & \dots & a_{2k-3} \\ : & 1 & a_2 & \dots & a_{2k-4} \\ : & : & : & \dots & : \\ 0 & 0 & 0 & \dots & a_k \end{bmatrix}$,

where $a_i = 0$ if $i > n$. Then all the roots of $P_n(\lambda)$ have a negative real part, if, $D_k > 0$ for all $k = 1, 2, ..., n$. Now, by applying this criterion when

- $n = 2$

  For $n = 2$, we have $P_2(\lambda) = \lambda^2 + a_1\lambda + a_2 = 0$, and hence, $D_1 = a_1$, $D_2 = \det \begin{bmatrix} a_1 & 0 \\ 1 & a_2 \end{bmatrix} = a_1a_2$. Thus, for $n = 2$, the necessary and sufficient conditions of all roots having negative real parts are $a_1 > 0$ and $a_2 > 0$.

- $n = 3$

  For $n = 3$, $P_3(\lambda) = \lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0$, and hence, $D_1 = a_1$, $D_2 = \det \begin{bmatrix} a_1 & a_3 \\ 1 & a_2 \end{bmatrix} = a_1a_2 - a_3$, $D_3 = \det \begin{bmatrix} a_1 & a_3 & 0 \\ 1 & a_2 & 0 \\ 0 & a_1 & a_3 \end{bmatrix} = (a_1a_2 - a_3)a_3$. Thus, for $n = 3$, the necessary and sufficient conditions for all roots having negative real parts are $a_1 > 0$, $a_3 > 0$ and $a_1a_2 - a_3 > 0$.

- $n = 4$

  Finally, for $n = 4$, we have $P_4(\lambda) = \lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 = 0$, and hence, $D_1 = a_1$, $D_2 = \det \begin{bmatrix} a_1 & a_3 \\ 1 & a_2 \end{bmatrix} = a_1a_2 - a_3$, $D_3 = \det \begin{bmatrix} a_1 & a_3 & 0 \\ 1 & a_2 & a_4 \\ 0 & a_1 & a_3 \end{bmatrix} = (a_1a_2 - a_3)a_3 - a_1^2a_4$,

  $$D_4 = \det \begin{bmatrix} a_1 & a_3 & 0 & 0 \\ 1 & a_2 & a_4 & 0 \\ 0 & a_1 & a_3 & 0 \\ 0 & 1 & a_2 & a_4 \end{bmatrix} = a_4(a_1a_2a_3 - a_3^2 - a_1^2a_4).$$

  Thus, for $n = 4$, the necessary and sufficient conditions for all roots having negative real part are $a_1 > 0$, $a_3 > 0$, $a_4 > 0$ and $(a_1a_2 - a_3)a_3 - a_1^2a_4 > 0$ [17].

Now, due to the above classification of an equilibrium point of the system (2.1), the domain of system (2.1) $D \subset R^n$ can be represented as the direct sum of three subspaces, which are defined as follows [18]:

$$\begin{aligned} E^s &= \text{span}\{e_1, e_2, ..., e_s\}, \\ E^u &= \text{span}\{e_{s+1}, e_{s+2}, ..., e_{s+u}\}, \\ E^c &= \text{span}\{e_{s+u+1}, e_{s+u+2}, ..., e_{s+u+c}\}, \end{aligned}$$

with $s+u+c=n$ is the dimension of the system. Here $\{e_1, e_2, ..., e_s\}$ are the eigenvectors of $J = dF(x^*)$ corresponding to the eigenvalues of $J = dF(x^*)$, having negative real parts, $\{e_{s+1}, e_{s+2}, ..., e_{s+u}\}$ are the eigenvectors of $J = dF(x^*)$ corresponding to eigenvalues of $J = dF(x^*)$, having positive real parts, and $\{e_{s+u+1}, e_{s+u+2}, ..., e_{s+u+c}\}$ are the eigenvectors of $J = dF(x^*)$ corresponding to the eigenvalues of $J = dF(x^*)$, having zero real parts. The subspaces E^s, E^u and E^c are referred to as the stable, unstable and centre subspace respectively.

2.3.3 Local stable and unstable manifold

To state the local stable manifold theorem, we need the following definition. Let x^* be a hyperbolic equilibrium point of the system (2.1). Then, the local stable and unstable manifolds of x^* are defined as follows:

$$W^s(x^*) = \{v \in U | \phi(t, v) \xrightarrow[t\to\infty]{} x^* \text{ and } \phi(t, v) \in U, \forall t \geq 0\},$$

$$W^u(x^*) = \{v \in U | \phi(t, v) \xrightarrow[t\to\infty]{} x^* \text{ and } \phi(t, v) \in U, \forall t \leq 0\},$$

where, $U \in R^n$ is a neighbourhood of the equilibrium point x^*. So the next theorem tells us that $W^s(x^*)$ and $W^u(x^*)$ are in fact tangent to E^s, E^u at x^* [19].

Theorem 2.3.1 *Suppose that system (2.1) has a hyperbolic equilibrium point x^*, then there exist a local stable and/or an unstable manifold $W^s(x^*)$, $W^u(x^*)$, of the same dimensions n_s and n_u as those of the eigenspaces E^s, E^u of the linearized system (2.1), and tangent to E^s, E^u at x^*. $W^s(x^*)$, $W^u(x^*)$ are as smooth as the function F of the system (2.1).*

The above theorem shows that the invariant manifolds $W^s(x^*)$ and $W^u(x^*)$ provide nonlinear analogues of the flat stable and unstable eigenspace E^s, E^u of the linear system (2.1).

2.3.4 Hartman-Grobman criterion

Let x^* be a hyperbolic equilibrium point of the system (2.1); then there is a homeomorphism h defined on some neighbourhood of x^* in R^n locally taking orbits of the nonlinear flow $\phi(t)$ of system (2.1) to those of the linear flow e^{tJ} of system (2.1). This homeomorphism preserves the sense of orbits and can also be chosen to preserve parameterisation by time, see [20]. Consequently, the orbit structure near a hyperbolic equilibrium point of the system (2.1) is qualitatively the same as the orbit structure given by the associated linearised dynamical system (2.2).

2.3.5 Lyapunov method

This method can be used to determine the stability and instability of an equilibrium point (especially of non-hyperbolic type) of nonlinear systems. It has also been utilized to study the stability of the equilibrium point for the linear system. Further, it works for finite and infinite dimensions, with the basic idea of the method being as follows. Suppose that; we have a vector field (2.1) with an equilibrium point x^*, then to determine whether or not x^* is stable, it is sufficient to find a neighbourhood of x^* for which the orbits are starting in U remain in there for all positive time. This condition would be satisfied, if we can show that the vector field is either tangent to the boundary of U or pointing inward toward x^*. Also, this situation should remain true even as we shrink U down onto x^*. Note that the way of showing this situation is known by the Lyapunov method. The general theorem for stability and instability of an equilibrium point which makes these ideas precise is given in the following.

Theorem 2.3.2 ***(Lyapunov stability)***

Let x^* be an equilibrium point of the system (2.1) and let $L : U \to R$ be a C^1 function defined on some neighbourhood of $x^*(U \subseteq R^n)$ such that:

1. *$L(x^*) = 0$ and $L(x) > 0$ if $x \neq x^*$ (that is mean L is a positive definite function).*

2. *$L^{'}(x) \leq 0$ in $U - \{x^*\}$. Then, x^* is stable, Moreover, if*

3. $L^{'}(x) < 0$ *in* $U - \{x^*\}$. *Then,* x^* *is asymptotically stable See [21].*

Note that, the function L given above is known as Lyapunov function. In addition, if U can be chosen to be all R^n, then x^* is said to be a globally asymptotically stable, if conditions (1) and (3) hold [22].

Theorem 2.3.3 ***(LaSalle invariance principle)***

Suppose that $x^* = 0$ *is an equilibrium point of system (2.1), and* V *is a Lyapunov function on some neighbourhood* U *of* $x^* = 0$*. If* $x_0 \in U$ *has its forward trajectory bounded with limit points in* U*, and* M *is the largest invariant set of* $E = \{x^* \in U : \dot{V}(x^*) = 0\}$*, then* $\phi(x_0, t) \to M$ *as* $t \to \infty$ *[23].*

2.3.6 Two-dimensional flow

Consider the following autonomous two-dimensional system:

$$\begin{aligned} \frac{dx}{dt} &= f(x, y) \\ \frac{dy}{dt} &= g(x, y) \end{aligned} \tag{2.3}$$

where, $(x, y) \in U \subseteq R^2$ with f and g are sufficiently smooth functions. According to the above discussion, the stability analysis of system (2.3) is well understood. In the following, two theorems that consider the constraints that grant the existence and non-existence of closed orbits in the plane are covered.

Theorem 2.3.4 ***(Poincare-Bendixson)*** *A nonempty compact* $\omega-$ *or* $\alpha-$ *limit set of a planar flow, which contains no equilibrium points is a closed orbit [24].*

Obviously, the Poincare-Bendixson theorem suggests that the solution of a system of two-dimensional autonomous differential equations of first order converges either to a point or closed curve.

Now, the non-existence condition of a closed orbit of the system (2.3) is established in the following theorem.

2.3.7 Bendixson-Dulic's criterion

Consider the planar dynamical system given by (2.3), where f and g are at least C^1. Let B be C^1 functioning in a simply connected region $D \subset R^2$. If $\partial(Bf)/\partial x + \partial(Bg)/\partial y$ is not identically zero and does not change sign in D, then the system has no closed orbits lying entirely in D [16].

2.3.8 Persistence and extinction

In general, the term persistence is a global property of the dynamical system; which does not depend upon interior solution space structure, but instead, upon solution behaviour near extinction boundaries. From the biological point of view, the persistence of a system means the survival of all its population at a future time. However, mathematically it implies that a strictly positive solution does not have an omega limit set in the boundary planes of a non-negative cone [25]. Accordingly, if the dynamical system does not persist, then the solution has an omega limit set on the boundary planes of the non-negative cone, and hence the dynamical system faces extinction. Moreover, a system is said to persist, if each component of the population does.

In this thesis, the Freedman and Waltman approach [26] for the persistence of a dynamical system is used. This approach is given below.

2.3.8.1 Freedman and Waltman approach

Consider the general ecological model of three interacting predator-prey populations defined as:

$$\begin{aligned}
\frac{dx}{dt} &= xf(x,y,z), \quad x(0) = x_0 \geq 0, \\
\frac{dy}{dt} &= yg(x,y,z), \quad y(0) = y_0 \geq 0, \\
\frac{dz}{dt} &= zh(x,y,z), \quad z(0) = z_0 \geq 0.
\end{aligned} \tag{2.4}$$

Here, x will always be a prey population, z will always be a predator population, and y will either a predator or prey or both. The abstract theorem for the persistence of a three-species system (2.4) is given in the following.

Theorem 2.3.5 *let the following hypotheses hold:*

- *f, g and h are C^1 in R^3_+;*
- *All the solutions of the system (2.4) with the non-negative initial condition are bounded in forward time;*
- *If there exists an equilibrium point on the x- and/or y-axis, then they are hyperbolic saddle points;*
- *Interior to each positive coordinate plane there is at most one equilibrium point, which if it exists, is unstable in the positive direction orthogonal to that plane, and around which there are no periodic orbits, then the system (2.4) persists.*

Lemma 1 ***(Butler-McGhee)*** *Let p be an isolated hyperbolic equilibrium point in the omega limit set $\Omega(x)$ of an orbit $o(x)$. Then either $\Omega(x) = p$ or there exist points q^+, q^- in $\Omega(x)$ with $q^+ \in M^+(p)$ and $q^- \in M^-(p)$.*

Here, $M^+(p)$ and $M^-(p)$ represent the stable and unstable manifolds of the hyperbolic equilibrium point p; $o(x)$ is the orbit throogh the point x [26] .

In the following subsection, the local bifurcation near the equilibrium point is studied.

2.3.9 Local bifurcation

Consider the following system:

$$x^{'} = F(x, \mu), \tag{2.5}$$

where, $x^{'} = \Big(dx_1/dt, dx_2/dt, ..., dx_n/dt\Big)^T$, $F = (F_1, F_2, ..., F_n,)^T$ and $\mu \in R$ is a parameter. We shall assume throughout this thesis that $F \in C^1(E \times I)$, where E is an open set in R^n, $n \in N$ and $I \subset R$ is an interval. We use $DF(x, \mu)$ to denote the Jacobian matrix and $F_\mu(x, \mu)$ to denote the vector of partial derivatives of the elements of F concerning the parameter μ. The term bifurcation is a qualitative change of the nature of the solution under variation of system's parameter [27].

2.3.9.1 Sotomayor approach

Suppose that $F(x^*, \mu_0) = 0$ and that $n \times n$ matrix $J \equiv DF(X^*, \mu_0)$ has a simple eigenvalue $\lambda = 0$ with eigenvector V and that the $n \times n$ matrix J^T has an eigenvector Ψ corresponding to the eigenvalue $\lambda = 0$. Furthermore, suppose that J has k eigenvalues with negative real part and $n - k - 1$ eigenvalues with the positive real part and that the following conditions are satisfied:

$$\Psi^T F_\mu(x^*, \mu_0) \neq 0, \Psi^T \lfloor D^2 F\Big(x^*, \mu_0\Big)(V, V)\rfloor \neq 0. \tag{2.6}$$

Then, the system (2.5) experiences a saddle-node bifurcation at the equilibrium point x^* as the parameter μ passes through the bifurcation value $\mu = \mu_0$. However, if the conditions given by (2.6) are changed to:

$$\Psi^T F_\mu(x^*, \mu_0) = 0, \Psi^T \Big[DF_\mu\Big(x^*, \mu_0\Big)V\Big] \neq 0, \Psi^T \Big[D^2 F\Big(x^*, \mu_0\Big)(V, V)\Big] \neq 0. \tag{2.7}$$

Then, the system (2.5) experiences a transcritical bifurcation at the equilibrium point x^* as the parameter μ passes through the bifurcation value $\mu = \mu_0$.

Finally, if the conditions given by (2.6) are changed to:

$$\begin{aligned}\Psi^T F_\mu(x^*, \mu_0) &= 0, \Psi^T\Big[DF_\mu\Big(x^*, \mu_0\Big)V\Big] \neq 0,\\ \Psi^T\Big[D^2F\Big(x^*, \mu_0\Big)(V, V)\Big] &= 0, \Psi^T\Big[D^3F\Big(x^*, \mu_0\Big)(V, V, V)\Big] \neq 0.\end{aligned}$$

Then, the system (2.5) experiences a pitchfork bifurcation at the equilibrium point x^* as the parameter μ passes through the bifurcation value $\mu = \mu_0$ [28]. In the following the conditions, the gradients that occur for a simple Hopf bifurcation in a dynamical system (2.5) are presented.

2.3.10 Hopf bifurcation

Let $F(x^*, \mu) = 0$ for all $\mu \in R$. A value $\mu = \tilde{\mu}$ is said to be a Hopf bifurcation value for a steady solution x^* of the system (2.5) if, the Jacobian matrix $DF(x^*, \tilde{\mu})$ has a simple pair of purely imaginary eigenvalues and no other eigenvalues with zero real parts, while the phase portrait of the system (2.5) will change as μ passes through $\tilde{\mu}$, where a periodic orbit is created in the neighbourhood of $\tilde{\mu}$ [29].

Consider the system (2.5) with an equilibrium point x^*. Then, if there exists a parameter $\mu \in I$ with $I \subset R$ and $F \in C^\alpha\Big(R^n \times R, R^2\Big)$ for some $\alpha \geq n$ with $F(x^*, \mu) = 0 \forall \mu \in R$, so that:

1. A simple pair of complex eigenvalues of the Jacobian matrix $J(x^*)$ of the system (2.5) at the equilibrium point x^* exists, say $\gamma(\mu) = \xi_1(\mu) \pm i\xi_2(\mu)$ whereby they become purely imaginary at $\mu = \mu_0$, while all the other eigenvalues remain real and negative.
2. $\frac{d\xi_1(\mu)}{d\mu}|_{\mu=\mu_0} \neq 0$, (this part called transversality condition) then the system (2.5) has a simple Hopf bifurcation at $\tilde{\mu}$.

2.3.10.1 Haque and Venturino methods

According to the above definition, the traditional simple Hopf bifurcation criterion is stated regarding the properties of eigenvalues. Since the computations of eigenvalues are sometimes difficult, it is worth having a criterion stated in relation to the coefficients of the characteristic equations. Haque and Venturino [30] derived a criterion for simple Hopf bifurcation using the properties of the coefficients of the characteristic equation, instead of those of eigenvalues. This is related to the Routh-Hurwitz criterion and is convenient in many applications. Their criterion is stated for $n = 3$ for more details see [30]. The criterion for $n = 4$ is stated regarding the properties of eigenvalues [31].

Consider the characteristic equation given by:

$$P_4(\tau) = \tau^4 + C_1\tau^3 + C_2\gamma^2 + C_3\gamma + C_4 = 0,$$

here, $C_1 = -tr\big(J(x^*)\big)$, $C_2 = M_1\big(J(x^*)\big)$, $C_3 = -M_2\big(J(x^*)\big)$ and $C_4 = det\big(J(x^*)\big)$ with $M_1\big(J(x^*)\big)$ and $M_2\big(J(x^*)\big)$ representing the sum of the principal minors of order two and three of $J(x^*)$, respectively. The first condition of Hop bifurcation holds if:

$$C_i > 0; i = 1, 3; \Delta_1 = C_1C_2 - C_3 > 0; C_1^3 - 4\Delta_1 > 0; \Delta_2 = C_3(C_1C_2 - C_3) - C_1^2C_4 = 0;$$

consequently, $C_4 = C_3(C_1C_2 - C_3)/C_1^2$. So, the characteristic equation becomes:

$$P_4(\tau) = \Big(\tau^2 + \frac{C_3}{C_1}\Big)\Big(\tau^2 + C_1\tau + \frac{\Delta_1}{C_1}\Big) = 0. \tag{2.8}$$

The roots of Eq.(2.8) are $\tau_{1,2} = \frac{1}{2}\Big(- C_1 \pm \sqrt{C_1^2 - 4\frac{\Delta_1}{C_1}}\Big)$, $\tau_{3,4} = \pm i\sqrt{\frac{C_3}{C_1}}$.

Now, to verify the transversality condition of Hopf bifurcation, we substitute $\tau(q) = \alpha(q) \pm i\alpha(q)$ into Eq.(2.8), and then calculating its derivative concerning the bifurcation parameter q, $P_4^{'} = (\tau(q)) = 0$, comparing the two sides of this equation and then equating their real and imaginary parts, we have:

$$\begin{aligned} \bar{\Psi}(q)\alpha_1^{'}(q) - \bar{\Phi}(q)\alpha_2^{'}(q) + \bar{C}(q) = 0, \\ \bar{\Phi}(q)\alpha_1^{'}(q) - \bar{\Psi}(q)\alpha_2^{'}(q) + \Gamma(q) = 0, \end{aligned} \tag{2.9}$$

where,

$$\begin{aligned}
\bar{\Psi}(q) &= 4(\alpha_1(q))^3 + 3C_1(q)(\alpha_1(q))^2 + C_3(q) + 2C_2(q)\alpha_1(q) - 12\alpha_1(q)\alpha_2^2(q) \\
&- 3C_1(q)(\alpha_2(q))^2, \\
\bar{\Phi}(q) &= 12(\alpha_1(q))^2\alpha_2(q) + 6C_1(q)\alpha_1(q)\alpha_2(q) + 2C_2(q)\alpha_2(q) - 4(\alpha_2(q))^3, \\
\bar{\Theta}(q) &= (\alpha_1(q))^3 C_1^{'}(q) + C_3^{'}(\mu)\alpha_1(q) + C_2^{'}(q)(\alpha_1(q))^2 + C_4^{'}(q) - 3C_1^{'}(q)\alpha_1(q)(\alpha_2(q))^2 \\
&- C_2^{'}(q)(\alpha_2(q))^2, \\
\bar{\Gamma}(q) &= 3(\alpha_1(q))^2\alpha_2(q)C_1^{'}(q) + C_3^{'}(q)\alpha_2(q) + 2C_2^{'}(q)\alpha_1(q)\alpha_2(q) - C_1{}'(q)(\alpha_2(q))^3.
\end{aligned}$$

Solving the linear system (2.9) by using Cramer's rule for the unknowns $\alpha_1^{'}(q)$ and $\alpha_2^{'}(\mu)$, gives that:

$$\begin{aligned}
\alpha_1^{'}(q) &= \frac{\bar{\Theta}(q)\bar{\Psi}(q) + \Gamma(q)\bar{\Phi}(q)}{(\bar{\Psi}(q))^2 + (\bar{\Phi}(q))^2}; \\
\alpha_2^{'}(\mu) &= \frac{-\Gamma(\mu)\bar{\Psi}(\mu) + \bar{\Theta}(\mu)\bar{\Phi}(\mu)}{(\bar{\Psi}(\mu))^2 + (\bar{\Phi}(\mu))^2}.
\end{aligned}$$

Hence, the transversality condition not being zero, if and only if:

$$\bar{\Theta}(\mu)\bar{\Psi}(\mu) + \bar{\Gamma}(\mu)\bar{\Phi}(\mu) \neq 0.$$

2.3.11 Gronwall lemma

Let $x(t)$ be a function that is satisfying the following differential inequality $x^{'} \leq ax + b$; $x(0) = x_0$ where a, b are constants. Then, for all $t \geq 0$ we have:

$$x(t) \leq x_0 e^{at} + \frac{b}{a}(e^{at} - 1); a \neq 0,$$

and,

$$x(t) \leq x_0 + bt; a = 0.$$

See [32] for more detail.

2.3.12 Descartes rule of signs

Let $p(x)$ define a characteristic polynomial with real coefficients and a nonzero constant term, with the terms being in descending powers of x. Hence, the number of positive real roots of $p(x) = 0$ either equals the number of variances in sign occurring in the coefficients of $p(x)$, or less than the number of variations by a positive even number. See [33] for more detail.

2.4 Summary

In this chapter, essential mathematical tools for analysing the solutions have been presented in detail, including local stability analysis, the Routh-Hurwitz criterion, the Lyapunov method, persistence and local bifurcations. They will be used in the next chapters to understand the behaviour of the proposed models and their solutions. The next chapter will review a selection of the relevant recent literature concerning modelling, analysis and numerical computation multi-species interaction models.

Chapter 3: Background and literature review

3.1 Introduction

A variety of mathematical models for multi-species interaction incorporating different factors to suit the varied environmental requirements is obtainable in the literature, such as predator-prey models, food chain models, food web models as well as models with a reserved zone. A selected historical background and a literature review regarding the dynamics of multi-component models is provided in this chapter. A practical model is one that meets the objectives, explains what is currently happening and predicts what will happen in future. Before presenting the literature, it is worth illustrating the general model simulating the first type of interaction between any two species. In the following, the most common form of the dynamics between any two-species having the prey-predator type of interaction will be described.

3.2 Prey predator model

It was just under a century ago that the very first endeavour to predict the existence of species and evolution was predicted mathematically. The physicist, Lotka [4], and mathematician, Volterra [5] were the first to explore that field. At that time, it constituted the dominant theme of the theoretical biology of population dynamics.

The dynamical system, which describes the interaction of two interacting species, can be broadly written as below:

$$\begin{aligned}\frac{dx}{dt} &= g_1(x) + f_1(x,y),\\ \frac{dy}{dt} &= g_2(y) + f_2(x,y),\end{aligned} \tag{3.1}$$

where, the population densities of the two interacting species at time t are denoted by $x(t)$ and $y(t)$. It is worth noting that measuring the rate of growth is divided into two terms, namely, $g_1(x)$, $g_2(y)$, representing the auto-growth/or decay part of the species in the absence of others and $f_1(x,y)$, $f_2(x,y)$ for the growth/decay due to the interactions between the two species. Since $f_1(x,y)$ and $f_2(x,y)$ account for the interactions between species that affect the growth rate of each in different ways, their ratio can be assumed as being a constant that differs from unity. Hence, consider that: $f_2(x,y) = kf_1(x,y)$, where, k is a constant then system (3.1) becomes:

$$\begin{aligned}\frac{dx}{dt} =& g_1(x) + f_1(x,y),\\ \frac{dy}{dt} =& g_2(y) + kf_1(x,y).\end{aligned} \tag{3.2}$$

The signs of g_1, g_2, f_1 and k depend on the way the species interact. With the reliance on the various formulae of $f1$, the system (3.2) represents different types of interactions. The classical type of interaction is called Lotka-Volterra, which describes the dynamic interaction between a prey population x and a predator one y, according to following differential equation:

$$\begin{aligned}\frac{dx}{dt} =& rx - axy,\\ \frac{dy}{dt} =& eaxy - hy,\end{aligned} \tag{3.3}$$

where, each term in the system (3.3) can be described as follows.

- $g_1(x) = rx$ represents the rate of growth of the prey population in the absence of predators. The rate of intrinsic of change of the prey (when the predator is absent) is represented by r. Thus, the prey population would increase exponentially in the absence of predators as: $x(t) = x_0 e^{rt}$.

- $kf_1(x,y) = eaxy$ is the production/growth rate of predator offspring, where (e) is the conversion rate of prey into predator.
- $g_2(y) = hy$ represents the predator's death rate in the absence of prey and h is the mortality rate per capita of a predator when prey is not present. Thus, predator decay exponentially in the absence of prey is: $y(t) = y_0 e^{-ht}$.

Over the last sixty years, several sophisticated models have been suggested to describe two or more interacting species based on the Lotka and Volterra models. This is done by considering the effects of age structure, crowding, time delay, switching, functional response and/or other factors [34–41]. The predator-prey relationships are considered as a type of interaction covering many kinds of natural enemies, such as parasitoid plants and herbivores, hosts and parasites, typical predators and their prey, etc. Despite the vital modelling work achieved by Lotka and Volterra, there has been far less quantitative-focused work on predation than on competition. This arises from the fact that it is far more challenging to integrate realistic biology into predation models in comparison to competing ones. Stability analysis for simple models often predict either the coexistence conditions or the competitive effect between the species. Whereas predator-prey models are more difficult to analyse as they are more complicated and it is often the case that their dynamics leads to periodic behaviour. In this thesis, the proposed models are concerned with the predator-prey type of interactions. The general form for modelling the continuous time predator-prey interactions has the following structure:

$$\begin{aligned} \frac{dx}{dt} &= g(x)x - f(x,y)y, \\ \frac{dy}{dt} &= ef(x,y)y - h(y)y, \end{aligned} \tag{3.4}$$

where, x and y represent the densities of prey and predator respectively. Moreover, $g(x)$ is the prey per-capita growth rate in the absence of predation and $f(x,y)$, represents the functional response in both the prey and predator equations. e is the conversion/growth rate of the consumed prey into the new predator, and $h(y)$ is the natural death-rate of the predator in the absence of prey. The dynamics of the two varieties in predator-prey models are based on the "trophic function" $f(x,y)$, which is represented in the prey equation as a functional response. This means a change in the prey's densities, which attack per unit of time per predator, while in the predator equation called numerical response (predator growth rate as a function of consumption of prey). The functional responses applied in ecological modelling, can be commonly classified into three forms, namely: prey-dependent, predator-dependent and ratio-dependent [42]. The most common trophic/ predation functions that are used in ecological modelling are described as below.

1. **Prey-Dependent Functions:**

   The term prey-dependent describes the consumption rate by each predator which only a function of prey that is $f(x,y) = f(x)$. In fact, there are many classifications of prey-dependent functional responses can be extensively found in the literature [43]. The most common types are identified as follows.

   - **Lotka-Volterra Type:**

     In this type, for each of individual predator, the rate of consumption grows linearly with the prey. Hence, this type of functional response can be written as:$f(x) = ax; x \geq 0$, where, $a > 0$ is the rate of consumption of prey by a predator.

   - **Holling Type-I:**

     This type is like the well-known Lotka-Volterra type, but with a fixed maximum or upper limit γ, being:

     $$f(x) = \begin{cases} ax & 0 < x < \alpha \\ \gamma & \alpha \leq x \end{cases} \tag{3.5}$$

     where, α is the constant amount of prey at which the predator overfeeds at γ.

     Despite the simplicity of the Type-I and Lotka-Volterra functional responses, they are still regularly used for manageable ecological models.

- **Holling Type-II Functional Response:**

  With this type, the consumption rate of each consumer rises at a reducing rate with prey density until it becomes constant at the saturation level. It is asymptotically approaching the maximal value $a = 1/h$, which is defined as:

  $$f(x) = \frac{Ax}{1 + Ahx} = \frac{ax}{b + x}, \tag{3.6}$$

  where, A represents the search rate, h is the time spent on the handling of one prey; a is the maximum attack/harvest rate, and $b = 1/Ah$ is the half saturation level, such that $f(b) = a/2$. In addition, Eq.(3.6) is one of the most widely deployed ones among ecologists, which is also known as the Michaelis-Menten type, due to it being proposed by Michaelis and Menten [44].

- **Holling Type-III Functional Response:**

  n this type, the consumption rate of an individual predator initially accelerates and then decelerates towards saturation level, which can be defined as:

  $$f(x) = \frac{Ax^2}{1 + Ahx^2} = \frac{ax^2}{b + x^2}, \tag{3.7}$$

2. **Ratio-Dependent Functions:**

   The prey-dependent type of functional responses does not integrate the predator abundance in its formula. Hence, Ginzberg and Arditi [45] suggested a new type of functional response known as ratio-dependent, in which the rate of prey feeding per predator depends on the ratio between both their densities, instead of depending only on that of the prey density. Their functional response can be written by using the ratio (x/y) instead of (x) in a Holling type-II functional response as follows:

   $$f(x, y) = \frac{A(x/y)}{1 + Ah(x/y)} = \frac{ax}{by + x}. \tag{3.8}$$

3. **Predator-Dependent Functions:**

   In this type, the functional response is dependent also on the densities of both the prey and predator. Mathematically, both of the prey-dependent and ratio-dependent functional responses could be considered as a limitation case for the general type of predator-dependent functional response. It has been noticed that high predator density leads to more recurrent encounters between predators [46, 47]. The first use of a predator-dependent functional response goes back to DeAngelis et al [48] and Beddington [49], which is now known as the DeAngelis-Beddington functional response and has the following form:

$$f(x,y) = \frac{ax}{\beta y + \alpha h x + 1} = \frac{ax}{by + x + c}, \tag{3.9}$$

   where, h describes the prey handling time, and β is an empirical constant, which can be defined as the product of the predator encounter rate and predator handling time. The main idea of this form is that the predators are wasting their time in handling prey as well as in dealing with other predators. Furthermore, Eq.(3.9) is ratio-dependent with small values of c and prey-dependent when b is minimal. In other words, ratio-dependence and prey–dependence are at opposite ends of the spectrum of predator-dependent functional/numerical responses that represent the general functions both of prey and predator densities, i.e.

$$f(x) \Leftarrow f(x,y) \Rightarrow f(x/y).$$

3.3 Logistic growth

After Lotka and Volterra formulated their model, Warder [50] presented his initial studies on under crowding dynamics, and it was widely acknowledged at that time that the growth of a single species has the following formula:

$$\frac{dN}{dt} = rN, \tag{3.10}$$

where, r is the growth rate per capita, N is the species' density. This equation is remaining true where the populations are not restricted by resources. With resource limitations, the ecologists Pierre F. Verhulst and biologist Raymond Pearl [51] modified (3.10) to the logistic of each species counting the intraspecific completion for resources as being:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{k}\right), \tag{3.11}$$

where, k represents the carrying capacity (maximum population density) that the environment can support. For high population densities, the per capita population growth rate is going to be negative. The logistic model has a unique globally stable positive equilibrium at the carrying capacity k. As a result, (3.11) has become a familiar with the concept of negative density, overcrowding and population limitation resources [52].

3.4 The behaviour of multi-species interactions

In the field of mathematical biology, the ecosystem models of predator-prey have been extensively discussed in the literature. The first development of a simple model describing the interaction between populations goes back to Lotka [4] and Volterra [5]. They first introduced their prey-predator system, which is a food chain of length two, as stated in Eq.(5.2). They demonstrated that for any initial condition the simple food chain models can permanently oscillate. Contemporary theorists now consider food chain models with lengths $n; n \geq 2$, which contain n interspecific interactions of populations consisting of n trophic levels, whereby each population except for the lowest gets its resources from those on the lower trophic levels. The resources are passed to the next population along a linear chain. A network of many intersecting food chains is also called a food web. Many food-chain/web models that have appeared are of the Lotka-Volterra type, with different terms for a functional response. For example, the consideration models in [53–57] include the Lotka-Volterra food-chain as special cases. Regarding general food chains with arbitrary length, early theoretical studies [58–60] were based on local behaviour stability. It has been noted from these analytical studies that even though a food chain model has a simple structure, it has very complicated dynamics. Moreover, Hastings and Powell [61] proposed a model of a food chain including a Holling type I functional response. It was noted that for long-term behaviour the proposed model exhibits to chaotic behaviour when reasonable biological parameter values have been chosen. After the appearance of chaos in their model, they concluded that the chaotic dynamics might be widespread in food web models. Furthermore, in [62] the dynamics of a food chain model of three species with Holling type-I and type-III functional responses for both of predator and super predator, respectively, were studied. The results elicited that the solutions had periodic behaviour around the steady states and possessed Hopf bifurcations. The persistence of the top species in their models is sensitively dependent on several sets of parameters, such that this species at specific values decreases over time to eventually dying out. Chaudhuri and Kar [63] proposed a model of two competing prey and one predator in which the former is affected by both of the existence of the latter and harvesting. The feeding rate of the predator in their model increases linearly with the density of prey and by using a Lyapunov method, they established the conditions for global stability of the system. They also recognised the requirements policy to get the optimal harvest by using Pontryagin's maximal principle. Green [64] formulated a system of two prey-one predator in which the former are replenished following a linear type of rate, instead of a logistic one. It was found out that the combined supply of prey to the predator a stabilise the system. This study also involved investigating some behaviour, such as limit cycles and chaos; however, the model does not consider either prey harvesting or competition amongst prey. Vlastmil and Eisner [65] proposed a tri-trophic food chain composed of a logistic supply of prey, a classical Lotka-Volterra functional response for prey and predator, and a Holling type-II functional response for predator and superpredator. For the study, the extinction of the lower resource due to the competition of prey was exhibited. Furthermore, the numerical analysis showed that by using the control parameter, it is possible to break the stable behaviour of the system, thus driving it into an unstable state. In another study of [66], a food chain model with a ratio-dependent functional response was considered. In this work, the population was separated into three different classes, namely: prey, predator and top-predator. In this model, the intra-specific competition among the predators has been incorporated. Moreover, the system exhibits saddle-node bifurcation, and Hopf bifurcation for some choices of the applicable parameters. Kabuye [67] proposed a four-species (lions, hyaenas, Ugandan kobs and waterbucks) model based on the interactions among them in the Queen Elizabeth National Park. The kobs and the waterbucks were the prey, while the lions and hyaenas were the predators. The author recognised the conditions for the stable existence of all the species by using the Routh-Hurwitz criteria. Moreover, he showed that how cooperation, as well as interspecific and intraspecific competition among the species, affected the dynamics around the equilibrium in the system. This system was based on the standard linear type predator-prey competition model, and terms such as logistic growth with carrying capacity and functional responses have been excluded. While, Edwin [68] proposed a three-species (lions, buffalo and Ugandan kobs) predator-prey model also based on the interactions among them in the Queen Elizabeth National Park. The kobs and buffalo were the prey, while the lions were the predator. The researcher exhibited that the three species could co-exist if one of the preys (Uganda Kobs) were not harvested. While, the numerical simulation result of the model shows the dynamical behaviour of the system could be changed from a stable to a limit cycle when values of some parameters such as natural death rate of the predator, the harvesting rate, and food conversion rate of the predator are varied. This system was based on Holling Type II functional response to one prey, and ratio-dependent functional response to the other prey. Terms such as logistic growth with carrying capacity and functional responses have been excluded. Furthermore, Schaffer and collaborators (Gilpin and Guckenheimer) [69–72] produced a much more significant complicated dynamics than ecologists had earlier believed could appear in a model with three species or more, which is called chaos. Later, this behaviour became familiar to most ecologists, such as May [73] and Schaffer and Kot [74] in that they investigated the arising of chaos in ecological models. Another exploration by Gilpin [75] confirmed that a system of two competing prey and one predator could exhibit chaotic behaviour.

One approach to studying an ecological community starts with the principles of a food web. However, theoretical studies of such webs have to contend with the question of how to combine a three number or more of interacting species. One approach to this type of research involves assuming the "building blocks" through which the species interacting are in a pairwise fashion see the influential books of May and Pimm [76, 77]. That is, the dynamic behaviour of the entire interacting community is assumed to arise from the coupling of these interacting pairs. Hence, this approach has the significant advantage that it is tractable for theoretical studies. Furthermore, the considerable intuition that researchers have developed over the decades with two-species models could also be applied to community food web questions. However, the dynamic behaviour that could be critical to organism function might emerge only through the interaction of three or more species. To understand plant-insect interactions, Price et al. [78] put forward a substantial case that this interaction must be based on three trophic-level structures or more. Also, the influential approaches of Paine [79] in relation to marine intertidal communities, determined the importance of higher trophic levels to lower ones in the food web model and similar results have arisen from experiments in freshwater.

3.5 The refuge in population dynamics

One of the most essential parts of biological activities is the biosphere, which is habitually responsible for the changes in environment and ecology. The interaction and co-existence of biological species have been widely studied via mathematical models by many investigators [80–84].

A variety of biological species has been taken to extinction, due to some causer such as overexploitation, over-predation, environmental pollution, mismanagement of the habitat etc. Regarding which, several researchers have reported that in many situations there needs to be a constant amount of prey protected from the effect of predation by a refuge. Accordingly, a number of mathematical models and investigation incorporate refugia, i.e. areas in which the prey survive and are not successfully suppressed by the predator. Moreover, these are aimed at decreasing the interaction between species [85].

The fundamental role of refuges/reserve area in the predator-prey model has received significant attention and has also been pointed to by several researchers [86–88] for studying the behaviour of coexistence of interacted species over the long-term. In particular, Collings [89] studied precisely the behaviour of a predator-prey system in the case of the existence of refuge to protect a constant amount of prey, with temperature dependent parameters appropriately chosen for a mite interaction with a fruit species. His study showed that the existence of a temperature interval such that the quantity of the refuge increases dynamically destabilises the proposed system. Furthermore, the interaction is not as much as likely to persist all the species on the part of this interval. Hence, the prey and predator have densities that are lower compared to when there is no refuge available. Krivan suggested a model of a predator-prey system for investigating the effects of the optimal antipredator behaviour of the prey. He detected from the behaviour of this system that it leads to a reduction of the oscillations that consequently, results in the persistence of all of the population densities [90]. Chattopadhyay et al. [91] suggested a predator-prey model with some cover for the prey species. It was demonstrated that the global stability of this model around the positive steady state does not mean that there is permanence of the system. Furthermore, Kar [92] studied a harvest of the predator-prey model together with a prey refuge. It was observed that using the harvesting effect as control, is more likely to break the cyclic behaviour of the system. However, in the investigations above, the dynamic behaviour of living prey together with the predator in the unreserved area has not been considered explicitly. In [93], the effects of prey protection on the behaviour of a predator-prey interaction with Holling type I functional responses are formulated. The results exhibited that the impact of having a refuge increases the prey population, while decreasing the density of the predators. It was also that the effect of the refuge could stabilise the proposed model, and destabilise it under an inadequate set of conditions. Furthermore, in [94] the effect of a prey refuge in the predator-prey model was analysed under the assumption that the rate of prey movement to the protection area is proportional to the density of predator. Subsequently, the results proved that the prey takes advantage of the protected area by increasing their density, while the predators decrease as refuge usage grows.

In fishery resources, the reserved zone plays a vital role in the aquatic environment by protecting them from overexploitation [95]. Regarding which, Dubey [96] proposed a mathematical model for studying the dynamic behaviour of a fishery resource in an aquatic environment involving two areas, namely, a free fishing zone and a reserve zone, where fishing was strictly not allowed. It was shown that the fish populations could be maintained at a proper equilibrium level in the habitation, even if the fishery is exploited incessantly in the unprotected area. Dubey [97] suggested a model of a predator-prey in the case of the existence of a reserved area. It was assumed that the habitation was also divided into two separate zones, namely: reserved and unreserved zones. The predators were not allowed to enter the last region, and they consumed the prey in the unreserved area according to the classic functional response of the Lotka-Volterra type. In his study, he concluded that the existence of the prey refuge takes advantage to stabilising the proposed model. Recently, Mukherjee [98], formulated and analysed a predator-prey model coupled with a reserved zone of prey and with a Holling type-II functional response for a predator, which entirely depended on the prey in the unreserved area. It was shown how the existence of the reserved zone fosters the stabilising of the proposed system. Later on, Agarwal and Pathak [99] proposed and analysed a system of two prey and one predator in which one of the former spread into two environment patches consisting both of reserved and unreserved areas of prey. Again, both studies confirmed how the reserved zone is responsible for stabilising their models.

Keeping that in view, in this thesis the idea of the reserved zone is adopted and developed to a new mathematical model by incorporating an additional equation. This equation represents the more general predator (top predator) in an unreserved area with the functional response of linear type which is coupled to a food chain predation process. Then, the coexistence and stability behaviour of the new system is studied in the next chapter in detail.

3.6 Summary

In this chapter, some types of Holling's interaction functions between species have been presented. The models, which describe the interaction between populations, have been presented in detail. Moreover, a selection of the relevant recent literature regarding multi-species models has been reviewed. It was shown that ecological situations consisting of three or more species have very complicated dynamics. In addition, dynamics behaviour, such as cycles, instability and chaos in several predator-prey models, has been explained. Further, the notion of refuge in population behaviour has been considered in one of the population species as a means of stabilising the behaviour of prey-predator interactions. That is, as a from the reviewed studies, it has emerged that the idea of refuge could be vital in populations, in particular, as a stabilising force in predator and prey population dynamics, being applicable to address some practical ecosystem challenges.

Chapter 4: The effect of the reserve zone on the behaviour of a food chain model

4.1 Introduction

In this chapter, the modelling of a food chain prey-predator model with reserve zone effect on the prey is proposed. A variety of analytical methods and tools are used to study the existence, uniqueness, boundedness, local stability, local bifurcation, and persistence of the solutions of the proposed model. The global dynamics of this model are investigated analytically as well as numerically. The model shows rich dynamics in the space of non-negative solutions. In particular, the dynamics around the different equilibrium points have been studied in detail, such as the strictly positive equilibrium, the equilibrium for which only the top predator vanishes and the remaining components are strictly positive, the equilibrium with two vanishing components and the trivial equilibrium. The long-term behaviour of the system has been studied, and conditions for persistence have been derived. Finally, the role of the reserved zone has been investigated in detail to achieve the coexistence of all species.

4.2 Mathematical model

Suppose there is a food chain consisting of prey, predator and a top predator, where the following assumptions have been made to formulate the model.

- The prey population has been separated into two classes: $x(t)$, which is the density of the prey in the non-reserved zone and $y(t)$, the density of the prey in the reserve region when predators are not allowed to enter.
- $z(t)$, $w(t)$ are the densities of predator and top predator species at a particular time, respectively.

Under the above assumptions, the model can be presented by the following system of differential equations:

$$\begin{aligned}
\frac{dx}{dt} &= rx\Big(1-\frac{x}{k}\Big) - \sigma_1 x + \sigma_2 y - \beta_1 xz = f_1(x,y,z,w),\\
\frac{dy}{dt} &= sy\Big(1-\frac{y}{l}\Big) + \sigma_1 x - \sigma_2 y = f_2(x,y,z,w),\\
\frac{dz}{dt} &= \beta_2 xz - \beta_0 z - \gamma_1 zw = f_3(x,y,z,w),\\
\frac{dw}{dt} &= \gamma_2 zw - \alpha w = f_4(x,y,z,w).
\end{aligned} \tag{4.1}$$

Here, the model (4.1) has been analysed with the initial conditions $x(0) \geq 0$, $y(0) \geq 0$, $z(0) \geq 0$ and $w(0) \geq 0$. $p(x) = \beta_1 x$ and $q(z) = \gamma_1 z$ are the Lotka-Volterra type of functional responses. All parameters of the model system (4.1) are assumed to be positive and described as follows.

k and l are the carrying capacities of the prey in the unreserved and reserved zone, respectively, with intrinsic growth rates r and s; σ_1 is the migration rate coefficient of the prey species from the unreserved to reserved area and σ_2 the migration rate coefficient of the prey species from the reserved to unreserved zone; β_1 is the attack rate of the predator on the prey in the unreserved region; β_2 is the conversion rate of the prey in the unreserved zone to a predator; γ_1 is the attack rate of the top predator on the predator; γ_2 is the conversion rate of the predator to the top predator; and finally, β_0 and α represent the predator and top predator's natural death rate, respectively .

Apparently, the functions on the right-hand side in the system (4.1) are continuously differentiable functions on $\mathbb{R}^4_+ = \big\{(x, y, z, w), x \geq 0, y \geq 0, z \geq 0, w \geq 0\big\}$ and hence, they are Lipschitzian. Therefore, a solution to the system (4.1) exists, which is unique. Further, all the solutions of the model (4.1) with any non-negative initial conditions are bounded, as shown in the following section.

