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Coexistence or extinction: Dynamics of multiple lizard species with competition, dispersal and intraguild predation

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Abstract

Biological invasions significantly impact native ecosystems, altering ecological processes and community behaviors through predation and competition. The introduction of non-native species can lead to either coexistence or extinction within local habitats. Our research develops a lizard population model that integrates aspects of competition, intraguild predation, and the dispersal behavior of intraguild prey. We analyze the model to determine the existence and stability of various ecological equilibria, uncovering the potential for bistability under certain conditions. By employing the dispersal rate as a bifurcation parameter, we reveal complex bifurcation dynamics associated with the positive equilibrium. Additionally, we conduct a two-parameter bifurcation analysis to investigate the combined impact of dispersal and intraguild predation on ecological structures. Our findings indicate that intraguild predation not only influences the movement patterns of brown anoles but also plays a crucial role in sustaining the coexistence of different lizard species in diverse habitats.

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1 Introduction

The increasing human impact on ecosystems has led to a significant challenge for ecological environments and biodiversity, as highlighted by multiple studies (Ceballos et al. 2015; Hautier et al. 2015; Cepic et al. 2022). Environmental pollution and dwindling resources have forced many species to abandon their native habitats in search of new areas to survive. Research into the biological effects of species invasions enhances our understanding of the ecological and evolutionary dynamics of the natural world and aids in formulating effective strategies for addressing ecological issues (Sax et al. 2007).

Biological invasions, considered a major factor in global change (Vitousek et al. 1997; Richardson and Pyšek 2008; Schirmel et al. 2016), significantly disrupt local ecosystem processes and functions (Nogales et al. 2006; Vilà et al. 2011; Zhang et al. 2020). Invasive species pose a threat to almost half of the endangered species in the United States (Wilcove et al. 1998) and contribute to the extinction of species both on the island and the mainland (Bellard et al. 2016). Research by (Duenas et al. 2018) supports the view that invasive species are a key driver in the decline of threatened species, and it is found that these species can negatively impact indigenous endangered or threatened species. However, (García-Gómez et al. 2021) identified some positive outcomes of biological invasions where introduced species successfully coexist with local communities. The role of spatial heterogeneity in influencing species activities and promoting coexistence is significant (Chesson 2000). Additionally, habitat diversity can facilitate the coexistence of exotic and native species (Kestrup and Ricciardi 2009; Chrétien and Chapman 2016). Therefore, the impact of biological invasions on local ecosystems can vary, being either negative or positive, depending on specific local conditions.

Predation and competition are two crucial interactions in species coexistence (Chase et al. 2002; Chesson and Kuang 2008; Laguna et al. 2015). Introduced species can compete with native species for resources, limiting diversity (Chesson and Kuang 2008), or act as predators on local species, impacting interspecific competition (Chase et al. 2002). Intraguild predation (IGP) is a common ecological interaction that encompasses both predation and competition (Arim and Marquet 2004; Holt and Huxel 2007). Studies show that top predators greatly influence species behavior (Gerber et al. 2012; Sommers and Chesson 2019; Dykstra et al. 2023), including dispersal in response to predation threats (Vanderwerf 2012; Orrock et al. 2013). In response to the threat from invasive black rats, native birds on islands adapt by altering their habitat and constructing nests at higher elevations to evade predation (Vanderwerf 2012). This behavior, motivated by the presence of a predator, leads prey species to limit their resource usage to areas with reduced predation risk. Such changes in behavior, without direct consumption, can have varied non-consumptive effects on the dynamics of the population (Orrock et al. 2013).

Mathematical models have been extensively used to study the impacts of species dispersal on ecological functions (Wang and Zou 2016; Alidousti and Ghahfarokhi 2019; Mai et al. 2019) and intraguild predation dynamics (Zhang and Dai 2019; Su

et al. 2020). (Yang et al. 2020) developed a two-patch mosquito model to assess the impact of dispersal rate on the effectiveness of sterile mosquito releases. (Ji et al. 2022) used an IGP model with IG prey dispersal to study lizard species coexistence, revealing complex dynamics. Moreover, the effects of time delay on IGP activities were investigated by (Shu et al. 2015), showing that delays can induce stability switches.