4.3 Boundedness

Theorem 4.3.1 *Assume that the conditions $\beta_1 \geq \beta_2$ and $\gamma_1 \geq \gamma_2$ hold, then all the solutions of the system (4.1) which initiate in $\mathbb{R}^4_+$ are bounded.*

Proof Let $(x(t), y(t), z(t), w(t))$ be an arbitrary solution of the system (4.1) with a non-negative initial condition. Then for $U(t) = x(t) + y(t) + z(t) + w(t)$, we have

$$\frac{dU}{dt} = rx - \frac{rx^2}{k} + sy - \frac{sy^2}{l} - (\beta_1 - \beta_2)xz - (\gamma_1 - \gamma_2)zw - \beta_0 z - \alpha w.$$

Hence, according to the assumptions of the theorem, the following is obtained:

$$\begin{aligned} \frac{dU}{dt} &\leq rx - \frac{rx^2}{k} + sy - \frac{sy^2}{l} - \beta_0 z - \alpha w \\ \frac{dU}{dt} + \xi U &\leq 2rx - \frac{rx^2}{k} + 2sy - \frac{sy^2}{l}, \end{aligned}$$

where, $\xi = \min\{r, s, \beta_0, \alpha\}$, then

$$\begin{aligned} \frac{dU}{dt} + \xi U &\leq rk - \frac{r}{k}\big(x - k\big)^2 + sl - \frac{s}{l}\big(y - l\big)^2 \\ &\leq rk + sl = \mu. \end{aligned}$$

Applying Gronwall's Inequality (see Subsection 2.3.11), the following is obtained:

$$0 \leq U\big(x(t), y(t), z(t), w(t)\big) \leq \frac{\mu}{\xi}\big(1 - e^{-\xi t}\big) + U(0)e^{-\xi t}.$$

Therefore,

$$0 \leq \limsup_{t\to\infty} U\big(t\big) \leq \frac{\mu}{\xi}.$$

Hence, all the solutions of the system (4.1) that are initiated in $\mathbb{R}^4_+$ are attracted to the region $\Omega = \big\{\big(x, y, z, w\big) \in \mathbb{R}^4_+ : U = x + y + z + w \leq \frac{\mu}{\xi}\big\}$ under the given conditions. Thus, these solutions are bounded, and the proof is complete. ∎

Remark

According to the above proof, the following can be noted:

- Since $\limsup_{t\to\infty} U\big(t\big)$ in the above theorem is independent of the initial condition, thus, in this case, the whole system can be said to be uniformly bounded.
- System (4.1) is dissipative (see Subsection 2.3.1).
- Since β_1 represents the depletion rate coefficient of prey due to its intake by the predator and β_2 denotes the growth rate coefficient of the predator due to its interaction with its prey, it is natural to assume that $\beta_1 \geq \beta_2$, and by the same argument $\gamma_1 \geq \gamma_2$ [97].

4.4 Positive invariance

Let $X = \big(x, y, z, w\big)^T \in \mathbb{R}^4$ and, $f(X) = \big[f_1(X), f_2(X), f_3(X), f_4(X)\big]^T$ where, $f(X) : \mathbb{R}^4_+ \to \mathbb{R}^4$ and $f \in C^{\infty}_+(\mathbb{R}^4_+)$. Then system (4.1) becomes:

$$\dot{X} = f(X), \tag{4.2}$$

with $X(0) = X_0 \in \mathbb{R}^4_+$. It is clear for any $X(0) \in \mathbb{R}^4_+$, such that $X_i = 0$, then $[f_i(X)]_{x_i=0} \geq 0$ (for $i = 1, 2, 3, 4$). Now, any solution of the Eq.(4.2) with $X_0 \in \mathbb{R}^4_+$, say $X(t) = X(t, X_0)$, is such that $X(t) \in \mathbb{R}^4_+$ for all $t > 0$ [100].

Lemma 2 ***(Main assumption)*** *it will be assumed that $r > \sigma_1$ and $s > \sigma_2$.*

Proof It is easy to validate that if $\sigma_2 = 0$, which means that there is no migration from the reserved to unreserved area, and $r - \sigma_1 < 0$, then $dx/dt < 0$. Similarly, when $\sigma_1 = 0$ and $r - \sigma_2 < 0$, then $dy/dt < 0$. The interest here lies in the case where dx/dt and dy/dt can be positive. Hence, the conditions that have been stated in the lemma will be taken as the main assumption. ■

In the following, the existence of the equilibrium points of the system (4.1) will be elucidated.

4.5 Existence of equilibria

The food chain prey-predator model with a reserved zone given by the system (4.1) has four nonnegative equilibrium points, namely:

- $F_0 = (0, 0, 0, 0)$ is the vanishing fixed point;
- $F_1 = (\hat{x}, \hat{y}, 0, 0)$ is the planar fixed point;
- $F_2 = (\bar{x}, \bar{y}, \bar{z}, 0)$ is the top predator-free fixed point;
- $F_3 = (x^*, y^*, z^*, w^*)$ is the interior fixed point.

The equilibrium $F_0 = (0, 0, 0, 0)$ obviously exists and the existence of F_1, F_2, and F_3 are now shown in the following.

4.5.1 The existence of the planar equilibrium point

The equilibrium point $F_1 = (\hat{x}, \hat{y}, 0, 0)$ exists in the interior of $\mathbb{R}^2_+$ of the xy- plane, if and only if, $\hat{x}$ and $\hat{y}$ represent the positive solution of the following set of algebraic equations:

$$r\left(1 - \frac{x}{k}\right) - \sigma_1 + \frac{\sigma_2 y}{x} = 0, \tag{4.3}$$

$$s\left(1 - \frac{y}{l}\right) - \sigma_2 + \frac{\sigma_1 x}{y} = 0. \tag{4.4}$$

From equation (4.3),

$$y = \frac{1}{\sigma_2}\Big[\frac{rx^2}{k} - (r-\sigma_1)x\Big]. \tag{4.5}$$

Now, substituting the value of y into Eq.(4.4), a little algebraic manipulation yields:

$$ax^3 + bx^2 + cx + d = 0, \tag{4.6}$$

where,

$$\begin{aligned} a &= \frac{sr^2}{l\sigma_2^2 k^2} > 0, \\ b &= \frac{-2rs(r-\sigma_1)}{lk\sigma_2^2} < 0, \\ c &= \frac{s(r-\sigma_1)^2}{l\sigma_2^2} - \frac{r(s-\sigma_2)}{k\sigma_2}, \\ d &= \frac{(r-\sigma_1)(s-\sigma_2)}{\sigma_2} - \sigma_1. \end{aligned}$$

Hence, by using Descartes rule of signs (see Subsection 2.3.12), Eq.(5.5) has a unique positive solution, say $x = \hat{x}$, if the following inequalities hold:

$$\frac{s(r-\sigma_1)^2}{l\sigma_2^2} < \frac{r(s-\sigma_2)}{k\sigma_2},$$
$$(r-\sigma_1)(s-\sigma_2) < \sigma_1\sigma_2.$$

Knowing the value of $\hat{x}$, the value of $\hat{y}$ is computed from Eq.(5.4). It should also be noted that for $\hat{y}$ to be positive, the following must be the case:

$$\hat{x} > \frac{k}{r}(r-\sigma_1). \tag{4.7}$$

Similarly, the value of $\hat{x}$ can be determined from Eq.(4.4) as:

$$\hat{x} = \frac{1}{\sigma_1}\Big[\frac{s\hat{y}^2}{l} - (s-\sigma_2)\hat{y}\Big].$$

While, $\hat{y}$ is a positive root that can be determined from Eq.(4.3), so that:

$$\hat{y} > \frac{l}{s}(s-\sigma_2). \tag{4.8}$$

Consequently, conditions (4.7) and (4.8) represent the necessary conditions for the existence of the planar equilibrium point F_1 in the interior of $\mathbb{R}^2_+$ of the xy-plane.

4.5.2 The existence of the top predator-free equilibrium point

The equilibrium point F_2 exists in the interior of $\mathbb{R}^3_+$ of the xyz-plane, if and only if, $\bar{x}, \bar{y}$ and $\bar{z}$ are the positive roots of the following set of algebraic equations:

$$\begin{aligned}
&r\Big(1-\frac{x}{k}\Big)-\sigma_1+\frac{\sigma_2 y}{x}-\beta_1 z=0,\\
&s\Big(1-\frac{y}{l}\Big)-\sigma_2+\frac{\sigma_1 x}{y}=0,\\
&\beta_2 x-\beta_0=0.
\end{aligned}$$

Solving the above equations, gives that:

$$\begin{aligned}
\bar{x}&=\frac{\beta_0}{\beta_2},\\
\bar{y}&=\frac{l}{2s\beta_2}\Big[l\beta_2(s-\sigma_2)+\sqrt{l^2\beta_2^2(s-\sigma_2)^2+4sl\beta_0\beta_2\sigma_1}\Big],\\
\bar{z}&=\frac{\beta_2}{\beta_0\beta_1}\Big[\frac{\beta_0(r-\sigma_1)}{\beta_2}-\frac{r\beta_0^2}{k\beta_2^2}+\sigma_2\bar{y}\Big].
\end{aligned}$$

Undoubtedly, for $\bar{z}$ to be positive, the following condition must holds:

$$\Big[\frac{\beta_0(r-\sigma_1)}{\beta_2}-+\sigma_2\bar{y}\Big]>-\frac{r\beta_0^2}{k\beta_2^2}, \tag{4.9}$$

It is clear that condition (4.9) gives a threshold value k of the carrying capacity in the free access area. Thus, the predator keeps surviving. Also, it should be noted that condition (4.9) could fail when k is small enough and hence, the existence of the top predator-free fixed point is violated.

4.5.3 The existence of the positive equilibrium point

The positive equilibrium point F_3 exists in the interior of $\mathbb{R}^4_+$, if and only if, x^*, y^*, z^* and w^* are the positive solutions of the following set of equations:

$$r\left(1-\frac{x}{k}\right)-\sigma_1+\frac{\sigma_2 y}{x}-\beta_1 z=0, \tag{4.10}$$

$$s\left(1-\frac{y}{l}\right)-\sigma_2+\frac{\sigma_1 x}{y}=0, \tag{4.11}$$

$$\beta_2 x-\beta_0-\gamma_1 w=0, \tag{4.12}$$

$$\gamma_2 z-\alpha=0. \tag{4.13}$$

From the above list of equations, the following is obtained:

$$y=\frac{l}{2s}\left[(s-\sigma_2)+\sqrt{(s-\sigma_2)^2+\frac{4s\sigma_1 x}{l}}\right], \tag{4.14}$$

$$z^*=\frac{\alpha}{\gamma_2}, \tag{4.15}$$

$$w=\frac{\beta_2 x-\beta_0}{\gamma_1}. \tag{4.16}$$

By substituting the values of y and z in Eq.(4.10), a little algebraic manipulation yields:

$$ax^3+bx^2+cx+d=0, \tag{4.17}$$

where,

$$\begin{aligned}
a&=\left(\frac{-r}{k}\right)^2>0,\\
b&=\frac{2r}{k}\left((r-\sigma_1)-\frac{\beta_1\alpha}{\gamma_2}\right),\\
c&=\frac{-2r}{k}\left(\frac{\sigma_2 l}{2s}(s-\sigma_2)\right)+\left((r-\sigma_1)-\frac{\beta_1\alpha}{\gamma_2}\right)^2,\\
d&=-\left[\frac{\sigma_2 l}{s}\left(s-\sigma_2\right)\left((r-\sigma_1)-\frac{\beta_1\alpha}{\gamma_2}\right)+\frac{\sigma_1\sigma_2^2 l}{s}\right].
\end{aligned}$$

By using Descartes rule of signs, Eq.(5.11) has a unique positive solution $x=x^*$, if the following inequality

$$\left(r-\sigma_1\right)>\frac{\beta_1\alpha}{\gamma_2}, \tag{4.18}$$

holds. Knowing the value of x^*, the values of y^* and w^* can be computed from

Equations (5.18) and (4.16), respectively. It should also be noted that for w^* to be positive, the following must be true:

$$\beta_2 x^* > \beta_0. \tag{4.19}$$

4.6 Local stability of the equilibrium points

In this section, the local dynamic behaviour of the system (4.1) around each of the above equilibrium points is discussed by making use of the eigenvalue method. The Jacobian matrix of system (4.1) at any point is given by:

$$J = \begin{bmatrix} r - \sigma_1 - \dfrac{2rx}{k} - \beta_1 z & \sigma_2 & -\beta_1 x & 0 \\ \sigma_1 & s - \sigma_2 - \dfrac{2sy}{l} & 0 & 0 \\ \beta_2 z & 0 & \beta_2 x - \beta_0 - \gamma_1 w & -\gamma_1 z \\ 0 & 0 & \gamma_2 w & \gamma_2 z - \alpha \end{bmatrix}, \tag{4.20}$$

and, the eigenvalues of the resulting matrix are computed as follows:

4.6.1 Local stability behaviour of F_0

In the following lemma, it is shown that F_0 is always a saddle point.

Lemma 3 *The vanishing equilibrium point* $F_0 = (0, 0, 0, 0)$ *is a saddle point in* $\mathbb{R}^4_+$.

Proof First, the Jacobian matrix of the system (4.1) at F_0 can be written by:

$$J(F_0) = \begin{bmatrix} r - \sigma_1 & \sigma_2 & 0 & 0 \\ \sigma_1 & s - \sigma_2 & 0 & 0 \\ 0 & 0 & -\beta_0 & 0 \\ 0 & 0 & 0 & -\alpha \end{bmatrix} \tag{4.21}$$

Then, it is easy to verify that, the eigenvalues of $J(F_0)$ satisfy the following relations:

$$\mathrm{T} = \lambda_{01} + \lambda_{02} = (r - \sigma_1) + (s - \sigma_2) > 0, \tag{4.22}$$

$$\mathrm{D} = \lambda_{01}.\lambda_{02} = (r - \sigma_1)(s - \sigma_2) - \sigma_1\sigma_2, \tag{4.23}$$

$$\lambda_{03} = -\beta_0 < 0, \tag{4.24}$$

$$\lambda_{04} = -\alpha < 0, \tag{4.25}$$

where, $\lambda_{0i} \quad (i = 1, 2, 3, 4)$ represent the eigenvalues that describe the dynamics in the directions of their eigenvectors. Note that, according to Eq.(4.23), the eigenvalues λ_{01} and λ_{02} are positive, provided that:

$$(r - \sigma_1)(s - \sigma_2) > \sigma_1\sigma_2,$$

and then, F_0 is the unstable point in the interior of $\mathbb{R}^2_+$ of the xy-plane. However, λ_{01} and λ_{01} have opposite signs, provided that:

$$(r - \sigma_1)(s - \sigma_2) < \sigma_1\sigma_2.$$

Hence, F_0 is a saddle point in the interior of $\mathbb{R}^2_+$ of the xy-plane. Further, according to Eqs. (4.24)-(4.25), the equilibrium point F_0 is a saddle point in the interior of $\mathbb{R}^4_+$. It should be also noted that the formulae of λ_{01} and λ_{02} are given by the following equations:

$$\lambda_{01,02} = \frac{\mathrm{T} \pm \sqrt{(\mathrm{T})^2 - 4\mathrm{D}}}{2}. \tag{4.26}$$

■

4.6.2 Local stability behaviour of F_1

In the following lemma, the local behaviour of the planar fixed point F_1 is shown.

Lemma 4 *The planar equilibrium point* $F_1 = (\hat{x}, \hat{y}, 0, 0)$ *is locally asymptotically stable in* $\mathbb{R}^4_+$*, whenever:*

$$\beta_2\hat{x} < \beta_0, \tag{4.27}$$

holds.

Proof The Jacobian matrix of system (4.1) at the equilibrium point F_1 is given by:

$$J(F_1) = \begin{bmatrix} r-\sigma_1-\frac{2r\hat{x}}{k} & \sigma_2 & -\beta_1\hat{x} & 0 \\ \sigma_1 & s-\sigma_2-\frac{2s\hat{y}}{l} & 0 & 0 \\ 0 & 0 & \beta_2\hat{x}-\beta_0 & 0 \\ 0 & 0 & 0 & -\alpha \end{bmatrix} \tag{4.28}$$

Straightforward computations show that the eigenvalues of the Jacobian matrix $J(F_1)$ satisfy the following relations:

$$\lambda_{11}+\lambda_{12} = -\Big(\frac{\sigma_2\hat{y}}{\hat{x}}+\frac{r\hat{x}}{k}+\frac{\sigma_1\hat{x}}{\hat{y}}+\frac{s\hat{y}}{l}\Big) < 0, \tag{4.29}$$

$$\lambda_{11}.\lambda_{12} = \left(\frac{rs(\hat{x})^2(\hat{y})^2+sk\sigma_2(\hat{y})^3+r\sigma_1(\hat{x})^3}{kl\hat{x}\hat{y}}\right) > 0, \tag{4.30}$$

$$\lambda_{13} = \beta_2\hat{x}-\beta_0, \tag{4.31}$$

$$\lambda_{14} = -\alpha < 0, \tag{4.32}$$

where, $\lambda_{1i} \quad (i=1,2,3,4)$ represent the eigenvalues that describe the dynamics in the directions of their eigenvectors. Note that, according to equations (4.29)-(4.32), all the eigenvalues of $J(F_1)$ have negative real parts and hence, F_1 is locally asymptotically stable in $\mathbb{R}^4_+$, if and only if, condition (4.27) holds. However, it is a saddle point in the interior of $\mathbb{R}^4_+$, if the condition (4.27) is violated. ■

4.6.3 Local stability behaviour of F_2

In the following lemma, the local behaviour of the top predator-free fixed point F_2 is shown.

Lemma 5 *The top predator-free equilibrium point* $F_2=(\bar{x},\bar{y},\bar{z},0)$ *is locally asymptotically stable in* $\mathbb{R}^4_+$ *whenever*

$$\gamma_2\bar{z} < \alpha. \tag{4.33}$$

holds.

Proof The Jacobian matrix of the system (4.1) at the equilibrium point $F_2 = (\bar{x}, \bar{y}, \bar{z}, 0)$ can be written as:

$$J(F_2) = \begin{bmatrix} a_{11} & a_{12} & a_{13} & 0 \\ a_{21} & a_{22} & 0 & 0 \\ a_{31} & 0 & 0 & a_{34} \\ 0 & 0 & 0 & a_{44} \end{bmatrix} \tag{4.34}$$

where,

$$a_{11} = -\Big(\frac{\sigma_2\bar{y}}{\bar{x}} + \frac{r\bar{x}}{k}\Big) < 0; a_{12} = \sigma_2 > 0; a_{13} = -\beta_1\bar{x} < 0; a_{21} = \sigma_1 > 0;$$
$$a_{22} = -\Big(\frac{\sigma_1\bar{x}}{\bar{y}} + \frac{s\bar{y}}{l}\Big) < 0; a_{31} = \beta_2\bar{z} > 0; a_{34} = -\gamma_1\bar{z} < 0; a_{44} = \gamma_2\bar{z} - \alpha.$$

The first root of the characteristic equation of $J(F_2)$ is $\gamma_2\bar{z} - \alpha$ and the other three roots are given by:

$$\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = 0.$$

The coefficients of the characteristic equation of $J(F_2)$ can be written as:

$A_1 = -(a_{11} + a_{22}) > 0,$

$A_2 = a_{11}a_{22} - a_{12}a_{21} - a_{13}a_{31},$

$A_3 = a_{22}a_{13}a_{31} > 0.$

Further,

$$\begin{aligned} \Delta &= A_1A_2 - A_3 = (a_{11} + a_{22})(a_{12}a_{21} + a_{11}a_{22}) + a_{11}a_{13}a_{31} \\ &= \left[\frac{kl\sigma_2(\bar{y})^2 + rl(\bar{x})^2\bar{y} + kl\sigma_1(\bar{x})^2 + sk\bar{x}(\bar{y})^2}{\bar{x}\bar{y}kl}\right]\left[\frac{sk\sigma_2(\bar{y})^3 + rl\sigma_1(\bar{x})^3 + rs(\bar{x})^2(\bar{y})^2}{\bar{x}\bar{y}kl}\right] \\ &+ \left(\frac{\beta_1\beta_2\bar{z}(k\sigma_2\bar{y} + r(\bar{x})^2)}{l}\right) > 0. \end{aligned}$$

Now, according to the Routh-Hurwitz criteria (see Subsection 2.3.2), all the eigenvalues of $J(F_2)$ have roots with negative real parts, provided that $A_i (i = 1, 3) > 0$ and $\Delta > 0$. Therefore, F_2 is locally asymptotically stable, if (4.33) holds. ∎

4.6.4 Local stability behaviour of F_3

In the following lemma, the local behaviour of the positive fixed point F_3 is shown.

Lemma 6 *The positive equilibrium point* $F_3 = (x^*, y^*, z^*, w^*)$ *is locally asymptotically stable in* $\mathbb{R}^4_+$ *whenever it exists.*

Proof The Jacobian matrix of the system (4.1), at the positive equilibrium point $F_3 = (x^*, y^*, z^*, w^*)$, can be written as:

$$J(F_3) = \begin{bmatrix} a_{11} & a_{12} & a_{13} & 0 \\ a_{21} & a_{22} & 0 & 0 \\ a_{31} & 0 & 0 & a_{34} \\ 0 & 0 & a_{43} & 0 \end{bmatrix} \tag{4.35}$$

where,

$$a_{11} = -\Big(\frac{\sigma_2 y^*}{x^*} + \frac{rx^*}{k}\Big) < 0; a_{12} = \sigma_2 > 0; a_{13} = -\beta_1 x^* < 0; a_{21} = \sigma_1 > 0;$$
$$a_{22} = -\Big(\frac{\sigma_1 x^*}{y^*} + \frac{sy^*}{l}\Big) < 0; a_{23} = 0; a_{31} = \beta_2 z^* > 0; a_{34} = -\gamma_1 z^* < 0; a_{43} = \gamma_2 w^*.$$

Accordingly, the characteristic equation of $J(F_3)$ is given by:

$$\lambda^4 + A_1\lambda^3 + A_2\lambda^2 + A_3\lambda + A_4 = 0.$$

Here,

$A_1 = -M_1 > 0,$

$A_2 = M_2 + M_3 > 0,$

$A_3 = a_{11}M_4 - a_{22}M_3,$

$A_4 = -M_2M_4,$

where,

$M_1 = a_{11} + a_{22} < 0,\ M_2 = a_{11}a_{22} - a_{12}a_{21} > 0,\ M_3 = -a_{13}a_{31} - a_{34}a_{43} > 0,$

$M_4 = a_{34}a_{43} < 0.$

Further,

$$\begin{aligned} \Delta &= A_1A_2A_3 - A_3^2 - A_1^2A_4 \\ &= \Big(a_{11}M_4 - a_{22}M_3\Big)\Big(a_{11}a_{13}a_{31} - M_1M_2\Big) + M_1^2M_2M_4 \\ &= a_{13}a_{31}\Big(a_{11}^2M_4 - a_{22}M_3 - a_{22}M_1M_2\Big) > 0. \end{aligned}$$

Now, according to the Routh-Hurwitz criteria, all the eigenvalues of $J(F_3)$ have roots with negative real parts, since $A_i(i = 1, 3, 4) > 0$ and $\Delta > 0$. Hence, F_3 is locally asymptotically stable in the interior of $\mathbb{R}^4_+$. ■

4.7 Global dynamical behaviour

In this section, the global stability of the local equilibrium points is investigated by using the Lyapunov direct method (see Subcection 2.3.5), as shown in the following theorems.

Theorem 4.7.1 *Assume that the equilibrium point F_1 is locally asymptotically stable in $\mathbb{R}^4_+$, then it is globally asymptotically stable in $\mathbb{R}^4_+$.*

Proof Consider the following positive definite function:

$$R_1(x, y, z, w) = c_1\Big(x - \hat{x} - \hat{x}\ln\frac{x}{\hat{x}}\Big) + c_2\Big(y - \hat{y} - \hat{y}\ln\frac{y}{\hat{y}}\Big) + c_3z + c_4w,$$

where, $c_i, (i = 1, 2, 3, 4)$ are positive constants to be determined. Now, the time derivative of R_1 along the trajectory of the system (4.1) can be written as:

$$
\begin{aligned}
\frac{dR_1}{dt} &= c_1\Big(\frac{x-\hat{x}}{x}\Big)\frac{dx}{dt} + c_2\Big(\frac{y-\hat{y}}{y}\Big)\frac{dy}{dt} + c_3\frac{dz}{dt} + c_4\frac{dw}{dt}\\
&= c_1\big(x-\hat{x}\big)\Big(r - \frac{rx}{k} - \sigma_1 + \frac{\sigma_2 y}{x} - \beta_1 z\Big)\\
&+ c_2\big(y-\hat{y}\big)\Big(s - \frac{sy}{l} + \frac{\sigma_1 x}{y} - \sigma_2\Big)\\
&+ c_3\big(\beta_2 xz - \beta_0 z - \gamma_1 zw\big) + c_4\big(\gamma_2 zw - \alpha w\big)\\
&= c_1\big(x-\hat{x}\big)\Big(\frac{-r}{k}\big(x-\hat{x}\big) + \sigma_2\Big(\frac{y}{x} - \frac{\hat{y}}{\hat{x}}\Big) - \beta_1 z\Big)\\
&+ c_2\big(y-\hat{y}\big)\Big(\frac{-s}{l}\big(y-\hat{y}\big) + \sigma_1\Big(\frac{x}{y} - \frac{\hat{x}}{\hat{y}}\Big)\Big)\\
&+ c_3\big(\beta_2 xz - \beta_0 z - \gamma_1 zw\big) + c_4\big(\gamma_2 zw - \alpha w\big).
\end{aligned}
$$

Therefore,

$$
\begin{aligned}
\frac{dR_1}{dt} &= \frac{-c_1 r}{k}\big(x-\hat{x}\big)^2 + c_1\sigma_2\big(x-\hat{x}\big)\Big(\frac{y\hat{x}-x\hat{y}}{x\hat{x}}\Big) - c_1\big(x-\hat{x}\big)\beta_1 z\Big)\\
&- \frac{c_2 s}{l}\big(y-\hat{y}\big)^2 + c_2\sigma_1\big(y-\hat{y}\big)\Big(\frac{x\hat{y}-y\hat{x}}{y\hat{y}}\Big)\\
&+ c_3\big(\beta_2 xz - \beta_0 z - \gamma_1 zw\big) + c_4\big(\gamma_2 zw - \alpha w\big).
\end{aligned}
$$

By choosing the positive constants as

$$
c_1 = 1, c_2 = \frac{\sigma_2\hat{y}}{\sigma_1\hat{x}}, c_3 = \frac{\beta_1}{\beta_2}, c_4 = \frac{\beta_1\gamma_1}{\beta_2\gamma_2},
$$

the following is obtained,

$$
\begin{aligned}
\frac{dR_1}{dt} &= -\Big(\frac{r}{k}\Big)\big(x-\hat{x}\big)^2 - \Big(\frac{\sigma_2}{x\hat{x}y}\Big)\big(x\hat{y}-y\hat{x}\big)^2 - \Big(\frac{s\sigma_2\hat{y}}{l\sigma_1\hat{x}}\Big)\big(y-\hat{y}\big)^2\\
&+ \Big(\hat{x} - \frac{\beta_0}{\beta_2}\Big)\beta_1 z - \Big(\frac{\alpha\beta_1\gamma_1}{\beta_2\gamma_2}\Big)w.
\end{aligned}
$$

Then, $\frac{dR_1}{dt} < 0$ under the local stability condition (4.27). Hence, R_1 is a Lyapunov function. Therefore, F_1 is globally asymptotically stable in $\mathbb{R}^4_+$. ■

The next theorem shows the global stability of the top predator-free equilibrium point F_2 in $\mathbb{R}^4_+$.

Theorem 4.7.2 *Assume that the equilibrium point F_2 is locally asymptotically stable in $\mathbb{R}^4_+$, then it is globally asymptotically stable in $\mathbb{R}^4_+$.*

Proof Consider the following positive definite function:

$$R_2(x,y,z,w)=c_1\Big(x-\bar{x}-\bar{x}\ln\frac{x}{\bar{x}}\Big)+c_2\Big(y-\bar{y}-\bar{y}\ln\frac{y}{\bar{y}}\Big)+c_3\Big(z-\bar{z}-\bar{z}\ln\frac{z}{\bar{z}}\Big)+c_4w,$$

where, $c_i,(i=1,2,3,4)$ are positive constants to be determined. Now the time derivative of R_2 along the trajectory of the system (4.1) can be written as:

$$\begin{aligned}
\frac{dR_2}{dt} &= c_1\Big(\frac{x-\bar{x}}{x}\Big)\frac{dx}{dt}+c_2\Big(\frac{y-\bar{y}}{y}\Big)\frac{dy}{dt}+c_3\Big(\frac{z-\bar{z}}{z}\Big)\frac{dz}{dt}+c_4\frac{dw}{dt}\\
&= c_1\big(x-\bar{x}\big)\Big(r-\frac{rx}{k}-\sigma_1+\frac{\sigma_2 y}{x}-\beta_1 z\Big)\\
&+ c_2\big(y-\bar{y}\big)\Big(s-\frac{sy}{l}+\frac{\sigma_1 x}{y}-\sigma_2\Big)\\
&+ c_3\big(z-\bar{z}\big)\big(\beta_2 x-\beta_0-\gamma_1 w\big)+c_4\big(\gamma_2 zw-\alpha w\big)\\
&= c_1\big(x-\bar{x}\big)\Big(\frac{-r}{k}\big(x-\bar{x}\big)+\sigma_2\Big(\frac{y}{x}-\frac{\bar{y}}{\bar{x}}\Big)-\beta_1\big(z-\bar{z}\big)\Big)\\
&+ c_2\big(y-\bar{y}\big)\Big(\frac{-s}{l}\big(y-\bar{y}\big)+\sigma_1\Big(\frac{x}{y}-\frac{\bar{x}}{\bar{y}}\Big)\Big)\\
&+ c_3\big(z-\bar{z}\big)\Big(\beta_2\big(x-\bar{x}\big)-\gamma_1 w\Big)+c_4\big(\gamma_2 zw-\alpha w\big).
\end{aligned}$$

Therefore,

$$\begin{aligned}
\frac{dR_2}{dt} &= \frac{-c_1 r}{k}\big(x-\bar{x}\big)^2+c_1\sigma_2\big(x-\bar{x}\big)\Big(\frac{y\bar{x}-x\bar{y}}{x\bar{x}}\Big)-c_1\beta_1\big(x-\bar{x}\big)\big(z-\bar{z}\big)\\
&- \frac{c_2 s}{l}\big(y-\bar{y}\big)^2+c_2\sigma_1\big(y-\bar{y}\big)\Big(\frac{x\bar{y}-y\bar{x}}{y\bar{y}}\Big)\\
&+ c_3\big(x-\bar{x}\big)\big(z-\bar{z}\big)-c_3\gamma_1 w\big(z-\bar{z}\big)+c_4\big(\gamma_2 zw-\alpha\big)w.
\end{aligned}$$

By choosing the positive constants as

$$c_1=1, c_2=\frac{\sigma_2\bar{y}}{\sigma_1\bar{x}}, c_3=\frac{\beta_1}{\beta_2}, c_4=\frac{\beta_1\gamma_1}{\beta_2\gamma_2},$$

the following is obtained

$$\begin{aligned}
\frac{dR_2}{dt} &= -\Big(\frac{r}{k}\Big)\big(x-\bar{x}\big)^2-\Big(\frac{\sigma_2}{x\bar{x}y}\Big)\big(x\bar{y}-y\bar{x}\big)^2\\
&- \Big(\frac{s\sigma_2\bar{y}}{l\sigma_1\bar{x}}\Big)\big(y-\bar{y}\big)^2+\Big(\gamma_2\bar{z}-\alpha\Big)\Big(\frac{\beta_1\gamma_1}{\beta_2\gamma_2}\Big)w.
\end{aligned}$$

Then, $\frac{dR_2}{dt}\le 0$ which is negative semi-definite under the local stability condition (4.33). Thus, F_2 is Lyapunov stable. However, the set $N_2=\Big\{(x,y,z,w)/\dot{R}_2(x,y,z,w)=$

$0\big\}$, which is the set $N_2 = \big\{(x, y, z, w)/x = \bar{x}, y = \bar{y}, w = 0\big\}$, does not contain any trajectory of the system except $F_2 = (\bar{x}, \bar{y}, \bar{z}, 0)$. Therefore, by LaSalle's invariance principle (see Theorem 2.3.3), F_2 is globally asymptotically stable in $\mathbb{R}^4_+$ if the local stability condition holds. ■

Finally, the global stability of the positive equilibrium point F_3 in the interior of $\mathbb{R}^4_+$ is investigated, as shown in the following theorem.

Theorem 4.7.3 *The equilibrium point F_3 is globally asymptotically stable in $\mathbb{R}^4_+$ whenever it exists.*

Proof Consider the following positive definite function:

$$\begin{aligned} R_3(x, y, z, w) &= c_1\Big(x - x^* - x^* \ln \frac{x}{x^*}\Big) + c_2\Big(y - y^* - y^* \ln \frac{y}{y^*}\Big) \\ &+ c_3\Big(z - z^* - z^* \ln \frac{z}{z^*}\Big) + c_4\Big(w - w^* - w^* \ln \frac{w}{w^*}\Big), \end{aligned}$$

where, $c_i, (i = 1, 2, 3, 4)$ are positive constants to be determined. Now, the time derivative of R_3 along the trajectory of the system (4.1) can be written as:

$$\begin{aligned} \frac{dR_3}{dt} &= c_1\Big(\frac{x - x^*}{x}\Big)\frac{dx}{dt} + c_2\Big(\frac{y - y^*}{y}\Big)\frac{dy}{dt} + c_3\Big(\frac{z - z^*}{z}\Big)\frac{dz}{dt} + c_4\Big(\frac{w - w^*}{w}\Big)\frac{dw}{dt} \\ &= c_1\big(x - x^*\big)\Big(r - \frac{rx}{k} - \sigma_1 + \frac{\sigma_2 y}{x} - \beta_1 z\Big) \\ &+ c_2\big(y - y^*\big)\Big(s - \frac{sy}{l} + \frac{\sigma_1 x}{y} - \sigma_2\Big) \\ &+ c_3\big(z - z^*\big)\big(\beta_2 x - \beta_0 - \gamma_1 w\big) + c_4\big(w - w^*\big)\big(\gamma_2 z - \alpha\big). \end{aligned}$$

Therefore,

$$\begin{aligned} \frac{dR_3}{dt} &= \frac{-c_1 r}{k}\big(x - x^*\big)^2 + c_1\sigma_2\big(x - x^*\big)\Big(\frac{yx^* - xy^*}{xx^*}\Big) - c_1\beta_1\big(x - x^*\big)\big(z - z^*\big) \\ &- \frac{c_2 s}{l}\big(y - y^*\big)^2 + c_2\sigma_1\big(y - y^*\big)\Big(\frac{xy^* - yx^*}{yy^*}\Big) + c_3\beta_2\big(x - x^*\big)\big(z - z^*\big) \\ &- c_3\gamma_1\big(z - z^*\big)\big(w - w^*\big) + c_4\gamma_2\big(z - z^*\big)\big(w - w^*\big). \end{aligned}$$

By choosing the positive constants as

$$c_1 = 1, c_2 = \frac{\sigma_2 y^*}{\sigma_1 x^*}, c_3 = \frac{\beta_1}{\beta_2}, c_4 = \frac{\beta_1\gamma_1}{\beta_2\gamma_2},$$

the following is obtained

$$\frac{dR_3}{dt} = -\Big(\frac{r}{k}\Big)\big(x-x^*\big)^2 - \Big(\frac{\sigma_2}{xx^*y}\Big)\big(xy^*-yx^*\big)^2 - \Big(\frac{s\sigma_2 y^*}{l\sigma_1 x^*}\Big)\big(y-y^*\big)^2.$$

Then, $\frac{dR_3}{dt} \leq 0$ which is negative semi-definite and thus F_3 is Lyapunov stable. However, the set $N_3 = \big\{(x,y,z,w)/\dot{R}_3(x,y,z,w) = 0\big\}$, which is the set $N_3 = \big\{(x,y,z,w)/x = x^*, y = y^*\big\}$, does not contain any trajectory of the system except $F_3 = (x^*, y^*, z^*, w^*)$. Therefore, by LaSalle's invariance principle F_3 is globally asymptotically stable in interior of $\mathbb{R}^4_+$. ■

4.8 Persistence analysis

In this section, the persistence conditions of system (4.1) are studied using the Freedman and Waltman approach (see Subsubsection 2.3.8.1). In general, the persistence of a system, from the mathematical point of view, means that strictly positive trajectories of it that initiate in the interior of $\mathbb{R}^4_+$ have no omega-limit sets on the boundary planes. Biologically, this implies the survival of all species of the system over the long-term.

Now, before establishing the persistence conditions of system (4.1), first, the stable behaviour of F_1 and F_2 in the boundary planes xy and xyz needs to be studied, which is undertaken through the following lemma.

Lemma 7 *Assume that conditions (4.27) and (4.33) are satisfied, which represent the local stability conditions for the equilibrium points F_1 and F_2, respectively. Then they are globally asymptotically stable in the interior of $\mathbb{R}^2_{+(\mathrm{xy})}$ and $\mathbb{R}^3_{+(\mathrm{xyz})}$, respectively.*

Proof The proof of the above Lemma is clear, and so omitted. ■

In the following theorem, the persistence condition of the system (4.1) is established.

Theorem 4.8.1 *If the conditions (4.27) and (4.33) are violated, then, the system (4.1) persists.*

Proof Suppose that q is a point in the interior of $\mathbb{R}^4_+$ and, $o(q)$ is the orbit through q. Let $\Omega(q)$ be the omega limit set of $o(q)$. Note that, $\Omega(q)$ is bounded due to the boundedness of the system (4.1). First, it is claimed that $F_0 \notin \Omega(q)$. Assume the contrary, and then, since F_0 is a saddle point, it cannot be the only point in $\Omega(q)$, and hence, according to the Butler-McGhee lemma (see Lemma 1, page 18) there is at least another point, say p, such that $p \in \omega^s(F_0) \cap \Omega(q)$, where, $\omega^s(F_0)$ is the stable manifold of F_0. Now, $\omega^s(F_0)$ is the space $\mathbb{R}^3_{+(\mathrm{xzw})}$ or $\mathbb{R}^3_{+(\mathrm{yzw})}$ and the entire orbit through p, which denoted by $o(p)$, is contained in $\Omega(q)$.

Suppose that $\omega^s(F_0)$ is the space $\mathbb{R}^3_{+(\mathrm{xzw})}$ (similar proof as when $\omega^s(F_0)$ is the space $\mathbb{R}^3_{+(\mathrm{yzw})}$). Then, if $p \in \partial\mathbb{R}^3_{+(\mathrm{xzw})}$ (i.e. on the boundary axes of $\mathbb{R}^3_{+(\mathrm{xzw})}$), this means that the particular positive axis (that containing p) is included in $\Omega(q)$, thus contradicting its boundedness. Now, let $p \in \mathrm{Int}.\mathbb{R}^3_{+(\mathrm{xzw})}$ (i.e. in the interior of $\mathbb{R}^3_{+(\mathrm{xzw})}$). Since there is no equilibrium point in the $\mathrm{Int}.\mathbb{R}^3_{+(\mathrm{xzw})}$, the orbit through p, which is contained in $\Omega(q)$, must be unbounded. Giving a contradiction too, this shows that $F_0 \notin \Omega(q)$.

Now, it is shown that $F_1 \notin \Omega(q)$ since F_1 is a saddle point when the equation (4.27) is violated. Then, again by the Butler-McGhee lemma, there is at least another point, say p_1, such that $p_1 \in \omega^s(F_1) \cap \Omega(q)$, also, where $\omega^s(F_1)$ is the space $\mathbb{R}^3_{+(\mathrm{xyw})}$. Note that, if $p_1 \in \partial\mathbb{R}^3_{+(\mathrm{xyw})}$, then a contradiction occurs, as in the first part of the proof. Let now, $p_1 \in \mathrm{Int}.\mathbb{R}^3_{+(\mathrm{xyw})}$, again, since there is no equilibrium point in the $\mathrm{Int}.\mathbb{R}^3_{+(\mathrm{xyw})}$, then the $o(p_1) \subset \Omega(q)$ is unbounded, which gives a contradiction to the boundedness of $\Omega(q)$. Thus, $F_1 \notin \Omega(q)$. Now, since F_2 is the saddle point in $\mathbb{R}^4_+$ if and only if equation (4.33) is violated. Then, by using the argument entirely analogous to the above yields that F_2 cannot be contained in $\Omega(q)$. Thus, $\Omega(q)$ must be in the interior of $\mathbb{R}^4_+$, which proves the persistence of the system (4.1). ■

4.9 Local bifurcation analysis

In this section, the effect of varying parameter values on the dynamical behaviour of the system (4.1) around each equilibrium point is studied. In the following theorems, an application of Sotomayor's hypothesis for local bifurcation is adapted (see Subsubsection 2.3.9.1).

Now, the Jacobian matrix of system (4.1) at each of the equilibrium points is given by:

$$J = DF = \begin{bmatrix} r - \sigma_1 - \dfrac{2rx}{k} - \beta_1 z & \sigma_2 & -\beta_1 x & 0 \\ \sigma_1 & s - \sigma_2 - \dfrac{2sy}{l} & 0 & 0 \\ \beta_2 z & 0 & \beta_2 x - \beta_0 - \gamma_1 w & -\gamma_1 z \\ 0 & 0 & \gamma_2 w & \gamma_2 z - \alpha \end{bmatrix}.$$

For any non-zero vector $V = (v_1, v_2, v_3, v_4)^T$:

$$D^2F(V,V) = \begin{bmatrix} -2v_1\left(\frac{rv_1}{k} - \beta_1 v_3\right) \\ -\frac{2s}{l}v_2^2 \\ 2v_3(\beta_2 v_1 - \gamma_1 v_4) \\ 2\gamma_2 v_3 v_4 \end{bmatrix} \tag{4.36}$$

and,

$$D^3F(V,V,V) = (0,0,0,0)^T.$$

So, according to Sotomayor's theorem the pitchfork bifurcation does not occur at any of the points $F_i, i = 0,1,2,3$.

Theorem 4.9.1 *Suppose that*

$$(r - \sigma_1)^2 - l\sigma_1^3 \neq 0. \tag{4.37}$$

Then, for the parameter value $\sigma_2^* = \dfrac{s(r - \sigma_1)}{r}$ *system (4.1), at the equilibrium point* F_0*, has a transcritical bifurcation.*

Proof According to the Jacobian matrix $J(F_0)$, given by (4.21), system (6.1), at the equilibrium point F_0, has a zero eigenvalue, say $\big(\lambda_{01}$ or $\lambda_{02}\big)$, at $\sigma_2 = \sigma_2^*$, and the Jacobian matrix $J(F_0)$, becomes:

$$J^*(F_0) = \begin{bmatrix} r-\sigma_1 & \sigma_2^* & 0 & 0 \\ \sigma_1 & s-\sigma_2^* & 0 & 0 \\ 0 & 0 & -\beta_0 & 0 \\ 0 & 0 & 0 & -\alpha \end{bmatrix}.$$

Now, suppose that $V^{[0]} = \left(v_1^{[0]}, v_2^{[0]}, v_3^{[0]}, v_4^{[0]}\right)^T$ is an eigenvector corresponding to the eigenvalue $\lambda_{01} = 0$ (same, if $\lambda_{02} = 0$). Thus, $\big(J^*(F_0) - \lambda_{01} I\big)V^{[0]} = 0$, which implies: $v_1^{[0]} = \dfrac{(\sigma_2^* - s)v_2^{[0]}}{\sigma_1}, v_3^{[0]} = v_4^{[0]} = 0$ and $v_2^{[0]}$ represents any non zero real number. Let $\psi^{[0]} = \big(\psi_1^{[0]}, \psi_2^{[0]}, \psi_3^{[0]}, \psi_4^{[0]}\big)^T$ be an eigenvector associated with the eigenvalue λ_{01} of the matrix $(J^*(F_0))^T$. Then, $\big((J^*(F_0))^T - \lambda_{01} I\big)\psi^{[0]} = 0$. Subsequently, by solving this equation for $\psi^{[0]}$, $\psi_1^{[0]} = \dfrac{(\sigma_2^* - s)\psi_2^{[0]}}{\sigma_2^*}, \psi_3^{[0]} = \psi_4^{[0]} = 0$ is obtained, where $\psi_2^{[0]}$, is any non-zero real number.

Now, to confirm that the conditions of Sotomayor's theorem for transcritical bifurcation are satisfied, the following is considered:

$$\frac{\partial f}{\partial \sigma_2} = f'_{\sigma_2}(X, \sigma_2) = \left(\frac{\partial f_1}{\partial \sigma_2}, \frac{\partial f_2}{\partial \sigma_2}, \frac{\partial f_3}{\partial \sigma_2}, \frac{\partial f_4}{\partial \sigma_2}\right)^T = (y, -y, 0, 0)^T.$$

Therefore, $f'_{\sigma_2}(F_0, \sigma_2^*) = (0,0,0,0)^T$ and hence, $(\psi^{[0]})^T f'_{\sigma_2}(F_0, \sigma_2^*) = 0$. Thus, according to Sotomayor's theorem, saddle-node bifurcation cannot occur, while the first condition of transcritical bifurcation is satisfied.

Now,

$$Df_{\sigma_2}(X, \sigma_2) = \begin{bmatrix} 0 & 1 & 0 & 0 \\ 0 & -1 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix},$$

where, $Df_{\sigma_2}(X, \sigma_2)$ represents the derivative of $f_{\sigma_2}(X, \sigma_2)$ with respect to $X = (x, y, z, w)^T$. Also, it is observed that:

$$Df_{\sigma_2}(F_0,\sigma_2^*)V^{[0]} = \begin{pmatrix} 0 & 1 & 0 & 0 \\ 0 & -1 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} v_1^{[0]} \\ v_2^{[0]} \\ 0 \\ 0 \end{pmatrix} = \begin{pmatrix} v_2^{[0]} \\ -v_2^{[0]} \\ 0 \\ 0 \end{pmatrix},$$

$$\begin{aligned} (\psi^{[0]})^T[Df_{\sigma_2}(F_0,\sigma_2^*)V^{[0]}] &= \Big(\psi_1^{[0]},\psi_2^{[0]},0,0\Big)\Big(v_2^{[0]},-v_2^{[0]},0,0\Big)^T \\ &= \Big(\frac{-s}{\sigma_2^*}\Big)\psi_2^{[0]}v_2^{[0]} \neq 0. \end{aligned}$$

Now, by substituting in (4.36), the following is obtained:

$$D^2f\big(F_0,\sigma_2^*\big)\big(V^{[0]},V^{[0]}\big) = \left(\frac{-2r\big(v_1^{[0]}\big)^2}{k}, \frac{-2s\big(v_2^{[0]}\big)^2}{l}, 0, 0\right)^T.$$

Hence, according to condition (4.37):

$$\begin{aligned} \big(\psi^{[0]}\big)^T\Big[D^2f(F_0,\sigma_2^*)\big(V^{[0]},V^{[0]}\big)\Big] &= \Big(\psi_1^{[0]},\psi_2^{[0]},0,0\Big)\left(\frac{-2r\big(v_1^{[0]}\big)^2}{k}, \frac{-2s\big(v_2^{[0]}\big)^2}{l}, 0, 0\right)^T \\ &= -2\big(v_1^{[0]}\big)^2\psi_2^{[0]}\Big(\frac{s^3}{r^2}\Big)\Big(-l\sigma_1^3+\big(r-\sigma_1\big)^2\Big) \neq 0. \end{aligned}$$

This means the second condition of transcritical bifurcation is satisfied. Thus, according to Sotomayor's theorem, system (4.1) has transcritical bifurcation at F_0 with the parameter $\sigma_2 = \sigma_2^*$. ■

Theorem 4.9.2 *Suppose that*

$$v_3^{[1]} \neq 0. \tag{4.38}$$

Then, for the parameter value $\beta_2^* = \beta_0/\hat{x}$, system (4.1), at the equilibrium point F_1, has a transcritical bifurcation.

Proof According to the Jacobian matrix $J(F_1)$ given by (4.28), system (4.1), at the equilibrium point F_1, has a zero eigenvalue, say λ_{13}, at $\beta_2 = \beta_2^*$ and the Jacobian matrix $J(F_1)$ becomes

$$J^*(F_1) = \begin{bmatrix} r-\sigma_1-\frac{2r\hat{x}}{k} & \sigma_2 & -\beta_1\hat{x} & 0 \\ \sigma_1 & s-\sigma_2-\frac{2s\hat{y}}{l} & 0 & 0 \\ 0 & 0 & -\beta_0 & 0 \\ 0 & 0 & 0 & -\alpha \end{bmatrix}.$$

Now, suppose that $V^{[1]} = \left(v_1^{[1]}, v_2^{[1]}, v_3^{[1]}, v_4^{[1]}\right)^T$ is an eigenvector corresponding to the eigenvalue λ_{13}. Then, $\big(J^*(F_1) - \lambda_{13}I\big)V^{[1]} = 0$, which implies

$$\begin{aligned} v_2^{[1]} &= \frac{\sigma_1 l v_1^{[1]}}{2s\hat{y}-(s-\sigma_2)l}, \\ v_3^{[1]} &= \left(\frac{(rk-2r\hat{x}-\sigma_1 k)(2s\hat{y}-(s-\sigma_2)l)+\sigma_1\sigma_2 lk}{\beta_1\hat{x}k(2s\hat{y}-(s-\sigma_2)l)}\right)v_1^{[1]}, \\ v_4^{[1]} &= 0, \end{aligned}$$

where, $v_1^{[1]}$ is any non-zero real number. Let $\psi^{[1]} = \big(\psi_1^{[1]}, \psi_2^{[1]}, \psi_3^{[1]}, \psi_4^{[1]}\big)^T$ be an eigenvector associated with the eigenvalue λ_{13} of the matrix $(J^*(F_1))^T$. Then, $\big((J^*(F_1))^T - \lambda_{13}I\big)\psi^{[1]} = 0$. By solving this equation for $\psi^{[1]}$, $\psi_1^{[1]} = \psi_2^{[1]} = \psi_4^{[1]} = 0$ is obtained, where $\psi_3^{[1]}$ is any non-zero real number.

Now, to confirm whether the conditions of Sotomayor's theorem for transcritical bifurcation are satisfied, the following is considered:

$$\frac{\partial f}{\partial \beta_2} = f'_{\beta_2}(X,\beta_2) = \left(\frac{\partial f_1}{\partial \beta_2}, \frac{\partial f_2}{\partial \beta_2}, \frac{\partial f_3}{\partial \beta_2}, \frac{\partial f_4}{\partial \beta_2}\right)^T = (0,0,xz,0)^T.$$

Thus, $f'_{\beta_2}(F_1,\beta_2^*) = (0,0,0,0)^T$ and hence, $(\psi^{[1]})^T f'_{\beta 2}(F_1,\beta_2^*) = 0$. Therefore, according to Sotomayor's theorem, saddle-node bifurcation cannot occur, while the first condition of transcritical bifurcation is satisfied.

Now,

$$Df_{\beta_2}(X,\beta_2) = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ z & 0 & x & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix},$$

where, $Df_{\beta_2}(X,\beta_2)$ represents the derivative of $f_{\beta_2}(X,\beta_2)$ with respect to $X = (x,y,z,w)^T$. Moreover, it is observed under condition (4.38) that:

$$Df_{\beta_2}(F_1,\beta_2^*)V^{[1]}=\begin{pmatrix}0&0&0&0\\0&0&0&0\\0&0&\hat{x}&0\\0&0&0&0\end{pmatrix}\begin{pmatrix}v_1^{[1]}\\v_2^{[1]}\\v_3^{[1]}\\0\end{pmatrix}=\begin{pmatrix}0\\0\\\hat{x}v_3^{[1]}\\0\end{pmatrix},$$

$$\begin{aligned}(\psi^{[1]})^T\Big[Df_{\beta_2}(F_1,\beta_2^*)V^{[1]}\Big] &= \Big(0,0,\psi_3^{[1]},0\Big)\Big(0,0,\hat{x}v_3^{[1]},0\Big)^T\\ &= \hat{x}\psi_3^{[1]}v_3^{[1]}\neq 0.\end{aligned}$$

Now, by substituting in (4.36), the following is obtained

$$D^2f\big(F_1,\beta_2^*\big)\big(V^{[1]},V^{[1]}\big)=\Bigg(-2v_1^{[1]}\Bigg(\frac{r\big(v_1^{[1]}\big)^2}{k}+\beta_1v_3^{[1]}\Bigg),\frac{-2s\big(v_2^{[1]}\big)^2}{l},2\beta_2^*v_1^{[1]}v_3^{[1]},0\Bigg)^T.$$

Hence, according to condition (4.38)

$$\big(\psi^{[1]}\big)^T\big[D^2f(F_1,\beta_2^*)\big(V^{[1]},V^{[1]}\big)\big]=-2\beta_2^*v_1^{[1]}v_3^{[1]}\psi_3^{[1]}\neq 0.$$

This means the second condition of transcritical bifurcation is satisfied. Thus, according to Sotomayor's theorem system, (4.1) has transcritical bifurcation at F_1 with the parameter $\beta_2=\beta_2^*$. ■

Theorem 4.9.3 *Suppose that*

$$v_3^{[2]}\neq 0. \tag{4.39}$$

Then, for the parameter value $\gamma_2^*=\dfrac{\alpha}{\bar{z}}$*, system (4.1), at the equilibrium point* F_2*, has transcritical bifurcation.*

Proof According to the Jacobian matrix $J(F_2)$, given by (4.34), system (4.1), at the equilibrium point F_2, has a zero eigenvalue, say λ_{24}, at $\gamma_2=\gamma_2^*$ and this matrix becomes

$$J^*(F_2)=\begin{bmatrix}r-\sigma_1-\frac{2r\bar{x}}{k}-\beta_1\bar{z}&\sigma_2&-\beta_1\bar{x}&0\\\sigma_1&s-\sigma_2-\frac{2s\bar{y}}{l}&0&0\\\beta_2\bar{z}&0&0&-\gamma_1\bar{z}\\0&0&0&0\end{bmatrix}.$$

Now, suppose that $V^{[2]} = \left(v_1^{[2]}, v_2^{[2]}, v_3^{[2]}, v_4^{[2]}\right)^T$ is an eigenvector corresponding to the eigenvalue λ_{24}. Thus, $\big(J^*(F_2) - \lambda_{24}I\big)V^{[2]} = 0$, which implies

$$\begin{aligned}
v_2^{[2]} &= \frac{\sigma_1 l v_1^{[2]}}{2s\bar{y} - (s-\sigma_2)l}, \\
v_3^{[2]} &= \left(\frac{(rk - 2r\bar{x} - \sigma_1 k - k\beta_1\bar{z})(2s\bar{y} - (s-\sigma_2)l) + \sigma_1\sigma_2 lk}{\beta_1\bar{x}k(2s\bar{y} - (s-\sigma_2)l)}\right)v_1^{[2]}, \\
v_4^{[2]} &= \frac{\beta_2 v_1^{[2]}}{\gamma_1},
\end{aligned}$$

where, $v_1^{[2]}$ is any non-zero real number and $2s\bar{y} \neq (s-\sigma_2)l$. Then, let $\psi^{[2]} = \big(\psi_1^{[2]}, \psi_2^{[2]}, \psi_3^{[2]}, \psi_4^{[2]}\big)^T$ be an eigenvector associated with the eigenvalue λ_{24} of the matrix $(J^*(F_2))^T$. So, $\big((J^*(F_2))^T - \lambda_{24}I\big)\psi^{[2]} = 0$ and by solving this equation for $\psi^{[2]}$, $\psi_1^{[2]} = \psi_2^{[2]} = \psi_3^{[2]} = 0$ is the result, where $\psi_4^{[2]}$ is any non-zero real number.

Now, to confirm that the conditions of Sotomayor's theorem for transcritical bifurcation are satisfied, the following is considered:

$$\frac{\partial f}{\partial \gamma_2} = f'_{\gamma_2}(X, \gamma_2) = \left(\frac{\partial f_1}{\partial \gamma_2}, \frac{\partial f_2}{\partial \gamma_2}, \frac{\partial f_3}{\partial \gamma_2}, \frac{\partial f_4}{\partial \gamma_2}\right)^T = (0,0,0,zw)^T.$$

Therefore, $f'_{\gamma_2}(F_2, \gamma_2^*) = (0,0,0,0)^T$ and hence, $(\psi^{[2]})^T f'_{\gamma 2}(F_2, \gamma_2^*) = 0$. So, according to Sotomayor's theorem, saddle-node bifurcation cannot occur, while the first condition of transcritical bifurcation is satisfied. Now,

$$Df_{\gamma_2}(X, \gamma_2) = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & w & z \end{bmatrix},$$

where, $Df_{\gamma_2}(X, \gamma_2)$ represent the derivative of $f_{\gamma_2}(X, \gamma_2)$ with respect to $X = (x, y, z, w)^T$. Further, it is observed under condition (4.39) that the following is obtained:

$$Df_{\gamma_2}(F_2, \gamma_2^*)V^{[2]} = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \bar{z} \end{pmatrix} \begin{pmatrix} v_1^{[2]} \\ v_2^{[2]} \\ v_3^{[2]} \\ v_4^{[2]} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \\ \bar{z}v_4^{[2]} \end{pmatrix},$$

$$(\psi^{[2]})^T\Big[Df_{\gamma_2}(F_2,\gamma_2^*)V^{[2]}\Big] = \Big(0,0,0,\psi_4^{[2]}\Big)\Big(0,0,0,\bar{z}v_4^{[2]}\Big)^T = \bar{z}\psi_4^{[2]}v_4^{[2]} \neq 0.$$

Now, by substituting in (4.36) it is found that

$$D^2 \quad f\big(F_2,\gamma_2^*\big)\big(V^{[2]},V^{[2]}\big) = \left(-2v_1^{[2]}\left(\frac{r\big(v_1^{[2]}\big)}{k}+\beta_1 v_3^{[2]}\right), \frac{-2s\big(v_2^{[2]}\big)^2}{l}, 2v_3^{[2]}\Big(\beta_2 v_1^{[2]}-\gamma_1 v_4^{[2]}\Big), 2\gamma_2^* v_3^{[2]}v_4^{[2]}\right)^T.$$

Hence, according to condition (4.39)

$$\big(\psi^{[2]}\big)^T\big[D^2 f(F_2,\gamma_2^*)\big(V^{[2]},V^{[2]}\big)\big] = -2\gamma_2^* v_3^{[2]}v_4^{[2]}\psi_4^{[2]} \neq 0.$$

This means the second condition of transcritical bifurcation is satisfied. Thus, according to Sotomayor's theorem, system (4.1) has transcritical bifurcation at F_2 with the parameter $\gamma_2 = \gamma_2^*$. ■

Remark

1. According to the Jacobian matrix $J(F_3)$, given by (4.35), all the eigenvalues of $J(F_3)$ have negative real parts at the equilibrium point F_3. Therefore, F_3 is a hyperbolic equilibrium point and thus, the system (4.1) has no bifurcation at F_3.

2. From the formula λ_{01} and λ_{02} given by (4.26), it is clear that $Re(\lambda_{01}) = Re(\lambda_{02}) = \lambda_{01}+\lambda_{02} \neq 0$ and both λ_{03} and λ_{04} are real eigenvalues (see Equations (4.24)-(4.25)). Hence, there is no possibility of Hopf bifurcation occurring at F_0.

3. According to the Jacobian matrix $J(F_1)$ given by (4.28), it is clear that $J(F_1)$ has four real eigenvalues (see Equations (4.29)-(4.32). Therefore, there is no possibility for Hopf bifurcation to occur at this point.

4. According to the Jacobian matrix $J(F_2)$ given by (4.34), it is clear that $J(F_2)$ has four real eigenvalues. Therefore, there is no possibility of Hopf bifurcation occurring at this point.

4.10 Numerical analysis

The main goal of this section is to find the key parameters of the system (4.1) that affects the behaviour of the proposed model by using numerical simulations. The dynamics of the system (4.1) is presented by solving the system numerically and then drawing the time series of the solutions of the system (4.1) for different sets of parameters.

Now, for the following set of parameters:

$$\begin{aligned} r =&1.5, k = 50, \sigma_1 = 0.5, \sigma_2 = 0.7, \beta_1 = 0.9, \beta_2 = 0.75,\\ \beta_0 =&0.01, s = 1.4, l = 40, \alpha = 0.4, \gamma_1 = 0.5, \gamma_2 = 0.2, \end{aligned} \tag{4.40}$$

the conditions (6.11) and (4.19) are satisfied. This shows that the positive equilibrium point F_3 exists, and it is given by: $(x^*, y^*, z^*, w^*) = (15.46, 27.91, 2.00, 23.17)$.

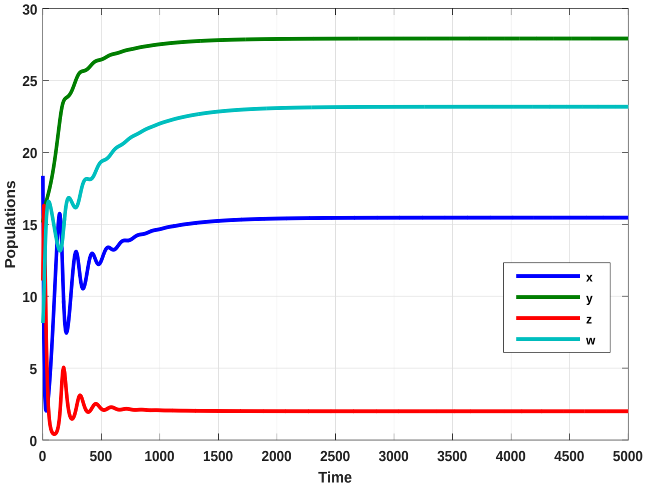

Fig. 4.1. Convergence of the solution of the system (4.1) to the positive equilibrium point with the data given by Eq.(4.40).

Figure 4.1, indicates that the solution of the system (4.1) oscillates for some small period and then, in the long-time limit, it asymptotically approaches the positive equilibrium point.

Now, to investigate the effect of the varying parameter values on the behaviour of system (4.1), the model has been solved numerically for the data given in Eq.(4.40),varying one parameter each time as will be shown in the following subsections.

4.10.1 The effect of varying the migration rate of the prey to the reserved area

Figure 4.2 shows the effect of migration to the reserved area, which is described by the parameter σ_1, on the behaviour of the system (4.1) with time. It is observed that for different values of σ_1, the solution initially oscillates for a small period and then, asymptotically approaches its equilibrium level in the interior of $\mathbb{R}^4_+$. As a result of rising the migration rate to the protected area, it can be seen that the density of the prey in the reserved zone increases. On the other hand, the populations of the top predator and the prey in the unreserved area decrease, while the third component has not affected.

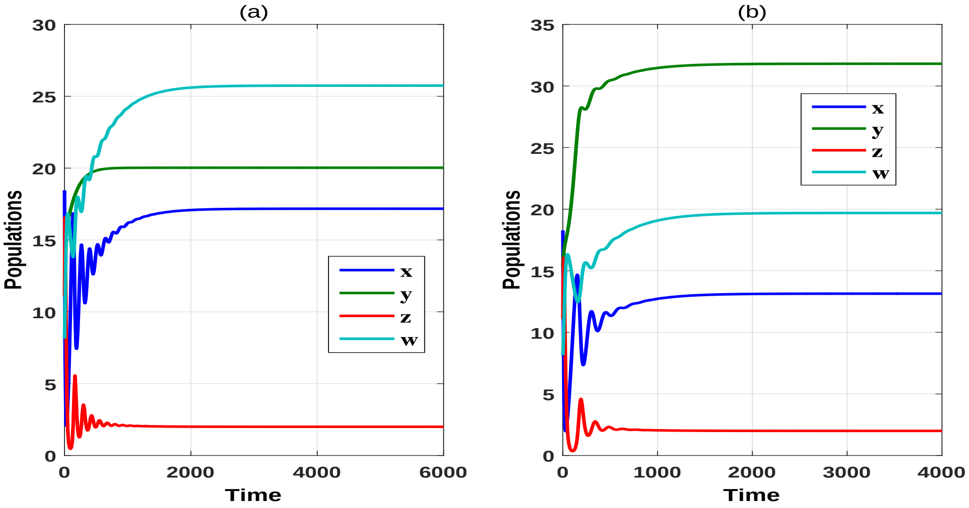

Fig. 4.2. Convergence of the solution of the system (4.1) for the data given by Eq.(4.40) with (a) $\sigma_1 = 0.001$ to the stable point(17.17, 20.02, 2.00, 25.74) in the interior of $\mathbb{R}^4_+$. (b) $\sigma_1 = 1$ to the stable point (13.14, 31.8, 2.00, 19.69) in the interior of $\mathbb{R}^4_+$.

4.10.2 The effect of varying the natural death rate of the predator

Now, the same analysis is used for different values of the predator's natural mortality, which is described by the parameter β_0, and the rest of the parameter values are kept the same as in Eq.(4.40). Figure 4.3 shows that for various values of β_0, the solution initially oscillates for a while and then, it settles down to its equilibrium level in the interior of $\mathbb{R}^4_+$. Due to the decrease of the predator's natural death-rate, the density of the top predator increases significantly. This means an abundance of the predator and hence, the food conversion rate of the predator to the top predator increases (and vice versa). On the other hand, the populations of the prey in both the reserved and unreserved zone, as well as the predator (the third component), are not affected.

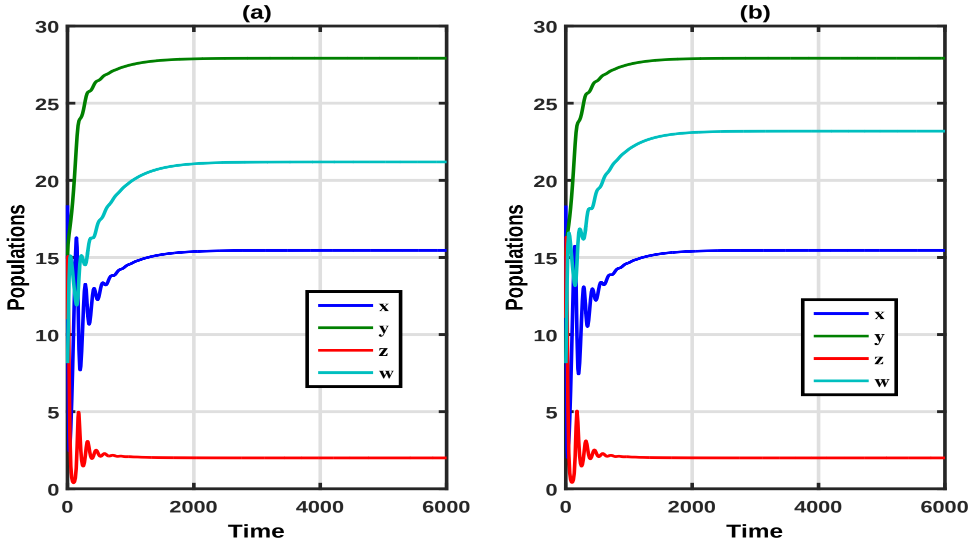

Fig. 4.3. Convergence of the solution of the system (4.1) for the data given by Eq.(4.40) with (a) $\beta_0 = 1$ to the stable point (15.46, 27.91,2.00, 21.19) in the interior of $\mathbb{R}^4_+$. (b) $\beta_0 = 0.001$ to the stable point (15.46, 27.91,2.00, 23.18) in the interior of $\mathbb{R}^4_+$.

4.10.3 The effect of varying the natural death rate of the top predator

The effect of varying α, which represents the top predator's natural death-rate, on the behaviour of the system (4.1), is also studied. From Figure 4.5, the following results can be observed. As α increases, the density of the top predator decreases and thus, the attack rate γ_1 by the top predator on the predator decreases, which implies that there is an abundance of the latter. Furthermore, as a result of the predator's density increase, the attack rate on the prey in the unreserved zone increases, which affects negatively their density in the unprotected area. Thus, the migration rate to the reserved zone is also affected. Also, for different values of α, the system (4.1) starts to oscillate for a particular time and then, attains the equilibrium level in the interior of $\mathbb{R}^4_+$. It follows that the system (4.1) persists for long-term behaviour.

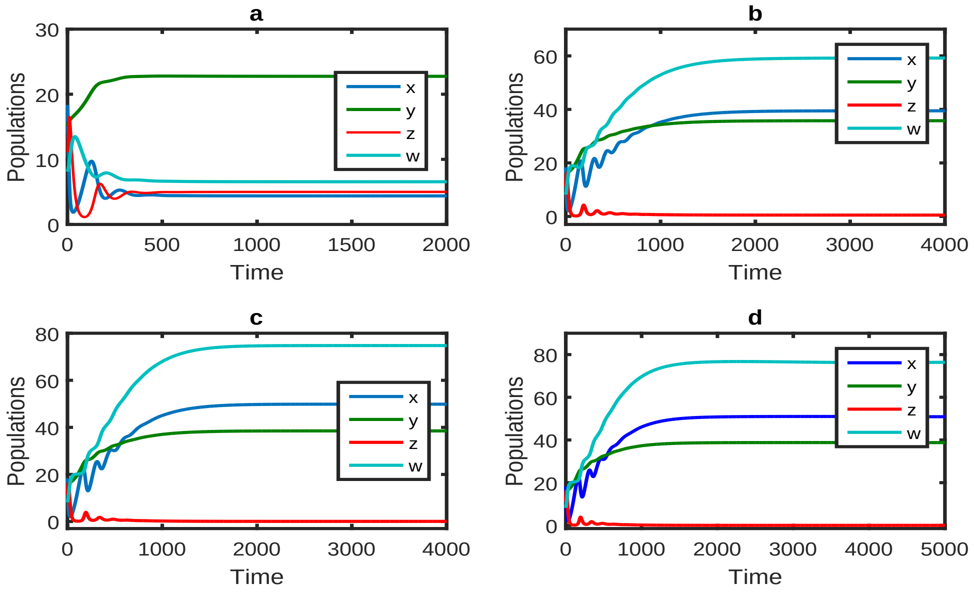

Fig. 4.4. Convergence of the solution of the system (4.1) for the data given by Eq.(4.40) with (a) $\alpha = 1$ to the stable point (4.38, 22.75, 5.00, 6.55) in the interior of $\mathbb{R}^4_+$. (b) $\alpha = 0.1$ to the stable point (39.47, 35.76, 0.5, 59.19) in the interior of $\mathbb{R}^4_+$. (c) $\alpha = 0.01$ to the stable point (44.85, 38.49, 0.05, 74.75) in the interior of $\mathbb{R}^4_+$. (d) $\alpha = 0.001$ to the stable point (50.94, 38.77, 0.005, 76.39) in the interior of $\mathbb{R}^4_+$.

4.10.4 The effect of varying the attack rate of the top predator on the predator

Figures 4.1 and 4.5 illustrate the effect of the top predator's attack rate on the predator, which is described by the parameter γ_1, in terms of the behaviour of the system (4.1) versus time. It can be noticed that for various values of γ_1, the solution initially oscillates, and after a specific time it attains its equilibrium level in the interior of $\mathbb{R}^4_+$. Also, when increasing γ_1, which means that the food conversion rate to the top predator increases and hence, its density is rapidly increasing. On the other hand, the densities both of the prey in the reserved and unreserved area, as well as the predator, are not affected. Once again, the system (4.1) persists for varying values of γ_1.

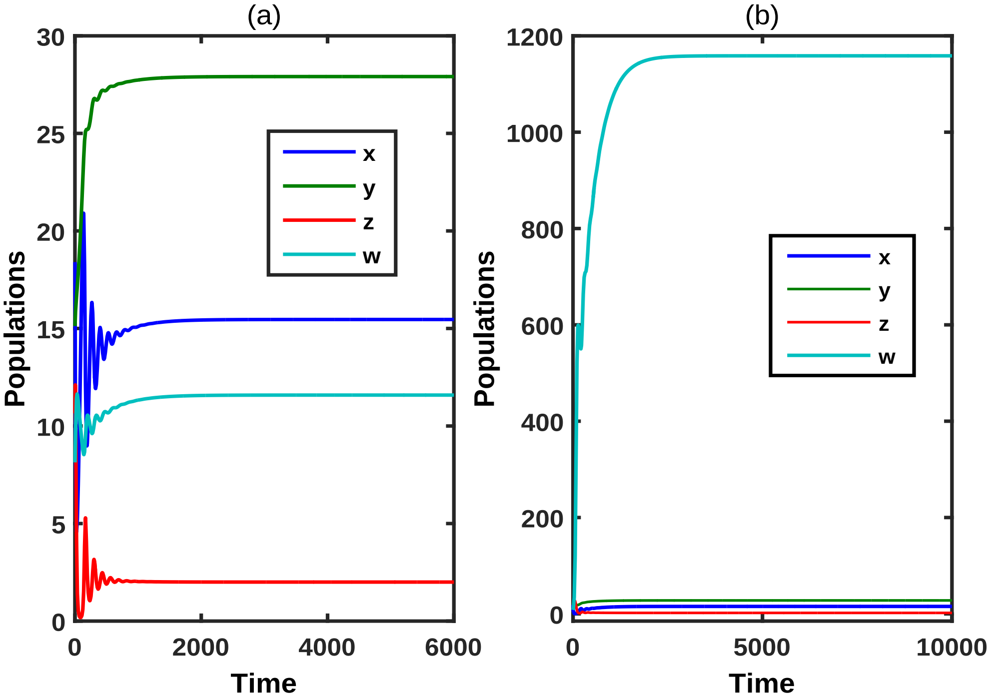

Fig. 4.5. Convergence of the solution of the system (4.1) for the data given by Eq.(4.40) with (a) $\gamma_1 = 0.001$ to the stable point (15.46, 27.91, 2.00, 11.58) in the interior of $\mathbb{R}^4_+$. (b) $\gamma_1 = 1$ to the stable point (15.46, 27.91, 2.00, 1158.1) in the interior of $\mathbb{R}^4_+$.

4.10.5 The effect of varying the conversion rate of the predator to the top predator

Now, Figure 4.6 studies the impact of the conversion rate of the predator to the top predator γ_2, on the behaviour of the species with t. When varying γ_2 and keeping the other parameters in Eq.(4.40) fixed, it can be observed that the solution of system (4.1) converges to the equilibrium point in the interior of $\mathbb{R}^3_+$ after oscillating for a certain amount of time. In this case, the w-component of the equilibrium point is strictly positive for $\gamma_2 \geq 0.0004$, but it becomes zero for $\gamma_2 < 0.00039$. Hence, the system (4.1) loses its persistence and the chain is broken.

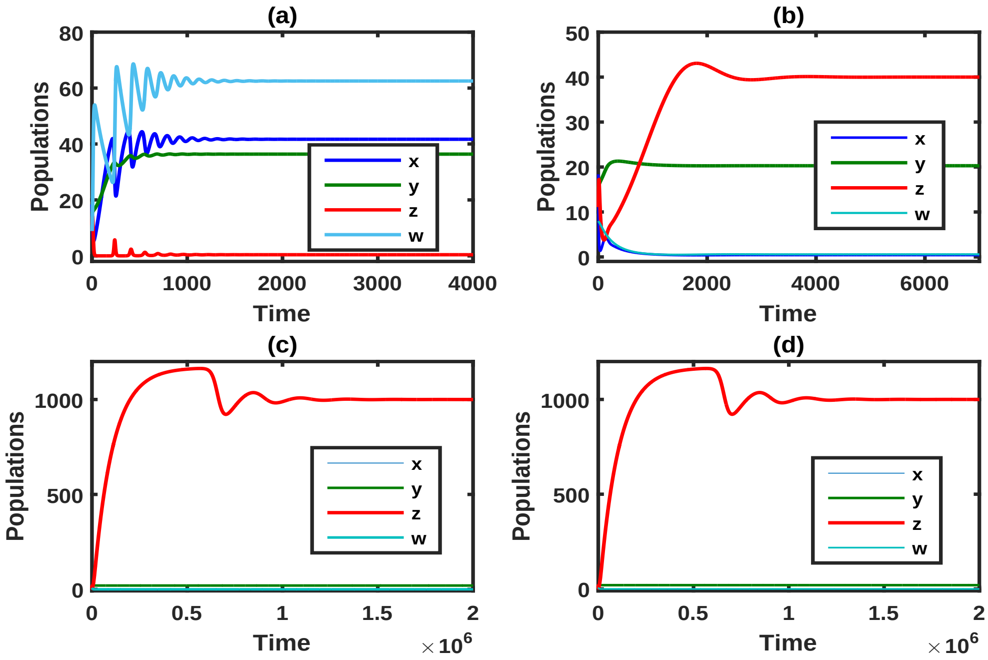

Fig. 4.6. Convergence of the solution of the system (4.1) for the data given by Eq.(4.40) with (a) $\gamma_2 = 1$ to the stable point (41.69, 36.37, 0.40, 62.51) in the interior of $\mathbb{R}^4_+$, (b) $\gamma_2 = 0.01$ to the stable point (0.44, 20.28, 40.00, 0.58) in the interior of $\mathbb{R}^4_+$, (c) $\gamma_2 = 0.0004$ to the stable point (0.01, 20.01, 999.38, 0.003) in the interior of $\mathbb{R}^4_+$, (d) $\gamma_2 = 0.00039$ to the stable point (0.01, 20, 1025.8, 0) in the interior of $\mathbb{R}^3_+$.

4.10.6 The effect of varying the unreserved area rate on the species

Similarly, for different values of σ_2, which represent the impact of the unreserved area on the behaviour of the species. When varying σ_2 and keeping the other parameters in (4.40) fixed, the solution of system (4.1) initially fluctuates for some time, and then, it converges to the equilibrium point. Furthermore, the top predator species w remains strictly positive for $\sigma_2 \geq 0.0003$, while it becomes zero for $\sigma_2 = 0.00029$. Hence, the system (4.1) loses its persistence, and the chain is broken (see Figure 4.7). Also, when decreasing σ_2, which means an abundance of prey, this negatively impacts on the density of the top predator. On the other hand, the densities of both of the prey in the reserved area and the predator are not affected.

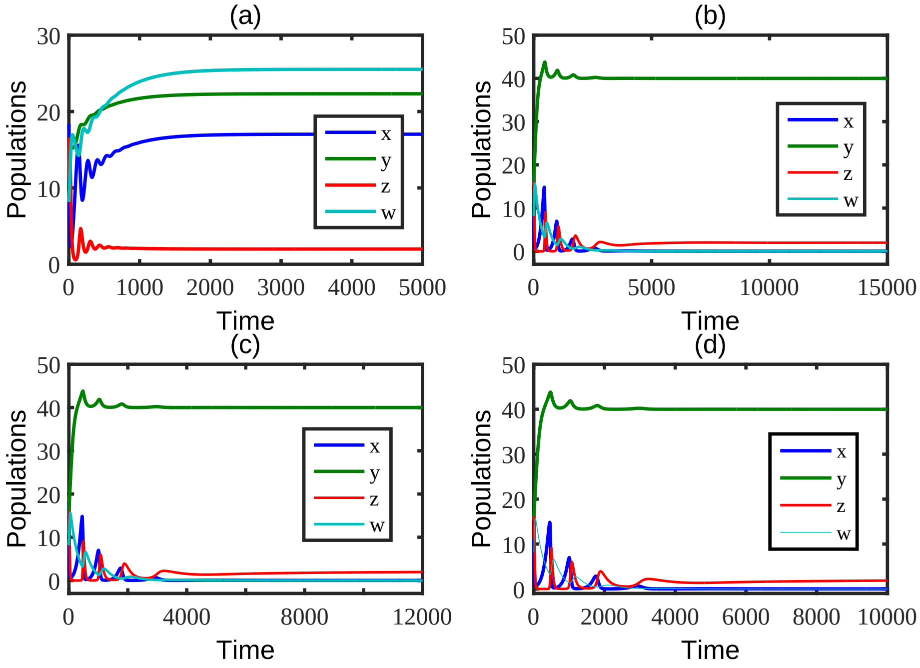

Fig. 4.7. Convergence of the solution of the system (4.1) for the data given by Eq.(4.40) with (a) $\sigma_2 = 1$ to the stable point (15.6, 27.58, 2.00, 23.38) in the interior of $\mathbb{R}^4_+$. (b) $\sigma_2 = 0.001$ to the stable point (0.04, 39.98, 2.00, 0.05) in the interior of $\mathbb{R}^4_+$. (c) $\sigma_2 = 0.0003$ to the stable point (0.01, 39.99, 2.00, 0.002) in the interior of $\mathbb{R}^4_+$, (d) $\sigma_2 = 0.00029$ to the stable point (0.01, 39.99, 1.82, 0) in the interior of $\mathbb{R}^3_+$.

4.10.7 The effect of varying the conversion rate of the prey in the unreserved zone to the predator

For the parameter values given in Eq.(4.40) with different β_2, which represent the conversion rate of the prey in the unreserved zone to the predator, system (4.1) again losses its persistence and the trajectory asymptotically approaches to the stable equilibrium point in the interior of $\mathbb{R}^3_+$. In this case, the z- and w- components of the equilibrium point are strictly positive for $\beta_2 \geq 0.0002$, but this becomes zero for $\beta_2 = 0.00019$. Hence, the system (4.1) loses its persistence, and the chain is broken. (See Figure 4.8).

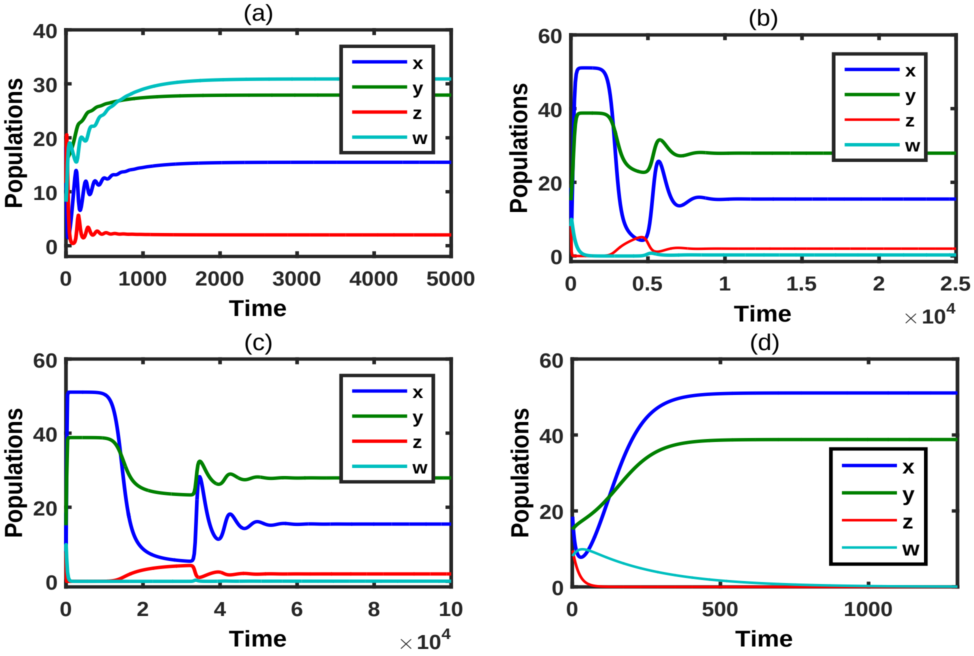

Fig. 4.8. Convergence of the solution of the system (4.1) for the data given by Eq.(4.40) with (a) $\beta_2 = 1$, to the stable point (15.6, 27.91, 2.00, 30.9) in the interior of $\mathbb{R}^4_+$. (b) $\beta_2 = 0.01$, to the stable point (15.46, 27.91, 2.00, 0.28) in the interior of $\mathbb{R}^4_+$. (c) $\beta_2 = 0.0002$, to the stable point (15.46, 27.91, 2.00, 0.04) in the interior of $\mathbb{R}^4_+$. (d) $\beta_2 = 0.00019$ to the stable point (51.05, 38.79, 0, 0) in the interior of $\mathbb{R}^2_+$.

4.10.8 The effect of varying the attack rate of the predator on the prey in the unreserve zone

Finally, Figure 4.9 shows the behaviour of the solution of system (4.1) for varying one of the most important parameters, namely β_1, due to the connection between the first component and the third in the chain. Since the fourth component totally depends on the third one, it is worth studying the dynamic behaviour of this parameter carefully. Again from Figure 4.9, it can be seen that as $\beta_1 \to 0$, the eigenvalues have the following forms:

For $\beta_1 = 0.1$,

$\lambda_1 = -0.2881 + 4.4316i, \lambda_2 = -0.2881 - 4.4316i, \lambda_3 = -1.0542, \lambda_4 = -2.2366.$

When $\beta_1 = 0.01$,

$\lambda_1 = -0.078 + 3.9688i, \lambda_2 = -0.0378 - 3.9688i, \lambda_3 = -2.5759, \lambda_4 = -1.4059.$

When $\beta_1 = 0.0001$,

$\lambda_1 = -0.0039 + 3.9190i, \lambda_2 = -0.0039 - 3.9190i, \lambda_3 = -2.6260, \lambda_4 = -1.4434.$

When $\beta_1 = 0.00001$,

$\lambda_1 = -0.0004 + 3.9041i, \lambda_2 = -0.0004 - 3.9041i, \lambda_3 = -2.6309, \lambda_4 = -1.4469.$

While the analytical expansion gives, $\lambda_{1,2} = \pm\sqrt{\gamma_1\gamma_2 z^* w^*}i = 3.904025$ (when $\beta_1 = 0$ as a limit). This result confirms the numerical calculations up to three decimal places. The numerical studies and the analytical expansion show that the real parts of the eigenvalues λ_1 and λ_2 are proportional to β_1 and their ratio is approximately -4. Together with the other eigenvalues, which have a negative real part that is not small, this means that for small β_1 the solution decays exponentially towards the equilibrium point F_3 at a rate, which is very small. On the other hand, the imaginary parts of λ_1 and λ_2 are not small and explain that the solution oscillates with a frequency $\sqrt{\gamma_1\gamma_2 z^* w^*}$, which is also not small. This observation is in agreement with the Routh-Hurwitz criteria, which show that all the eigenvalues of $J(F_3)$ have a negative real part and hence, F_3 is a hyperbolic equilibrium point. Figure 4.9 also indicates that the slow-decaying and oscillating components are z and w, whereas x and y converge fast to their equilibrium and do not oscillate.

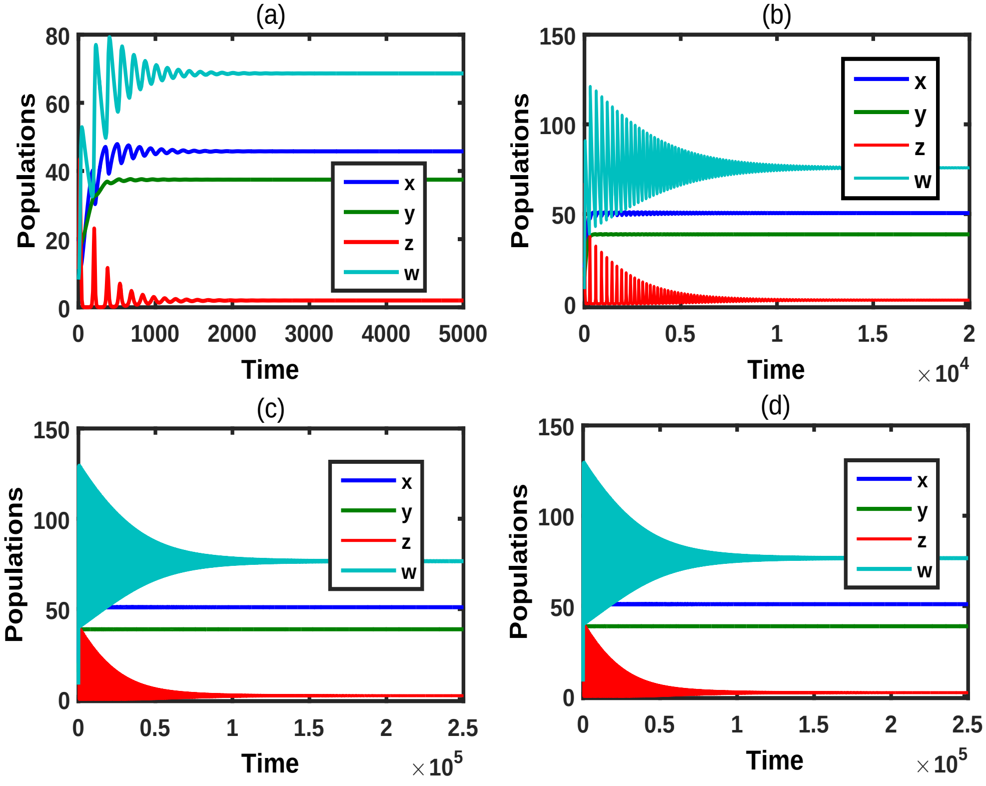

Fig. 4.9. Convergence of the solution of the system (4.1) for the data given by Eq.(4.40) with (a) $\beta_1 = 0.1$ to the stable point (45.76, 37.45, 2.00, 68.62) in the interior of $\mathbb{R}^4_+$. (b) $\beta_1 = 0.01$ to the stable point (50.52, 38.66, 2.00, 75.76) in the interior of $\mathbb{R}^4_+$. (c) $\beta_1 = 0.0001$ to the stable point (51.05, 38.79, 2.01, 76.58) in the interior of $\mathbb{R}^4_+$. (d) $\beta_1 = 0.00001$ to the stable point (51.05, 38.79, 1.99, 76.59) in the interior of $\mathbb{R}^4_+$.

4.11 Conclusion

An ecological model, which describes the effect of the reserved zone on the dynamical behaviour of a food chain prey-predator model with a Lotka-Volterra type of functional response, has been proposed and studied. The boundedness of system (4.1) has been shown, and the possible dynamical behaviour of this system has been investigated analytically at the equilibrium points. The persistence conditions of the proposed system have been derived. It has been proven that the solutions of system (4.1) possess transcritical bifurcation. To confirm the analytical results, system (4.1) has been solved numerically, and the effects of various parameters on the dynamical behaviour of the proposed system have been performed, with the following results being obtained.

1. The persistence of the top predator w hinges solely on the parameters β_2, σ_2 and γ_2. In particular, if $\beta_2 = 0.0019$, then this species decreases over time, eventually dying out, and the solution of system (4.1) is attained asymptotically to the equilibrium point in $\mathbb{R}^3_+$, while this species survives when $\beta_2 \geq 0.002$.

2. The existence of the predator z relies solely on the conversion rate β_2 of the prey in the unreserved zone to the third component in the chain. This species decreases over time until it faces extinction, and this causes the chain to break. Hence, the solution of system (4.1) settles down asymptotically to the equilibrium point in $\mathbb{R}^2_+$. In particular, if $\beta_2 = 0.0019$, then this species decreases over time and dies out, whilst it survives when $\beta_2 \geq 0.002$.

3. Both the prey species x in the unreserved zone and the prey species y in the reserved area are persistent under all conditions.

4. It is observed that the dynamic behaviour of system (4.1) does not change if one of the parameters σ_1, β_0, α, β_1 and γ_1 is varied.

Overall, the system with the reserved zone, as shown in this chapter, converges to a steady state for a wide range of parameters.