In a comprehensive six-year experiment by (Pringle et al. 2019), the biological consequences of predator introduction were studied on 16 Bahamian islands. The study involved introducing green anoles (GA, *Anolis smaragdinus*) and curly-tailed lizards (CT, *Leiocephalus carinatus*) to islands inhabited by brown anoles (*Anolis sagrei*). These species, feeding on various arthropods, interact differently in the ecosystem (Takimoto et al. 2008).

Brown anoles, identified as trunk-ground ecomorphs, possess long legs that aid in their dispersal and allow them to inhabit a variety of surfaces (Losos and Spiller 1999; Knouft et al. 2006). These lizards typically consume both terrestrial and arboreal resources throughout their lifetime. In the absence of predators, the movement of brown anoles between arboreal and terrestrial habitats is largely driven by foraging behavior shifts. However, the introduction of CT lizards can result in non-consumptive effects (Peckarsky et al. 2008) on brown anoles, compelling them to shift to higher perches and consume more arboreal resources (Schoener et al. 2005). CT lizards not only consume terrestrial resources but also prey on brown anoles (Schoener et al. 1982), indicating the emergence of intraguild predation where CT lizards become both top predators and intraguild predators. Facing threats from these predators, ground-dwelling brown anoles may alter their habitat to trees, thereby competing with GA lizards for arboreal resources. For study purposes, brown anoles are categorized into two groups: BA lizards, representing those in arboreal habitats, and BT lizards, representing those in terrestrial habitats.

Two ecological models are described in (Pringle et al. 2019) to understand lizard species interactions. The keystone-predation model (Paine 1966) suggests that intense predation by CT lizards on BT lizards keeps the populations of BT and BA lizards low, reducing competition for GA lizards and indirectly benefiting them. This implies that the intraguild predation may stabilize the coexistence of lizard species. The refuge-competition model (Orrock et al. 2013) posits that while the predation of CT lizards on BT lizards is weak, interspecific competition is strong, keeping the populations of BA lizards high and potentially leading to the extinction of GA lizards due to resource competition. In this study, we aim to employ mathematical modeling, numerical simulations, and data fitting techniques to explore how CT lizards indirectly influence the persistence or extinction of GA lizards. This investigation will focus on understanding the impact of CT lizards through their predation upon and competition with BT lizards.

Motivated by the works in (Pringle et al. 2019; Ji et al. 2022), we propose a mathematical model incorporating the competition between GA and BA lizards, as well as BT and CT lizards, intraguild predation by CT lizards on BT lizards, and the dispersal behavior of brown anoles to investigate lizards population dynamics under interaction effects.

$$u'_{GA}(T) = r_{GA}u_{GA}\left(1 - \frac{u_{GA}}{K_{GA}}\right) - q_{GA}u_{GA}u_{BA},$$

$$u'_{BA}(T) = r_{BA}u_{BA}\left(1 - \frac{u_{BA}}{K_{BA}}\right) - q_{BA}u_{GA}u_{BA} - m_{BA}u_{BA} + m_{BT}u_{BT},$$

$$u'_{BT}(T) = r_{BT}u_{BT}\left(1 - \frac{u_{BT}}{K_{BT}}\right) - q_{BT}u_{BT}u_{CT} - p_{BT}u_{BT}u_{CT} - m_{BT}u_{BT} + m_{BA}u_{BA},$$

$$u'_{CT}(T) = r_{CT}u_{CT}\left(1 - \frac{u_{CT}}{K_{CT}}\right) - q_{CT}u_{BT}u_{CT} + p_{CT}u_{BT}u_{CT}, \tag{1.1}$$