Chapter 5: The effect of the reserve zone on the partially dependent predator-prey model

5.1 Introduction

In this chapter, we study the effect of a reserve zone on the food chain prey-predator model introduced earlier. We propose to model such an effect by introducing a partial dependence of the predator population (z) on the prey in the unprotected zone (x). In this case, the latter represents an alternative resource for the predator. As before, we discuss the existence of equilibrium points and perform carry out the stability analysis by making use of the eigenvalue method, Routh-Hurwitz criteria and Lyapunov direct method. The model shows rich dynamics in the space of non-negative solutions. We find that in addition to the equilibrium with two vanishing components and the trivial equilibrium (which have been already discussed before) there are two new equilibria. One is the equilibrium for which only the top predator vanishes and the remaining components are strictly positive, and the other is when only the last two components are strictly positive and the other two are zero. The long-term behaviour of the system is studied, and conditions for persistence are derived.

Finally, the simulations of this model show that for large-time the solutions approach the strictly positive steady state.

5.2 Mathematical model

Similarly to the previous chapter, we consider a food chain consisting of prey in the unreserved zones, prey in the reserved zone (which predators are not allowed to enter), predator and a top predator. The corresponding densities are denoted by $x(t)$, $y(t)$, $z(t)$ and $w(t)$. Now, however, the predator population (z) is allowed to partially depend on the prey in the unreserved zone (x). This is modelled by an extra logistic term added to the first component of the system of differential equations:

$$\begin{aligned} \frac{dx}{dt} &= rx\Big(1-\frac{x}{k}\Big) - \sigma_1 x + \sigma_2 y - \beta_1 xz = f_1(x,y,z,w),\\ \frac{dy}{dt} &= sy\Big(1-\frac{y}{l}\Big) + \sigma_1 x - \sigma_2 y = f_2(x,y,z,w),\\ \frac{dz}{dt} &= az\Big(1-\frac{z}{m}\Big) + \beta_2 xz - \beta_0 z - \gamma_1 zw = f_3(x,y,z,w),\\ \frac{dw}{dt} &= \gamma_2 zw - \alpha w = f_4(x,y,z,w). \end{aligned} \tag{5.1}$$

Here, m and a are two new model parameters: m is the carrying capacity of the predator, wheres a is the intrinsic growth rate. The other model parameters are the same as in Chapter 4. The proposed model (5.1) has been analysed with the initial conditions $x(0) \geq 0$, $y(0) \geq 0$, $z(0) \geq 0$ and $w(0) \geq 0$, $p(x) = \beta_1 x$ and $q(z) = \gamma_1 z$ are the Lotka-Volterra type of functional responses. All parameters of the model system (5.1) are again assumed to be positive.

Under the above assumptions, the functions on the right-hand side in the system (5.1) are continuously differentiable functions on $\mathbb{R}^4_+ = \big\{(x,y,z,w), x \geq 0, y \geq 0, z \geq 0, w \geq 0\big\}$ and hence, they are Lipschitzian. Therefore, a solution to the system (5.1) exists, which is unique. Further, all the solutions of the model (5.1) with any non-negative initial conditions are bounded, as is shown in the following section.

5.3 Boundedness

Theorem 5.3.1 *Assume that the conditions* $\beta_1 \geq \beta_2$ *and* $\gamma_1 \geq \gamma_2$ *hold, then all the solutions of the system (5.1) which initiate in* $\mathbb{R}_+^4$ *are uniformly bounded.*

Proof Let $(x(t), y(t), z(t), w(t))$ be an arbitrary solution of the system (5.1) with a non-negative initial condition. Then for $U(t) = x(t) + y(t) + z(t) + w(t)$, we have

$$\frac{dU}{dt} = rx - \frac{rx^2}{k} + sy - \frac{sy^2}{l} + az - \frac{az^2}{m} - (\beta_1 - \beta_2)xz - (\gamma_1 - \gamma_2)zw - \beta_0 z - \alpha w.$$

Hence, according to the assumptions of the theorem, the following is obtained:

$$\begin{aligned} \frac{dU}{dt} &\leq rx - \frac{rx^2}{k} + sy - \frac{sy^2}{l} + az - \frac{az^2}{m} - \beta_0 z - \alpha w \\ \frac{dU}{dt} + \xi U &\leq 2rx - \frac{rx^2}{k} + 2sy - \frac{sy^2}{l}, \end{aligned}$$

where, $\xi = \min\{r, s, \beta_0, \alpha, a\}$, then

$$\begin{aligned} \frac{dU}{dt} + \xi U &\leq rk - \frac{r}{k}\big(x - k\big)^2 + sl - \frac{s}{l}\big(y - l\big)^2 \\ &\leq rk + sl = \mu. \end{aligned}$$

Applying Gronwall's Inequality, the following is obtained:

$$0 \leq U\big(x(t), y(t), z(t), w(t)\big) \leq \frac{\mu}{\xi}\big(1 - e^{-\xi t}\big) + U(0)e^{-\xi t}.$$

Therefore,

$$0 \leq \limsup_{t \to \infty} U\big(t\big) \leq \frac{\mu}{\xi}.$$

Hence, all the solutions of the system (5.1) that are initiated in the $\mathbb{R}_+^4$ are attracted to the region $\Omega = \Big\{\big(x, y, z, w\big) \in \mathbb{R}_+^4 : U = x + y + z + w \leq \frac{\mu}{\xi}\Big\}$ under the given conditions. Thus, these solutions are bounded, and the proof is complete. ■

5.4 Positive invariance

See Subsection (4.4).

In the following, the existence of the equilibrium points of the system (5.1) will be elucidated.

5.5 Existence of equilibria

The system, which given by (5.1), has six nonnegative equilibrium points, namely:

- $F_0 = (0, 0, 0, 0)$ is the vanishing fixed point;
- $F_1 = (\hat{x}, \hat{y}, 0, 0)$ is the xy planar fixed point;
- $F_2 = (0, 0, \ddot{z}, 0)$ is the axial fixed point;
- $F_3 = (0, 0, \tilde{z}, \tilde{w})$ is the zw planar fixed point;
- $F_4 = (\bar{x}, \bar{y}, \bar{z}, 0)$ is the top predator-free fixed point;
- $F_5 = (x^*, y^*, z^*, w^*)$ is the interior fixed point.

The existence of $F_0 = (0, 0, 0, 0)$ and $F_1 = (\hat{x}, \hat{y}, 0, 0)$ are similar to that in Subsection 4.5.1, and hence omitted, while the existence of F_2, F_3, F_4 and F_5 are now shown as follows:

5.5.1 The existence of the axial equilibrium point

The equilibrium point F_2 exists on z axis of if and only if, $\ddot{z}$ is the positive root of the following algebraic equation: $a - \left(\frac{az}{m}\right) - \beta_0 = 0$. Solving this equation gives that:

$$\ddot{z} = \frac{(a - \beta_0)m}{a}.$$

It should also be noted that for $\ddot{z} > 0$ to be positive, the following must be the case:

$$a > \beta_0.$$

Thus, in the absence of prey in the reserved and unreserved zone and the top predator, the intrinsic growth rate of the predator must be higher than its natural mortality rate for the equilibrium point F_2 to exist.

5.5.2 The existence of the $zw-$ planar equilibrium point

The equilibrium point $F_3 = (0, 0, \tilde{z}, \tilde{w})$ exists in the interior of $\mathbb{R}^2_+$ of the zw-plane, if and only if, $\tilde{z}$ and $\tilde{w}$ represent the positive solution of the following set of algebraic equations:

$$\begin{aligned} a\left(1 - \frac{z}{m}\right) - \beta_0 - \gamma_1 w &= 0, && (5.2) \\ \gamma_2 z - \alpha &= 0. && (5.3) \end{aligned}$$

From equation (5.3),

$$\tilde{z} = \frac{\alpha}{\gamma_2}. \tag{5.4}$$

Now, substituting the value of $\tilde{z}$ into Eq.(5.2), a little algebraic manipulation yields:

$$\tilde{w} = \frac{m\gamma_2(a - \beta_0) - a\alpha}{m\gamma_1\gamma_2}, \tag{5.5}$$

It should also be noted that for $\tilde{w} > 0$ to be positive, the following must be the case:

$$am\gamma_2 > a\alpha + m\beta_0\gamma_2.$$

5.5.3 The existence of the top predator-free equilibrium point

The equilibrium point F_4 exists in the interior of $\mathbb{R}^3_+$ of the xyz-plane, if and only if, $\bar{x}, \bar{y}$ and $\bar{z}$ are the positive roots of the following set of algebraic equations:

$$r\left(1 - \frac{x}{k}\right) - \sigma_1 + \frac{\sigma_2 y}{x} - \beta_1 z = 0, \tag{5.6}$$

$$s\left(1 - \frac{y}{l}\right) - \sigma_2 + \frac{\sigma_1 x}{y} = 0, \tag{5.7}$$

$$a\left(1 - \frac{z}{m}\right) + \beta_2 x - \beta_0 = 0. \tag{5.8}$$

From the above list of equations, the following is obtained:

$$y = \frac{l}{2s}\left[(s-\sigma_2) + \sqrt{(s-\sigma_2)^2 + \frac{4s\sigma_1 x}{l}}\right], \tag{5.9}$$

$$z = \frac{\big(a + \beta_2 x - \beta_0\big)m}{a}. \tag{5.10}$$

By substituting the values of y and z in Eq.(5.6), a little algebraic manipulation yields:

$$ax^3 + bx^2 + cx + d = 0, \tag{5.11}$$

where,

$$\begin{aligned}
a &= \left[\frac{r}{k} + \frac{\beta_1\beta_2 m}{a}\right]^2 > 0,\\
b &= 2\left(\frac{r}{k} + \frac{\beta_1\beta_2 m}{a}\right) + \left(r - \sigma_1 - m\beta_1 + \frac{m\beta_0\beta_1}{a}\right),\\
c &= -2\left(\frac{r}{k} + \frac{\beta_1\beta_2 m}{a}\right)\left[\frac{l\sigma_2(s-\sigma_2)}{2s}\right] + \left(r - \sigma_1 - m\beta_1 + \frac{m\beta_0\beta_1}{a}\right)^2,\\
d &= -\left[\frac{l\sigma_2(s-\sigma_2)}{2s}\right]\left(r - \sigma_1 - m\beta_1 + \frac{m\beta_0\beta_1}{a}\right) + \left(\frac{\sigma_1\sigma_2^2 l}{s}\right).
\end{aligned}$$

By using Descartes rule of signs, Eq.(5.11) has a unique positive solution $x = \bar{x}$, if the following inequality

$$\left(\frac{\sigma_1\sigma_2}{s-\sigma_2}\right) + \beta_1 m < \big(r - \sigma_1\big) + \left[\frac{\beta_0\beta_1 m}{a}\right], \tag{5.12}$$

holds. Knowing the value of $\bar{x}$, the values of $\bar{y}$ and $\bar{z}$ can be computed from Equations (5.9) and (5.10), respectively. It should also be noted that for $\bar{z}$ to be positive, the following must be true:

$$a + \beta_2\bar{x} > \beta_0. \tag{5.13}$$

5.5.4 The existence of the positive equilibrium point

The positive equilibrium point F_5 exists in the interior of $\mathbb{R}^4_+$, if and only if, x^*, y^*, z^* and w^* are the positive solutions of the following set of equations:

$$r\Big(1-\frac{x}{k}\Big)-\sigma_1+\frac{\sigma_2 y}{x}-\beta_1 z=0, \tag{5.14}$$

$$s\Big(1-\frac{y}{l}\Big)-\sigma_2+\frac{\sigma_1 x}{y}=0, \tag{5.15}$$

$$a\Big(1-\frac{z}{m}\Big)+\beta_2 x-\beta_0-\gamma_1 w=0, \tag{5.16}$$

$$\gamma_2 z-\alpha=0. \tag{5.17}$$

From the above list of equations, the following is obtained:

$$y=\frac{l}{2s}\left((s-\sigma_2)+\sqrt{(s-\sigma_2)^2+\frac{4s\sigma_1 x}{l}}\right), \tag{5.18}$$

$$z^*=\frac{\alpha}{\gamma_2}, \tag{5.19}$$

$$w=\frac{\gamma_2 m\big(a+\beta_2 x\big)-\big(a\alpha+\beta_0\gamma_2 m\big)}{\gamma_1\gamma_2 m}. \tag{5.20}$$

By substituting the values of y and z in Eq.(5.14), a little algebraic manipulation yields:

$$ax^3+bx^2+cx+d=0, \tag{5.21}$$

where,

$$a=\Big(\frac{-r}{k}\Big)^2>0,$$
$$b=\frac{2r}{k}\Big((r-\sigma_1)-\frac{\beta_1\alpha}{\gamma_2}\Big),$$
$$c=\frac{2r}{k}\Big(\frac{\sigma_2 l}{2s}(s-\sigma_2)\Big)+\Big((r-\sigma_1)-\frac{\beta_1\alpha}{\gamma_2}\Big)^2,$$
$$d=\frac{\sigma_2 l}{s}\Big(s-\sigma_2\Big)\left((r-\sigma_1)-\frac{\beta_1\alpha}{\gamma_2}\right)+\frac{\sigma_1\sigma_2^2 l}{s}.$$

By using Descartes rule of signs, Eq.(5.21) has a unique positive solution $x=x^*$, if the following inequality

$$\Big(r - \sigma_1\Big) > \frac{\beta_1 \alpha}{\gamma_2}, \tag{5.22}$$

holds. Knowing the value of x^*, the values of y^* and w^* can be computed from Equations (5.9) and (5.22), respectively. It should also be noted that for w^* to be positive, the following must be true:

$$\gamma_2 m\big(a + \beta_2 x^*\big) > \big(a\alpha + \beta_0 \gamma_2 m\big). \tag{5.23}$$

5.6 Local stability of the equilibrium points

Similarly to the previous chapter, the local dynamic behaviour of the system (5.1) is discussed by making use of the eigenvalue method and Routh-Hurwitz criteria. The Jacobian matrix of the system (5.1) at any point is given by

$$J = \begin{bmatrix} r - \sigma_1 - \dfrac{2rx}{k} - \beta_1 z & \sigma_2 & -\beta_1 x & 0 \\ \sigma_1 & s - \sigma_2 - \dfrac{2sy}{l} & 0 & 0 \\ \beta_2 z & 0 & a - \frac{2az}{m} + \beta_2 x - \beta_0 - \gamma_1 w & -\gamma_1 z \\ 0 & 0 & \gamma_2 w & \gamma_2 z - \alpha \end{bmatrix},$$

and, the eigenvalues of the resulting matrix are computed as follows:

5.6.1 Local stability behaviour of F_0

In the following lemma, it is shown that F_0 is always a saddle point.

Lemma 8 *The vanishing equilibrium point* $F_0 = (0, 0, 0, 0)$ *is a saddle point in the* $\mathbb{R}^4_+$.

Proof First, the Jacobian matrix of the system (5.1) at F_0 can be written by:

$$J(F_0) = \begin{bmatrix} r-\sigma_1 & \sigma_2 & 0 & 0 \\ \sigma_1 & s-\sigma_2 & 0 & 0 \\ 0 & 0 & a-\beta_0 & 0 \\ 0 & 0 & 0 & -\alpha \end{bmatrix} \tag{5.24}$$

Then, it is easy to verify that, the eigenvalues of $J(F_0)$ satisfy the following relations:

$$\lambda_{01} + \lambda_{02} = (r-\sigma_1) + (s-\sigma_2) > 0, \tag{5.25}$$

$$\lambda_{01}.\lambda_{02} = (r-\sigma_1)(s-\sigma_2) - \sigma_1\sigma_2, \tag{5.26}$$

$$\lambda_{03} = a - \beta_0, \tag{5.27}$$

$$\lambda_{04} = -\alpha < 0, \tag{5.28}$$

where, $\lambda_{0i} \quad (i = 1, 2, 3, 4)$ represent the eigenvalues that describe the dynamics in the directions of their eigenvectors. Note that, according to Eq.(5.26), the eigenvalues λ_{01} and λ_{02} are positive, provided that:

$$(r-\sigma_1)(s-\sigma_2) > \sigma_1\sigma_2,$$

and then, F_0 is the unstable point in the interior of $\mathbb{R}^2_+$ of the xy-plane. However, λ_{01} and λ_{01} have opposite signs, provided that:

$$(r-\sigma_1)(s-\sigma_2) < \sigma_1\sigma_2.$$

Hence, F_0 is a saddle point in the interior of $\mathbb{R}^2_+$ of the xy-plane. Further, according to Eqs. (4.24)-(4.25), the equilibrium point F_0 is a saddle point in the interior of $\mathbb{R}^4_+$.
■

5.6.2 Local stability behaviour of F_1

In the following lemma, the local behaviour of the xy- planar fixed point F_1 is shown.

Lemma 9 *The planar equilibrium point* $F_1 = (\hat{x}, \hat{y}, 0, 0)$ *is locally asymptotically stable in* $\mathbb{R}^4_+$*, whenever:*

$$a + \beta_2 \hat{x} < \beta_0, \tag{5.29}$$

holds.

Proof The Jacobian matrix of system (5.1) at the equilibrium point F_1 is given by:

$$J(F_1) = \begin{bmatrix} r - \sigma_1 - \frac{2r\hat{x}}{k} & \sigma_2 & -\beta_1 \hat{x} & 0 \\ \sigma_1 & s - \sigma_2 - \frac{2s\hat{y}}{l} & 0 & 0 \\ 0 & 0 & a + \beta_2 \hat{x} - \beta_0 & 0 \\ 0 & 0 & 0 & -\alpha \end{bmatrix} \tag{5.30}$$

Straightforward computations show that the eigenvalues of the Jacobian matrix $J(F_1)$ satisfy the following relations:

$$\lambda_{11} + \lambda_{12} = -\Big(\frac{\sigma_2 \hat{y}}{\hat{x}} + \frac{r\hat{x}}{k} + \frac{\sigma_1 \hat{x}}{\hat{y}} + \frac{s\hat{y}}{l}\Big) < 0, \tag{5.31}$$

$$\lambda_{11}.\lambda_{12} = \left(\frac{rs(\hat{x})^2(\hat{y})^2 + sk\sigma_2(\hat{y})^3 + r\sigma_1(\hat{x})^3}{kl\hat{x}\hat{y}}\right) > 0, \tag{5.32}$$

$$\lambda_{13} = a + \beta_2 \hat{x} - \beta_0, \tag{5.33}$$

$$\lambda_{14} = -\alpha < 0, \tag{5.34}$$

where, $\lambda_{1i} \quad (i = 1, 2, 3, 4)$ represent the eigenvalues that describe the dynamics in the directions of their eigenvectors. Note that, according to equations (5.31)-(5.34), all the eigenvalues of $J(F_1)$ have negative real parts and hence, F_1 is locally asymptotically stable in $\mathbb{R}^4_+$, if and only if, condition (5.29) holds. However, it is a saddle point in the interior of $\mathbb{R}^4_+$, if the condition (5.29) is violated. ■

5.6.3 Local stability behaviour of F_2

In the following lemma, the local behaviour of the z- axial fixed point F_2 is shown.

Lemma 10 *The axial equilibrium point* $F_2 = (0, 0, \ddot{z}, 0)$ *is locally stable in* $\mathbb{R}^4_+$*, whenever:*

$$\begin{aligned} &r - \sigma_1 + s - \sigma_2 < \beta_1 \ddot{z}, \\ &\big(r - \sigma_1 - \beta_1 \ddot{z}\big)\big(s - \sigma_2\big) - \sigma_1 \sigma_2 > 0, \\ &\gamma_2 \ddot{z} < \alpha, \end{aligned} \tag{5.35}$$

hold.

Proof The Jacobian matrix of system (5.1) at the equilibrium point F_2 is given by:

$$J(F_2) = \begin{bmatrix} r - \sigma_1 - \beta_1 \ddot{z} & \sigma_2 & 0 & 0 \\ \sigma_1 & s - \sigma_2 & 0 & 0 \\ \beta_2 \ddot{z} & 0 & 0 & -\gamma_1 \ddot{z} \\ 0 & 0 & 0 & \gamma_2 \ddot{z} - \alpha \end{bmatrix} \tag{5.36}$$

Straightforward computations show that the eigenvalues of the Jacobian matrix $J(F_2)$ satisfy the following relations:

$$\lambda_{21} + \lambda_{22} = (r - \sigma_1) - \beta_1 \ddot{z} + (s - \sigma_2), \tag{5.37}$$

$$\lambda_{21}.\lambda_{22} = (r - \sigma_1 - \beta_1 \ddot{z}).(s - \sigma_2) - \sigma_1 \sigma_2, \tag{5.38}$$

$$\lambda_{23} = 0, \tag{5.39}$$

$$\lambda_{24} = \gamma_2 \ddot{z} - \alpha, \tag{5.40}$$

where, $\lambda_{1i} \quad (i = 1, 2, 3, 4)$ represent the eigenvalues that describe the dynamics in the directions of their eigenvectors. Note that, according to equations (5.37)-(5.40), the eigenvalues $\big(\lambda_{21}, \lambda_{22}$ and $\lambda_{24}\big)$ of $J(F_2)$ have negative real parts and hence, F_2 is locally stable in $\mathbb{R}^4_+$, if and only if, conditions (5.35) hold. However, it is a saddle point in the interior of $\mathbb{R}^4_+$, if one of the conditions in (5.35) is violated. ■

5.6.4 Local stability behaviour of F_3

In the following lemma, the local behaviour of the zw- planar fixed point F_3 is shown.

Lemma 11 *The planar equilibrium point* $F_3 = (0, 0, \tilde{z}, \tilde{w})$ *is locally asymptotically stable in* $\mathbb{R}^4_+$*, whenever:*

$$\begin{aligned} &r - \sigma_1 + s - \sigma_2 < \beta_1 \tilde{z}, \\ &\big(r - \sigma_1 - \beta_1 \tilde{z}\big)\big(s - \sigma_2\big) - \sigma_1\sigma_2 > 0, \end{aligned} \tag{5.41}$$

hold.

Proof The Jacobian matrix of system (5.1) at the equilibrium point F_3 is given by:

$$J(F_3) = \begin{bmatrix} r - \sigma_1 - \beta_1\tilde{z} & \sigma_2 & 0 & 0 \\ \sigma_1 & s - \sigma_2 & 0 & 0 \\ \beta_2\tilde{z} & 0 & -\frac{a\tilde{z}}{m} & -\gamma_1\tilde{z} \\ 0 & 0 & \gamma_2\tilde{w} & 0 \end{bmatrix} \tag{5.42}$$

Straightforward computations show that the eigenvalues of the Jacobian matrix $J(F_3)$ satisfy the following relations:

$$\lambda_{31} + \lambda_{32} = (r - \sigma_1) - \beta_1\ddot{z} + (s - \sigma_2), \tag{5.43}$$

$$\lambda_{31}.\lambda_{32} = (r - \sigma_1 - \beta_1\ddot{z}).(s - \sigma_2) - \sigma_1\sigma_2, \tag{5.44}$$

$$\lambda_{33} + \lambda_{34} = \frac{-a\tilde{z}}{m} < 0, \tag{5.45}$$

$$\lambda_{33}.\lambda_{34} = \gamma_1\gamma_2\tilde{z}\tilde{w} > 0, \tag{5.46}$$

where, $\lambda_{3i} \quad (i = 1, 2, 3, 4)$ represent the eigenvalues that describe the dynamics in the directions of their eigenvectors. Note that, according to equations (5.43)-(5.46), all the eigenvalues of $J(F_3)$ have negative real parts and hence, F_3 is locally asymptotically stable in $\mathbb{R}^4_+$, if and only if, condition (5.41) holds. However, it is a saddle point in the interior of $\mathbb{R}^4_+$, if one of the conditions in (5.41) is violated. ■

5.6.5 Local stability behaviour of F_4

In the following lemma, the local behaviour of the top predator-free fixed point F_4 is shown.

Lemma 12 *The top predator-free equilibrium point* $F_4 = (\bar{x}, \bar{y}, \bar{z}, 0)$ *is locally asymptotically stable in* $\mathbb{R}^4_+$ *whenever*

$$\gamma_2 \bar{z} < \alpha. \tag{5.47}$$

holds.

Proof The Jacobian matrix of the system (5.1) at the equilibrium point $F_4 = (\bar{x}, \bar{y}, \bar{z}, 0)$ can be written as:

$$J(F_4) = \begin{bmatrix} a_{11} & a_{12} & a_{13} & 0 \\ a_{21} & a_{22} & 0 & 0 \\ a_{31} & 0 & a_{33} & a_{34} \\ 0 & 0 & 0 & a_{44} \end{bmatrix} \tag{5.48}$$

where,

$$a_{11} = -\Big(\frac{\sigma_2 \bar{y}}{\bar{x}} + \frac{r\bar{x}}{k}\Big) < 0; a_{12} = \sigma_2 > 0; a_{13} = -\beta_1 \bar{x} < 0;$$
$$a_{21} = \sigma_1 > 0; a_{22} = -\Big(\frac{\sigma_1 \bar{x}}{\bar{y}} + \frac{s\bar{y}}{l}\Big) < 0; a_{31} = \beta_2 \bar{z} > 0;$$
$$a_{32} = 0; a_{33} = -\Big(\frac{a\bar{z}}{m}\Big); a_{34} = -\gamma_1 \bar{z} < 0; a_{44} = \gamma_2 \bar{z} - \alpha.$$

The first root of the characteristic equation of $J(F_4)$ is $\gamma_2 \bar{z} - \alpha$ and the other three roots are given by:

$$\lambda^3 + A_1 \lambda^2 + A_2 \lambda + A_3 = 0.$$

The coefficients of the characteristic equation of $J(F_4)$ can be written as:

$A_1 = -(a_{11} + a_{22} + a_{33}) > 0,$

$A_2 = a_{11}a_{33} + a_{22}a_{33} - a_{13}a_{31} + M_1 > 0,$

$A_3 = a_{13}a_{31}a_{22} - a_{33}M_1 > 0,$

where, $M_1 = a_{11}a_{22} - a_{12}a_{21} > 0$. Further,

$$\begin{aligned} \Delta &= A_1A_2 - A_3 = (a_{11} + a_{33})(a_{13}a_{31} + a_{11}a_{33}) \\ &- (a_{11} + a_{22})\big[M_1 + a_{22}a_{33}\big] - 2a_{11}a_{22}a_{33} > 0. \end{aligned}$$

Now, according to the Routh-Hurwitz criteria, all the eigenvalues of $J(F_4)$ have roots with negative real parts, provided that $A_i(i=1,3) > 0$ and $\Delta > 0$. Therefore, F_4 is locally asymptotically stable, if (5.47) holds. ■

5.6.6 Local stability behaviour of F_5

In the following lemma, the local behaviour of the positive fixed point F_5 is shown.

Lemma 13 *The positive equilibrium point* $F_5 = (x^*, y^*, z^*, w^*)$ *is locally asymptotically stable in* $\mathbb{R}^4_+$ *whenever it exists.*

Proof The Jacobian matrix of the system (5.1), at the positive equilibrium point $F_5 = (x^*, y^*, z^*, w^*)$, can be written as:

$$J(F_5) = \begin{bmatrix} a_{11} & a_{12} & a_{13} & 0 \\ a_{21} & a_{22} & 0 & 0 \\ a_{31} & 0 & a_{33} & a_{34} \\ 0 & 0 & a_{43} & 0 \end{bmatrix} \tag{5.49}$$

where,

$$a_{11} = -\Big(\frac{\sigma_2 y^*}{x^*} + \frac{rx^*}{k}\Big) < 0; a_{12} = \sigma_2 > 0; a_{13} = -\beta_1 x^* < 0;$$
$$a_{21} = \sigma_1 > 0; a_{22} = -\Big(\frac{\sigma_1 x^*}{y^*} + \frac{sy^*}{l}\Big) < 0; a_{31} = \beta_2 z^* > 0;$$
$$a_{33} = -\Big(\frac{a\bar{z}}{m}\Big); a_{34} = -\gamma_1 z^* < 0; a_{43} = \gamma_2 w^*.$$

Accordingly, the characteristic equation of $J(F_5)$ is given by:

$$\lambda^4 + A_1\lambda^3 + A_2\lambda^2 + A_3\lambda + A_4 = 0.$$

Here,

$$A_1 = -\big(a_{33} + M_2\big) > 0,$$
$$A_2 = a_{33}M_2 + M_1 - a_{13}a_{31} - a_{34}a_{43} > 0,$$
$$A_3 = a_{43}a_{34}M_2 - a_{33}M_1 + a_{13}a_{31}a_{22} > 0,$$
$$A_4 = -a_{34}a_{43}M_1 > 0,$$

where,

$M_1 = a_{11}a_{22} - a_{12}a_{21} > 0,\ M_2 = a_{11} + a_{22} < 0.$

Further,

$$\begin{aligned} \Delta &= A_1A_2A_3 - A_3^2 - A_1^2A_4 \\ &= \Big[- M_2\Big(a_{33}(a_{33} + M_2) + M_1\Big) + a_{13}a_{31}(a_{11} + a_{33}) + a_{33}a_{34}a_{43}\Big] \\ \Big(& \quad a_{43}a_{34}M_2 - a_{33}M_1 + a_{31}a_{13}a_{22}\Big) + a_{34}a_{43}M_1(a_{33} + M_2)^2 > 0. \end{aligned}$$

Now, according to the Routh-Hurwitz criteria, all the eigenvalues of $J(F_5)$ have roots with negative real parts since $A_i (i = 1, 3, 4) > 0$ and $\Delta > 0$. Hence, F_5 is locally asymptotically stable in the interior of $\mathbb{R}_+^4$. ■

5.7 Global dynamical behaviour

In this section, the global stability of the local equilibrium points is investigated by using the Lyapunov direct method, as shown in the following theorems.

Theorem 5.7.1 *Assume that the equilibrium point F_1 is locally asymptotically stable in $\mathbb{R}_+^4$, then it is globally asymptotically stable in $\mathbb{R}_+^4$.*

Proof Consider the following positive definite function:

$$R_1(x, y, z, w) = c_1\Big(x - \hat{x} - \hat{x}\ln\frac{x}{\hat{x}}\Big) + c_2\Big(y - \hat{y} - \hat{y}\ln\frac{y}{\hat{y}}\Big) + c_3z + c_4w,$$

where, $c_i, (i = 1, 2, 3, 4)$ are positive constants to be determined. Now, the time derivative of R_1 along the trajectory of the system (5.1) can be written as:

$$
\begin{aligned}
\frac{dR_1}{dt} &= c_1\Big(\frac{x-\hat{x}}{x}\Big)\frac{dx}{dt}+c_2\Big(\frac{y-\hat{y}}{y}\Big)\frac{dy}{dt}+c_3\frac{dz}{dt}+c_4\frac{dw}{dt}\\
&= c_1\big(x-\hat{x}\big)\Big(r-\frac{rx}{k}-\sigma_1+\frac{\sigma_2 y}{x}-\beta_1 z\Big)\\
&+ c_2\big(y-\hat{y}\big)\Big(s-\frac{sy}{l}+\frac{\sigma_1 x}{y}-\sigma_2\Big)\\
&+ c_3\Big(az-\frac{a(z)^2}{m}+\beta_2 xz-\beta_0 z-\gamma_1 zw\Big)+c_4\big(\gamma_2 zw-\alpha w\big)\\
&= c_1\big(x-\hat{x}\big)\Big(\frac{-r}{k}\big(x-\hat{x}\big)+\sigma_2\Big(\frac{y}{x}-\frac{\hat{y}}{\hat{x}}\Big)-\beta_1 z\Big)\\
&+ c_2\big(y-\hat{y}\big)\Big(\frac{-s}{l}\big(y-\hat{y}\big)+\sigma_1\Big(\frac{x}{y}-\frac{\hat{x}}{\hat{y}}\Big)\Big)\\
&+ c_3\Big(az-\frac{a(z)^2}{m}+\beta_2 xz-\beta_0 z-\gamma_1 zw\Big)+c_4\big(\gamma_2 zw-\alpha w\big).
\end{aligned}
$$

Therefore,

$$
\begin{aligned}
\frac{dR_1}{dt} &= \frac{-c_1 r}{k}\big(x-\hat{x}\big)^2+c_1\sigma_2\big(x-\hat{x}\big)\Big(\frac{y\hat{x}-x\hat{y}}{x\hat{x}}\Big)-c_1\big(x-\hat{x}\big)\beta_1 z\Big)\\
&- \frac{c_2 s}{l}\big(y-\hat{y}\big)^2+c_2\sigma_1\big(y-\hat{y}\big)\Big(\frac{x\hat{y}-y\hat{x}}{y\hat{y}}\Big)\\
&+ c_3\Big(az-\frac{a(z)^2}{m}+\beta_2 xz-\beta_0 z-\gamma_1 zw\Big)+c_4\big(\gamma_2 zw-\alpha w\big).
\end{aligned}
$$

By choosing the positive constants as

$$
c_1=1, c_2=\frac{\sigma_2\hat{y}}{\sigma_1\hat{x}}, c_3=\frac{\beta_1}{\beta_2}, c_4=\frac{\beta_1\gamma_1}{\beta_2\gamma_2},
$$

the following is obtained,

$$
\begin{aligned}
\frac{dR_1}{dt} &= -\Big(\frac{r}{k}\Big)\big(x-\hat{x}\big)^2-\Big(\frac{\sigma_2}{x\hat{x}y}\Big)\big(x\hat{y}-y\hat{x}\big)^2-\Big(\frac{s\sigma_2\hat{y}}{l\sigma_1\hat{x}}\Big)\big(y-\hat{y}\big)^2\\
&+ \Big(\beta_2\hat{x}+a-\beta_0\Big)\Big(\frac{\beta_2}{\beta_1}\Big)z-\Big(\frac{a\beta_1}{m\beta_2}\Big)z^2-\Big(\frac{\alpha\beta_1\gamma_1}{\beta_2\gamma_2}\Big)w.
\end{aligned}
$$

Then, $\frac{dR_1}{dt}<0$ under the local stability condition (5.29) and hence, R_1 is a Lyapunov function. Therefore, F_1 is globally asymptotically stable in $\mathbb{R}^4_+$. ■

The next theorem shows the global stability of the top predator-free equilibrium point F_4 in $\mathbb{R}^4_+$.

Theorem 5.7.2 *Assume that the equilibrium point F_4 is locally asymptotically stable in $\mathbb{R}^4_+$, then it is globally asymptotically stable in $\mathbb{R}^4_+$.*

Proof Consider the following positive definite function:

$$R_2(x,y,z,w) = c_1\Big(x-\bar{x}-\bar{x}\ln\frac{x}{\bar{x}}\Big) + c_2\Big(y-\bar{y}-\bar{y}\ln\frac{y}{\bar{y}}\Big) + c_3\Big(z-\bar{z}-\bar{z}\ln\frac{z}{\bar{z}}\Big) + c_4 w,$$

where, $c_i, (i = 1,2,3,4)$ are positive constants to be determined. Now the time derivative of R_4 along the trajectory of the system (5.1) can be written as:

$$\begin{aligned}
\frac{dR_2}{dt} &= c_1\Big(\frac{x-\bar{x}}{x}\Big)\frac{dx}{dt} + c_2\Big(\frac{y-\bar{y}}{y}\Big)\frac{dy}{dt} + c_3\Big(\frac{z-\bar{z}}{z}\Big)\frac{dz}{dt} + c_4\frac{dw}{dt} \\
&= c_1\big(x-\bar{x}\big)\Big(r - \frac{rx}{k} - \sigma_1 + \frac{\sigma_2 y}{x} - \beta_1 z\Big) \\
&+ c_2\big(y-\bar{y}\big)\Big(s - \frac{sy}{l} + \frac{\sigma_1 x}{y} - \sigma_2\Big) \\
&+ c_3\big(z-\bar{z}\big)\Big(a - \frac{az}{m} + \beta_2 x - \beta_0 - \gamma_1 w\Big) + c_4\big(\gamma_2 zw - \alpha w\big) \\
&= c_1\big(x-\bar{x}\big)\Big(\frac{-r}{k}\big(x-\bar{x}\big) + \sigma_2\Big(\frac{y}{x} - \frac{\bar{y}}{\bar{x}}\Big) - \beta_1\big(z-\bar{z}\big)\Big) \\
&+ c_2\big(y-\bar{y}\big)\Big(\frac{-s}{l}\big(y-\bar{y}\big) + \sigma_1\Big(\frac{x}{y} - \frac{\bar{x}}{\bar{y}}\Big)\Big) \\
&+ c_3\big(z-\bar{z}\big)\Big(-\frac{a}{m}\big(z-\bar{z}\big) + \beta_2\big(x-\bar{x}\big) - \gamma_1 w\Big) + c_4\big(\gamma_2 zw - \alpha w\big).
\end{aligned}$$

Therefore,

$$\begin{aligned}
\frac{dR_2}{dt} &= \frac{-c_1 r}{k}\big(x-\bar{x}\big)^2 + c_1\sigma_2\big(x-\bar{x}\big)\Big(\frac{y\bar{x}-x\bar{y}}{x\bar{x}}\Big) - c_1\beta_1\big(x-\bar{x}\big)\big(z-\bar{z}\big) \\
&- \frac{c_2 s}{l}\big(y-\bar{y}\big)^2 + c_2\sigma_1\big(y-\bar{y}\big)\Big(\frac{x\bar{y}-y\bar{x}}{y\bar{y}}\Big) - c_3\Big(\frac{a}{m}\Big)\big(z-\bar{z}\big)^2 \\
&+ c_3\big(x-\bar{x}\big)\big(z-\bar{z}\big) - c_3\gamma_1 w\big(z-\bar{z}\big) + c_4\big(\gamma_2 zw - \alpha w\big).
\end{aligned}$$

By choosing the positive constants as

$$c_1 = 1, c_2 = \frac{\sigma_2\bar{y}}{\sigma_1\bar{x}}, c_3 = \frac{\beta_1}{\beta_2}, c_4 = \frac{\beta_1\gamma_1}{\beta_2\gamma_2},$$

the following is obtained

$$\begin{aligned}
\frac{dR_2}{dt} &= -\Big(\frac{r}{k}\Big)\big(x-\bar{x}\big)^2 - \Big(\frac{\sigma_2}{x\bar{x}y}\Big)\big(x\bar{y}-y\bar{x}\big)^2 - \Big(\frac{a\beta_1}{m\beta_2}\Big)\big(z-\bar{z}\big)^2 \\
&- \Big(\frac{s\sigma_2\bar{y}}{l\sigma_1\bar{x}}\Big)\big(y-\bar{y}\big)^2 + \Big(\gamma_2\bar{z}-\alpha\Big)\Big(\frac{\beta_1\gamma_1}{\beta_2\gamma_2}\Big)w.
\end{aligned}$$

Then, $\frac{dR_2}{dt} < 0$ under the local stability condition (5.47) and hence, R_2 is a Lyapunov function. Therefore, F_4 is globally asymptotically stable in $\mathbb{R}^4_+$. ■

Finally, the global stability of the positive equilibrium point F_5 in the interior of $\mathbb{R}^4_+$ is investigated, as shown in the following theorem.

Theorem 5.7.3 *The equilibrium point F_5 is globally asymptotically stable in $\mathbb{R}^4_+$ whenever it exists.*

Proof Consider the following positive definite function:

$$\begin{aligned} R_3(x,y,z,w) &= c_1\Big(x - x^* - x^* \ln\frac{x}{x^*}\Big) + c_2\Big(y - y^* - y^* \ln\frac{y}{y^*}\Big) \\ &+ c_3\Big(z - z^* - z^* \ln\frac{z}{z^*}\Big) + c_4\Big(w - w^* - w^* \ln\frac{w}{w^*}\Big), \end{aligned}$$

where, $c_i, (i = 1,2,3,4)$ are positive constants to be determined. Now, the time derivative of R_2 along the trajectory of the system (4.1) can be written as:

$$\begin{aligned} \frac{dR_3}{dt} &= c_1\Big(\frac{x-x^*}{x}\Big)\frac{dx}{dt} + c_2\Big(\frac{y-y^*}{y}\Big)\frac{dy}{dt} + c_3\Big(\frac{z-z^*}{z}\Big)\frac{dz}{dt} + c_4\Big(\frac{w-w^*}{w}\Big)\frac{dw}{dt} \\ &= c_1\big(x-x^*\big)\Big(r - \frac{rx}{k} - \sigma_1 + \frac{\sigma_2 y}{x} - \beta_1 z\Big) \\ &+ c_2\big(y-y^*\big)\Big(s - \frac{sy}{l} + \frac{\sigma_1 x}{y} - \sigma_2\Big) \\ &+ c_3\big(z-z^*\big)\big(a - \frac{az}{m} + \beta_2 x - \beta_0 - \gamma_1 w\big) + c_4\big(w-w^*\big)\big(\gamma_2 z - \alpha\big). \end{aligned}$$

Therefore,

$$\begin{aligned} \frac{dR_3}{dt} &= \frac{-c_1 r}{k}\big(x-x^*\big)^2 + c_1\sigma_2\big(x-x^*\big)\Big(\frac{yx^*-xy^*}{xx^*}\Big) - c_1\beta_1\big(x-x^*\big)\big(z-z^*\big) \\ &- \frac{c_2 s}{l}\big(y-y^*\big)^2 + c_2\sigma_1\big(y-y^*\big)\Big(\frac{xy^*-yx^*}{yy^*}\Big) + c_3\beta_2\big(x-x^*\big)\big(z-z^*\big) \\ &- \frac{c_3 a}{m}\big(z-z^*\big)^2 - c_3\gamma_1\big(z-z^*\big)\big(w-w^*\big) + c_4\gamma_2\big(z-z^*\big)\big(w-w^*\big). \end{aligned}$$

By choosing the positive constants as

$$c_1 = 1, c_2 = \frac{\sigma_2 y^*}{\sigma_1 x^*}, c_3 = \frac{\beta_1}{\beta_2}, c_4 = \frac{\beta_1\gamma_1}{\beta_2\gamma_2},$$

the following is obtained

$$\frac{dR_3}{dt} = -\Big(\frac{r}{k}\Big)\big(x-x^*\big)^2 - \Big(\frac{\sigma_2}{xx^*y}\Big)\big(xy^*-yx^*\big)^2 - \Big(\frac{s\sigma_2 y^*}{l\sigma_1 x^*}\Big)\big(y-y^*\big)^2.$$

Then, $\frac{dR_3}{dt} \leq 0$ which is negative semi-definite and then F_5 is Lyapunov stable. However, the set $N_3 = \big\{(x, y, z, w)/\dot{R}_3(x, y, z, w) = 0\big\}$, which is the set $N_3 = \big\{(x, y, z, w)/x = x^*, y = y^*\big\}$, does not contain any trajectory of the system except $F_5 = (x^*, y^*, z^*, w^*)$. Therefore, by LaSalle's invariance principle F_5 is globally asymptotically stable in interior of $\mathbb{R}^4_+$. ■

5.8 Persistence analysis

Similarly to the previous chapter, the persistence conditions of the system (5.1) are studied using the Freedman and Waltman approach.

In the following theorem, the persistence condition of the system (5.1) is established.

Theorem 5.8.1 *If the conditions (5.29), (5.35), (5.41) and (5.47) are violated, then, the system (5.1) persists.*

Proof Followed directly by the application of Freedman and Waltman persistence theorem. ■

5.9 Local bifurcation analysis

In this section, the effect of varying parameter values on the dynamical behaviour of the system (5.1) around each equilibrium point is studied. In the following theorems, an application of Sotomayor's hypothesis for local bifurcation is adapted.

Now, the Jacobian matrix of system (5.1) at each of the equilibrium points is given by:

$$J = DF = \begin{bmatrix} r - \sigma_1 - \dfrac{2rx}{k} - \beta_1 z & \sigma_2 & -\beta_1 x & 0 \\ \sigma_1 & s - \sigma_2 - \dfrac{2sy}{l} & 0 & 0 \\ \beta_2 z & 0 & a - \frac{2az}{m} + \beta_2 x - \beta_0 - \gamma_1 w & -\gamma_1 z \\ 0 & 0 & \gamma_2 w & \gamma_2 z - \alpha \end{bmatrix}.$$

For any non-zero vector $V = (v_1, v_2, v_3, v_4)^T$:

$$D^2F(V,V) = \begin{bmatrix} -2v_1\Big(\frac{rv_1}{k} - \beta_1 v_3\Big) \\ -\frac{2s}{l}v_2^2 \\ 2v_3\Big(\beta_2 v_1 - \frac{aV_3}{m} - \gamma_1 v_4\Big) \\ 2\gamma_2 v_3 v_4 \end{bmatrix} \tag{5.50}$$

and,

$$D^3F(V,V,V) = (0,0,0,0)^T.$$

So, according to Sotomayor's theorem the pitchfork bifurcation does not occur at any of the points $F_i, i = 0, 1, 2, 3, 4, 5$.

Theorem 5.9.1 *Suppose that*

$$(r - \sigma_1)^2 - l\sigma_1^3 \neq 0. \tag{5.51}$$

Then, for the parameter value $\sigma_2^* = \dfrac{s(r-\sigma_1)}{r}$ *system (5.1), at the equilibrium point* F_0*, has a transcritical bifurcation.*

Proof Similar to the proof of the Theorem 4.9.1. ■

Theorem 5.9.2 *Suppose that*

$$v_3^{[1]} \neq 0. \tag{5.52}$$

Then, for the parameter value $\beta_2^* = \frac{\beta_0 - a}{\hat{x}}$*, system (5.1), at the equilibrium point* F_1*, has a transcritical bifurcation.*

Proof Similar to the proof of the Theorem 4.9.2. ■

Theorem 5.9.3 *Suppose that*

$$v_1^{[2]}\Big(\frac{rv_1^{[2]}}{k} + \beta_1 v_3^{[2]}\Big)\psi_1^{[2]} + \Big(\frac{s}{l}\Big)\big(v_2^{[2]}\big)^2\psi_2^{[2]} \neq 0. \tag{5.53}$$

Then, for the parameter value $\gamma_2 = \alpha/\ddot{z}$*, system (5.1), at the equilibrium point* F_2*, has a transcritical bifurcation.*

Proof According to the Jacobian matrix $J(F_2)$, system (5.1), at the equilibrium point F_2, has a zero eigenvalue, say λ_{24}, at $\gamma_2 = \gamma_2^*$ and the Jacobian matrix $J(F_2)$ becomes:

$$J^*(F_2) = \begin{bmatrix} r - \sigma_1 - \beta_1 \ddot{z} & \sigma_2 & 0 & 0 \\ \sigma_1 & s - \sigma_2 & 0 & 0 \\ \beta_2 \ddot{z} & 0 & 0 & -\gamma_1 \ddot{z} \\ 0 & 0 & 0 & 0 \end{bmatrix}.$$

Now, suppose that $V^{[2]} = \left(v_1^{[2]}, v_2^{[2]}, v_3^{[2]}, v_4^{[2]}\right)^T$ is an eigenvector corresponding to the eigenvalue λ_{24}. Then, $\big(J^*(F_2) - \lambda_{24} I\big)V^{[2]} = 0$, which implies:

$$\begin{aligned} v_2^{[2]} &= \frac{\sigma_1 v_1^{[2]}}{(\sigma_2 - s)}, \\ v_4^{[2]} &= \frac{\beta_2 v_1^{[2]}}{\gamma_1}, \end{aligned}$$

where, $v_1^{[2]}$ is any non-zero real number. Let $\psi^{[2]} = \left(\psi_1^{[2]}, \psi_2^{[2]}, \psi_3^{[2]}, \psi_4^{[2]}\right)^T$ be an eigenvector associated with the eigenvalue λ_{24} of the matrix $(J^*(F_2))^T$. Then, $\big((J^*(F_2))^T - \lambda_{24} I\big)\psi^{[2]} = 0$. By solving this equation for $\psi^{[2]}$, $\psi_2^{[2]} = \frac{\sigma_2 \psi_1^{[2]}}{\sigma_2 - s}, \psi_3^{[2]} = 0$ are obtained, where $\psi_1^{[2]}$ is any non-zero real number.

Now, to confirm whether the conditions of Sotomayor's theorem for transcritical bifurcation are satisfied, the following is considered:

$$\frac{\partial f}{\partial \gamma_2} = f'_{\gamma_2}(X, \gamma_2) = \left(\frac{\partial f_1}{\partial \gamma_2}, \frac{\partial f_2}{\partial \gamma_2}, \frac{\partial f_3}{\partial \gamma_2}, \frac{\partial f_4}{\partial \gamma_2}\right)^T = (0, 0, 0, zw)^T.$$

Thus, $f'_{\gamma_2}(F_2, \gamma_2^*) = (0, 0, 0, 0)^T$ and hence, $(\psi^{[2]})^T f'_{\gamma_2}(F_2, \gamma_2^*) = 0$. Therefore, according to Sotomayor's theorem, saddle-node bifurcation cannot occur, while the first condition of transcritical bifurcation is satisfied.

Now,

$$Df_{\gamma_2}(X, \gamma_2) = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & w & z \end{bmatrix},$$

where, $Df_{\gamma_2}(X,\gamma_2)$ represents the derivative of $f_{\gamma_2}(X,\gamma_2)$ with respect to $X=(x,y,z,w)^T$. Moreover, it is observed under condition (5.53) that:

$$Df_{\gamma_2}(F_2,\gamma_2^*)V^{[2]} = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \ddot{z} \end{pmatrix} \begin{pmatrix} v_1^{[2]} \\ v_2^{[2]} \\ v_3^{[2]} \\ v_4^{[2]} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \\ \ddot{z}v_4^{[2]} \end{pmatrix},$$

$$\begin{aligned} (\psi^{[2]})^T\Big[Df_{\gamma_2}(F_2,\gamma_2^*)V^{[2]}\Big] &= \Big(\psi_1^{[2]},\psi_2^{[2]},0,\psi_4^{[2]}\Big)\Big(0,0,0,\ddot{z}v_4^{[2]}\Big)^T \\ &= \ddot{z}\psi_4^{[2]}v_4^{[2]} \neq 0. \end{aligned}$$

Now, by substituting in (5.50) and according to condition (5.53), the following is obtained:

$$\big(\psi^{[2]}\big)^T\big[D^2f(F_2,\gamma_2^*)\big(V^{[2]},V^{[2]}\big)\big] = -2v_1^{[2]}\Big(\frac{rv_1^{[2]}}{k}+\beta_1v_3^{[2]}\Big)\psi_1^{[2]} - 2\Big(\frac{s}{l}\Big)\big(v_2^{[2]}\big)^2\psi_2^{[2]} \neq 0.$$

This means the second condition of transcritical bifurcation is satisfied. Thus, according to Sotomayor's theorem system, (5.1) has transcritical bifurcation at F_2 with the parameter $\gamma_2=\gamma_2^*$. ■

Theorem 5.9.4 *Suppose that*

$$rl(s-\sigma_2)^3 \neq ks\sigma_2(\sigma_1)^2. \qquad (5.54)$$

Then, for the parameter value $\beta_1^*=\frac{(r-\sigma_1)(s-\sigma_2)-\sigma_1\sigma_2}{(s-\sigma_2)\tilde{z}}$, *system (5.1), at the equilibrium point* F_3, *has a transcritical bifurcation.*

Proof According to the Jacobian matrix $J(F_3)$, system (5.1), at the equilibrium point F_3, has a zero eigenvalue, say λ_{31}, at $\beta_1=\beta_1^*$ and the Jacobian matrix $J(F_3)$ becomes

$$J^*(F_3) = \begin{bmatrix} r-\sigma_1-\beta_1\tilde{z} & \sigma_2 & 0 & 0 \\ \sigma_1 & s-\sigma_2 & 0 & 0 \\ \beta_2\tilde{z} & 0 & \frac{-2a\tilde{z}}{m} & -\gamma_1\tilde{z} \\ 0 & 0 & \gamma_2\tilde{w} & 0 \end{bmatrix}.$$

Now, suppose that $V^{[3]} = \left(v_1^{[3]}, v_2^{[3]}, v_3^{[3]}, v_4^{[3]}\right)^T$ is an eigenvector corresponding to the eigenvalue λ_{31}. Then, $\big(J^*(F_3) - \lambda_{31} I\big)V^{[3]} = 0$, which implies

$$\begin{aligned} v_2^{[3]} &= \frac{\sigma_1 v_1^{[3]}}{(\sigma_2 - s)}, \\ v_3^{[3]} &= 0 \\ v_4^{[3]} &= \frac{\beta_2 v_1^{[3]}}{\gamma_1}, \end{aligned}$$

where, $v_1^{[3]}$ is any non-zero real number. Let $\psi^{[3]} = \big(\psi_1^{[3]}, \psi_2^{[3]}, \psi_3^{[3]}, \psi_4^{[3]}\big)^T$ be an eigenvector associated with the eigenvalue λ_{31} of the matrix $(J^*(F_3))^T$. Then, $\big((J^*(F_3))^T - \lambda_{31} I\big)\psi^{[3]} = 0$. By solving this equation for $\psi^{[3]}$, $\psi_2^{[3]} = \frac{\sigma_2 \psi_1^{[3]}}{\sigma_2 - s}$, $\psi_3^{[3]} = \psi_4^{[3]} = 0$ are obtained, where $\psi_1^{[3]}$ is any non-zero real number.

Now, to confirm whether the conditions of Sotomayor's theorem for saddle-node bifurcation are satisfied, the following is considered:

$$\frac{\partial f}{\partial \beta_1} = f'_{\beta_1}(X, \beta_1) = \left(\frac{\partial f_1}{\partial \beta_1}, \frac{\partial f_2}{\partial \beta_1}, \frac{\partial f_3}{\partial \beta_1}, \frac{\partial f_4}{\partial \beta_1}\right)^T = (-z, 0, 0, 0)^T.$$

Thus, $f'_{\beta_1}(F_3, \beta_1^*) = (-\tilde{z}, 0, 0, 0)^T$ and hence,

$$(\psi^{[3]})^T f'_{\beta_1}(F_3, \beta_1^*) = (\psi_1^{[3]}, \psi_2^{[3]}, 0, 0)^T (-\tilde{z}, 0, 0, 0)^T = -\psi_1^{[3]} \tilde{z} \neq 0$$

Therefore, according to Sotomayor's theorem, transcritical bifurcation cannot occur, while the first condition of saddle-node bifurcation is satisfied.

Now,

$$Df_{\beta_1}(X, \beta_1) = \begin{bmatrix} 0 & 0 & -1 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix},$$

where, $Df_{\beta_1}(X, \beta_1)$ represents the derivative of $f_{\beta_1}(X, \beta_1)$ with respect to $X = (x, y, z, w)^T$. Moreover, it is observed under condition (5.54) that:

$$Df_{\beta_1}(F_3, \beta_1^*)V^{[3]} = \begin{pmatrix} 0 & 0 & -1 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} v_1^{[3]} \\ v_2^{[3]} \\ 0 \\ v_4^{[3]} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \end{pmatrix},$$

$$(\psi^{[3]})^T \Big[Df_{\beta_1}(F_3, \beta_1^*)V^{[3]} \Big] = \Big(\psi_1^{[3]}, \psi_2^{[3]}, 0, 0 \Big) \Big(0, 0, 0, 0 \Big)^T = 0.$$

Now, by substituting in (5.50) and according to condition (5.54), the following is obtained:

$$\big(\psi^{[3]}\big)^T \big[D^2 f(F_3, \beta_1^*) \big(V^{[3]}, V^{[3]} \big) \big] = 2\psi_1^{[3]} \Big(v_1^{[3]} \Big)^2 \Big(\frac{-r}{k} + \frac{s\sigma_2(\sigma_1)^2}{l(s-\sigma_2)^3} \Big) \neq 0.$$

This means the second condition of saddle-node bifurcation is satisfied. Thus, according to Sotomayor's theorem system, (5.1) has saddle-node bifurcation at F_3 with the parameter $\beta_1 = \beta_1^*$. ■

Theorem 5.9.5 *Suppose that*

$$v_3^{[4]}, v_4^{[4]} \neq 0. \tag{5.55}$$

Then, for the parameter value $\gamma_2^* = \dfrac{\alpha}{\bar{z}}$*, system (5.1), at the equilibrium point* F_4*, has transcritical bifurcation.*

Proof According to the Jacobian matrix $J(F_4)$, given by (5.48), system (5.1), at the equilibrium point F_4, has a zero eigenvalue, say λ_{44}, at $\gamma_2 = \gamma_2^*$ and this matrix becomes

$$J^*(F_4) = \begin{bmatrix} r - \sigma_1 - \frac{2r\bar{x}}{k} - \beta_1\bar{z} & \sigma_2 & -\beta_1\bar{x} & 0 \\ \sigma_1 & s - \sigma_2 - \frac{2s\bar{y}}{l} & 0 & 0 \\ \beta_2\bar{z} & 0 & \frac{-a\bar{z}}{m} & -\gamma_1\bar{z} \\ 0 & 0 & 0 & 0 \end{bmatrix}.$$

Now, suppose that $V^{[4]} = \left(v_1^{[4]}, v_2^{[4]}, v_3^{[4]}, v_4^{[4]}\right)^T$ is an eigenvector corresponding to the eigenvalue λ_{44}. Thus, $\big(J^*(F_4) - \lambda_{44} I\big)V^{[4]} = 0$, which implies:

$$\begin{aligned} v_2^{[4]} &= \frac{\sigma_1 l v_1^{[4]}}{2s\bar{y} - (s-\sigma_2)l}, \\ v_3^{[4]} &= \left(\frac{(rk - 2r\bar{x} - \sigma_1 k - k\beta_1\bar{z})(2s\bar{y} - (s-\sigma_2)l) + \sigma_1\sigma_2 lk}{\beta_1\bar{x}k(2s\bar{y} - (s-\sigma_2)l)}\right) v_1^{[4]}, \\ v_4^{[4]} &= \frac{m\beta_2 v_1^{[4]} - a v_3^{[4]}}{m\gamma_1}, \end{aligned}$$

where, $v_1^{[4]}$ is any non-zero real number and $2s\bar{y} \neq (s-\sigma_2)l$. Then, let $\psi^{[4]} = \big(\psi_1^{[4]}, \psi_2^{[4]}, \psi_3^{[4]}, \psi_4^{[4]}\big)^T$ be an eigenvector associated with the eigenvalue λ_{44} of the matrix $(J^*(F_4))^T$. So, $\big((J^*(F_4))^T - \lambda_{44} I\big)\psi^{[4]} = 0$ and by solving this equation for $\psi^{[4]}$, $\psi_1^{[4]} = \psi_2^{[4]} = \psi_3^{[4]} = 0$ is the result, where $\psi_4^{[4]}$ is any non-zero real number.

Now, to confirm that the conditions of Sotomayor's theorem for transcritical bifurcation are satisfied, the following is considered:

$$\frac{\partial f}{\partial \gamma_2} = f'_{\gamma_2}(X, \gamma_2) = \left(\frac{\partial f_1}{\partial \gamma_2}, \frac{\partial f_2}{\partial \gamma_2}, \frac{\partial f_3}{\partial \gamma_2}, \frac{\partial f_4}{\partial \gamma_2}\right)^T = (0, 0, 0, zw)^T.$$

Therefore, $f'_{\gamma_2}(F_4, \gamma_2^*) = (0, 0, 0, 0)^T$ and hence, $(\psi^{[4]})^T f'_{\gamma 2}(F_4, \gamma_2^*) = 0$. So, according to Sotomayor's theorem, saddle-node bifurcation cannot occur, while the first condition of transcritical bifurcation is satisfied. Now,

$$Df_{\gamma_2}(X, \gamma_2) = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & w & z \end{bmatrix},$$

where, $Df_{\gamma_2}(X, \gamma_2)$ represent the derivative of $f_{\gamma_2}(X, \gamma_2)$ with respect to $X = (x, y, z, w)^T$. Further, it is observed under condition (5.55) that the following is obtained:

$$Df_{\gamma_2}(F_4, \gamma_2^*)V^{[4]} = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \bar{z} \end{pmatrix} \begin{pmatrix} v_1^{[4]} \\ v_2^{[4]} \\ v_3^{[4]} \\ v_4^{[4]} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \\ \bar{z} v_4^{[2]} \end{pmatrix},$$

$$\begin{aligned}(\psi^{[4]})^T\Big[Df_{\gamma_2}(F_4,\gamma_2^*)V^{[4]}\Big] &= \Big(0,0,0,\psi_4^{[4]}\Big)\Big(0,0,0,\bar{z}v_4^{[4]}\Big)^T \\ &= \bar{z}\psi_4^{[4]}v_4^{[4]} \neq 0.\end{aligned}$$

Now, by substituting in (5.50) and according to condition (5.55), it is found that:

$$\big(\psi^{[4]}\big)^T\big[D^2f(F_4,\gamma_2^*)\big(V^{[4]},V^{[4]}\big)\big] = -2\gamma_2^* v_3^{[4]}v_4^{[4]}\psi_4^{[4]} \neq 0.$$

This means the second condition of transcritical bifurcation is satisfied. Thus, according to Sotomayor's theorem, system (5.1) has transcritical bifurcation at F_4 with the parameter $\gamma_2 = \gamma_2^*$. ■

Remark

1. According to the Jacobian matrix $J(F_5)$, given by (5.49), all the eigenvalues of $J(F_5)$ have negative real parts at the equilibrium point F_5. Therefore, F_5 is a hyperbolic equilibrium point and thus, the system (5.1) has no bifurcation at F_5.
2. According to the Jacobian matrices $J(F_0)$, $J(F_1)$, $J(F_2)$, $J(F_3)$ and $J(F_4)$ given by (5.24), (5.30), (5.36), (5.42) and (5.48) respectively, it is clear that $J(F_i), \quad i = 0,1,2,3,4$ has four real eigenvalues. Therefore, there is no possibility of Hopf bifurcation occurring at this points.

5.10 Numerical analysis

The main goal of this section is to find the key parameters of the system (5.1) that affects the behaviour of the proposed model by using numerical simulations. The dynamics of the system (5.1) is presented by solving the system numerically and then drawing the time series of the solutions of the system (5.1) are drawn for different sets of parameters.

Now, for the following set of parameters:

$$\begin{aligned} r =&1.5, k = 50, \sigma_1 = 0.5, \sigma_2 = 0.7, \beta_1 = 0.9, \beta_2 = 0.75, \beta_0 = 0.01, \\ s =&1.4, l = 40, \alpha = 0.4, \gamma_1 = 0.5, \gamma_2 = 0.1, a = 1.5, m = 45, \end{aligned} \tag{5.56}$$

the conditions (5.22) and (5.23) are satisfied. This shows that the positive equilibrium point F_3 exists, and it is given by: $(x^*, y^*, z^*, w^*) = (5.94, 23.59, 4.00, 11.63)$.

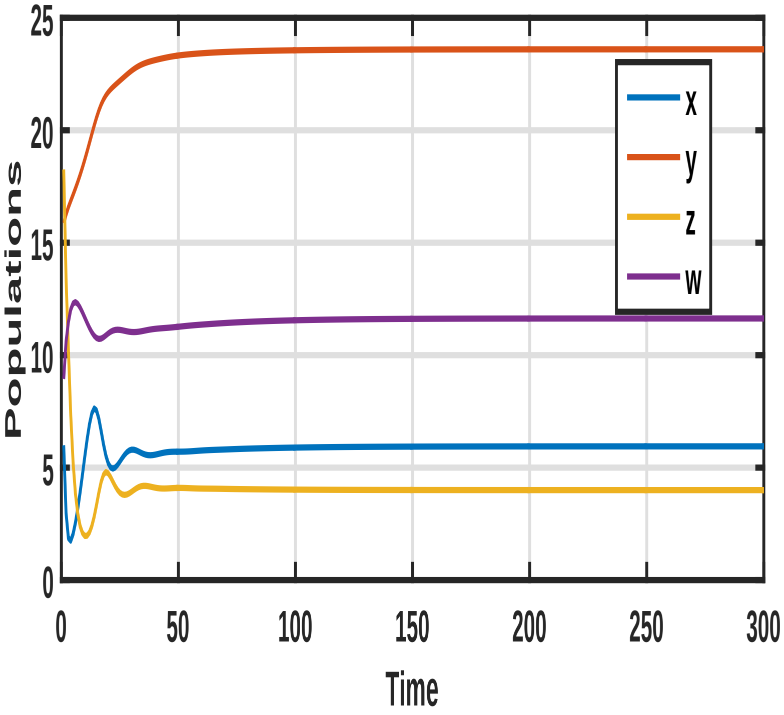

Fig. 5.1. Convergence of the solution of the system (5.1) to the positive equilibrium point with the data given by Eq.(5.56).

Figure 5.1, indicates that the solution of the system (5.1) oscillates for some small period and then, in the long-time limit, it asymptotically approaches the positive equilibrium point.

Now, to investigate the effect of the varying parameter values on the behaviour of the system (5.1), the model has been solved numerically for the data given in Eq.(5.56), varying one parameter each time in the following subsections.

5.10.1 The effect of varying the migration rate of the prey to the reserved area

Figure 5.2 shows the effect of migration to the reserved area, which is described by the parameter σ_1, on the behaviour of the system (5.1) with time. It is observed that for different values of σ_1, the solution initially oscillates for a small period and then, asymptotically approaches its equilibrium level in the interior of $\mathbb{R}^4_+$. As a result of rising the migration rate to the protected area, it can be seen that the density of the prey in the reserved zone increases. On the other hand, the populations of the top predator and the prey in the unreserved area slightly decrease, while the third component has not affected.

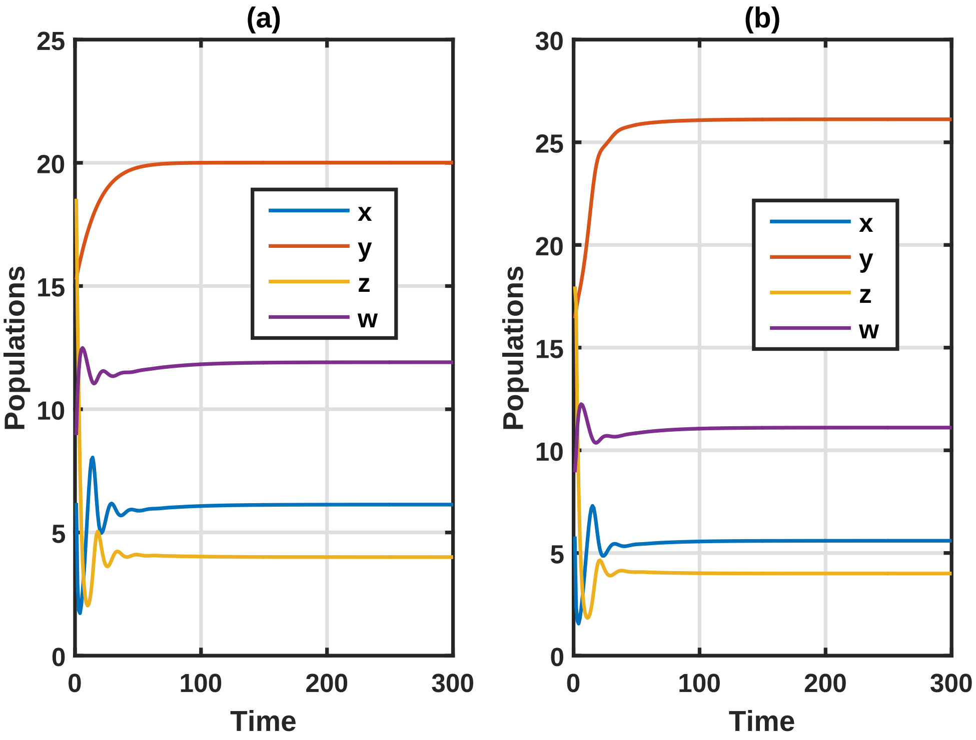

Fig. 5.2. Convergence of the solution of the system (5.1) for the data given by Eq.(5.56) with (a) $\sigma_1 = 0.001$ to the stable point(6.12, 20.00, 4.00, 11.90) in the interior of $\mathbb{R}^4_+$. (b) $\sigma_1 = 1$ to the stable point (5.59, 26.12, 4.00, 11.10) in the interior of $\mathbb{R}^4_+$.

5.10.2 The effect of varying the natural death rate of the predator

Now the same analysis is used for different values of the predator's natural mortality, which is described by the parameter β_0, and the rest of the parameter values are kept the same as in Eq.(5.56). Figure 5.3 shows that for various values of β_0, the solution initially oscillates for a while and then it settles down to its equilibrium level in the interior of $\mathbb{R}^4_+$. Due to the decrease of the predator's natural death-rate, the density of the top predator increases. This means an abundance of the predator and hence, the food conversion rate of the predator to the top predator increases (and vice versa). On the other hand, the populations of the prey in the reserved and unreserved zone, as well as the predator (the third component), are not affected.

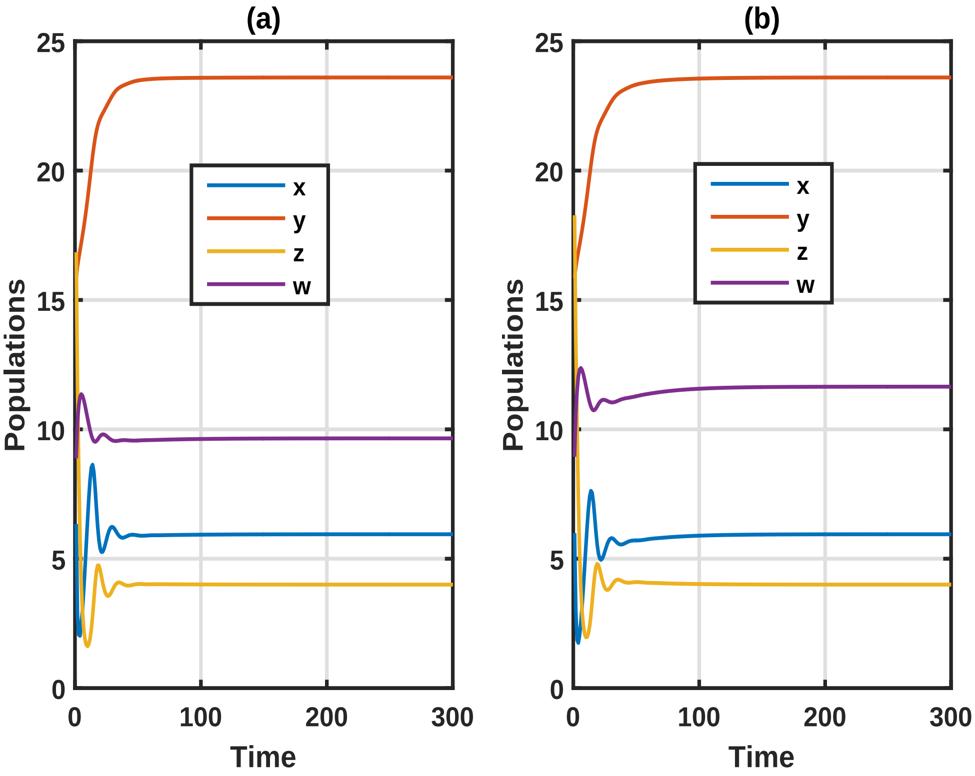

Fig. 5.3. Convergence of the solution of the system (5.1) for the data given by Eq.(5.56) with (a) $\beta_0 = 1$ to the stable point (5.94, 23.59, 4.00, 9.65) in the interior of $\mathbb{R}^4_+$. (b) $\beta_0 = 0.001$ to the stable point (5.94, 23.59, 4.00, 11.64) in the interior of $\mathbb{R}^4_+$.

5.10.3 The effect of varying the natural death rate of the top predator

The effect of varying α, which represents the top predator's natural death-rate, on the behaviour of the system (5.1), is also studied. From Figure 5.4, the following results can be observed. As α increases, the density of the top predator decreases and thus, the attack rate γ_1 by the top predator on the predator decreases, which implies that there is an abundance of the latter. Furthermore, as a result of the predator's density increasing, the attack rate on the prey in the unreserved zone increases, which affects negatively their density in the unprotected area. Thus, the migration rate to the reserved zone is also affected. Further, for different values of α, the system (5.1) starts to oscillate for a particular time and then, attains the equilibrium level in the interior of $\mathbb{R}^4_+$. It follows that the system (5.1) persists for long-term behaviour.

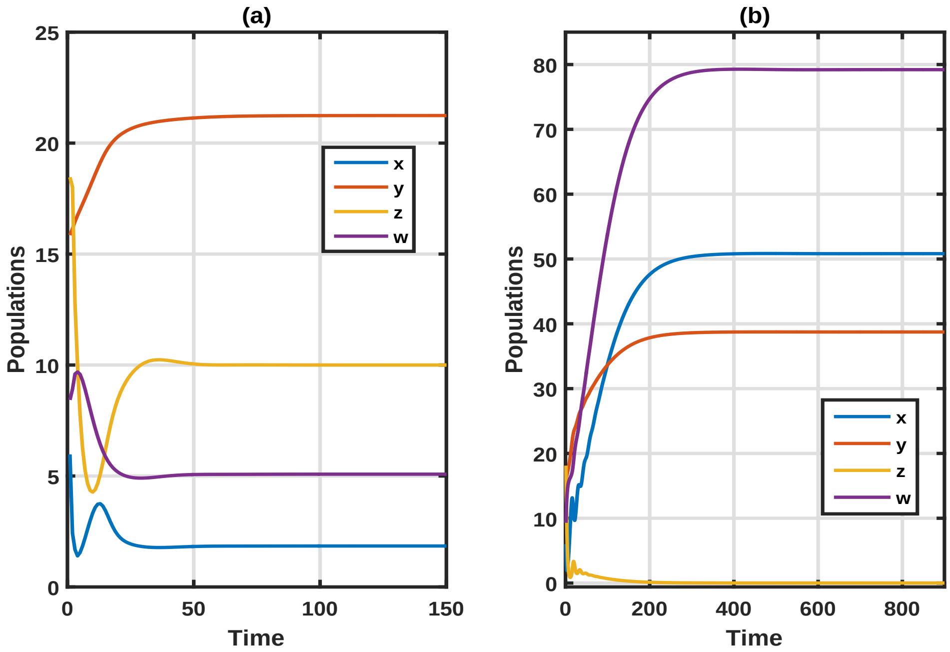

Fig. 5.4. Convergence of the solution of the system (5.1) for the data given by Eq.(5.56) with (a) $\alpha = 1$ to the stable point (1.84, 21.24, 10.00, 5.08) in the interior of $\mathbb{R}^4_+$. (b) $\alpha = 0.0001$ to the stable point (50.82, 38.74, 0.01, 79.20) in the interior of $\mathbb{R}^4_+$.

5.10.4 The effect of varying the attack rate of the top predator on the predator

Figure 5.4 illustrates the effect of the top predator's attack rate on the predator, which is described by the parameter γ_1, in terms of the behaviour of the system (5.1) versus time. It can be noticed that for various values of γ_1, the solution initially oscillates, and after a specific time it attains its equilibrium level in the interior of $\mathbb{R}^4_+$. Also, when increasing γ_1, which means that the food conversion rate to the top predator increases and hence, its density is rapidly increasing. On the other hand, the densities of the prey in the reserved and unreserved area, as well as the predator, are not affected. Once again, the system (5.1) persists for varying values of γ_1.

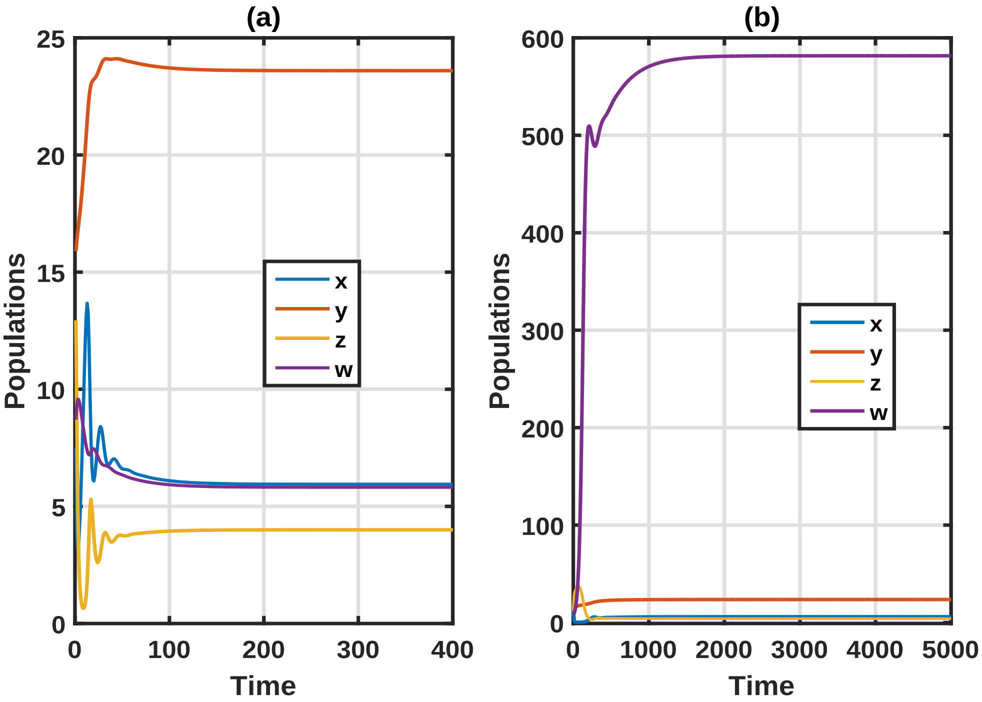

Fig. 5.5. Convergence of the solution of the system (5.1) for the data given by Eq.(5.56) with (a) $\gamma_1 = 0.01$ to the stable point (5.94, 23.59, 4.00, 581.59) in the interior of $\mathbb{R}^4_+$. (b) $\gamma_1 = 1$ to the stable point (5.94, 23.59, 4.00, 5.81) in the interior of $\mathbb{R}^4_+$.

5.10.5 The effect of varying the conversion rate of the predator to the top predator

Now, Figure 5.6 studies the impact of the conversion rate of the predator to the top predator γ_2, on the behaviour of the species with t. When varying γ_2 and keeping the other parameters in Eq.(5.56) fixed, it can be observed that the solution of system (5.1) converges to the equilibrium point in the interior of $\mathbb{R}^4_+$ after oscillating for a certain amount of time. Due to the decreasing of γ_2, the densities of the top predator, the prey in the reserved and unreserved zone decrease. On the other hand, the population of the predator (the third component) increases significantly.

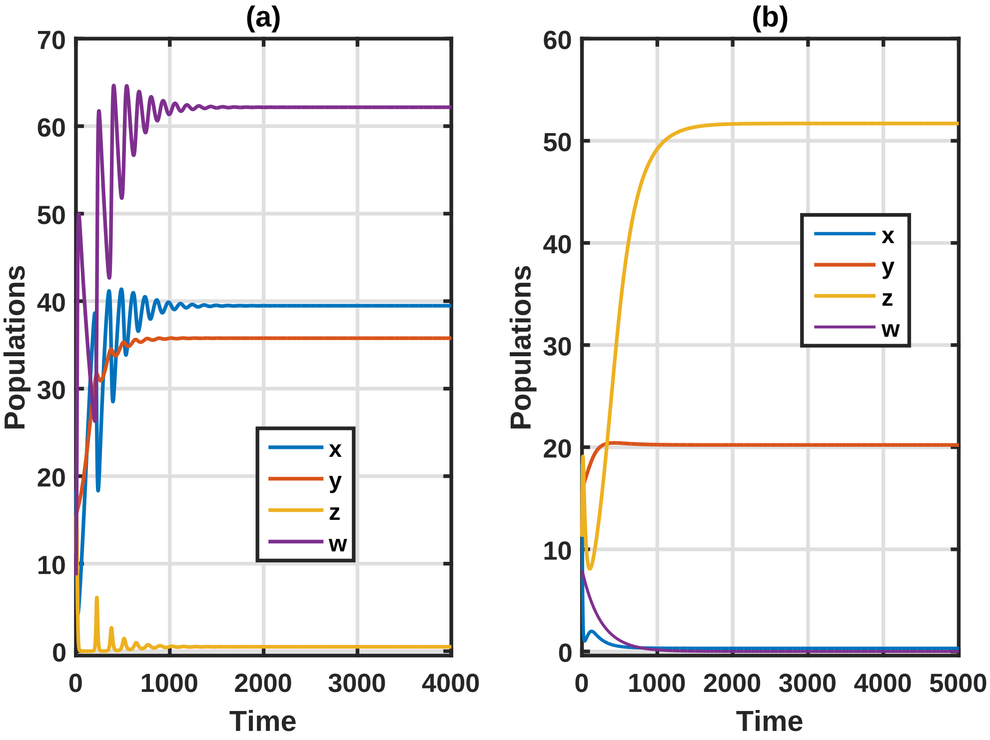

Fig. 5.6. Convergence of the solution of the system (5.1) for the data given by Eq.(5.56) with (a) $\gamma_2 = 1$ to the stable point (39.47, 35.76, 0.50, 62.589) in the interior of $\mathbb{R}^4_+$, (b) $\gamma_2 = 0.0001$ to the stable point (0.30, 20.21, 51.69, 0.41) in the interior of $\mathbb{R}^4_+$.

5.10.6 The effect of varying the unreserved area rate on the species

Similarly, for different values of σ_2, which represent the impact of the unreserved area on the behaviour of the species. When varying σ_2 and keeping the other parameters in (5.56) fixed, the solution of system (5.1) initially fluctuates for some time, and then, it converges to the equilibrium point. Furthermore, Due to the decreasing of σ_2, the densities of the top predator and the prey in the unreserved area decrease. On the other hand, the population of the prey in the reserved zone increases, while, the third component is not affected (see Figure 5.7).

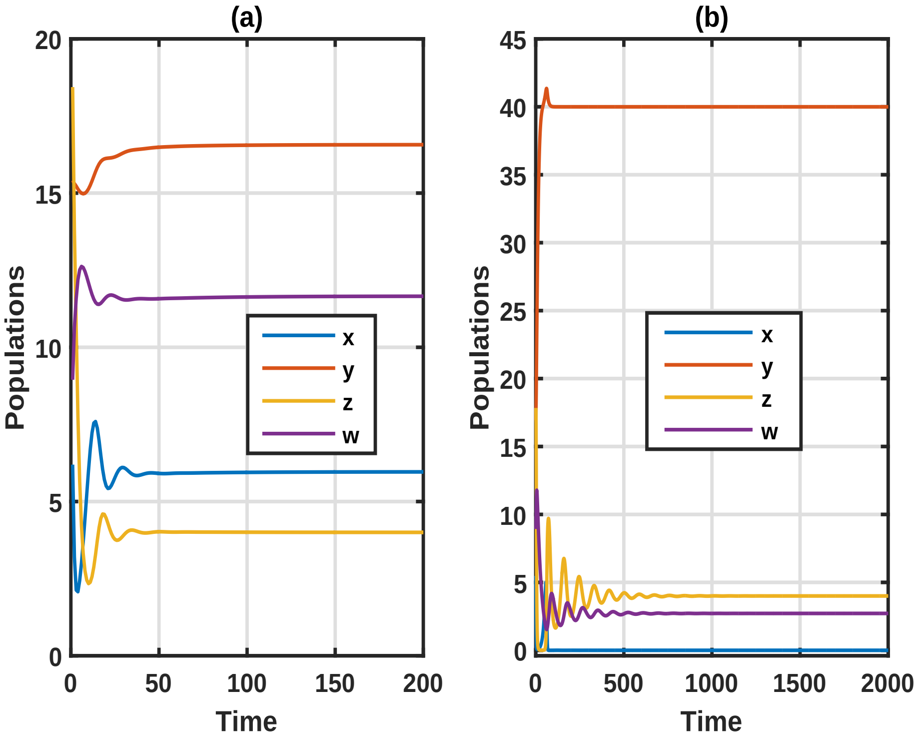

Fig. 5.7. Convergence of the solution of the system (5.1) for the data given by Eq.(5.56) with (a) $\sigma_2 = 1$ to the stable point (5.96, 16.56, 4.00, 11.65) in the interior of $\mathbb{R}^4_+$. (b) $\sigma_2 = 0.0001$ to the stable point (0.01, 39.99, 4.00, 2.70) in the interior of $\mathbb{R}^4_+$.

5.10.7 The effect of varying the conversion rate of the prey in the unreserved zone to the predator

For the parameter values given in Eq.(5.56) with different β_2, which represent the conversion rate of the prey in the unreserved zone to the predator, the following results can be observed. As β_2 decreases, the population of the top predator affects negatively, which implies the decreases of their density. Furthermore, the densities of the prey in the reserved and unreserved zone as well as the predator are not affected. Also, for different values of α, the system (5.1) starts to oscillate for a particular time and then, attains the equilibrium level in the interior of $\mathbb{R}_+^4$. It follows that the system (5.1) persists for long-term behaviour (see Figure 5.8).

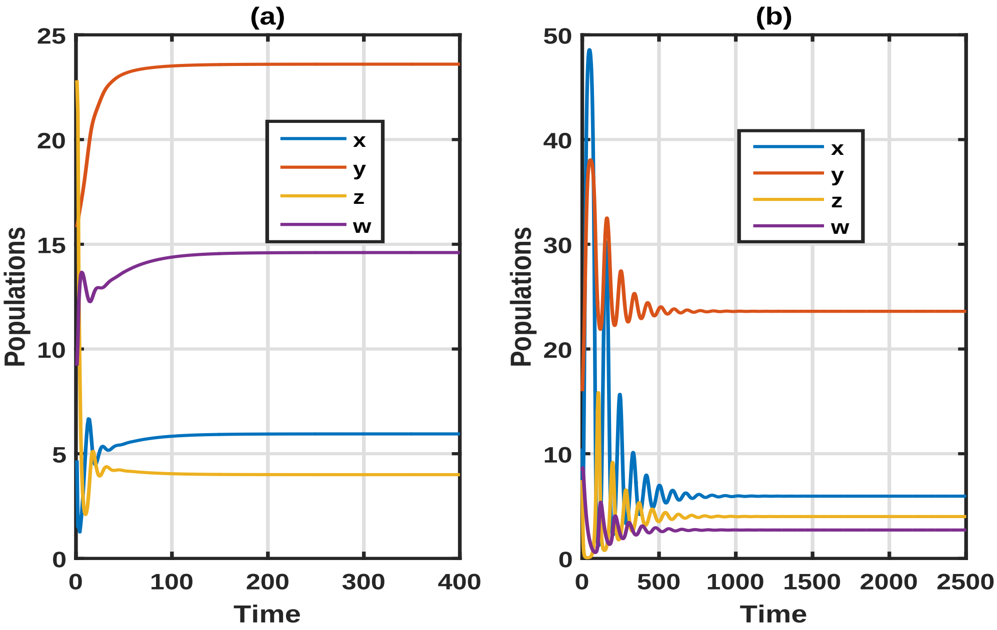

Fig. 5.8. Convergence of the solution of the system (5.1) for the data given by Eq.(5.56) with (a) $\beta_2 = 1$, to the stable point (5.94, 23.59, 4.00, 14.60) in the interior of $\mathbb{R}_+^4$. (b) $\beta_2 = 0.0001$, to the stable point (5.94, 23.59, 4, 2.70) in the interior of $\mathbb{R}_+^4$.

5.10.8 The effect of varying the attack rate of the predator on the prey in the unreserve zone

Finally, Figure 5.9 shows the behaviour of the solution of system (5.1) for varying β_1, which connects the first component with the third in the chain. Figure 5.9 indicates that the slow-decaying and oscillating components are z and w, whereas x and y converge fast to their equilibrium level.

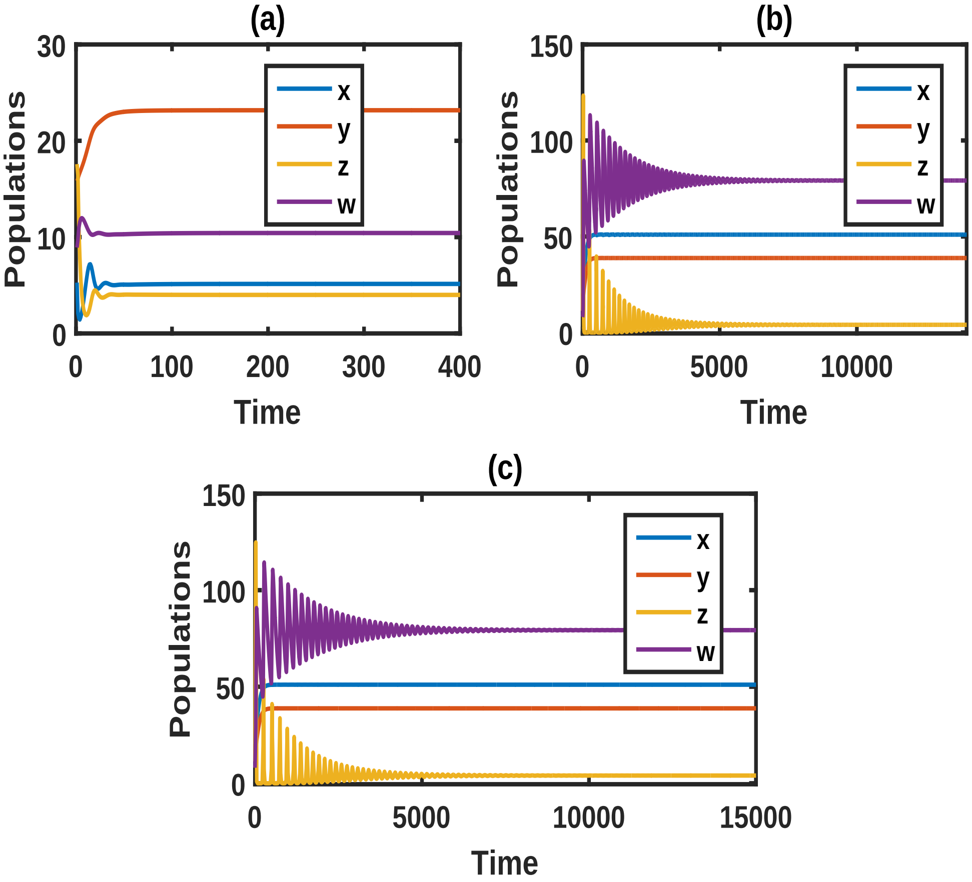

Fig. 5.9. Convergence of the solution of the system (5.1) for the data given by Eq.(5.56) with (a) $\beta_1 = 1$ to the stable point (5.14, 23.17, 4.00, 10.42) in the interior of $\mathbb{R}^4_+$. (b) $\beta_1 = 0.001$ to the stable point (50.95, 38.77, 4.00, 79.14) in the interior of $\mathbb{R}^4_+$. (c) $\beta_1 = 0.0001$ to the stable point (51.05, 38.79, 4.00, 79.29) in the interior of $\mathbb{R}^4_+$.

5.11 Conclusion

An ecological model, which describes the effect of the reserved zone on the dynamical behaviour of a food chain prey-predator model when the third component is partially dependent on the prey in the unprotected zone, has been proposed and studied. The boundedness of system (5.1) has been shown, and the possible dynamical behaviour of this system has been investigated analytically at the equilibrium points. The persistence conditions of the proposed system have been derived. It has been proven that the solutions of system (5.1) possess transcritical bifurcation. To confirm the analytical results, system (5.1) has been solved numerically, and the effects of various parameters on the dynamical behaviour of the proposed system have been performed, with the following results being obtained.

1. The prey species x in the unreserved zone, the prey species y in the reserved area, the predator z and the top predator w are persistent under all conditions.
2. It is observed that the dynamic behaviour of system (5.1) does not change if one of the parameters σ_1, σ_2, β_0, α, β_1, β_2, γ_1 and γ_2 is varied.
3. The positive equilibrium point, whenever it exists, is always globally asymptotically stable.

Overall, the system with the reserved zone, as shown in this chapter, shows that an alternative supply for the third component leads to the persistence of the proposed system as a whole.