where $u_{GA}(T)$, $u_{BA}(T)$, $u_{BT}(T)$ and $u_{CT}(T)$ represent the densities of green anoles (GA), arboreal brown anoles (BA), terrestrial brown anoles (BT) and curly-tailed lizards (CT) at time T, respectively. We employ logistic terms to measure the intrinsic growth of all lizard species and bilinear incidence functions to describe the predation and competition interactions. The GA, BA, BT, and CT lizards grow with the intrinsic growth rate r_j and carrying capacity K_j, for $j = GA, BA, BT, CT$, respectively. Here K_j represents the intrinsic carrying capacity, which is specific to each lizard species j and its corresponding resource. For example, K_{GA} is the carrying capacity of GA lizards in the absence of competing species such as BA lizards, and K_{BA} is the carrying capacity of BA lizards in the absence of GA lizards, assuming dispersal behavior is ignored. Similarly, K_{BT} (and K_{CT}) represents the intrinsic carrying capacity of BT (and CT) lizards in the absence of other lizard species. Parameters q_{GA}, q_{BA}, q_{BT}, and q_{CT} are the interspecific competition coefficients from BA, GA, CT, and BT lizards, respectively. The CT lizards prey on the BT lizards with a bilinear function $p_{BT}u_{BT}u_{CT}$ and recruit at the rate of $p_{CT}u_{BT}u_{CT}$. Parameter m_{BA} (m_{BT}) represents the migration/movement rate of brown anoles from the tree (ground) to the ground (tree). All parameters of (1.1) are positive and their descriptions are listed in Table 1. The interactions among lizard species are depicted in Fig. 1. We also assume that the predation of CT lizards on BT lizards is stronger than the competition of BT lizards with CT lizards; namely, $p_{CT} > q_{CT}$.

To reduce the number of parameters and conduct mathematical analysis, we scale the state variables and the time variable as follows:

$$G_A = \frac{u_{GA}}{K_{GA}}, \quad B_A = \frac{u_{BA}}{K_{BA}}, \quad B_T = \frac{u_{BT}}{K_{BT}}, \quad C_T = \frac{u_{CT}}{K_{CT}}, \quad t = r_{GA}T.$$

System (1.1) becomes

$$\begin{aligned}
G'_A(t) &= G_A(1 - G_A) - \alpha G_A B_A, \\
B'_A(t) &= r_1 B_A(1 - B_A) - \beta G_A B_A - m_1 B_A + m_2\theta B_T, \\
B'_T(t) &= r_2 B_T(1 - B_T) - \gamma B_T C_T - m_2 B_T + \frac{m_1}{\theta}B_A, \\
C'_T(t) &= r_3 C_T(1 - C_T) + \sigma B_T C_T,
\end{aligned} \tag{1.2}$$

Table 1 The parameter description of Model (1.1)

| Parameter	Description	Unit
r_{GA}	Intrinsic growth rate of GA lizards	1/year
r_{BA}	Intrinsic growth rate of BA lizards	1/year
r_{BT}	Intrinsic growth rate of BT lizards	1/year
r_{CT}	Intrinsic growth rate of CT lizards	1/year
K_{GA}	Carrying capacity of GA lizards	[GA]
K_{BA}	Carrying capacity of BA lizards	[BA]
K_{BT}	Carrying capacity of BT lizards	[BT]
K_{CT}	Carrying capacity of CT lizards	[CT]
q_{GA}	BA competition rate for arboreal resource	1/year/[BA]
q_{BA}	GA competition rate for arboreal resource	1/year/[GA]
q_{BT}	CT competition rate for terrestrial resource	1/year/[CT]
q_{CT}	BT competition rate for terrestrial resource	1/year/[BT]
m_{BA}	Movement rate of BA lizards	1/year
m_{BT}	Movement rate of BT lizards	1/year
p_{BT}	Intraguild predation rate on BT lizards	1/year/[CT]
p_{CT}	CT recruitment rate by intraguild predation	1/year/[BT]
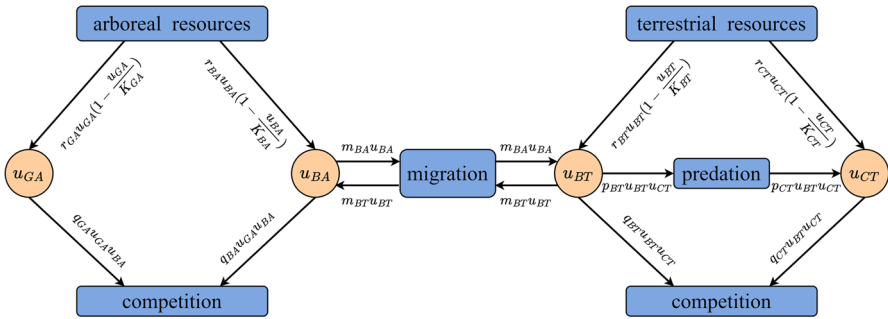
Fig. 1 A flow diagram of interactions among lizard species in model (1.1)