Chapter 6: The effect of the reserve zone on the behaviour of a food web model

6.1 Introduction

In this Chapter, the modelling of a four species food web model with reserve zone effect on the prey is proposed. It is assumed that the third level predator (z) feeds on the prey species in the first level (x) only and hence it is known as a specialist predator, while the predator species in the fourth level (w) takes the food from the species in the first and third level and hence it is known as a generalist predator. The boundedness, existence and uniqueness of the solution of the model under consideration are studied. The existences of equilibria and stability analysis are discussed with the help of the stability theory of ordinary differential equations. The dynamical behaviour of the solution is found to be very sensitive to parameter values and initial data, in particular, the stability of equilibrium points. Now, all the equilibrium points are obtained, which correspond to those in Chapter four plus a new equilibrium point, for which only the third component vanishes and the remaining components are strictly positive.

6.2 Mathematical model

In this chapter, we consider a food web model which consists of prey in the unreserved zones, prey in the reserved zone, specialist predator and a generalist predator. The corresponding densities are denoted by $x(t)$, $y(t)$, $z(t)$ and $w(t)$. Now, however, the generalist predator population (z) is allowed to feed directly on the first prey (x). This is modelled by adding two more terms of Holling type 1 functional response to the first component of the main system of differential equations:

$$\begin{aligned}
\frac{dx}{dt} &= rx\Big(1-\frac{x}{k}\Big) - \sigma_1 x + \sigma_2 y - \beta_1 xz - \alpha_1 xw = f_1(x,y,z,w),\\
\frac{dy}{dt} &= sy\Big(1-\frac{y}{l}\Big) + \sigma_1 x - \sigma_2 y = f_2(x,y,z,w),\\
\frac{dz}{dt} &= \beta_2 xz - \beta_0 z - \gamma_1 zw = f_3(x,y,z,w),\\
\frac{dw}{dt} &= \alpha_2 xw + \gamma_2 zw - \alpha w = f_4(x,y,z,w),
\end{aligned} \tag{6.1}$$

Here, α_1 and α_2 are two new model parameters: α_1 is the attack rate of the generalist predator on the prey in the unreserved region, wheres α_2 is the conversion rate of latter to a generalist predator. The other model parameters are the same as in Chapter 4. The proposed model (6.1) has been analysed with the initial conditions $x(0) \geq 0$, $y(0) \geq 0$, $z(0) \geq 0$ and $w(0) \geq 0$, $p_1(x) = \alpha_1 x$, $p_2(x) = \beta_1 x$ and $q(z) = \gamma_1 z$ are the Lotka-Volterra type of functional responses. All parameters of the model system (5.1) are again assumed to be positive.

Apparently, the functions on the right-hand side in the system (6.1) are continuously differentiable functions on $\mathbb{R}^4_+ = \big\{(x,y,z,w), x \geq 0, y \geq 0, z \geq 0, w \geq 0\big\}$ and hence, they are Lipschitzian. Therefore, a solution to the system (6.1) exists, which is unique. Further, all the solutions of the model (6.1) with any non-negative initial conditions are bounded, as shown in the following section.

6.3 Boundedness

Theorem 6.3.1 *Assume that the conditions $\alpha_1 \geq \alpha_2$, $\beta_1 \geq \beta_2$ and $\gamma_1 \geq \gamma_2$ hold, then all the solutions of the system (6.1) which initiate in the $\mathbb{R}^4_+$ are uniformly bounded.*

Proof Let $(x(t), y(t), z(t), w(t))$ be an arbitrary solution of the system (6.1) with a non-negative initial condition. Then for $U(t) = x(t) + y(t) + z(t) + w(t)$, we have

$$\frac{dU}{dt} = rx - \frac{rx^2}{k} + sy - \frac{sy^2}{l} - (\alpha_1 - \alpha_2)xw - (\beta_1 - \beta_2)xz - (\gamma_1 - \gamma_2)zw - \beta_0 z - \alpha w.$$

Hence, according to the given condition the following is obtained:

$$\begin{aligned} \frac{dU}{dt} &\leq rx - \frac{rx^2}{k} + sy - \frac{sy^2}{l} - \beta_0 z - \alpha w, \\ \frac{dU}{dt} + \xi U &\leq 2rx - \frac{rx^2}{k} + 2sy - \frac{sy^2}{l}, \end{aligned}$$

where, $\xi = \min\{r, s, \beta_0, \alpha\}$, then

$$\begin{aligned} \frac{dU}{dt} + \xi U &\leq rk - \frac{r}{k}\big(x-k\big)^2 + sl - \frac{s}{l}\big(y-l\big)^2 \\ &\leq rk + sl = \mu. \end{aligned}$$

Applying Gronwall's Inequality, the following is obtained:

$$0 \leq U\big(x(t), y(t), z(t), w(t)\big) \leq \frac{\mu}{\xi}\big(1 - e^{-\xi t}\big) + U(0)e^{-\xi t}.$$

Therefore,

$$0 \leq \limsup_{t \to \infty} U\big(t\big) \leq \frac{\mu}{\xi}.$$

Hence, all the solutions of the system (6.1) that are initiated in $\mathbb{R}^4_+$ are attracted to the region $\Omega = \Big\{\big(x, y, z, w\big) \in \mathbb{R}^4_+ : U = x + y + z + w \leq \frac{\mu}{\xi}\Big\}$ under the given conditions. Thus, these solutions are bounded, and the proof is complete. ■

6.4 Positive invariance

See Subsection (4.4).

In the following, the existence of the equilibrium points of the system (6.1) will be elucidated.

6.5 Existence of equilibria

The food web prey-predator model with a reserved zone given by the system (6.1) has five nonnegative equilibrium points, namely:

- $F_0 = (0, 0, 0, 0)$ is the vanishing fixed point;
- $F_1 = (\hat{x}, \hat{y}, 0, 0)$ is the planar fixed point;
- $F_2 = (\bar{x}, \bar{y}, \bar{z}, 0)$ is the generalist predator-free fixed point;
- $F_3 = (\dot{x}, \dot{y}, 0, \dot{w})$ is the specialist predator-free fixed point;
- $F_4 = (x^*, y^*, z^*, w^*)$ is the interior fixed point.

The existence of $F_0 = (0, 0, 0, 0)$, $F_1 = (\hat{x}, \hat{y}, 0, 0)$ and $F_2 = (\bar{x}, \bar{y}, \bar{z}, 0)$ are similar to that in Subsection 4.5.1 and 4.5.2, and hence omitted, while the existence of F_3 and F_4 are now shown as follows:

6.5.1 The existence of the specialist predator-free equilibrium point

The equilibrium point F_3 exists in the interior of $\mathbb{R}^3_+$ of the xyw-plane if and only if, $\dot{x}, \dot{y}$ and $\dot{w}$ are the positive roots of the following set of algebraic equations:

$$\begin{aligned}
&r\Big(1 - \frac{x}{k}\Big) - \sigma_1 + \frac{\sigma_2 y}{x} - \alpha_1 w = 0,\\
&s\Big(1 - \frac{y}{l}\Big) - \sigma_2 + \frac{\sigma_1 x}{y} = 0,\\
&\quad \alpha_2 x - \alpha = 0.
\end{aligned}$$

Solving the above equations, gives that:

$$\begin{aligned}
\dot{x} &= \frac{\alpha}{\alpha_2},\\
\dot{y} &= \frac{l}{2s\alpha_2}\Big[l\alpha_2(s-\sigma_2)+\sqrt{l^2\alpha_2^2(s-\sigma_2)^2+4sl\alpha\alpha_2\sigma_1}\Big],\\
\dot{w} &= \frac{\alpha_2}{\alpha\alpha_1}\Big[\frac{\alpha(r-\sigma_1)}{\alpha_2}-\frac{r\alpha^2}{k\alpha_2^2}+\sigma_2\dot{y}\Big].
\end{aligned}$$

Undoubtedly, for $\dot{w}$ to be positive, the following condition must holds:

$$\Big[\frac{\alpha(r-\sigma_1)}{\alpha_2}+\sigma_2\dot{y}\Big] > \frac{r\alpha^2}{k\alpha_2^2}, \tag{6.2}$$

It is clear that condition (6.2) gives a threshold value of the carrying capacity k in the free access area. Thus, the generalist predator species keeps surviving. Also, it should be noted that condition (6.2) could fail when k is small enough and hence, the existence of the specialist predator-free fixed point is violated.

6.5.2 The existence of the positive equilibrium point

The positive equilibrium point F_4 exists in the interior of $\mathbb{R}^4_+$, if and only if, x^*, y^*, z^* and w^* are the positive solutions of the following set of equations:

$$r\Big(1-\frac{x}{k}\Big)-\sigma_1+\frac{\sigma_2 y}{x}-\beta_1 z-\alpha_1 w=0, \tag{6.3}$$

$$s\Big(1-\frac{y}{l}\Big)-\sigma_2+\frac{\sigma_1 x}{y}=0, \tag{6.4}$$

$$\beta_2 x-\beta_0-\gamma_1 w=0, \tag{6.5}$$

$$\alpha_2 x+\gamma_2 z-\alpha=0. \tag{6.6}$$

From the above list of equations, the following is obtained:

$$y=\frac{l}{2s}\Big[(s-\sigma_2)+\sqrt{(s-\sigma_2)^2+\frac{4s\sigma_1 x}{l}}\Big], \tag{6.7}$$

$$z=\frac{\alpha-\alpha_2 x}{\gamma_2}, \tag{6.8}$$

$$w=\frac{\beta_2 x-\beta_0}{\gamma_1}. \tag{6.9}$$

By substituting the values of y, z and w in Eq.(6.3), a little algebraic manipulation yields:

$$ax^3 + bx^2 + cx + d = 0, \tag{6.10}$$

where,

$$\begin{aligned}
a &= \Big(\frac{\alpha_2\beta_1}{\gamma_2} - \frac{r}{k} - \frac{\alpha_1\beta_1}{\gamma_1}\Big)^2 > 0,\\
b &= -2\Big(\frac{\alpha_2\beta_1}{\gamma_2} - \frac{r}{k} - \frac{\alpha_1\beta_1}{\gamma_1}\Big)\Big((r-\sigma_1) - \frac{\alpha\beta_1}{\gamma_2} + \frac{\alpha_1\beta_0}{\gamma_1}\Big),\\
c &= \Big(\frac{l\sigma_2(s-\sigma_2)}{s}\Big)\Big(\frac{\alpha_2\beta_1}{\gamma_2} - \frac{r}{k} - \frac{\alpha_1\beta_1}{\gamma_1}\Big) + \Big((r-\sigma_1) - \frac{\alpha\beta_1}{\gamma_2} + \frac{\alpha_1\beta_0}{\gamma_1}\Big)^2,\\
d &= -\frac{l\sigma_2}{s}\Big((s-\sigma_2)\Big((r-\sigma_1) - \frac{\alpha\beta_1}{\gamma_2} + \frac{\alpha_1\beta_0}{\gamma_1}\Big) + \sigma_1\sigma_2\Big).
\end{aligned}$$

By using Descartes rule of signs, Eq.(6.10) has a unique positive solution $x = x^*$, if the following inequality

$$\frac{\beta_1}{\gamma_2} < \min\Big\{\frac{r\gamma_1 + \alpha_1\beta_1 k}{\alpha_2\gamma_1 k}, \frac{(r-\sigma_1)\gamma_1 + \alpha_1\beta_0}{\alpha\gamma_1}\Big\}, \tag{6.11}$$

holds. Knowing the value of x^*, the values of y^*, z^* and w^* can be computed from Equations (6.7)-(6.9), respectively. It should also be noted that for z^* and w^* to be positive, the following must be true:

$$\frac{\beta_0}{\beta_2} < x^* < \frac{\alpha}{\alpha_2}. \tag{6.12}$$

6.6 Local stability of the equilibrium points

Similarly to the previous chapter, the local dynamic behaviour of the system (6.1) is discussed by making use of the eigenvalue method and Routh-Hurwitz criteria. The Jacobian matrix of the system (6.1) at any point is given by

$$J = \begin{bmatrix} r - \sigma_1 - \dfrac{2rx}{k} - \beta_1 z - \alpha_1 w & \sigma_2 & -\beta_1 x & -\alpha_1 x \\ \sigma_1 & s - \sigma_2 - \dfrac{2sy}{l} & 0 & 0 \\ \beta_2 z & 0 & \beta_2 x - \beta_0 - \gamma_1 w & -\gamma_1 z \\ \alpha_2 w & 0 & \gamma_2 w & \alpha_2 x + \gamma_2 z - \alpha \end{bmatrix},$$

and, the eigenvalues of the resulting matrix are computed as follows:

6.6.1 Local stability behaviour of F_0

In the following lemma, it is shown that F_0 is always a saddle point.

Lemma 14 *The vanishing equilibrium point* $F_0 = (0, 0, 0, 0)$ *is a saddle point in the* $\mathbb{R}^4_+$.

Proof The proof of this lemma is similar to that in Subsection 5.6.1 , and hence omitted. ■

6.6.2 Local stability behaviour of F_1

In the following lemma, the local behaviour of the planar fixed point F_1 is shown.

Lemma 15 *The planar equilibrium point* $F_1 = (\hat{x}, \hat{y}, 0, 0)$ *is locally asymptotically stable in* $\mathbb{R}^4_+$*, whenever:*

$$\hat{x} < min\left\{\frac{\alpha}{\alpha_2}, \frac{\beta_0}{\beta_2}\right\}, \tag{6.13}$$

holds.

Proof The Jacobian matrix of system (6.1) at the equilibrium point F_1 is given by:

$$J(F_1) = \begin{bmatrix} r - \sigma_1 - \frac{2r\hat{x}}{k} & \sigma_2 & -\beta_1\hat{x} & -\alpha_1\hat{x} \\ \sigma_1 & s - \sigma_2 - \frac{2s\hat{y}}{l} & 0 & 0 \\ 0 & 0 & \beta_2\hat{x} - \beta_0 & 0 \\ 0 & 0 & 0 & \alpha_2\hat{x} - \alpha \end{bmatrix} \tag{6.14}$$

Straightforward computations show that the eigenvalues of the Jacobian matrix $J(F_1)$ satisfy the following relations:

$$\lambda_{11} + \lambda_{12} = -\Big(\frac{\sigma_2 \hat{y}}{\hat{x}} + \frac{r\hat{x}}{k} + \frac{\sigma_1 \hat{x}}{\hat{y}} + \frac{s\hat{y}}{l}\Big) < 0, \tag{6.15}$$

$$\lambda_{11}.\lambda_{12} = \left(\frac{rs(\hat{x})^2(\hat{y})^2 + sk\sigma_2(\hat{y})^3 + r\sigma_1(\hat{x})^3}{kl\hat{x}\hat{y}}\right) > 0, \tag{6.16}$$

$$\lambda_{13} = \beta_2\hat{x} - \beta_0, \tag{6.17}$$

$$\lambda_{14} = \alpha_2\hat{x} - \alpha < 0. \tag{6.18}$$

where, $\lambda_{1i} \quad (i = 1, 2, 3, 4)$ represent the eigenvalues that describe the dynamics in the directions of their eigenvectors. Note that, according to equations (6.15)-(6.18), all the eigenvalues of $J(F_1)$ have negative real parts and hence, F_1 is locally asymptotically stable in $\mathbb{R}^4_+$, if and only if, condition (6.13) holds. However, it is a saddle point in the interior of $\mathbb{R}^4_+$, if the condition (6.13) is violated. ■

6.6.3 Local stability behaviour of F_2

In the following lemma, the local behaviour of the generalist predator-free fixed point F_2 is shown.

Lemma 16 *The generalist predator-free equilibrium point $F_2 = (\bar{x}, \bar{y}, \bar{z}, 0)$ is locally asymptotically stable in $\mathbb{R}^4_+$ whenever*

$$\alpha_2\bar{x} + \gamma_2\bar{z} < \alpha, \tag{6.19}$$

holds.

Proof The Jacobian matrix of the system (6.1) at the equilibrium point $F_2 = (\bar{x}, \bar{y}, \bar{z}, 0)$ can be written as:

$$J(F_2) = \begin{bmatrix} a_{11} & a_{12} & a_{13} & a_{14} \\ a_{21} & a_{22} & 0 & 0 \\ a_{31} & 0 & 0 & a_{34} \\ 0 & 0 & 0 & a_{44} \end{bmatrix}, \tag{6.20}$$

where,

$$a_{11} = -\Big(\frac{\sigma_2\bar{y}}{\bar{x}} + \frac{r\bar{x}}{k}\Big) < 0; a_{12} = \sigma_2 > 0; a_{13} = -\beta_1\bar{x} < 0;$$

$$a_{14} = -\alpha_1\bar{x}; a_{21} = \sigma_1 > 0; a_{22} = -\Big(\frac{\sigma_1\bar{x}}{\bar{y}} + \frac{s\bar{y}}{l}\Big) < 0;$$

$$a_{31} = \beta_2\bar{z} > 0; a_{32} = 0; a_{34} = -\gamma_1\bar{z} < 0; a_{44} = \alpha_2\bar{x} + \gamma_2\bar{z} - \alpha.$$

The first root of the characteristic equation of $J(F_2)$ is $\alpha_2\bar{x} + \gamma_2\bar{z} - \alpha$ and, the other three roots are given by:

$$\lambda^3 + A_1\lambda^2 + A_2\lambda + A_3 = 0.$$

The coefficients of the characteristic equation of $J(F_2)$ can be written as:

$A_1 = -(a_{11} + a_{22}) > 0,$

$A_2 = a_{11}a_{22} - a_{12}a_{21} - a_{13}a_{31},$

$A_3 = a_{22}a_{13}a_{31} > 0.$

Further,

$$\begin{aligned}\Delta &= A_1A_2 - A_3 = (a_{11} + a_{22})(a_{12}a_{21} + a_{11}a_{22}) + a_{11}a_{13}a_{31}\\ &= \Big[\frac{kl\sigma_2(\bar{y})^2 + rl(\bar{x})^2\bar{y} + kl\sigma_1(\bar{x})^2 + sk\bar{x}(\bar{y})^2}{\bar{x}\bar{y}kl}\Big]\Big[\frac{sk\sigma_2(\bar{y})^3 + rl\sigma_1(\bar{x})^3 + rs(\bar{x})^2(\bar{y})^2}{\bar{x}\bar{y}kl}\Big]\\ &+ \Big(\frac{\beta_1\beta_2\bar{z}(k\sigma_2\bar{y} + r(\bar{x})^2)}{l}\Big) > 0.\end{aligned}$$

Now, according to the Routh-Hurwitz criteria, all the eigenvalues of $J(F_2)$ have roots with negative real parts, provided that $A_i(i = 1, 3) > 0$ and $\Delta > 0$. Therefore, F_2 is locally asymptotically stable, if (6.19) holds. ■

6.6.4 Local stability behaviour of F_3

In the following lemma, the local behaviour of the specialist predator-free fixed point F_3 is shown.

Lemma 17 *The specialist predator-free equilibrium point* $F_3 = (\dot{x}, \dot{y}, 0, \dot{w})$ *is locally asymptotically stable in* $\mathbb{R}^4_+$ *whenever*

$$\beta_2\dot{x} < \beta_0 + \gamma_1\dot{w}, \tag{6.21}$$

holds.

Proof The Jacobian matrix of the system (6.1) at the equilibrium point $F_3 = (\dot{x}, \dot{y}, 0, \dot{w})$ can be written as:

$$J(F_3) = \begin{bmatrix} a_{11} & a_{12} & a_{13} & a_{14} \\ a_{21} & a_{22} & 0 & 0 \\ 0 & 0 & a_{33} & 0 \\ a_{41} & 0 & a_{43} & 0 \end{bmatrix} \tag{6.22}$$

where,

$$a_{11} = -\Big(\frac{\sigma_2 \dot{y}}{\dot{x}} + \frac{r\dot{x}}{k}\Big) < 0; a_{12} = \sigma_2 > 0; a_{13} = -\beta_1 \dot{x} < 0; a_{14} = -\alpha_1 \dot{x}; a_{21} = \sigma_1 > 0;$$
$$a_{22} = -\Big(\frac{\sigma_1 \dot{x}}{\dot{y}} + \frac{s\dot{y}}{l}\Big) < 0; a_{33} = \beta_2 \dot{x} - \beta_0 - \gamma_1 \dot{w}; a_{41} = \alpha_2 \dot{w}; a_{43} = \gamma_2 \dot{w}.$$

The first root of the characteristic equation of $J(F_3)$ is $\beta_2 \dot{x} - \beta_0 - \gamma_1 \dot{w}$ and, the other three roots are given by:

$$\lambda^3 + A_1 \lambda^2 + A_2 \lambda + A_3 = 0.$$

The coefficients of the characteristic equation of $J(F_3)$ can be written as:

$A_1 = -(a_{11} + a_{22}) > 0,$

$A_2 = a_{11}a_{22} - a_{12}a_{21} - a_{14}a_{41},$

$A_3 = a_{22}a_{14}a_{41} > 0.$

Further,

$$\begin{aligned} \Delta &= A_1 A_2 - A_3 = (a_{11} + a_{22})(a_{12}a_{21} + a_{11}a_{22}) + a_{11}a_{14}a_{41} \\ &= \Big[\frac{kl\sigma_2(\dot{y})^2 + rl(\dot{x})^2\dot{y} + kl\sigma_1(\dot{x})^2 + sk\dot{x}(\dot{y})^2}{\dot{x}\dot{y}kl}\Big]\Big[\frac{sk\sigma_2(\dot{y})^3 + rl\sigma_1(\dot{x})^3 + rs(\dot{x})^2(\dot{y})^2}{\dot{x}\dot{y}kl}\Big] \\ &+ \Big(\frac{\alpha_1\alpha_2\dot{w}(k\sigma_2\dot{y} + r(\dot{x})^2)}{k}\Big) > 0. \end{aligned}$$

Now, according to the Routh-Hurwitz criteria, all the eigenvalues of $J(F_3)$ have roots with negative real parts, provided that $A_i (i = 1, 3) > 0$ and $\Delta > 0$. Therefore, F_3 is locally asymptotically stable, if (6.21) holds. ■

6.6.5 Local stability behaviour of F_4

In the following lemma, the local behaviour of the positive fixed point F_4 is shown.

Lemma 18 *The positive equilibrium point* $F_4 = (x^*, y^*, z^*, w^*)$ *is locally asymptotically stable in* $\mathbb{R}^4_+$ *when the following conditions hold as :* $A_3 > 0, A_4 > 0, \big(A_1A_2 - A_3\big)A_3 - A_4A_1^2 > 0$, *where* A_i*'s are given in the proof of this lemma.*

Proof The Jacobian matrix of the system (6.1), at the positive equilibrium point $F_4 = (x^*, y^*, z^*, w^*)$, can be written as:

$$J(F_4) = \begin{bmatrix} a_{11} & a_{12} & a_{13} & a_{14} \\ a_{21} & a_{22} & 0 & 0 \\ a_{31} & 0 & 0 & a_{34} \\ a_{41} & 0 & a_{43} & a_{44} \end{bmatrix} \tag{6.23}$$

where,

$$a_{11} = -\Big(\frac{\sigma_2 y^*}{x^*} + \frac{rx^*}{k}\Big) < 0; a_{12} = \sigma_2 > 0; a_{13} = -\beta_1 x^* < 0; a_{14} = -\alpha_1 x^* < 0;$$

$$a_{21} = \sigma_1 > 0; a_{22} = -\Big(\frac{\sigma_1 x^*}{y^*} + \frac{sy^*}{l}\Big) < 0; a_{31} = \beta_2 z^* > 0; a_{33} = 0; a_{34} = -\gamma_1 z^* < 0;$$

$$a_{41} = \alpha_2 w^*; a_{43} = \gamma_2 w^*; a_{44} = \alpha_2 w^* + \gamma_2 z^* - \alpha.$$

Accordingly, the characteristic equation of $J(F_4)$ is given by:

$$\lambda^4 + A_1\lambda^3 + A_2\lambda^2 + A_3\lambda + A_4 = 0. \tag{6.24}$$

Here,

$A_1 = -M_1 > 0,$

$A_2 = M_2 + M_3 > 0,$

$A_3 = a_{11}M_5 - a_{22}M_3 - M_4,$

$A_4 = -M_2M_5 + a_{22}M_4,$

$\Delta_1 = A_1A_2 - A_3 = -\big(M_1M_2 + M_4 - a_{11}a_{14}a_{41} - a_{11}a_{13}a_{31}\big)$

where,

$M_1 = a_{11} + a_{22} < 0$, $M_2 = a_{11}a_{22} - a_{12}a_{21} > 0$, $M_3 = -a_{13}a_{31} - a_{34}a_{43} - a_{14}a_{41} > 0,$

$M_4 = a_{13}a_{34}a_{41} + a_{14}a_{31}a_{43}$, $M_5 = a_{34}a_{43} < 0$.

Further,

$$\begin{aligned}\Delta_2 &= A_1A_2A_3 - A_3^2 - A_1^2A_4 \\ &= \Big(a_{22}M_3 + M_4\Big)\Big(M_1M_2 + M_4 - a_{11}a_{14}a_{41} - a_{11}a_{13}a_{31}\Big) \\ &- M_5\Big[a_{11}M_4 - a_{11}^2\big(a_{14}a_{41} + a_{13}a_{31}\big) - a_{22}M_1(M_2 - M_1)\Big].\end{aligned}$$

Now, according to the Routh-Hurwitz criteria, all the eigenvalues of $J(F_4)$ have roots with negative real parts when $A_i(i = 1, 3, 4) > 0$ and $\Delta_2 > 0$. Hence, F_4 is locally asymptotically stable in the interior of $\mathbb{R}_+^4$ if the conditions that have been stated in the lemma hold. ■

A consequence of above lemma is the statement in the next corollary.

Corollary 6.6.0.1 *The positive equilibrium point* $F_4 = (x^*, y^*, z^*, w^*)$ *is locally asymptotically stable in* $\mathbb{R}_+^4$ *whenever*

$$\alpha_1\gamma_2\beta_2 = \alpha_2\gamma_1\beta_1, \tag{6.25}$$

holds.

Proof If the case $M_4 = \alpha_1\gamma_2\beta_2 - \alpha_2\gamma_1\beta_1 = 0$ is taken in the above lemma and re-written M_i as:

$M_1 = a_{11} + a_{22} < 0$,

$M_2 = a_{13}a_{31} + a_{14}a_{41} < 0$,

$M_3 = a_{12}a_{21} - a_{11}a_{22} < 0$,

then, the following is obtained:

$$\begin{aligned}
A_1 &= -M_1 > 0,\\
A_2 &= -\big(M_2 + M_3 + a_{34}a_{43}\big) > 0,\\
A_3 &= a_{34}a_{43}M_1 + a_{22}M_2 > 0,\\
A_4 &= a_{34}a_{43}M_3 > 0,\\
\Delta_1 &= A_1A_2 - A_3 = \big(M_1M_3 + a_{11}M_2\big) > 0,\\
\Delta_2 &= A_1A_2A_3 - A_3^2 - A_1^2A_4\\
&= \big(a_{22}M_1M_2M_3 + a_{11}a_{34}a_{43}M_1M_2 + a_{11}a_{22}M_2^2\big) > 0.
\end{aligned}$$

Now, according to the Routh-Hurwitz criteria, all the eigenvalues of $J(F_4)$ have roots with negative real parts, when $A_i(i = 1, 3, 4) > 0$ and $\Delta_2 > 0$. Hence, F_4 is locally asymptotically stable in the interior of $\mathbb{R}^4_+$ if (6.25) holds. ■

6.7 Global dynamical behaviour

In this section, the global stability of the local equilibrium points is investigated by using the Lyapunov direct method, as shown in the following theorems.

Theorem 6.7.1 *Assume that the equilibrium point F_1 is locally asymptotically stable in $\mathbb{R}^4_+$, then it is globally asymptotically stable in $\mathbb{R}^4_+$ whenever*

$$\alpha_1\gamma_2\beta_2 \leq \alpha_2\gamma_1\beta_1, \tag{6.26}$$

holds.

Proof Consider the following positive definite function:

$$R_1(x, y, z, w) = c_1\Big(x - \hat{x} - \hat{x}\ln\frac{x}{\hat{x}}\Big) + c_2\Big(y - \hat{y} - \hat{y}\ln\frac{y}{\hat{y}}\Big) + c_3z + c_4w,$$

where, $c_i, (i = 1, 2, 3, 4)$ are positive constants to be determined. Now, the time derivative of R_1 along the trajectory of the system (6.1) can be written as:

$$
\begin{aligned}
\frac{dR_1}{dt} &= c_1\Big(\frac{x-\hat{x}}{x}\Big)\frac{dx}{dt} + c_2\Big(\frac{y-\hat{y}}{y}\Big)\frac{dy}{dt} + c_3\frac{dz}{dt} + c_4\frac{dw}{dt} \\
&= c_1\big(x-\hat{x}\big)\Big(r - \frac{rx}{k} - \sigma_1 + \frac{\sigma_2 y}{x} - \beta_1 z - \alpha_1 w\Big) \\
&+ c_2\big(y-\hat{y}\big)\Big(s - \frac{sy}{l} + \frac{\sigma_1 x}{y} - \sigma_2\Big) \\
&+ c_3\big(\beta_2 xz - \beta_0 z - \gamma_1 zw\big) + c_4\big(\alpha_2 xw + \gamma_2 zw - \alpha w\big) \\
&= c_1\big(x-\hat{x}\big)\Big(\frac{-r}{k}\big(x-\hat{x}\big) + \sigma_2\Big(\frac{y}{x} - \frac{\hat{y}}{\hat{x}}\Big) - \beta_1 z - \alpha_1 w\Big) \\
&+ c_2\big(y-\hat{y}\big)\Big(\frac{-s}{l}\big(y-\hat{y}\big) + \sigma_1\Big(\frac{x}{y} - \frac{\hat{x}}{\hat{y}}\Big)\Big) \\
&+ c_3\big(\beta_2 xz - \beta_0 z - \gamma_1 zw\big) + c_4\big(\alpha_2 xw + \gamma_2 zw - \alpha w\big).
\end{aligned}
$$

Therefore,

$$
\begin{aligned}
\frac{dR_1}{dt} &= \frac{-c_1 r}{k}\big(x-\hat{x}\big)^2 + c_1\sigma_2\big(x-\hat{x}\big)\Big(\frac{y\hat{x} - x\hat{y}}{x\hat{x}}\Big) - c_1\big(x-\hat{x}\big)\beta_1 z - c_1\big(x-\hat{x}\big)\alpha_1 w\Big) \\
&- \frac{c_2 s}{l}\big(y-\hat{y}\big)^2 + c_2\sigma_1\big(y-\hat{y}\big)\Big(\frac{x\hat{y} - y\hat{x}}{y\hat{y}}\Big) \\
&+ c_3\big(\beta_2 xz - \beta_0 z - \gamma_1 zw\big) + c_4\big(\alpha_2 xw + \gamma_2 zw - \alpha w\big).
\end{aligned}
$$

By choosing the positive constants as:

$$
c_1 = 1, c_2 = \frac{\sigma_2\hat{y}}{\sigma_1\hat{x}}, c_3 = \frac{\beta_1}{\beta_2}, c_4 = \frac{\alpha_1}{\alpha_2},
$$

the following is obtained,

$$
\begin{aligned}
\frac{dR_1}{dt} &= -\Big(\frac{r}{k}\Big)\big(x-\hat{x}\big)^2 - \Big(\frac{\sigma_2}{x\hat{x}y}\Big)\big(x\hat{y} - y\hat{x}\big)^2 - \Big(\frac{s\sigma_2\hat{y}}{l\sigma_1\hat{x}}\Big)\big(y-\hat{y}\big)^2 \\
&+ \Big(\hat{x} - \frac{\beta_0}{\beta_2}\Big)\beta_1 z + \Big(\hat{x} - \frac{\alpha_0}{\alpha_2}\Big)\alpha_1 w - \Big(\frac{\alpha_2\beta_1\gamma_1 - \alpha_1\beta_2\gamma_2}{\alpha_2\beta_2}\Big)zw.
\end{aligned}
$$

Then, $\frac{dR_1}{dt} < 0$ under the local stability condition (6.13) and (6.26). Hence, R_1 is a Lyapunov function. Therefore, F_1 is globally asymptotically stable in $\mathbb{R}^4_+$. ■

Condition (6.26) shows how the two chains ($x \to z \to w$) and ($x \to w$) interact with to each other.

The next theorem shows the global stability of the generalist predator-free equilibrium point F_2 in $\mathbb{R}^4_+$.

Theorem 6.7.2 *Assume that the equilibrium point F_2 is locally asymptotically stable in $\mathbb{R}^4_+$, then it is globally asymptotically stable in $\mathbb{R}^4_+$ whenever condition*

$$\alpha_1\gamma_2\beta_2 = \alpha_2\gamma_1\beta_1, \tag{6.27}$$

holds.

Proof Consider the following positive definite function:

$$R_2(x,y,z,w) = c_1\Big(x-\bar{x}-\bar{x}\ln\frac{x}{\bar{x}}\Big) + c_2\Big(y-\bar{y}-\bar{y}\ln\frac{y}{\bar{y}}\Big) + c_3\Big(z-\bar{z}-\bar{z}\ln\frac{z}{\bar{z}}\Big) + c_4 w,$$

where, $c_i, (i = 1,2,3,4)$ are positive constants to be determined. Now the time derivative of R_2 along the trajectory of the system (6.1) can be written as:

$$\begin{aligned}
\frac{dR_2}{dt} &= c_1\Big(\frac{x-\bar{x}}{x}\Big)\frac{dx}{dt} + c_2\Big(\frac{y-\bar{y}}{y}\Big)\frac{dy}{dt} + c_3\Big(\frac{z-\bar{z}}{z}\Big)\frac{dz}{dt} + c_4\frac{dw}{dt} \\
&= c_1\big(x-\bar{x}\big)\Big(r - \frac{rx}{k} - \sigma_1 + \frac{\sigma_2 y}{x} - \beta_1 z - \alpha_1 w\Big) \\
&+ c_2\big(y-\bar{y}\big)\Big(s - \frac{sy}{l} + \frac{\sigma_1 x}{y} - \sigma_2\Big) \\
&+ c_3\big(z-\bar{z}\big)\big(\beta_2 x - \beta_0 - \gamma_1 w\big) + c_4\big(\alpha_2 xw + \gamma_2 zw - \alpha w\big) \\
&= c_1\big(x-\bar{x}\big)\Big(\frac{-r}{k}\big(x-\bar{x}\big) + \sigma_2\Big(\frac{y}{x} - \frac{\bar{y}}{\bar{x}}\Big) - \beta_1\big(z-\bar{z}\big) - \alpha_1 w\Big) \\
&+ c_2\big(y-\bar{y}\big)\Big(\frac{-s}{l}\big(y-\bar{y}\big) + \sigma_1\Big(\frac{x}{y} - \frac{\bar{x}}{\bar{y}}\Big)\Big) \\
&+ c_3\big(z-\bar{z}\big)\Big(\beta_2\big(x-\bar{x}\big) - \gamma_1 w\Big) + c_4\big(\alpha_2 xw + \gamma_2 zw - \alpha w\big).
\end{aligned}$$

Therefore,

$$\begin{aligned}
\frac{dR_2}{dt} &= \frac{-c_1 r}{k}\big(x-\bar{x}\big)^2 + c_1\sigma_2\big(x-\bar{x}\big)\Big(\frac{y\bar{x}-x\bar{y}}{x\bar{x}}\Big) - c_1\beta_1\big(x-\bar{x}\big)\big(z-\bar{z}\big) - c_1\alpha_1 w\big(x-\bar{x}\big) \\
&- \frac{c_2 s}{l}\big(y-\bar{y}\big)^2 + c_2\sigma_1\big(y-\bar{y}\big)\Big(\frac{x\bar{y}-y\bar{x}}{y\bar{y}}\Big) \\
&+ c_3\big(x-\bar{x}\big)\big(z-\bar{z}\big) - c_3\gamma_1 w\big(z-\bar{z}\big) + c_4\big(\alpha_2 xw + \gamma_2 zw - \alpha w\big).
\end{aligned}$$

By choosing the positive constants as:

$$c_1 = 1, c_2 = \frac{\sigma_2\bar{y}}{\sigma_1\bar{x}}, c_3 = \frac{\beta_1}{\beta_2}, c_4 = \frac{\alpha_1}{\alpha_2},$$

the following is obtained:

$$\frac{dR_2}{dt} = -\Big(\frac{r}{k}\Big)\big(x-\bar{x}\big)^2 - \Big(\frac{\sigma_2}{x\bar{x}y}\Big)\big(x\bar{y}-y\bar{x}\big)^2 - \Big(\frac{s\sigma_2\bar{y}}{l\sigma_1\bar{x}}\Big)\big(y-\bar{y}\big)^2.$$

Then, $\frac{dR_2}{dt} \leq 0$ which is negative semi-definite under the local stability condition (6.19) and (6.27). Thus, F_2 is Lyapunov stable. However, the set

$N_2 = \big\{(x,y,z,w)/\dot{R}_2(x,y,z,w) = 0\big\}$, which is the set $N_2 = \big\{(x,y,z,w)/x = \bar{x}, y = \bar{y}\big\}$, does not contain any trajectory of the system except $F_2 = (\bar{x},\bar{y},\bar{z},0)$. Therefore, by LaSalle's invariance principle, F_2 is globally asymptotically stable in $\mathbb{R}^4_+$ if the local stability condition (6.19) and (6.25) hold. ■

The next theorem shows the global stability of the specialist predator-free equilibrium point F_3 in $\mathbb{R}^4_+$.

Theorem 6.7.3 *Assume that the equilibrium point F_3 is locally asymptotically stable in $\mathbb{R}^4_+$, then it is globally asymptotically stable in $\mathbb{R}^4_+$ whenever condition (6.27) holds.*

Proof Consider the following positive definite function:

$$R_3(x,y,z,w) = c_1\Big(x - \dot{x} - \dot{x}\ln\frac{x}{\dot{x}}\Big) + c_2\Big(y - \dot{y} - \dot{y}\ln\frac{y}{\dot{y}}\Big) + c_3 z + c_4\Big(w - \dot{w} - \dot{w}\ln\frac{w}{\dot{w}}\Big),$$

where, $c_i, (i = 1,2,3,4)$ are positive constants to be determined. Now the time derivative of R_3 along the trajectory of the system (6.1) can be written as:

$$\begin{aligned}
\frac{dR_3}{dt} &= c_1\Big(\frac{x-\dot{x}}{x}\Big)\frac{dx}{dt} + c_2\Big(\frac{y-\dot{y}}{y}\Big)\frac{dy}{dt} + c_3\frac{dz}{dt} + c_4\Big(\frac{w-\dot{w}}{w}\Big)\frac{dw}{dt} \\
&= c_1\big(x-\dot{x}\big)\Big(\frac{-r}{k}\big(x-\dot{x}\big) + \sigma_2\Big(\frac{y}{x} - \frac{\dot{y}}{\dot{x}}\Big) - \beta_1 z - \alpha_1\big(w-\dot{w}\big)\Big) \\
&+ c_2\big(y-\dot{y}\big)\Big(\frac{-s}{l}\big(y-\dot{y}\big) + \sigma_1\Big(\frac{x}{y} - \frac{\dot{x}}{\dot{y}}\Big)\Big) \\
&+ c_3 z\Big(\beta_2 x - \gamma_1 w - \beta_0\Big) + c_4\big(w-\dot{w}\big)\Big(\alpha_2\big(x-\dot{x}\big) + \gamma_2 z\Big).
\end{aligned}$$

By choosing the positive constants as:

$$c_1 = 1, c_2 = \frac{\sigma_2\dot{y}}{\sigma_1\dot{x}}, c_3 = \frac{\beta_1}{\beta_2}, c_4 = \frac{\alpha_1}{\alpha_2},$$

the following is obtained:

$$\frac{dR_3}{dt} = -\Big(\frac{r}{k}\Big)\big(x-\dot{x}\big)^2 - \Big(\frac{\sigma_2}{x\dot{x}y}\Big)\big(x\dot{y} - y\dot{x}\big)^2 - \Big(\frac{s\sigma_2\dot{y}}{l\sigma_1\dot{x}}\Big)\big(y-\dot{y}\big)^2.$$

Then, $\frac{dR_3}{dt} \leq 0$ which is negative semi-definite under the local stability condition (6.21) and (6.27). Thus, F_3 is Lyapunov stable. However, the set

$N_3 = \{(x,y,z,w)/\dot{R}_3(x,y,z,w) = 0\}$, which is the set $N_3 = \{(x,y,z,w)/x = \dot{x}, y = \dot{y}\}$, does not contain any trajectory of the system except $F_3 = (\dot{x}, \dot{y}, 0, \dot{w})$. Therefore, by LaSalle's invariance principle, F_3 is globally asymptotically stable in $\mathbb{R}^4_+$ if the local stability condition (6.21) and (6.27) hold. ■

Finally, the global stability of the positive equilibrium point F_4 in the interior of $\mathbb{R}^4_+$ is investigated, as shown in the following theorem.

Theorem 6.7.4 *The equilibrium point* F_4 *is globally asymptotically stable in* $\mathbb{R}^4_+$ *whenever it exists.*

Proof Consider the following positive definite function:

$$\begin{aligned} R_4(x,y,z,w) &= c_1\Big(x - x^* - x^* \ln\frac{x}{x^*}\Big) + c_2\Big(y - y^* - y^* \ln\frac{y}{y^*}\Big) \\ &+ c_3\Big(z - z^* - z^* \ln\frac{z}{z^*}\Big) + c_4\Big(w - w^* - w^* \ln\frac{w}{w^*}\Big), \end{aligned}$$

where, $c_i, (i = 1,2,3,4)$ are positive constants to be determined. Now, the time derivative of R_4 along the trajectory of the system (6.1) can be written as:

$$\begin{aligned} \frac{dR_4}{dt} &= c_1\Big(\frac{x-x^*}{x}\Big)\frac{dx}{dt} + c_2\Big(\frac{y-y^*}{y}\Big)\frac{dy}{dt} + c_3\Big(\frac{z-z^*}{z}\Big)\frac{dz}{dt} + c_4\Big(\frac{w-w^*}{w}\Big)\frac{dw}{dt} \\ &= c_1\big(x-x^*\big)\Big(r - \frac{rx}{k} - \sigma_1 + \frac{\sigma_2 y}{x} - \beta_1 z\Big) \\ &+ c_2\big(y-y^*\big)\Big(s - \frac{sy}{l} + \frac{\sigma_1 x}{y} - \sigma_2\Big) \\ &+ c_3\big(z-z^*\big)\big(\beta_2 x - \beta_0 - \gamma_1 w\big) + c_4\big(w-w^*\big)\big(\gamma_2 z - \alpha\big). \end{aligned}$$

Therefore,

$$\begin{aligned} \frac{dR_4}{dt} &= \frac{-c_1 r}{k}\big(x-x^*\big)^2 + c_1\sigma_2\big(x-x^*\big)\Big(\frac{yx^* - xy^*}{xx^*}\Big) - c_1\beta_1\big(x-x^*\big)\big(z-z^*\big) \\ &- \frac{c_2 s}{l}\big(y-y^*\big)^2 + c_2\sigma_1\big(y-y^*\big)\Big(\frac{xy^* - yx^*}{yy^*}\Big) + c_3\beta_2\big(x-x^*\big)\big(z-z^*\big) \\ &- c_3\gamma_1\big(z-z^*\big)\big(w-w^*\big) + c_4\gamma_2\big(z-z^*\big)\big(w-w^*\big). \end{aligned}$$

By choosing the positive constants as:

$$c_1 = 1, c_2 = \frac{\sigma_2 y^*}{\sigma_1 x^*}, c_3 = \frac{\beta_1}{\beta_2}, c_4 = \frac{\alpha_1}{\alpha_2},$$

the following is obtained:

$$\frac{dR_4}{dt} \quad = \quad -\Big(\frac{r}{k}\Big)\big(x - x^*\big)^2 - \Big(\frac{\sigma_2}{xx^*y}\Big)\big(xy^* - yx^*\big)^2 - \Big(\frac{s\sigma_2 y^*}{l\sigma_1 x^*}\Big)\big(y - y^*\big)^2.$$

Then, $\frac{dR_4}{dt} \leq 0$ which is negative semi-definite and thus F_4 is Lyapunov stable. However, the set $N_4 = \big\{(x, y, z, w)/\dot{R}_4(x, y, z, w) = 0\big\}$, which is the set $N_4 = \big\{(x, y, z, w)/x = x^*, y = y^*\big\}$, does not contain any trajectory of the system except $F_4 = (x^*, y^*, z^*, w^*)$. Therefore, by LaSalle's invariance principle F_4 is globally asymptotically stable in interior of $\mathbb{R}^4_+$ if the local stability holds. ■

6.8 Persistence analysis

Similarly to the previous chapter, the persistence conditions of the system (6.1) are studied using the Freedman and Waltman approach.

Now, before establishing the persistence conditions of the system (6.1), first, the stable behaviour of F_1 and F_2 in the boundary planes xy and xyz needs to be studied, which is undertaken through the following lemma.

Lemma 19 *Assume that conditions (4.27) and (4.33) are satisfied, which represent the local stability conditions for the equilibrium points F_1, F_2 and F_3, respectively. Then they are globally asymptotically stable in the interior of $\mathbb{R}^2_{+(\mathrm{xy})}$, $\mathbb{R}^3_{+(\mathrm{xyz})}$ and $\mathbb{R}^3_{+(\mathrm{xyw})}$, respectively.*

Proof The proof of the above Lemma is clear, and so omitted. ■

In the following theorem, the persistence condition of the system (6.1) is established.

Theorem 6.8.1 *If the conditions (6.13), (6.19) and (6.21) are violated, then, the system (6.1) persists.*

Proof Followed by the application of Freedman and Waltman persistence theorem. ■

6.9 Local bifurcation analysis

In this section, the effect of varying parameter values on the dynamical behaviour of the system (6.1) around each equilibrium point is studied. In the following theorems, an application of Sotomayor's hypothesis for local bifurcation is adapted.

Now, the Jacobian matrix of system (6.1) at each of the equilibrium points is given by:

$$J = DF = \begin{bmatrix} r - \sigma_1 - \dfrac{2rx}{k} - \beta_1 z - \alpha_1 w & \sigma_2 & -\beta_1 x & -\alpha_1 x \\ \sigma_1 & s - \sigma_2 - \dfrac{2sy}{l} & 0 & 0 \\ \beta_2 z & 0 & \beta_2 x - \beta_0 - \gamma_1 w & -\gamma_1 z \\ \alpha_2 w & 0 & \gamma_2 w & \alpha_2 x + \gamma_2 z - \alpha \end{bmatrix}.$$

For any non-zero vector $V = (v_1, v_2, v_3, v_4)^T$:

$$D^2F(V,V) = \begin{bmatrix} -2v_1\Big(\frac{rv_1}{k} - \beta_1 v_3 + \alpha_1 v_4\Big) \\ -\frac{2s}{l} v_2^2 \\ 2v_3\Big(\beta_2 v_1 - \gamma_1 v_4\Big) \\ 2v_4\Big(\alpha_2 v_1 + \gamma_2 v_3\Big) \end{bmatrix} \tag{6.28}$$

and,

$$D^3F(V,V,V) = (0,0,0,0)^T.$$

So, according to Sotomayor's theorem the pitchfork bifurcation does not occur at any of the points $F_i, i = 0,1,2,3$.

Theorem 6.9.1 *Suppose that*

$$(r - \sigma_1)^2 - l\sigma_1^3 \neq 0. \tag{6.29}$$

Then, for the parameter value $\sigma_2^* = \dfrac{s(r-\sigma_1)}{r}$ *system (6.1), at the equilibrium point* F_0*, has a transcritical bifurcation.*

Proof The proof of this theorem is similar to that of Theorem 4.9.1, and hence omitted. ■

Theorem 6.9.2 *Suppose that*

$$v_3^{[1]} \neq 0, \tag{6.30}$$

Then, for the parameter value $\beta_2^* = \frac{\beta_0}{\hat{x}}$, *system (6.1), at the equilibrium point* F_1, *has a transcritical bifurcation.*

Proof According to the Jacobian matrix $J(F_1)$ given by (6.14), system (6.1), at the equilibrium point F_1, has a zero eigenvalue, say λ_{13}, at $\beta_2 = \beta_2^*$ and the Jacobian matrix $J(F_1)$ becomes:

$$J^*(F_1) = \begin{bmatrix} r - \sigma_1 - \frac{2r\hat{x}}{k} & \sigma_2 & -\beta_1\hat{x} & -\alpha_1\hat{x} \\ \sigma_1 & s - \sigma_2 - \frac{2s\hat{y}}{l} & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \alpha_2\hat{x} - \alpha \end{bmatrix}$$

Now, suppose that $V^{[1]} = \left(v_1^{[1]}, v_2^{[1]}, v_3^{[1]}, v_4^{[1]}\right)^T$ is an eigenvector corresponding to the eigenvalue λ_{13}. Then, $\big(J^*(F_1) - \lambda_{13}I\big)V^{[1]} = 0$, which implies:

$$\begin{aligned} v_2^{[1]} &= \frac{\sigma_1 l v_1^{[1]}}{2s\hat{y} - (s - \sigma_2)l}, \\ v_3^{[1]} &= \left(\frac{(rk - 2r\hat{x} - \sigma_1 k)(2s\hat{y} - (s - \sigma_2)l) + \sigma_1\sigma_2 lk}{\beta_1\hat{x}k(2s\hat{y} - (s - \sigma_2)l)}\right)v_1^{[1]}, \\ v_4^{[1]} &= 0, \end{aligned}$$

where, $v_1^{[1]}$ is any non-zero real number. Let $\psi^{[1]} = \big(\psi_1^{[1]}, \psi_2^{[1]}, \psi_3^{[1]}, \psi_4^{[1]}\big)^T$ be an eigenvector associated with the eigenvalue λ_{13} of the matrix $(J^*(F_1))^T$. Then, $\big((J^*(F_1))^T - \lambda_{13}I\big)\psi^{[1]} = 0$. By solving this equation for $\psi^{[1]}$, $\psi_1^{[1]} = \psi_2^{[1]} = \psi_4^{[1]} = 0$ is obtained, where $\psi_3^{[1]}$ is any non-zero real number.

Now, to confirm whether the conditions of Sotomayor's theorem for transcritical bifurcation are satisfied, the following is considered:

$$\frac{\partial f}{\partial \beta_2} = f_{\beta_2}(X, \beta_2) = \left(\frac{\partial f_1}{\partial \beta_2}, \frac{\partial f_2}{\partial \beta_2}, \frac{\partial f_3}{\partial \beta_2}, \frac{\partial f_4}{\partial \beta_2}\right)^T = (0, 0, xz, 0)^T.$$

Thus, $f'_{\beta_2}(F_1, \beta_2^*) = (0,0,0,0)^T$ and hence, $(\psi^{[1]})^T f'_{\beta 2}(F_1, \beta_2^*) = 0$. Therefore, according to Sotomayor's theorem, saddle-node bifurcation cannot occur, while the first condition of transcritical bifurcation is satisfied.

Now,

$$Df_{\beta_2}(X, \beta_2) = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ z & 0 & x & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

where, $Df_{\beta_2}(X, \beta_2)$ represents the derivative of $f_{\beta_2}(X, \beta_2)$ with respect to $X = (x, y, z, w)^T$. Moreover, it is observed under condition (6.30) that:

$$Df_{\beta_2}(F_1, \beta_2^*)V^{[1]} = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & \hat{x} & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} v_1^{[1]} \\ v_2^{[1]} \\ v_3^{[1]} \\ 0 \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ \hat{x}v_3^{[1]} \\ 0 \end{pmatrix}$$

$$\begin{aligned} (\psi^{[1]})^T \Big[Df_{\beta_2}(F_1, \beta_2^*)V^{[1]}\Big] &= \Big(0, 0, \psi_3^{[1]}, 0\Big)\Big(0, 0, \hat{x}v_3^{[1]}, 0\Big)^T \\ &= \hat{x}\psi_3^{[1]}v_3^{[1]} \neq 0. \end{aligned}$$

Now, by substituting in (6.28), the following is obtained:

$$D^2 f\big(F_1, \beta_2^*\big)\big(V^{[1]}, V^{[1]}\big) = \left[-2v_1^{[1]}\left(\frac{rv_1^{[1]}}{k} + \beta_1 v_3^{[1]}\right), \frac{-2s\big(v_2^{[1]}\big)^2}{l}, 2\beta_2^* v_1^{[1]} v_3^{[1]}, 0 \right]^T.$$

Hence, according to condition (6.30):

$$\big(\psi^{[1]}\big)^T \big[D^2 f(F_1, \beta_2^*)\big(V^{[1]}, V^{[1]}\big)\big] = 2\beta_2^* v_1^{[1]} v_3^{[1]} \psi_3^{[1]} \neq 0.$$

This means the second condition of transcritical bifurcation is satisfied. Thus, according to Sotomayor's theorem system, (6.1) has transcritical bifurcation at F_1 with the parameter $\beta_2 = \beta_2^*$. ■

Theorem 6.9.3 *Suppose that*

$$\alpha_2 v_1^{[2]} + \gamma_2^* v_3^{[2]} \neq 0. \tag{6.31}$$

Then, for the parameter value $\gamma_2^* = \frac{\alpha - \alpha_2 \bar{x}}{\bar{z}}$*, system (6.1), at the equilibrium point* F_2*, has transcritical bifurcation.*

Proof According to the Jacobian matrix $J(F_2)$, given by (6.20), system (6.1), at the equilibrium point F_2, has a zero eigenvalue, say λ_{24}, at $\gamma_2 = \gamma_2^*$ and this matrix becomes

$$J^*(F_2) = \begin{bmatrix} r - \sigma_1 - \frac{2r\bar{x}}{k} - \beta_1 \bar{z} & \sigma_2 & -\beta_1 \bar{x} & -\alpha_1 \bar{x} \\ \sigma_1 & s - \sigma_2 - \frac{2s\bar{y}}{l} & 0 & 0 \\ \beta_2 \bar{z} & 0 & 0 & -\gamma_1 \bar{z} \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

Now, suppose that $V^{[2]} = \left(v_1^{[2]}, v_2^{[2]}, v_3^{[2]}, v_4^{[2]}\right)^T$ is an eigenvector corresponding to the eigenvalue λ_{24}. Thus, $\big(J^*(F_2) - \lambda_{24} I\big) V^{[2]} = 0$, which implies

$$\begin{aligned} v_2^{[2]} &= \frac{\sigma_1 l v_1^{[2]}}{2s\bar{y} - (s - \sigma_2) l}, \\ v_3^{[2]} &= \left[\left(\frac{(rk - 2r\bar{x} - \sigma_1 k - k\beta_1 \bar{z})(2s\bar{y} - (s - \sigma_2)l)\gamma_1 + \sigma_1 \sigma_2 l k \bar{x} \beta_1 \gamma_1}{\bar{x} k \beta_1 \gamma_1 (2s\bar{y} - (s - \sigma_2) l)}\right)\right. \\ &- \left.\left(\frac{(\bar{x}\alpha_1 k \beta_1 v_1^{[2]} (2s\bar{y} - (s - \sigma_2) l)}{\bar{x} k \beta_1 \gamma_1 (2s\bar{y} - (s - \sigma_2) l)}\right)\right] v_1^{[2]}, \\ v_4^{[2]} &= \frac{\beta_2 v_1^{[2]}}{\gamma_1}, \end{aligned}$$

where, $v_1^{[2]}$ is any non-zero real number and $\left[2s\bar{y} - (s - \sigma_2) l\right] \neq 0$. Then, let $\psi^{[2]} = \left(\psi_1^{[2]}, \psi_2^{[2]}, \psi_3^{[2]}, \psi_4^{[2]}\right)^T$ be an eigenvector associated with the eigenvalue λ_{24} of the matrix $(J^*(F_2))^T$. So, $\big((J^*(F_2))^T - \lambda_{24} I\big)\psi^{[2]} = 0$ and by solving this equation for $\psi^{[2]}$, $\psi_1^{[2]} = \psi_2^{[2]} = \psi_3^{[2]} = 0$ is obtained, where $\psi_4^{[2]}$ is any non-zero real number.

Now, to confirm that the conditions of Sotomayor's theorem for transcritical bifurcation are satisfied, the following is considered:

$$\frac{\partial f}{\partial \gamma_2} = f'_{\gamma_2}(X, \gamma_2) = \left(\frac{\partial f_1}{\partial \gamma_2}, \frac{\partial f_2}{\partial \gamma_2}, \frac{\partial f_3}{\partial \gamma_2}, \frac{\partial f_4}{\partial \gamma_2}\right)^T = (0, 0, 0, zw)^T.$$

Therefore, $f'_{\gamma_2}(F_2,\gamma_2^*) = (0,0,0,0)^T$ and hence, $(\psi^{[2]})^T f'_{\gamma_2}(F_2,\gamma_2^*) = 0$. So, according to Sotomayor's theorem, saddle-node bifurcation cannot occur, while the first condition of transcritical bifurcation is satisfied. Now,

$$Df_{\gamma_2}(X,\gamma_2) = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & w & z \end{bmatrix}$$

where, $Df_{\gamma_2}(X,\gamma_2)$ represent the derivative of $f_{\gamma_2}(X,\gamma_2)$ with respect to $X = (x,y,z,w)^T$. Further, it is observed under condition (6.31) that the following is obtained:

$$Df_{\gamma_2}(F_2,\gamma_2^*)V^{[2]} = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \bar{z} \end{pmatrix} \begin{pmatrix} v_1^{[2]} \\ v_2^{[2]} \\ v_3^{[2]} \\ v_4^{[2]} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ 0 \\ \bar{z}v_4^{[2]} \end{pmatrix}$$

$$\begin{aligned} (\psi^{[2]})^T \Big[Df_{\gamma_2}(F_2,\gamma_2^*)V^{[2]}\Big] &= \Big(0,0,0,\psi_4^{[2]}\Big)\Big(0,0,0,\bar{z}v_4^{[2]}\Big)^T \\ &= \psi_4^{[2]}\bar{z}v_4^{[2]} \neq 0. \end{aligned}$$

Now, by substituting in (6.28) it is found that

$$D^2 f\big(F_2,\gamma_2^*\big)\big(V^{[2]},V^{[2]}\big) \begin{bmatrix} -2v_1^{[2]}\left(\frac{r\left(v_1^{[2]}\right)}{k} + \beta_1 v_3^{[2]} + \alpha_1 v_4^{[2]}\right) \\ \frac{-2s\left(v_2^{[2]}\right)^2}{l} \\ 2v_3^{[2]}\left(\beta_2 v_1^{[2]} - \gamma_1 v_4^{[2]}\right) \\ 2v_4^{[2]}\left(\alpha_2 v_1^{[2]} + \gamma_2^* v_3^{[2]}\right) \end{bmatrix}$$

Hence, according to condition (6.31)

$$\big(\psi^{[2]}\big)^T\big[D^2 f(F_2,\gamma_2^*)\big(V^{[2]},V^{[2]}\big)\big] = 2v_4^{[2]}\Big(\alpha_2 v_1^{[2]} + \gamma_2^* v_3^{[2]}\Big)\psi_4^{[2]} \neq 0.$$

This means the second condition of transcritical bifurcation is satisfied. Thus, according to Sotomayor's theorem, system (6.1) has transcritical bifurcation at F_2 with the parameter $\gamma_2 = \gamma_2^*$. ■

Theorem 6.9.4 *Suppose that*

$$\beta_2 v_1^{[3]} \neq \gamma_1 v_4^{[3]}. \tag{6.32}$$

Then, for the parameter value $\gamma_1^* = \dfrac{\beta_2\dot{x} - \beta_0}{\dot{w}}$*, system (6.1), at the equilibrium point* F_3*, has transcritical bifurcation.*

Proof According to the Jacobian matrix $J(F_3)$, given by (6.22), system (6.1), at the equilibrium point F_3, has a zero eigenvalue, say λ_{33}, at $\gamma_1 = \gamma_1^*$ and this matrix becomes

$$J^*(F_3) = \begin{bmatrix} r - \sigma_1 - \frac{2r\dot{x}}{k} - \gamma_1\dot{w} & \sigma_2 & -\beta_1\dot{x} & -\alpha_1\dot{x} \\ \sigma_1 & s - \sigma_2 - \frac{2s\dot{y}}{l} & 0 & 0 \\ 0 & 0 & 0 & 0 \\ \alpha_2\dot{w} & 0 & \gamma_2\dot{w} & 0 \end{bmatrix}$$

Now, suppose that $V^{[3]} = \left(v_1^{[3]}, v_2^{[3]}, v_3^{[3]}, v_4^{[3]}\right)^T$ is an eigenvector corresponding to the eigenvalue λ_{33}. Thus, $\big(J^*(F_3) - \lambda_{33}I\big)V^{[3]} = 0$, which implies:

$$\begin{aligned} v_2^{[3]} &= \frac{\sigma_1 l v_1^{[3]}}{2s\dot{y} - (s - \sigma_2)l}, \\ v_3^{[3]} &= \frac{-\alpha_2 v_1^{[3]}}{\gamma_2}, \\ v_4^{[3]} &= \left(\frac{\Big[(s-\sigma_2)l - 2s\dot{y}\Big]\Big((rk - 2r\dot{x} - \sigma_1 k)\gamma_2 + k\alpha_2\beta_1\dot{x}\Big) - \sigma_1\sigma_2 kl\gamma_2}{k\gamma_2(2s\dot{y} - (s-\sigma_2)l)}\right)v_1^{[3]}, \end{aligned}$$

where, $v_1^{[3]}$ is any non-zero real number and $\big[2s\dot{y} - (s - \sigma_2)l\big] \neq 0$. Then, let $\psi^{[3]} = \big(\psi_1^{[3]}, \psi_2^{[3]}, \psi_3^{[3]}, \psi_4^{[3]}\big)^T$ be an eigenvector associated with the eigenvalue λ_{33} of the matrix $(J^*(F_3))^T$. So, $\big((J^*(F_3))^T - \lambda_{33}I\big)\psi^{[3]} = 0$ and by solving this equation for $\psi^{[3]}$, $\psi_1^{[3]} = \psi_2^{[3]} = \psi_4^{[3]} = 0$ is the result, where $\psi_3^{[3]}$ is any non-zero real number.

Now, to confirm that the conditions of Sotomayor's theorem for transcritical bifurcation are satisfied, the following is considered:

$$\frac{\partial f}{\partial \gamma_1} = f'_{\gamma_1}(X, \gamma_1) = \left(\frac{\partial f_1}{\partial \gamma_1}, \frac{\partial f_2}{\partial \gamma_1}, \frac{\partial f_3}{\partial \gamma_1}, \frac{\partial f_4}{\partial \gamma_1}\right)^T = (0, 0, -zw, 0)^T.$$

Therefore, $f'_{\gamma_1}(F_3,\gamma_1^*) = (0,0,0,0)^T$ and hence, $(\psi^{[3]})^T f'_{\gamma 1}(F_3,\gamma_1^*) = 0$. So, according to Sotomayor's theorem, saddle-node bifurcation cannot occur, while the first condition of transcritical bifurcation is satisfied. Now,

$$Df_{\gamma_1}(X,\gamma_1) = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & -w & -z \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

where, $Df_{\gamma_1}(X,\gamma_1)$ represent the derivative of $f_{\gamma_1}(X,\gamma_1)$ with respect to $X = (x,y,z,w)^T$. Further, it is observed under condition (6.32) that the following is obtained:

$$Df_{\gamma_1}(F_3,\gamma_1^*)V^{[3]} = \begin{pmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & -\dot{w} & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} v_1^{[3]} \\ v_2^{[3]} \\ v_3^{[3]} \\ v_4^{[3]} \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ -\dot{w}v_3^{[3]} \\ 0 \end{pmatrix}$$

$$\begin{aligned} (\psi^{[3]})^T\Big[Df_{\gamma_1}(F_3,\gamma_1^*)V^{[3]}\Big] &= \Big(0,0,\psi_3^{[3]},0\Big)\Big(0,0,-\dot{w}v_3^{[3]},0\Big)^T \\ &= -\dot{w}\psi_3^{[3]}v_3^{[3]} \neq 0. \end{aligned}$$

Now, by substituting in (6.28) and according to condition (6.32), it is found that

$$\big(\psi^{[3]}\big)^T\big[D^2f(F_3,\gamma_1^*)\big(V^{[3]},V^{[3]}\big)\big] = 2v_3^{[3]}\Big(\beta_2 v_1^{[3]} - \gamma_1^* v_4^{[3]}\Big)\psi_3^{[3]} \neq 0.$$

This means the second condition of transcritical bifurcation is satisfied. Thus, according to Sotomayor's theorem, system (6.1) has transcritical bifurcation at F_3 with the parameter $\gamma_1 = \gamma_1^*$. ■

Theorem 6.9.5 *Suppose that*

$$\big(\psi^{[4]}\big)^T\big[D^2f(F_4,\gamma_2^*)\big(V^{[4]},V^{[4]}\big)\big] \neq 0. \tag{6.33}$$

Then, for the parameter value $\gamma_2^* = \dfrac{a_{22}M_4}{a_{34}M_2w^*}$, *system (6.1), at the equilibrium point* F_4, *has saddle-node bifurcation.*

Proof According to the Jacobian matrix $J(F_4)$, given by (6.23), system (6.1), at the equilibrium point F_4, has a zero eigenvalue, say λ_{44}, at $\gamma_2 = \gamma_2^*$ and this matrix becomes

$$J^*(F_4) = \begin{bmatrix} r - \sigma_1 - \frac{2rx^*}{k} - \beta_1 z^* - \gamma_1 w^* & \sigma_2 & -\beta_1 x^* & -\alpha_1 x^* \\ \sigma_1 & s - \sigma_2 - \frac{2sy^*}{l} & 0 & 0 \\ \beta_2 z^* & 0 & 0 & -\gamma_1 z^* \\ \alpha_2 w^* & 0 & \gamma_2^* w^* & 0 \end{bmatrix}$$

Now, suppose that $V^{[4]} = \left(v_1^{[4]}, v_2^{[4]}, v_3^{[4]}, v_4^{[4]}\right)^T$ is an eigenvector corresponding to the eigenvalue λ_{44}. Thus, $\big(J^*(F_4) - \lambda_{44} I\big)V^{[4]} = 0$, which implies

$$\begin{aligned} v_2^{[4]} &= \frac{-\sigma_1 l v_1^{[4]}}{(s-\sigma_2)l - 2sy^*}, \\ v_3^{[4]} &= \frac{-\alpha_2 v_1^{[4]}}{\gamma_2}, \\ v_4^{[4]} &= \frac{\beta_2 v_1^{[4]}}{\gamma_1}, \end{aligned}$$

where, $v_1^{[4]}$ is any non-zero real number and $(s-\sigma_2)l - 2sy^* \neq 0$. Then, let $\psi^{[4]} = \big(\psi_1^{[4]}, \psi_2^{[4]}, \psi_3^{[4]}, \psi_4^{[4]}\big)^T$ be an eigenvector associated with the eigenvalue λ_{44} of the matrix $(J^*(F_4))^T$. So, $\big((J^*(F_4))^T - \lambda_{44} I\big)\psi^{[4]} = 0$ and by solving this equation for $\psi^{[4]}$,

$$\begin{aligned} \psi_2^{[4]} &= \frac{-\sigma_2 l \psi_1^{[4]}}{(s-\sigma_2)l - 2sy^*}, \\ \psi_3^{[4]} &= \frac{-\alpha_1 x^* \psi_1^{[4]}}{\gamma_1 z^*}, \\ \psi_4^{[4]} &= \frac{\beta_1 x^* \psi_1^{[4]}}{\gamma_2 w^*}, \end{aligned}$$

is obtained, where $\psi_1^{[4]}$ is any non-zero real number.

Now, to confirm that the conditions of Sotomayor's theorem for saddle-node bifurcation are satisfied, the following is considered:

$$\frac{\partial f}{\partial \gamma_2} = f'_{\gamma_2}(X, \gamma_2) = \left(\frac{\partial f_1}{\partial \gamma_2}, \frac{\partial f_2}{\partial \gamma_2}, \frac{\partial f_3}{\partial \gamma_2}, \frac{\partial f_4}{\partial \gamma_2}\right)^T = (0, 0, zw, 0)^T.$$

Therefore, $f'_{\gamma_2}(F_4,\gamma_2^*) = (0,0,z^*w^*,0)^T$ and hence,

$(\psi^{[4]})^T f'_{\gamma 2}(F_4,\gamma_2^*) = z^*w^*\psi_3^{[4]} \neq 0$. So, according to Sotomayor's theorem, transcritical bifurcation cannot occur, while the first condition of saddle-node bifurcation is satisfied. Further, it is observed under condition (6.33) that the following is obtained:

$$\begin{aligned}\left(\psi^{[4]}\right)^T\left[D^2 f(F_4,\gamma_2^*)\left(V^{[4]},V^{[4]}\right)\right] &= -2v_1^{[4]}\psi_1^{[4]}\left(\tfrac{r}{k}v_1^{[4]}+\beta_1 v_3^{[4]}+\alpha_1 v_4^{[4]}\right) \quad -\left[\frac{2s(v_2^{[4]})^2\psi_2^{[4]}}{l}\right]\\ &+2v_3^{[4]}\psi_3^{[4]}\left(\beta_2 v_1^{[4]}-\gamma_1^* v_4^{[4]}\right)+2v_4^{[4]}\psi_4^{[4]}\left(\alpha_2 v_1^{[4]}+\gamma_2^* v_3^{[4]}\right)\neq 0.\end{aligned}$$

This means the second condition of saddle-node bifurcation is satisfied. Thus, according to Sotomayor's theorem, system (6.1) has saddle-node bifurcation at F_4 with the parameter $\gamma_2 = \gamma_2^*$. ■

6.10 The Hopf bifurcation analysis

In this section, the conditions for the Jacobian matrix that a simple Hopf bifurcation for a dynamical system (6.1) occurs, are presented. In the following theorems, an application of Haque and Venturino methods for Hopf bifurcation is adapted (see Subsubsection 2.3.10.1).

6.10.1 The Hopf bifurcation analysis near $F_i(i = 0,1,2,3)$

According to the Jacobian matrices of system (6.1) at $F_i,(i = 0,1,2,3)$, given by (4.21), (6.14), (6.20) and (6.22), all the eigenvalues of $J(F_i),(i = 0,1,2,3)$ have negative real parts at the equilibrium point F_i. Therefore, there is no possibility for Hopf bifurcation to occur at this points.

The possibility of Hopf bifurcation to occur near F_4 is discussed in the next theorem.

6.10.2 The Hopf bifurcation analysis near the positive equilibrium point

Theorem 6.10.1 *Suppose that the following conditions are satisfied*

$$A_3 \quad > 0, \tag{6.34}$$

$$\Delta_1 \quad = A_1A_2 - A_3 > 0, \tag{6.35}$$

$$\Delta_2 \quad = \big(A_1A_2 - A_3\big)A_3 - A_4A_1^2 = 0, \tag{6.36}$$

$$\gamma_2^* \quad > 0, \tag{6.37}$$

where A_i's are given in the proof of the lemma 18 and the formula of γ_2^* is given in the following proof. Then, system (6.1) has a Hopf bifurcation at $\gamma_2 = \gamma_2^*$ for F_4.

Proof Consider the characteristic equation of the system (6.1) at F_4 which is given by Eq.(6.24). Now, to verify the necessary and sufficient conditions for a Hopf bifurcation to occur, we need to find a parameter sush that $\Delta_2 = 0$ is satisfied. It is observed that $\Delta_2 = 0$ gives:

$$\gamma_2^* = \frac{\Big(a_{22}M_3 + M_4\Big)\Big(a_{11}a_{14}a_{41} + a_{11}a_{13}a_{31} - M_1M_2 - M_4\Big)}{\gamma_1 z^* w^*\Big(a_{11}M_4 - a_{11}^2\big(a_{14}a_{41} + a_{13}a_{31}\big) - a_{22}M_1(M_2 - M_1)\Big)}.$$

Clearly, $\gamma_2^* > 0$ provided that the condition (6.37) holds. Now, at $\gamma_2 = \gamma_2^*$ the characteristic equation given by Eq.(6.24) can be written as

$$\left(\lambda_4^2 + \frac{A_3}{A_1}\right)\left(\lambda_4^2 + A_1\lambda_4 + \frac{\Delta_1}{A_1}\right) = 0, \tag{6.38}$$

which has four roots

$$\lambda_{4_{1,2}} = \pm i\sqrt{\frac{A_3}{A_1}}, \lambda_{4_{3,4}} = \frac{1}{2}\ \Bigg(\ -A_1 \pm \sqrt{A_1^2 - 4\frac{\Delta_1}{A_1}}\ \Bigg)\ .$$

Clearly, at $\gamma_2 = \gamma_2^*$ there are two purely imaginary eigenvalues λ_{41} and λ_{42} and two eigenvalues λ_{43} and λ_{44} which have negative real parts. Now for all values of γ_2 in the neighborhood of γ_2^*, the roots in general have the following forms:

$$\lambda_{4_{1,2}} = \alpha_1 \pm i\alpha_2, \lambda_{4_{3,4}} = \frac{1}{2}\ \Bigg(\ -A_1 \pm \sqrt{A_1^2 - 4\frac{\Delta_1}{A_1}}\ \Bigg)\ .$$

Clearly, Re$(\lambda_{4_{1,2}})|_{\gamma_2=\gamma_2^*} = \alpha_1(\gamma_2^*) = 0$ that means the first condition of the necessary and sufficient conditions for Hopf bifurcation is satisfied at $\gamma_2 = \gamma_2^*$. Now to verify the transversality condition we substitute $\alpha_1 \pm i\alpha_2$ into Eq.(6.38), and then calculate its derivative with respect to the bifurcation parameter γ_2^*, $\bar{\Theta}\,(\gamma_2^*)\ \bar{\Psi}\,(\gamma_2^*) + \bar{\Gamma}\,(\gamma_2^*)\ \bar{\Phi}\,(\gamma_2^*) \neq 0$, where the form of $\bar{\Theta}$, $\bar{\Psi}$, $\bar{\Gamma}$ and $\bar{\Phi}$ are given in Subsubsection 2.3.10.1. Note that for $\gamma_2 = \gamma_2^*$, we have $\alpha_1 = 0$ and $\alpha_2 = \sqrt{\frac{A_3}{A_1}}$, substitution into gives the following simplifications:

$$\begin{aligned}
\bar{\Psi}\,(\gamma_2^*) &= -2A_3(\gamma_2^*);\\
\bar{\Phi}\,(\gamma_2^*) &= \frac{2\alpha_2(\gamma_2^*)}{A_1(\gamma_2^*)}\Bigg(\ A_1(\gamma_2^*)A_2(\gamma_2^*) - 2A_3(\gamma_2^*)\ \Bigg);\\
\bar{\Theta}\,(\gamma_2^*) &= A_4^{'}(\gamma_2^*) - \Bigg(\ \frac{A_3(\gamma_2^*)A_2^{'}(\gamma_2^*)}{A_1(\gamma_2^*)}\ \Bigg);\\
\bar{\Gamma}\,(\gamma_2^*) &= \alpha_2(\gamma_2^*)A_3^{'}(\gamma_2^*),
\end{aligned}$$

where,

$$\begin{aligned}
A_1^{'}(\gamma_2^*) &= 0;\\
A_2^{'}(\gamma_2^*) &= \gamma_1 z^* w^*;\\
A_3^{'}(\gamma_2^*) &= \Bigg(\ a_{34}M_1 - a_{14}a_{31}\ \Bigg)\ w^*;\\
A_4^{'}(\gamma_2^*) &= \Bigg(\ a_{22}a_{14}a_{31} - a_{34}M_2\ \Bigg)\ w^*.
\end{aligned}$$

Hence,

$$\begin{aligned}
\bar{\Theta}\,(\gamma_2^*)\ \bar{\Psi}\,(\gamma_2^*) + \bar{\Gamma}\,(\gamma_2^*)\ \bar{\Phi}\,(\gamma_2^*) &= \Bigg(\ \Big(a_{22}a_{14}a_{31} - a_{34}M_2 + \tfrac{a_{34}A_3(\gamma_2^*)}{A_1(\gamma_2^*)}\Big)\Big(-2A_3(\gamma_2^*)w^*\Big)\ \Bigg)\\
&+ \Bigg(\ \tfrac{2\alpha_2^2(\gamma_2^*)w^*}{A_1(\gamma_2^*)}\ \Bigg)\ \Big(a_{34}M_1 - a_{14}a_{31}\Big)\Big(A_1(\gamma_2^*)A_2(\gamma_2^*) - 2A_3(\gamma_2^*)\Big) \neq 0.
\end{aligned}$$

This means that Hopf bifurcation has occurred. ■

6.11 Numerical analysis

The main goal of this section is to find the key parameters of the system (6.1) that affects the behaviour of the proposed model by using numerical simulations.

The dynamics of the system (6.1) is presented by solving the system numerically and then drawing the time series of the solutions of the system (6.1) for different sets of parameters.

Now, for the following set of parameters:

$$\begin{aligned}&r=2, k=50, \sigma_1=0.4, \sigma_2=0.7, \beta_1=0.5, \beta_2=0.3, \beta_0=0.01,\\&s=1.4, l=40, \alpha=0.25, \gamma_1=0.05, \gamma_2=0.01, \alpha_1=0.1, \alpha_2=0.05,\end{aligned} \tag{6.39}$$

the conditions that have been stated in lemma 18 are satisfied. This shows that the positive equilibrium point F_4 exists, and it is given by:

$$(x^*, y^*, z^*, w^*) = (2.15, 21.16, 14.21, 12.74).$$

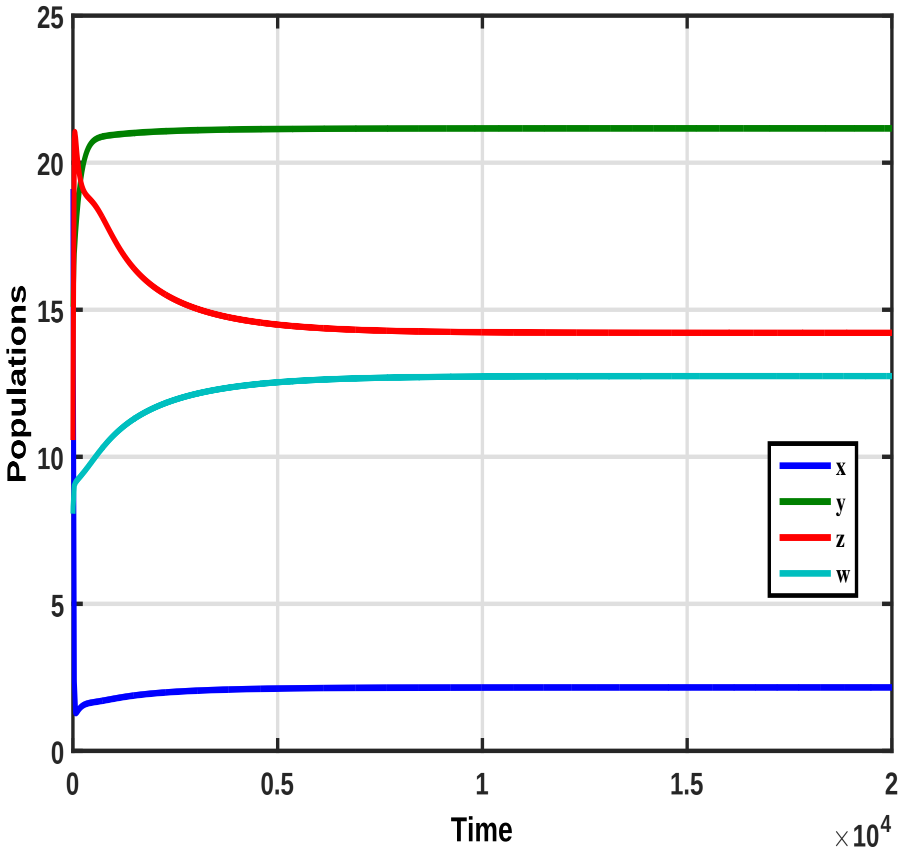

Fig. 6.1. Convergence of the solution of the system (6.1) to the positive equilibrium point with the data given by Eq.(6.39).

Figure 6.1, indicates that the solution of the system (6.1) oscillates for some small period and then, in the long-time limit, it asymptotically approaches the positive equilibrium point.

Now, to investigate the effect of the varying parameter values on the behaviour of the system (6.1), the model has been solved numerically for the data given in Eq.(6.39), varying one parameter each time, as:

6.11.1 The effect of varying the migration rate of the prey to the reserved area

Figure 6.2 shows the effect of migration to the reserved area, which is described by the parameter σ_1, on the behaviour of the system (6.1) with time. It is observed that for different values of σ_1, the solution initially oscillates for a small period and then, asymptotically approaches its equilibrium level in the interior of $\mathbb{R}^4_+$. As the result of rising migration rate to the protected area, it can be seen that the density of the prey in the reserved zone increases. On the other hand, the populations of the generalist predator and the prey in the unreserved area decrease, while the third component has slightly increased.

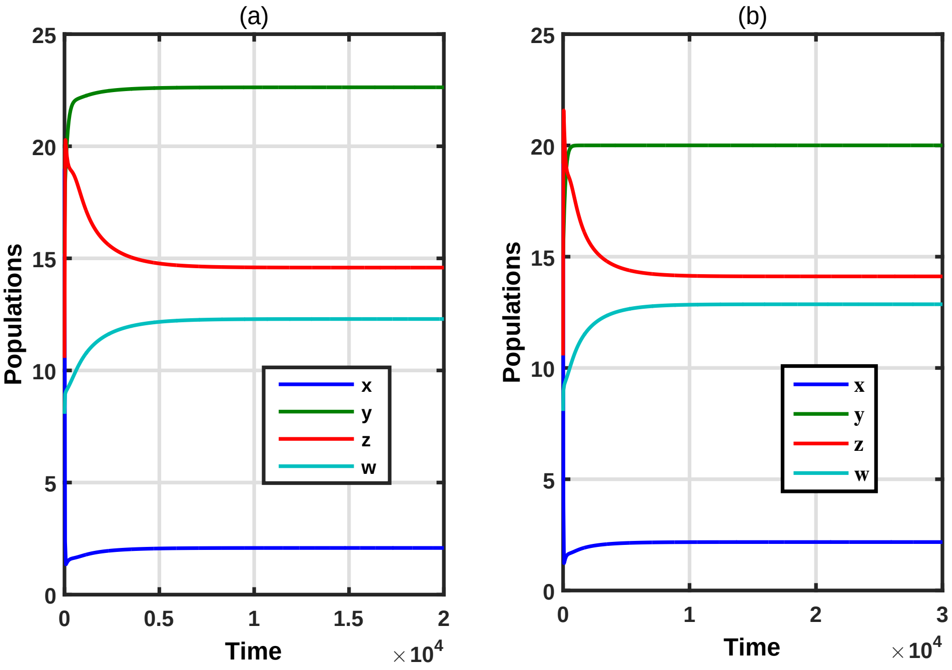

Fig. 6.2. Convergence of the solution of the system (6.1) for the data given by Eq.(6.39) with (a) $\sigma_1 = 1$ to the stable point (2.08,22.62,14.58,12.29) in the interior of $\mathbb{R}^4_+$, (b) $\sigma_1 = 0.001$ to the stable point (2.17,20,14.11,12.86) in the interior of $\mathbb{R}^4_+$.

6.11.2 The effect of varying the natural death rate of the specialist predator

Now the same analysis is used for different values of the specialist predator's natural mortality, which is described by the parameter β_0, and the rest of the parameter values are kept the same as in Eq.(6.39). Figure 6.3 shows that for various values of β_0, the solution initially oscillates for a while and then it settles down to its equilibrium level. Furthermore, the specialist predator species z remains strictly positive for $\beta_0 \leq 0.160$, while it becomes zero for $\beta_0 = 0.161$. Hence, the system (6.1) loses its persistence, and the chain is broken. Due to the increase of the specialist predator's natural death-rate, the densities of the prey in the unreserved area and the generalist predator increase significantly. This means an abundance of the prey in an unprotected area and hence, the food conversion rate of the prey to the generalist predator increases (and vice versa). On the other hand, the prey in the private zone is slightly affected.

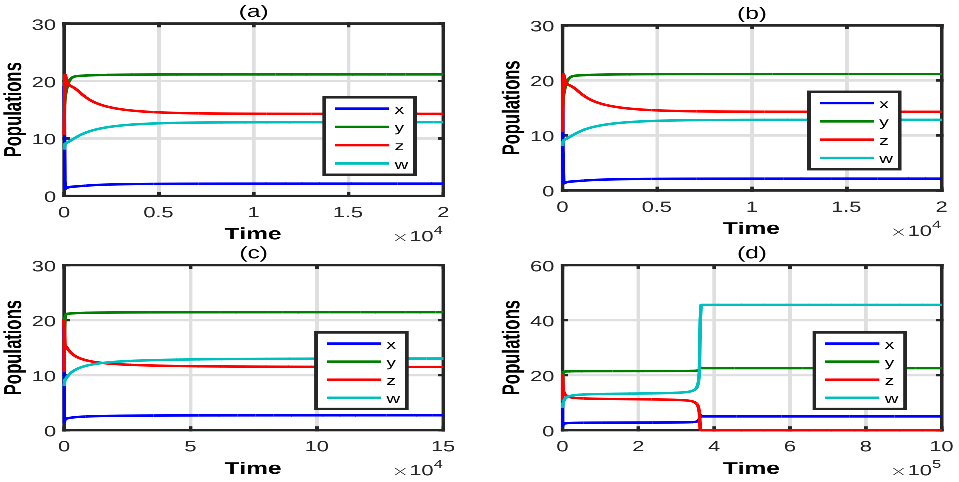

Fig. 6.3. Convergence of the solution of the system (6.1) for the data given by Eq.(6.39) with (a) $\beta_0 = 0.001$ to the stable point (2.14, 21.55, 14.28, 12.83) in the interior of $\mathbb{R}^4_+$, (b) $\beta_0 = 0.0001$ to the stable point (2.14, 21.15, 14.29, 12.84) in the interior of $\mathbb{R}^4_+$, (c) $\beta_0 = 0.16$ to the stable point (2.7, 21.44, 11.47, 13) in the interior of $\mathbb{R}^4_+$, (d) $\beta_0 = 0.161$ to the stable point (5, 22.53, 0, 45.54) in the interior of $\mathbb{R}^3_+$.

6.11.3 The effect of varying the natural death rate of the generalist predator

The effect of varying α, which represents the top predator's natural death-rate, on the behaviour of the system (6.1), is also studied. From Figure 6.4, the following results can be observed. For various values of α, the solution starts to oscillate for a particular time and then, attains the equilibrium level. Furthermore, the specialist predator species z remains strictly positive for $\alpha \geq 0.25$, while it becomes zero for $\alpha = 0.24$. Hence, the system (6.1) loses its persistence, and the chain is broken. Due to the decrease of the generalist predator's natural death-rate, the densities of the prey in the reserved, unreserved area and the generalist predator increases significantly. This means an abundance of the prey in an unprotected area and hence, the food conversion rate of the prey to the generalist predator increases (and vice versa). Furthermore, the migration rate to the reserved zone is also affected, which also showes an abundance of prey in the protected area.

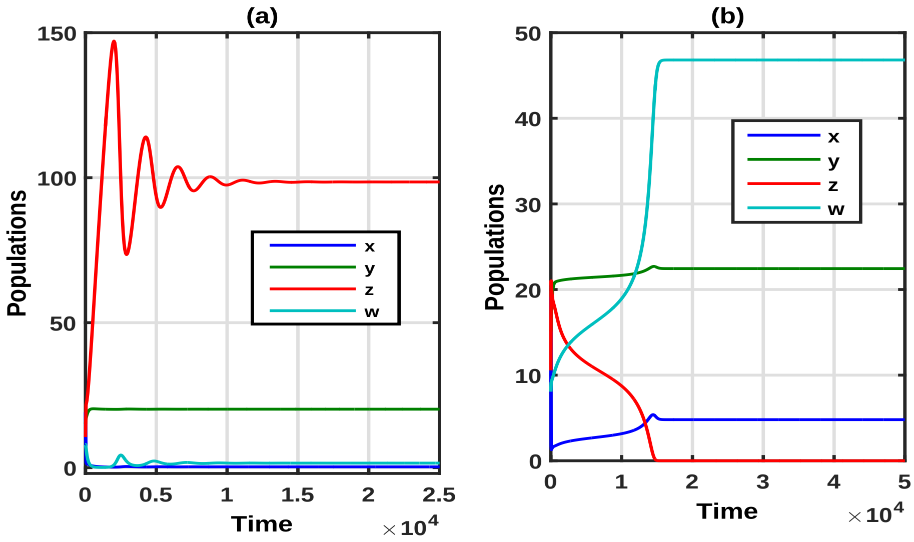

Fig. 6.4. Convergence of the solution of the system (6.1) for the data given by Eq.(6.39) with (a) $\alpha = 1$ to the stable point (0.29, 20.16, 98.52, 1.57) in the interior of $\mathbb{R}^4_+$, (b) $\alpha = 0.24$ to the stable point (4.8, 22.44, 0, 56.81) in the interior of $\mathbb{R}^3_+$.

6.11.4 The effect of varying the attack rate of the generalist predator on the specialist predator

Figure 6.5 illustrates the effect of the generalist predator's attack rate on the specialist predator, which is described by the parameter γ_1, in terms of the behaviour of the system (6.1) versus time. It can be noticed that for various values of γ_1, the solution initially oscillates, and after a specific time it attains its equilibrium level. Also, the specialist predator species z remains strictly positive for $\gamma_1 \leq 0.061$, while it becomes zero for $\gamma_1 = 0.062$. Hence, the system (6.1) loses its persistence, and the chain is broken. On the other hand, the system (6.1) persists when decreasing γ_1. Further, the density of the generalist predator rapidly increases, which means that the food conversion rate to the latter increases. Hence, the system (6.1) loses its persistence and the chain is broken.

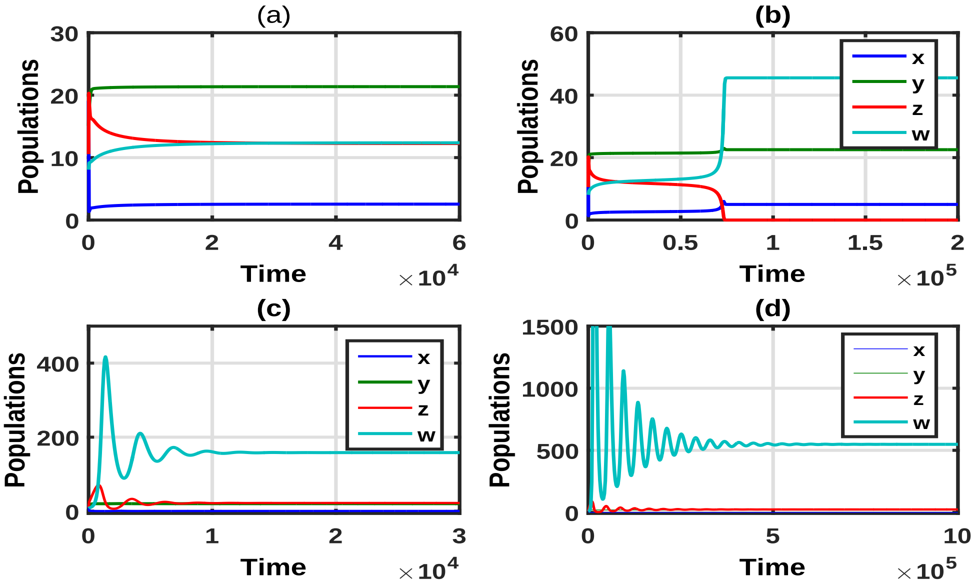

Fig. 6.5. Convergence of the solution of the system (6.1) for the data given by Eq.(6.39) with (a) $\gamma_1 = 0.061$ to the stable point (2.54, 21.36, 12.25, 12.37) in the interior of $\mathbb{R}^4_+$, (b) $\gamma_1 = 0.062$ to the stable point (5, 22.53, 0, 45.54) in the interior of $\mathbb{R}^3_+$, (c) $\gamma_1 = 0.001$ to the stable point (0.56, 20.31, 22.19, 158.29) in the interior of $\mathbb{R}^4_+$, (d) $\gamma_1 = 0.0001$ to the stable point (0.23, 20.1, 23.78, 530.24) in the interior of $\mathbb{R}^4_+$.