where the non-dimensional parameters are defined as

$$\alpha = \frac{q_{GA}K_{BA}}{r_{GA}}, \ \beta = \frac{q_{BA}K_{GA}}{r_{GA}}, \ \gamma = \frac{(q_{BT} + p_{BT})K_{CT}}{r_{GA}}, \ \sigma = \frac{(p_{CT} - q_{CT})K_{BT}}{r_{GA}},$$

$$r_1 = \frac{r_{BA}}{r_{GA}}, \ r_2 = \frac{r_{BT}}{r_{GA}}, \ r_3 = \frac{r_{CT}}{r_{GA}}, \ m_1 = \frac{m_{BA}}{r_{GA}}, \ m_2 = \frac{m_{BT}}{r_{GA}}, \ \theta = \frac{K_{BT}}{K_{BA}}.$$

The structure of this paper is outlined as follows: In Sect. 2, we establish the non-negativity and boundedness of solutions for (1.2) and examine the existence of feasible equilibria. Section 3 is dedicated to the stability analysis of each equilibrium and the investigation of potential bistability scenarios. Numerical simulations are conducted in Sect. 4 to support and illustrate our theoretical findings. The application of our model

to experimental data in the literature for parameters estimation is presented in Sect. 5. The paper concludes with Sect. 6, where we summarize our main results and offer insights and discussions based on our study.

2 Well-posedness and equilibria

We first state the following preliminary results on the nonnegativity and boundedness of the solutions of system (1.2).

Theorem 2.1 *For any initial condition* $(G_A(0), B_A(0), B_T(0), C_T(0)) \in \mathbb{R}_+^4$, *the system (1.2) admits a unique solution, which is nonnegative and ultimately bounded in* $\mathbb{R}_+^4$. *Furthermore, if* $G_A(0) > 0$, *then* $G_A(t) > 0$ *for all* $t \geq 0$; *if* $C_T(0) > 0$, *then* $C_T(t) > 0$ *for all* $t \geq 0$; *if* $B_A(0) + B_T(0) > 0$, *then* $B_A(t) > 0$ *and* $B_T(t) > 0$ *for all* $t \geq 0$.

Proof Since the right-hand sides of system (1.2) are polynomial functions of the state variables, we obtain from the standard theory of ordinary differential equations that the solution of system (1.2) with an initial condition in $\mathbb{R}_+^4$ exists globally and is unique.

From the first equation in (1.2), we have the integral representation

$$G_A(t) = G_A(0) \exp\left(\int_0^t (1 - G_A(\theta) - \alpha B_A(\theta))d\theta\right),$$

which implies $G_A(t) \geq 0$ for all $t \geq 0$. Moreover, if $G_A(0) > 0$ then $G_A(t) > 0$ for all $t \geq 0$. Similarly, we obtain from the fourth equation in (1.2) that $C_T(t) \geq 0$ for all $t \geq 0$, and if $C_T(0) > 0$ then $C_T(t) > 0$ for all $t \geq 0$.

Next, we let $\varepsilon > 0$ be small and consider the perturbed system

$$
\begin{aligned}
(G_A^\varepsilon)'(t) &= G_A^\varepsilon \left(1 - G_A^\varepsilon\right) - \alpha G_A^\varepsilon B_A^\varepsilon, \\
(B_A^\varepsilon)'(t) &= r_1 B_A^\varepsilon \left(1 - B_A^\varepsilon\right) - \beta G_A^\varepsilon B_A^\varepsilon - m_1 B_A^\varepsilon + m_2 \theta B_T^\varepsilon + \varepsilon, \\
(B_T^\varepsilon)'(t) &= r_2 B_T^\varepsilon \left(1 - B_T^\varepsilon\right) - \gamma B_T^\varepsilon C_T^\varepsilon - m_2 B_T^\varepsilon + \frac{m_1}{\theta} B_A^\varepsilon + \varepsilon, \\
(C_T^\varepsilon)'(t) &= r_3 C_T^\varepsilon \left(1 - C_T^\varepsilon\right) + \sigma B_T^\varepsilon C_T^\varepsilon,
\end{aligned}
$$

together with the same nonnegative initial condition as in the original system. We claim that $B_A^\varepsilon(t) \geq 0$ and $B_T^\varepsilon(t) \geq 0$ for all $t \geq 0$. Otherwise, there exists a $t_0 \geq 0$ such that both $B_A^\varepsilon(t)$ and $B_T^\varepsilon(t)$ are nonnegative for $t \in [0, t_0]$ while either $B_A^\varepsilon(t)$ or $B_T^\varepsilon(t)$ becomes negative when $t - t_0$ is positive and small. If $B_A^\varepsilon(t) < 0$ for small $t - t_0 > 0$, then $B_A^\varepsilon(t_0) = 0$ and $0 \geq (B_A^\varepsilon)'(t_0) = m_2 \theta B_T^\varepsilon(t_0) + \varepsilon > 0$, a contradiction. Similarly, if $B_T^\varepsilon(t) < 0$ for small $t - t_0 > 0$, then $B_T^\varepsilon(t_0) = 0$ and $0 \geq (B_T^\varepsilon)'(t_0) = (m_1/\theta) B_A^\varepsilon(t_0) + \varepsilon > 0$, a contradiction again. Hence, our claim is true. For each $t \geq 0$, we let $\varepsilon \to 0^+$ to find $B_A(t) \geq 0$ and $B_T(t) \geq 0$. This proves the non-negativeness of the solution.

Now, we assume $B_A(0) + B_T(0) > 0$. It follows from the second and third equations of (1.2) that $B_A(t) > 0$ and $B_T(t) > 0$ for sufficiently small $t > 0$. Let

$$U(t, s) = e^{\int_s^t \{r_1[1 - B_A(\tau)] - \beta G_A(\tau) - m_1\} d\tau} > 0$$

for $t \geq s \geq 0$. We obtain from the second equation of (1.2) that

$$B_A(t) = U(t, 0) B_A(0) + \int_0^t [U(t, s) m_2 \theta B_T(s)] ds > 0$$

for all $t > 0$. Similarly, we obtain from the third equation of (1.2) that

$$B_T(t) = V(t, 0) B_T(0) + \int_0^t [V(t, s)(m_1/\theta) B_A(s)] ds > 0 \quad \text{for all } t > 0,$$

where $V(t, s) = e^{\int_s^t \{r_2[1 - B_T(\tau)] - \gamma C_T(\tau) - m_2\} d\tau} > 0$ for $t \geq s \geq 0$.