6.11.5 The effect of varying the conversion rate of the specialist predator to the generalist predator

Now, Figure 6.6 studies the impact of the conversion rate of the specialist predator to the generalist predator γ_2, on the behaviour of the species with t. When varying γ_2 and keeping the other parameters in Eq.(6.39) fixed, it can be observed that the solution of system (6.1) converges to the equilibrium point after oscillating for a certain amount of time. Further, the w-component of the equilibrium point is strictly positive for $\gamma_2 \geq 0.0099$, but it becomes zero for $\gamma_2 = 0.00010$. On the other hand, the z-component of the equilibrium point is strictly positive for $\gamma_2 \leq 0.01$, but it becomes zero for $\gamma_2 = 0.011$. Hence, the system (6.1) loses its persistence and the chain is broken.

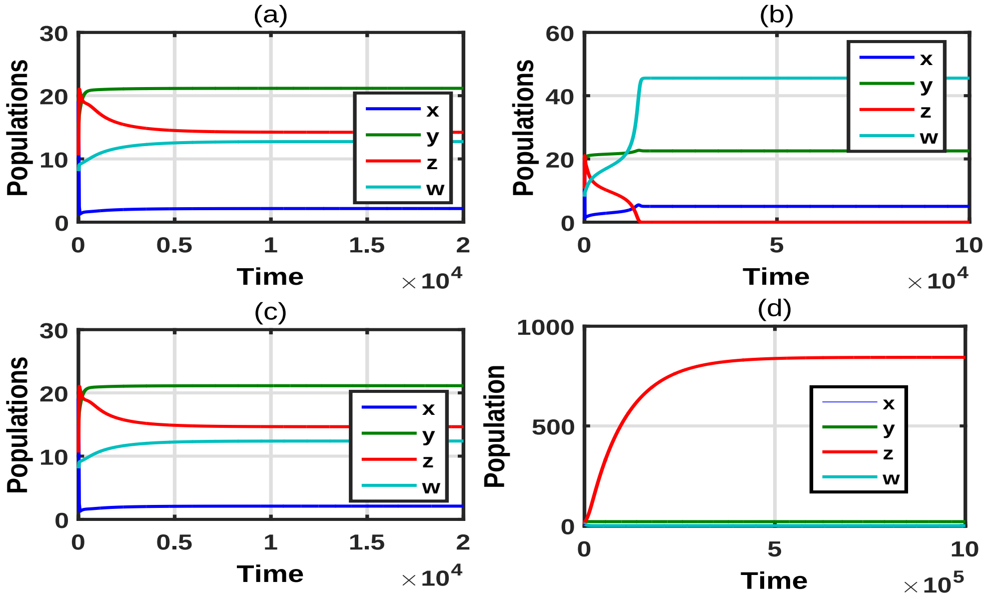

Fig. 6.6. Convergence of the solution of the system (6.1) for the data given by Eq.(6.39) with (a) $\gamma_2 = 0.1$ to the stable point (2.15, 21.16, 14.21, 12.74) in the interior of $\mathbb{R}^4_+$, (b) $\gamma_2 = 0.011$ to the stable point (5, 22.53, 0, 45.54) in the interior of $\mathbb{R}^3_+$, (c) $\gamma_2 = 0.0099$ to the stable point (2.09, 21.13, 14.65, 12.39) in the interior of $\mathbb{R}^4_+$. (d) $\gamma_2 = 0.0001$ to the stable point (0.03, 20.02, 825.28, 0) in the interior of $\mathbb{R}^3_+$.

6.11.6 The effect of varying the unreserved area rate on the species

Similarly, for different values of σ_2, which represent the impact of the unreserved area on the behaviour of the species. When varying σ_2 and keeping the other parameters in (6.39) fixed, the solution of system (6.1) initially fluctuates for some time, and then, it converges to the equilibrium level. Furthermore, the generalist predator species w remains strictly positive for $\sigma_2 \geq 0.09$, while it becomes zero for $\sigma_2 = 0.08$. Hence, the system (6.1) loses its persistence, and the chain is broken (see Figure 6.7). Also, when decreasing σ_2, the density of the prey in unreserved zone decreases, this negatively impacts on the density of the generalist predator. On the other hand, the decrease of σ_2 has positive impact on the density of the prey in the reserved area.

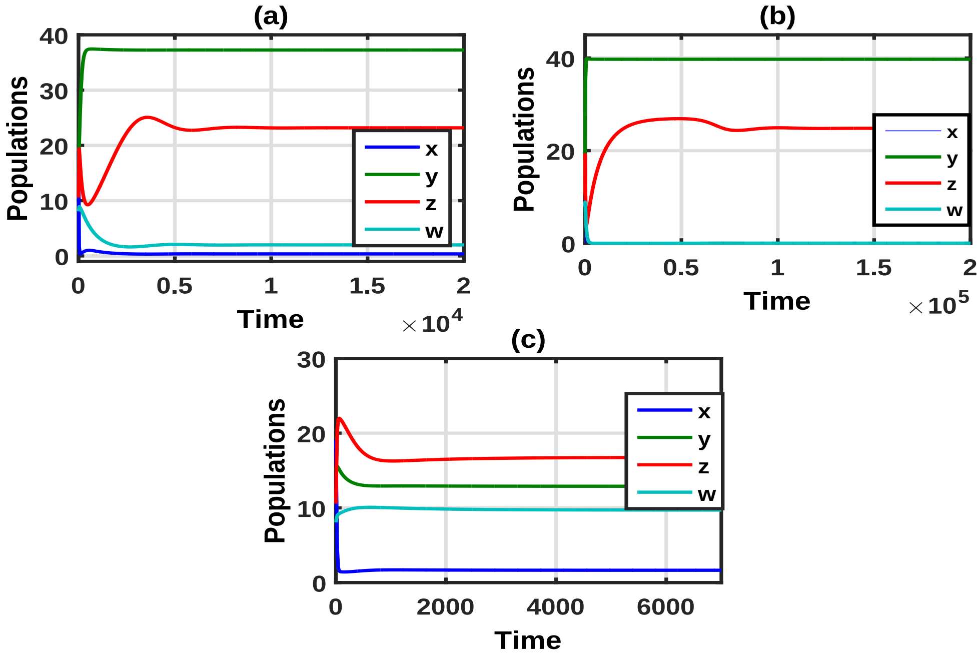

Fig. 6.7. Convergence of the solution of the system (6.1) for the data given by Eq.(6.39) with (a) $\sigma_2 = 0.09$ to the stable point (0.36, 37.25, 23.17, 1.9) in the interior of $\mathbb{R}^4_+$, (b) $\sigma_2 = 0.08$ to the stable point (0.03, 39.72, 26.59, 0) in the interior of $\mathbb{R}^3_+$, (c) $\sigma_2 = 1$ to the stable point (1.6, 12.89, 16.74, 9.7) in the interior of $\mathbb{R}^4_+$.

6.11.7 The effect of varying the attack rate of the specialist predator on the prey in the unreserve zone

Figure 6.8 shows the behaviour of the solution of system (6.1) with different β_1, which represent the attack rate of the specialist predator on the prey in the unreserve zone. For varying β_1, the solution of system (6.1) converges to the equilibrium level after oscillating for a certain amount of time. In this case, the z-component of the equilibrium point is strictly positive for $\beta_1 \geq 0.48$ and hence, system (6.1) persists. While, it becomes zero for $\beta_1 = 0.47$, hence, the system (6.1) loses its persistence and the chain is broken. On the other hand, the decrease of β_1 has positive impact on the densities of the prey in the unreserved area and the generalist predator.

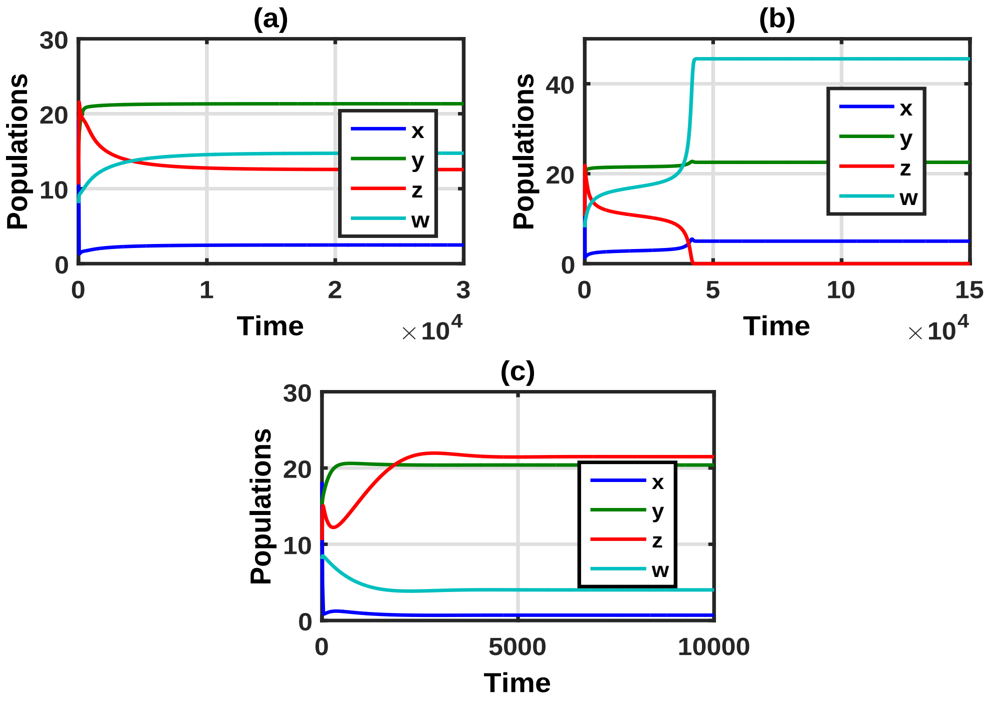

Fig. 6.8. Convergence of the solution of the system (6.1) for the data given by Eq.(6.39) with (a) $\beta_1 = 0.48$ to the stable point (2.48, 21.33, 12.55, 14.73) in the interior of $\mathbb{R}^4_+$, (b) $\beta_1 = 0.47$ to the stable point (5, 22.53, 0, 45.54) in the interior of $\mathbb{R}^3_+$, (c) $\beta_1 = 1$ to the stable point (0.7, 20.39, 21.48, 4.01) in the interior of $\mathbb{R}^4_+$.

6.11.8 The effect of varying the conversion rate of the prey in unreserve area to the specialist predator

Now, Figure 6.9 studies the impact of the conversion rate of the prey in unreserve area to the specialist predator β_2, on the behaviour of the species with t. When varying β_2 and keeping the other parameters in Eq.(6.39) fixed, it is observed that the solution initially oscillates for a small period and then, asymptotically approaches its equilibrium level. It can be observed that the solution of system (6.1) converges to the equilibrium level after oscillating for a certain amount of time. In this case, the z-component of the equilibrium point is strictly positive for $\beta_2 \geq 0.25$, and hence the system (6.1) persists. On the other hand, it becomes zero for $\beta_2 = 0.24$, therefore, the system (6.1) loses its persistence and the chain is broken. On the other hand, the decrease of β_2 has positive impact on the densities of the prey in the reserved and unreserved area as well as the generalist predator.

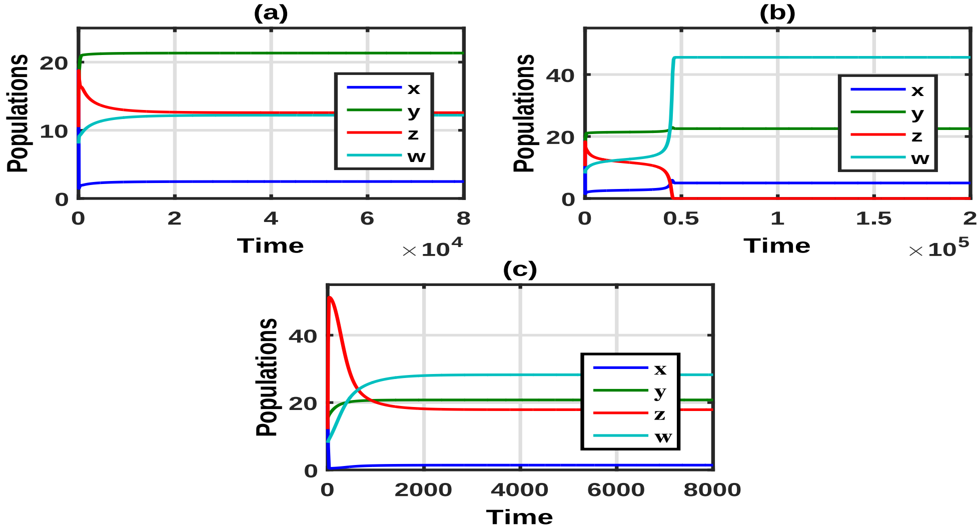

Fig. 6.9. Convergence of the solution of the system (6.1) for the data given by Eq.(6.39) with (a) $\beta_2 = 0.25$ to the stable point (2.48, 21.33, 12.58, 12.21) in the interior of $\mathbb{R}^4_+$, (b) $\beta_2 = 0.24$ to the stable point (5, 22.53, 0, 45.54) in the interior of $\mathbb{R}^3_+$, (c) $\beta_2 = 1$ to the stable point (1.42, 20.78, 17.88, 28.25) in the interior of $\mathbb{R}^4_+$.

6.11.9 The effect of varying the attack rate of the generalist predator on the specialist predator

Figure 6.10 shows the behaviour of the solution of system (6.1) with different α_1, which represent the attack rate of the generalist predator on the specialist predator. For varying α_1, the solution of system (6.1) converges to the equilibrium level after oscillating for a certain amount of time. In this case, the z-component of the equilibrium point is strictly positive for $\alpha_1 \geq 0.01$ and hence, system (6.1) persists. While, it becomes zero for $\alpha_1 = 0.09$, hence, the system (6.1) loses its persistence and the chain is broken. On the other hand, the decrease of α_1 has positive impact on the densities of the prey in the reserved and unreserved area as well as the generalist predator.

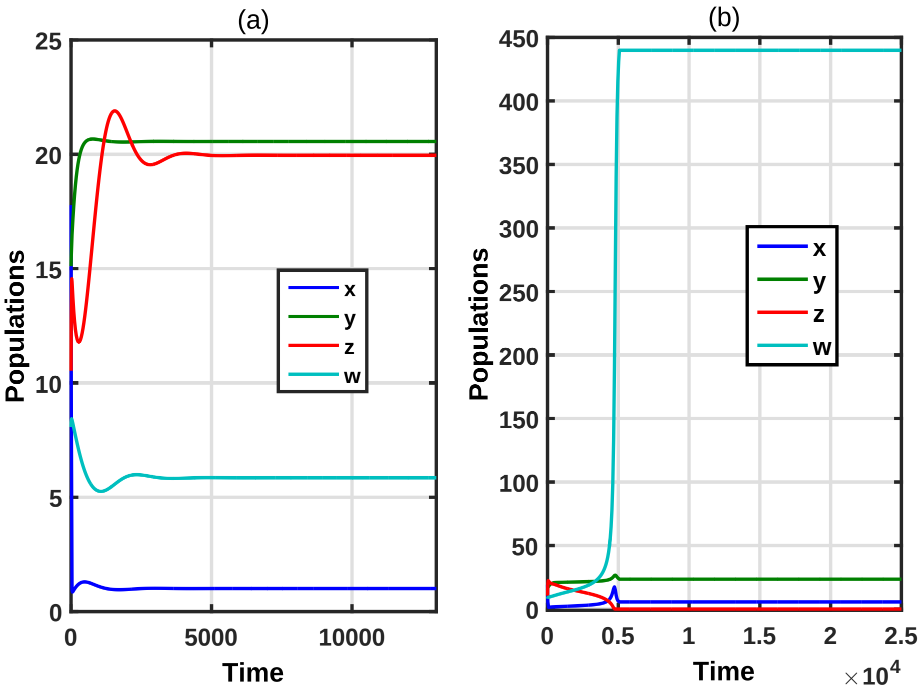

Fig. 6.10. Convergence of the solution of the system (6.1) for the data given by Eq.(6.39) with (a) $\alpha_1 = 1$ to the stable point (1, 20.56, 19.95, 5.85) in the interior of $\mathbb{R}^4_+$, (b) $\alpha_1 = 0.09$ to the stable point (5.61, 23.51, 0, 439.86) in the interior of $\mathbb{R}^3_+$.

6.11.10 The effect of varying the conversion rate of the prey in unreserve area to the generalist predator

Now, Figure 6.11 studies the impact of the conversion rate of the prey in unreserve area to the generalist predator α_2, on the behaviour of the species with t. When varying α_2 and keeping the other parameters in Eq.(6.39) fixed, it can be observed that the solution of system (6.1) converges to the equilibrium level after oscillating for a certain amount of time. In this case, the z-component of the equilibrium point is strictly positive for $\alpha_2 \leq 0.05$, and hence the system (6.1) persists. While, it becomes zero for $\alpha_2 = 0.06$, therefore, the system (6.1) loses its persistence and the chain is broken. On the other hand, the decreasing of α_2 has negatinv impact on the densities of the prey in the unreserved area and the generalist predator.

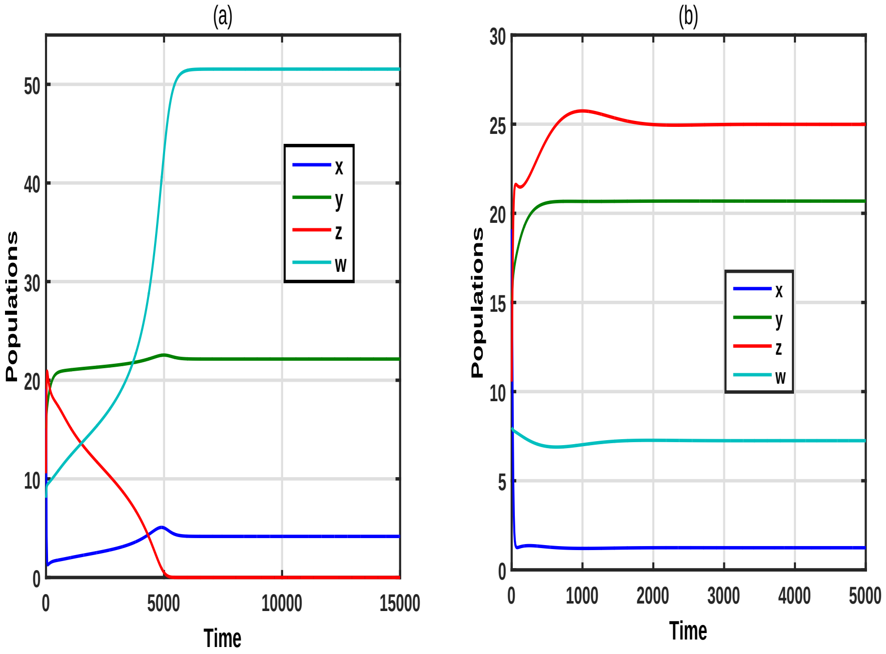

Fig. 6.11. Convergence of the solution of the system (6.1) for the data given by Eq.(6.39) with (a) $\alpha_2 = 0.06$ to the stable point (4.16, 22.14, 0, 51.54) in the interior of $\mathbb{R}^3_+$, (b) $\alpha_2 = 0.0001$ to the stable point (1.24, 20.68, 24.98, 7.24) in the interior of $\mathbb{R}^4_+$.

6.12 Conclusion

An ecological model, which describes the effect of the reserved zone on the dynamical behaviour of a food web prey-predator model with a Lotka-Volterra type of functional response, has been proposed and studied. The boundedness of system (6.1) has been shown, and the possible dynamical behaviour of this system has been investigated analytically at the equilibrium points. The persistence conditions of the proposed system have been derived. It has been proven that the solutions of system (6.1) possess transcritical bifurcation. To confirm the analytical results, system (6.1) has been solved numerically, and the effects of various parameters on the dynamical behaviour of the proposed system have been performed, with the following results being obtained.

1. The persistence of the generalist predator w hinges solely on the parameters σ_2 and γ_2. In particular, if $\sigma_2 = 0.08$, then this species decreases over time, eventually dying out, and the solution of system (6.1) is attained asymptotically to the equilibrium point in $\mathbb{R}^3_+$, while this species survives when $\sigma_2 \geq 0.09$.
2. The existence of the specialist predator z relies solely on the parameters β_1, β_2, β_0, α_1, α_2, α, γ_1 and γ_2. In particular, if $\beta_0 \leq 0.016$ This species decreases over time until it faces extinction, and this causes the chain to break. Hence, the solution of system (6.1) settles down asymptotically to the equilibrium point in $\mathbb{R}^3_+$. Further, this species survives when $\beta_0 = 0.061$.
3. Both the prey species x in the unreserved zone and the prey species y in the reserved area are persistent under all conditions.
4. It is observed that the dynamic behaviour of system (6.1) does not change if the σ_1 is varied.

Overall, the dynamical behaviour of the system with the reserved zone, as shown in this chapter, is found to be sensitive to parameter values and initial data.

Chapter 7: Conclusions and future works

7.1 Summary of the thesis and conclusions

In ecological systems, the coexistence of all species is a vital issue for the management of existing resources and the prediction of the long-term survival of each species. In prey-predator systems, it is well known that the solutions have a periodic dynamics as many publications show in the literature. On the other hand, although the food chain has a simple structure compared with the food web, it has complex dynamics. In order to control the prey population level, three ecological models are proposed and analysed within this thesis. The first model is a food chain predator-prey model with prey refuge in the case when the predator entirely depends on the prey in the protected area, while in the second model, the predator partially depends on the prey. Finally, the third model discusses the food web predator-prey interaction with prey refuge. These models have established that conditions for which the reserved zone can stabilise the predator-prey systems. By using a variety of analytical methods and tools for ordinary differential equations, the following results have been shown:

1. The uniqueness and boundedness of the proposed systems have been shown.
2. The existence and the dynamics around the different equilibrium points have been studied in detail.

3. The long-term behaviour of the systems has been studied, and conditions for persistence have been derived.

4. The possible local bifurcations around the equilibrium points have been studied in detail. In particular, it has been proven that the solutions of the proposed systems possess transcritical bifurcation.

The systems have been solved numerically in MATLAB®, and the effects of various parameters on the dynamical behaviour of the proposed systems have been performed. The models show rich dynamics in the space of non-negative solutions and the following results were obtained.

- In model (4.1), when the predator entirely depends on the first component in the chain, the prey species in the unreserved zone and the prey species in the reserved area are persistent under all conditions. The existence of the top predator hinges solely on the parameters β_2, σ_2 and γ_2. Moreover, the persistence of the predator relies solely on the conversion rate β_2 of the prey in the unreserved zone to the third component in the chain. Furthermore, the positive equilibrium point, whenever it exists, is always globally asymptotically stable. This behaviour shows that the role of the reserved zone has a positive impact on stabilising the dynamics of the food chain predator-prey system.

- In model (5.1), when the predator partially depends on the first component in the chain, the prey species in the unreserved zone, the prey species in the reserved area, the predator and the top predator are persistent under all conditions. This means that an alternative resource for the third component leads to the persistence of all species in the proposed system. Furthermore, the positive equilibrium point, whenever it exists, is always globally asymptotically stable which implies that the influences of the reserved zone can be beneficial for the species' survival.

- In the last model (6.1), when there is a direct connection between the first component in the chain and the third one, the prey species in the unreserved zone and the prey species in the reserved area are persistent under all conditions. The dynamical behaviour is found to be very sensitive to parameter values and initial data, in particular, the existence of the specialist and generalist predators. This shows that the multi-connection between the species can lead to the loss of persistence for some components.

7.2 Suggestions and recommendations for future work

In the next project, the proposed models (4.1), (5.1) and (6.1) can be further extended to investigate the effect of the combination of two different types of functional response on the dynamic behaviour of the food chain and food web prey-predator models with the reserved area. In this case, the new mathematical models can be described as follows:

- In this model, it is assumed that there is a standard Lotka-Volterra functional response between the predator and top predator, and a Holling type-II functional response between the prey in the unreserved zone and the third component in the chain as

$$\begin{aligned}\frac{dx}{dt} &= rx\Big(1-\frac{x}{k}\Big) - \sigma_1 x + \sigma_2 y - \Big(\frac{\beta_1 xz}{\alpha_0 + x}\Big),\\ \frac{dy}{dt} &= sy\Big(1-\frac{y}{l}\Big) + \sigma_1 x - \sigma_2 y,\\ \frac{dz}{dt} &= \Big(\frac{\beta_2 xz}{\alpha_0 + x}\Big) - \beta_0 z - \gamma_1 zw,\\ \frac{dw}{dt} &= \gamma_2 zw - \alpha.\end{aligned}$$

  Here, α_0 represents the half saturation level coefficient and the other parameters are the same as in model (4.1).

- The same combination of functional responses are used for the second model. In this case, model (5.1) can be re-writen as

$$\begin{aligned}
\frac{dx}{dt} &= rx\Big(1-\frac{x}{k}\Big) - \sigma_1 x + \sigma_2 y - \Big(\frac{\beta_1 xz}{\alpha_0 + x}\Big),\\
\frac{dy}{dt} &= sy\Big(1-\frac{y}{l}\Big) + \sigma_1 x - \sigma_2 y,\\
\frac{dz}{dt} &= az\Big(1-\frac{z}{m}\Big) + \Big(\frac{\beta_2 xz}{\alpha_0 + x}\Big) - \beta_0 z - \gamma_1 zw,\\
\frac{dw}{dt} &= \gamma_2 zw - \alpha.
\end{aligned}$$

- In this model, It is assumed that there is a standard Lotka-Volterra functional response between the specialist predator and generalist predator, also between the prey ,in the unreserved zone and a generalist predator. On the other hand, a Holling type-II functional response is assumed between the prey in the unreserved zone and the third component in the web. In this case, (6.1) can be re-writen as

$$\begin{aligned}
\frac{dx}{dt} &= rx\Big(1-\frac{x}{k}\Big) - \sigma_1 x + \sigma_2 y - \Big(\frac{\beta_1 xz}{\alpha_0 + x}\Big) - \alpha_1 xw,\\
\frac{dy}{dt} &= sy\Big(1-\frac{y}{l}\Big) + \sigma_1 x - \sigma_2 y,\\
\frac{dz}{dt} &= \Big(\frac{\beta_2 xz}{\alpha_0 + x}\Big) - \beta_0 z - \gamma_1 zw,\\
\frac{dw}{dt} &= \alpha_2 xw + \gamma_2 zw - \alpha.
\end{aligned}$$

Then we can compare the new results with the once we have drived in this thesis.

LIST OF REFERENCES

LIST OF REFERENCES

[1] R. Sinha, "Unit-2 basic concepts of ecology," IGNOU, 2018.

[2] N. F. Britton, *Essential mathematical biology.* Springer Science & Business Media, 2012.

[3] J. C. Moore, P. C. de Ruiter, K. S. McCann, and V. Wolters, *Food Webs.* Cambridge University Press, 2017.

[4] A. Lotka, "Elements of physical biology: Williams and wilkins company," *Baltimore, Maryland*, 1925.

[5] V. Volterra, *Fluctuations in the abundance of a species considered mathematically.* Nature Publishing Group, 1926.

[6] M. K. A. Gavina, T. Tahara, K.-i. Tainaka, H. Ito, S. Morita, G. Ichinose, T. Okabe, T. Togashi, T. Nagatani, and J. Yoshimura, "Multi-species coexistence in lotka-volterra competitive systems with crowding effects," *Scientific reports*, vol. 8, no. 1, p. 1198, 2018.

[7] Y. Lv and Z. Du, "Existence and global attractivity of a positive periodic solution to a lotka–volterra model with mutual interference and holling iii type functional response," *Nonlinear Analysis: Real World Applications*, vol. 12, no. 6, pp. 3654–3664, 2011.

[8] V. Castellanos and R. E. Chan-López, "Existence of limit cycles in a three level trophic chain with lotka–volterra and holling type ii functional responses," *Chaos, Solitons & Fractals*, vol. 95, pp. 157–167, 2017.

[9] J. Levinton and G. Lopez, "A model of renewable resources and limitation of deposit-feeding benthic populations," *Oecologia*, vol. 31, no. 2, pp. 177–190, 1977.

[10] D. Mukherjee, "Bifurcation and stability analysis of a prey-predator system with a reserved area," *World Journal of Modelling and Simulation*, vol. 8, no. 4, pp. 285–292, 2012.

[11] D. Arrowsmith and C. M. Place, *Dynamical systems: differential equations, maps, and chaotic behaviour*, vol. 5. CRC Press, 1992.

[12] P. Hiver, “Attractor states,” *Motivational dynamics in language learning*, pp. 20–28, 2015.

[13] C. Place, *Dynamical Systems: Differential Equations, Maps, and Chaotic Behaviour*. Routledge, 2017.

[14] E. Knobloch, “Spatial localization in dissipative systems,” *conmatphys*, vol. 6, no. 1, pp. 325–359, 2015.

[15] A. Knauf, “Dynamical systems,” in *Mathematical Physics: Classical Mechanics*, pp. 11–29, Springer, 2018.

[16] K.-P. Hadeler, *Topics in Mathematical Biology*. Springer, 2017.

[17] E. X. DeJesus and C. Kaufman, “Routh-hurwitz criterion in the examination of eigenvalues of a system of nonlinear ordinary differential equations,” *Physical Review A*, vol. 35, no. 12, p. 5288, 1987.

[18] G. Fusco, M. Iannelli, and L. Salvadori, *Advanced Topics in the Theory of Dynamical Systems: Notes and Reports in Mathematics in Science and Engineering*, vol. 6. Elsevier, 2016.

[19] S. Wiggins, *Introduction to applied nonlinear dynamical systems and chaos*, vol. 2. Springer Science & Business Media, 2003.

[20] P. Hartman, *Ordinary differential equations*. SIAM, 2002.

[21] V. Lakshmikantham, S. Leela, and A. A. Martynyuk, *Stability analysis of nonlinear systems*. Springer, 1989.

[22] M. Hirsch, “S. smale differential equations,” *Dynamical Systems and Linear Algebra, Academic Press, New York*, 1974.

[23] J. P. LaSalle, “Stability theory for ordinary differential equations,” *Journal of Differential Equations*, vol. 4, no. 1, pp. 57–65, 1968.

[24] G. F. Simmons, *Differential equations with applications and historical notes*. CRC Press, 2016.

[25] A. Seidman, *College student retention: Formula for student success*. Greenwood Publishing Group, 2005.

[26] H. Freedman and P. Waltman, “Persistence in models of three interacting predator-prey populations,” *Mathematical Biosciences*, vol. 68, no. 2, pp. 213–231, 1984.

[27] Y. A. Kuznetsov, *Elements of applied bifurcation theory*, vol. 112. Springer Science & Business Media, 2013.

[28] L. Perko, *Differential equations and dynamical systems*, vol. 7. Springer Science & Business Media, 2013.

[29] C. G. Rong *et al.*, *Hopf bifurcation analysis: a frequency domain approach*, vol. 21. World Scientific, 1996.

[30] M. Haque, E. Venturino, *et al.*, “Increase of the prey may decrease the healthy predator population in presence of a disease in the predator,” in *Hermis*, vol. 7, pp. 38–59, LEA., Athens, 2006.

[31] R. L. Tayeh and R. K. Naji, “Mathematical study of eco–epidemiological system,” *Mathematical Theory and Modeling*, vol. 4, no. 14, pp. 2225–0522, 2014.

[32] A. Quarteroni and A. Valli, *Introduction.* Springer, 1994.

[33] G. Jameson, “Counting zeros of generalised polynomials: Descartes’ rule of signs and laguerre’s extensions,” *The Mathematical Gazette*, vol. 90, no. 518, pp. 223–234, 2006.

[34] M. L. Rosenzweig, “Paradox of enrichment: destabilization of exploitation ecosystems in ecological time,” *Science*, vol. 171, no. 3969, pp. 385–387, 1971.

[35] R. M. May, “Qualitative stability in model ecosystems,” *Ecology*, vol. 54, no. 3, pp. 638–641, 1973.

[36] J. M. Cushing, “Two species competition in a periodic environment,” *Journal of Mathematical Biology*, vol. 10, no. 4, pp. 385–400, 1980.

[37] R. Arditi, J. Abillon, and J. V. Da Silva, “A predator-prey model with satiation and intraspecific competition,” *Ecological Modelling*, vol. 5, no. 3, pp. 173–191, 1978.

[38] A. Roy and F. Solimano, “Global stability and oscillations in classical lotka-volterra loops,” *Journal of Mathematical Biology*, vol. 24, no. 6, pp. 603–616, 1987.

[39] B. Rai and P. Khare, “Mathematical-analysis of a 2 species model with a differential nature of interaction,” *INDIAN JOURNAL OF PURE & APPLIED MATHEMATICS*, vol. 22, no. 8, pp. 669–678, 1991.

[40] D. Kesh, A. Sarkar, and A. Roy, “Persistence of two prey–one predator system with ratio-dependent predator influence,” *Mathematical methods in the applied sciences*, vol. 23, no. 4, pp. 347–356, 2000.

[41] B. Dennis, R. A. Desharnais, J. Cushing, S. M. Henson, and R. Costantino, “Estimating chaos and complex dynamics in an insect population,” *Ecological Monographs*, vol. 71, no. 2, pp. 277–303, 2001.

[42] H. G. Fransz, *The functional response to prey density in an acarine system.* Pudoc, 1974.

[43] C. S. Holling, “Some characteristics of simple types of predation and parasitism,” *The Canadian Entomologist*, vol. 91, no. 7, pp. 385–398, 1959.

[44] L. Michaelis and M. L. Menten, “The kinetics of the inversion effect,” *Biochem. Z*, vol. 49, pp. 333–369, 1913.

[45] R. Arditi and L. R. Ginzburg, “Coupling in predator-prey dynamics: ratio-dependence,” *Journal of theoretical biology*, vol. 139, no. 3, pp. 311–326, 1989.

[46] M. Hassell and G. Varley, “New inductive population model for insect parasites and its bearing on biological control,” *Nature*, vol. 223, no. 5211, p. 1133, 1969.

[47] J. R. Beddington, “Mutual interference between parasites or predators and its effect on searching efficiency,” *The Journal of Animal Ecology*, pp. 331–340, 1975.

[48] D. L. DeAngelis, R. Goldstein, and R. O’neill, “A model for tropic interaction,” *Ecology*, vol. 56, no. 4, pp. 881–892, 1975.

[49] J. R. Beddington, “Mutual interference between parasites or predators and its effect on searching efficiency,” *The Journal of Animal Ecology*, pp. 331–340, 1975.

[50] W. C. Allee *et al.*, “Animal aggregations,” 1931.

[51] J. R. Miner, “Pierre-françois verhulst, the discoverer of the logistic curve,” *Human Biology*, vol. 5, no. 4, p. 673, 1933.

[52] J. S. Cramer, “The origins and development of the logit model,” *Logit models from economics and other fields*, vol. 2003, pp. 1–19, 2003.

[53] G. W. Harrison, “Global stability of food chains,” *The American Naturalist*, vol. 114, no. 3, pp. 455–457, 1979.

[54] T. C. Gard and T. G. Hallam, “Persistence in food webs—i lotka-volterra food chains,” *Bulletin of Mathematical Biology*, vol. 41, no. 6, pp. 877–891, 1979.

[55] H. I. Freedman, *Deterministic mathematical models in population ecology.* M. Dekker New York, 1980.

[56] K.-S. Cheng, S.-B. Hsu, and S.-S. Lin, “Some results on global stability of a predator-prey system,” *Journal of Mathematical Biology*, vol. 12, no. 1, pp. 115–126, 1982.

[57] J. M. Cushing, “Two species competition in a periodic environment,” *Journal of Mathematical Biology*, vol. 10, no. 4, pp. 385–400, 1980.

[58] T. C. Gard, “Persistence in food chains with general interactions,” *Mathematical Biosciences*, vol. 51, no. 1-2, pp. 165–174, 1980.

[59] T. C. Gard, “Uniform persistence in multispecies population models,” *Mathematical biosciences*, vol. 85, no. 1, pp. 93–104, 1987.

[60] P. Saijnders and M. Bazin, “On the stability of food chains,” *Journal of theoretical biology*, vol. 52, no. 1, pp. 121–142, 1975.

[61] A. Hastings and T. Powell, “Chaos in a three-species food chain,” *Ecology*, vol. 72, no. 3, pp. 896–903, 1991.

[62] M. Sunaryo, Z. Salleh, and M. Mamat, “Mathematical model of three species food chain with holling type-iii functional response,” *International Journal of Pure and Applied Mathematics*, vol. 89, no. 5, pp. 647–657, 2013.

[63] T. K. Kar and K. Chaudhuri, “On non-selective harvesting of two competing fish species in the presence of toxicity,” *Ecological Modelling*, vol. 161, no. 1-2, pp. 125–137, 2003.

[64] E. Green, “The effect of asmart’predator in a one predator, two prey system,” *Rose-Hulman Undergraduate Mathematics Journal*, vol. 5, no. 2, p. 5, 2004.

[65] V. Křivan and J. Eisner, “The effect of the holling type ii functional response on apparent competition,” *Theoretical Population Biology*, vol. 70, no. 4, pp. 421–430, 2006.

[66] N. Ali, M. Haque, E. Venturino, and S. Chakravarty, “Dynamics of a three species ratio-dependent food chain model with intra-specific competition within the top predator,” *Computers in biology and medicine*, vol. 85, pp. 63–74, 2017.

[67] R. Kabuye, *Mathematical Analysis of interaction within a four species Ecosystem.* PhD thesis, Doctoral dissertation, Department of Mathematics, Makerere University, Kampala, Uganda, 1995.

[68] A. EDWIN, *Modeling and analysis of a two prey-one predator system with harvesting, Holling Type II and ratio-dependent responses.* PhD thesis, Doctoral dissertation, Makerere University, 2010.

[69] A. Hastings and T. Powell, “Chaos in a three-species food chain,” *Ecology*, vol. 72, no. 3, pp. 896–903, 1991.

[70] W. M. Schaffer, “Order and chaos in ecological systems,” *Ecology*, vol. 66, no. 1, pp. 93–106, 1985.

[71] M. E. Gilpin, “Spiral chaos in a predator-prey model,” *The American Naturalist*, vol. 113, no. 2, pp. 306–308, 1979.

[72] J. Guckenheimer and P. Holmes, “Local bifurcations,” in *Nonlinear oscillations, dynamical systems, and bifurcations of vector fields*, pp. 117–165, Springer, 1983.

[73] R. M. May, “Biological populations with nonoverlapping generations: stable points, stable cycles, and chaos,” *Science*, vol. 186, no. 4164, pp. 645–647, 1974.

[74] M. Kot, W. M. Schaffer, G. L. Truty, D. J. Graser, and L. F. Olsen, “Changing criteria for imposing order,” *Ecological Modelling*, vol. 43, no. 1-2, pp. 75–110, 1988.

[75] M. E. Gilpin, “Spiral chaos in a predator-prey model,” *The American Naturalist*, vol. 113, no. 2, pp. 306–308, 1979.

[76] R. M. May, *Stability and complexity in model ecosystems*, vol. 6. Princeton university press, 2001.

[77] S. L. Pimm, “Food webs,” in *Food webs*, pp. 1–11, Springer, 1982.

[78] P. W. Price, C. E. Bouton, P. Gross, B. A. McPheron, J. N. Thompson, and A. E. Weis, “Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies,” *Annual review of Ecology and Systematics*, vol. 11, no. 1, pp. 41–65, 1980.

[79] R. T. Paine, “Food web complexity and species diversity,” *The American Naturalist*, vol. 100, no. 910, pp. 65–75, 1966.

[80] G. W. Harrison, "Multiple stable equilibria in a predator-prey system," *Bulletin of Mathematical Biology*, vol. 48, no. 2, pp. 137–148, 1986.

[81] S. Hsu, "Predator-mediated coexistence and extinction," *Mathematical Biosciences*, vol. 54, no. 3-4, pp. 231–248, 1981.

[82] B. Rai and P. Khare, "Mathematical-analysis of a 2 species model with a differential nature of interaction," *INDIAN JOURNAL OF PURE & APPLIED MATHEMATICS*, vol. 22, no. 8, pp. 669–678, 1991.

[83] J. Shukla, A. Agrawal, B. Dubey, and P. Sinha, "Existence and survival of two competing species in a polluted environment: A mathematical model," *Journal of Biological Systems*, vol. 9, no. 02, pp. 89–103, 2001.

[84] T. H. Fay and J. C. Greeff, "Lion, wildebeest and zebra: A predator–prey model," *ecological modelling*, vol. 196, no. 1-2, pp. 237–244, 2006.

[85] A. R. Hausrath, "Analysis of a model predator-prey system with refuges," *Journal of mathematical analysis and applications*, vol. 181, no. 2, pp. 531–545, 1994.

[86] M. Agarwal and R. Pathak, "Influence of prey reserve in two preys and one predator system," *International Journal of Engineering, Science and Technology*, vol. 6, no. 2, pp. 1–19, 2014.

[87] R. K. Naji and S. R. Jawad, "The dynamics of prey-predator model with a reserved zone," *World Journal of Modelling and Simulation*, vol. 12, no. 3, pp. 175–188, 2016.

[88] D. Jana, R. Pathak, and M. Agarwal, "On the stability and hopf bifurcation of a prey-generalist predator system with independent age-selective harvesting," *Chaos, Solitons & Fractals*, vol. 83, pp. 252–273, 2016.

[89] J. B. Collings, "Bifurcation and stability analysis of a temperature-dependent mite predator-prey interaction model incorporating a prey refuge," *Bulletin of mathematical biology*, vol. 57, no. 1, pp. 63–76, 1995.

[90] V. Křivan, "Effects of optimal antipredator behavior of prey on predator–prey dynamics: the role of refuges," *Theoretical population biology*, vol. 53, no. 2, pp. 131–142, 1998.

[91] J. Chattopadhyay, N. Bairagi, and R. R. Sarkar, "A predator-prey model with some cover on prey species," *NONLINEAR PHENOMENA IN COMPLEX SYSTEMS-MINSK-*, vol. 3, no. 4, pp. 407–420, 2000.

[92] T. K. Kar, "Stability analysis of a prey-predator model with delay and harvesting," *Journal of Biological Systems*, vol. 12, no. 01, pp. 61–71, 2004.

[93] T. K. Kar, "Modelling and analysis of a harvested prey–predator system incorporating a prey refuge," *Journal of Computational and Applied Mathematics*, vol. 185, no. 1, pp. 19–33, 2006.

[94] Z. Ma and S. Wang, "Stability analysis: The effect of prey refuge in predator–prey model," *Ecological Modelling*, vol. 247, pp. 95–97, 2012.

[95] T. K. Kar and S. Misra, "Influence of prey reserve in a prey–predator fishery," *Nonlinear Analysis: Theory, Methods & Applications*, vol. 65, no. 9, pp. 1725–1735, 2006.

[96] B. Dubey, P. Chandra, and P. Sinha, "A model for fishery resource with reserve area," *Nonlinear Analysis: Real World Applications*, vol. 4, no. 4, pp. 625–637, 2003.

[97] B. Dubey, "A prey-predator model with a reserved area," *Nonlin. Anal. Model& control*, vol. 12, pp. 479–494, 2007.

[98] D. Mukherjee, "Bifurcation and stability analysis of a prey-predator system with a reserved area," *World Journal of Modelling and Simulation*, vol. 8, no. 4, pp. 285–292, 2012.

[99] M. Agarwal and R. Pathak, "Influence of prey reserve in two preys and one predator system," *International Journal of Engineering, Science and Technology*, vol. 6, no. 2, pp. 1–19, 2014.

[100] B. Sahoo and S. Poria, "Diseased prey predator model with general holling type interactions," *Applied Mathematics and Computation*, vol. 226, pp. 83–100, 2014.

list of Publications

[**1**] **S. R. Jawad**, and Mattias Winter, "the effect of reserved zone on the behavior of food web model", Poster presentation in *Brunel University London research student conference*, 4-5 July 2017.

[**2**] **S. R. Jawad**, and Mattias Winter, "the effect of reserved zone on the behavior of food chain model", Poster presentation in *Mathematical modeling in life science-A probability summer school - Pisa*, 13-15 September 2017.

[**3**] R. K. Naji and **S. R. Jawad**, "The dynamics of prey-predator model with a reserved zone", *World Journal of Modelling and Simulation*, vol. 12, no. 3, pp. 175-188, 2016.

[**4**] Alhumaima, R. S., **J., Shireen** and Al-Raweshidy, H. S., "Evaluating the Energy Efficiency of Virtualised 5G Networks, *Nova Science Publishers*, Book ch., Id 46182, 2017.