Finally, we denote $X(t) = G_A(t) + B_A(t) + \theta B_T(t) + (\theta \gamma / \sigma) C_T(t)$. It follows from (1.2) that

$$X'(t) \leq G_A(1 - G_A) + r_1 B_A(1 - B_A) + \theta r_2 B_T(1 - B_T) + \frac{\theta r_3 \gamma}{\sigma} C_T(1 - C_T)$$

$$\leq 1 - G_A + r_1(1 - B_A) + \theta r_2(1 - B_T) + \frac{\theta r_3 \gamma}{\sigma}(1 - C_T) \leq M - \delta X(t),$$

where $M = 1 + r_1 + \theta r_2 + \theta r_3 \gamma / \sigma > 0$ and $\delta = \min\{1, r_1, r_2, r_3\} > 0$. By comparison principle, we have $\limsup_{t \to \infty} X(t) \leq M/\delta$. This ends the proof. $\qquad \square$

System (1.2) always admits the following four equilibria, namely, a trivial equilibrium $E_0 = (0, 0, 0, 0)$, a CT equilibrium $E_{01} = (0, 0, 0, 1)$, a GA equilibrium $E_{10} = (1, 0, 0, 0)$, and a GA-CT equilibrium $E_{20} = (1, 0, 0, 1)$.

Now, we investigate the existence of BA-BT equilibrium $E_{02} = (0, \hat{B}_A, \hat{B}_T, 0)$, where $\hat{B}_T = \hat{B}_A(r_1 \hat{B}_A + m_1 - r_1)/(m_2 \theta)$ and $\hat{B}_A$ is a positive zero of the cubic polynomial

$$F_{02}(x) = a_3 x^3 + a_2 x^2 + a_1 x + a_0$$

with $a_3 = r_1^2 r_2 > 0$, $a_2 = 2r_1 r_2(m_1 - r_1)$, $a_1 = r_1 m_2 \theta(m_2 - r_2) + r_2(r_1 - m_1)^2$ and $a_0 = m_2 \theta(r_1 r_2 - r_1 m_2 - r_2 m_1)$. We shall make use of the following lemma.

Lemma 2.1 *Let $F(x) = a_3 x^3 + a_2 x^2 + a_1 x + a_0$ be a cubic polynomial with a positive leading coefficient $a_3 > 0$. Denote by $x_c := -a_2/(3a_3)$ the turning point such that $F''(x_c) = 0$. Given $x_b \geq x_c$, if $F(x_b) < 0$, then $F(x)$ has a unique zero in (x_b, ∞); if $F(x_b) \geq 0$ and $F'(x_b) \geq 0$, then $F(x)$ has no zero in (x_b, ∞).*

Proof Assume $F(x_b) < 0$. Since $F(x) \to \infty$ as $x \to \infty$, there exists at least one zero of $F(x)$ in (x_b, ∞). If $F(x)$ has two or three zeros in (x_b, ∞), then we obtain from

$F(x_b) < 0$ that $F'(x)$ has two zeros in (x_b, ∞). By Rolle's theorem, $F''(x)$ has a zero in (x_b, ∞), which contradicts $x_b \geq x_c$. Hence, the zero of $F(x)$ in (x_b, ∞) is unique.

Now we assume $F(x_b) \geq 0$ and $F'(x_b) \geq 0$. If $F(x)$ has at least one zero in (x_b, ∞), then $F'(x)$ has two zeros in $[x_b, \infty)$. By Rolle's theorem, $F''(x)$ has a zero in (x_b, ∞), a contradiction to $x_c \leq x_b$. Hence, $F(x)$ has no zero in (x_b, ∞). This completes the proof.   □

Denote

$$\hat{x}_b = \frac{r_1 - m_1}{r_1}, \quad \hat{x}_c = \frac{2(r_1 - m_1)}{3r_1}. \tag{2.1}$$

Then the existence of E_{02} can be presented in the following result.

Theorem 2.2 *System (1.2) always admits a unique BA-BT equilibrium $E_{02} = (0, \hat{B}_A, \hat{B}_T, 0)$.*

Proof Taking the second derivative of $y = F_{02}(x)$ yields $y = F_{02}''(x)$, which satisfies $F_{02}''(\hat{x}_c) = 0$ with $\hat{x}_c$ defined in (2.1). Thus $\hat{x}_c$ is the turning point of $F_{02}(x)$. Moreover, $\hat{B}_T > 0$ if and only if $\hat{B}_A > \max\{0, \hat{x}_b\}$.

We now consider two different cases to prove that $F_{02}(x)$ has a unique positive zero that is bigger than $\hat{x}_b$. If $r_1 \geq m_1$, then $\hat{x}_b \geq \hat{x}_c \geq 0$. Since $F_{02}(\hat{x}_b) = -m_1 m_2^2 \theta < 0$, we obtain from Lemma 2.1 that $F_{02}(x)$ has a unique positive zero that is bigger than $\hat{x}_b$. If $r_1 < m_1$, then $\hat{x}_b < \hat{x}_c < 0$ and $F_{02}(0) = a_0 < 0$. It again follows from Lemma 2.1 that $F_{02}(x)$ has a unique positive zero. In conclusion, a unique BA-BT equilibrium E_{02} exists for system (1.2).   □

Next, we explore the existence of BA-BT-CT equilibrium $E_{03} = (0, \bar{B}_A, \bar{B}_T, \bar{C}_T)$. From the second and fourth equations of (1.2), we obtain

$$\bar{B}_T = \frac{\bar{B}_A}{m_2 \theta}(r_1 \bar{B}_A + m_1 - r_1), \quad \bar{C}_T = 1 + \frac{\sigma}{r_3} \bar{B}_T. \tag{2.2}$$

It then follows from the third equation of (1.2) that $\bar{B}_A$ is the positive zero of the cubic polynomial

$$F_{03}(x) = b_3 x^3 + b_2 x^2 + b_1 x + b_0 \tag{2.3}$$

with $b_3 = r_1^2(r_2 r_3 + \gamma \sigma) > 0$, $b_2 = 2r_1(r_2 r_3 + \gamma \sigma)(m_1 - r_1)$, $b_1 = r_1 r_3 m_2 \theta(-r_2 + \gamma + m_2) + (r_2 r_3 + \gamma \sigma)(r_1 - m_1)^2$ and $b_0 = r_3 m_2 \theta((r_1 - m_1)(r_2 - \gamma) - r_1 m_2)$. Denote

$$\bar{m}_2 = \frac{(r_1 - m_1)(r_2 - \gamma)}{r_1}. \tag{2.4}$$

Theorem 2.3 *Let $\bar{m}_2$ be defined in (2.4). If $r_1 \geq m_1$ or $m_2 > \bar{m}_2$, then system (1.2) admits a unique BA-BT-CT equilibrium $E_{03} = (0, \bar{B}_A, \bar{B}_T, \bar{C}_T)$. If $r_1 < m_1$ and $m_2 \leq \bar{m}_2$, then system (1.2) has no BA-BT-CT equilibrium.*

Proof Note from (2.2) that $\bar{B}_T > 0$ if and only if $\bar{B}_A > \max\{0, \hat{x}_b\}$, where $\hat{x}_b$ is given in (2.1). By (2.3), we can rewrite $F_{03}(x)$ by

$$F_{03}(x) = (r_2 r_3 + \gamma\sigma)(r_1 x - (r_1 - m_1))^2 x - r_3 m_2 \theta (r_2 - \gamma - m_2)(r_1 x - (r_1 - m_1)) - r_3 m_1 m_2^2 \theta.$$

Substituting $x = \hat{x}_b$ into $F_{03}(x)$ yields $F_{03}(\hat{x}_b) = -r_3 m_1 m_2^2 \theta < 0$. Moreover, we calculate $F_{03}''(x) = 6b_3 x + 2b_2 = 2r_1(r_2 r_3 + \gamma\sigma)(3r_1 x - 2(r_1 - m_1))$, thus $F_{03}''(\hat{x}_c) = 0$, where $\hat{x}_c$ is defined in (2.1).

If $r_1 \geq m_1$, then $\hat{x}_b \geq \hat{x}_c \geq 0$. This together with $F_{03}(\hat{x}_b) < 0$ and Lemma 2.1 implies that $F_{03}(x)$ has a unique zero in $(\hat{x}_b, \infty)$. If $r_1 < m_1$, then $\hat{x}_b < \hat{x}_c < 0$. We need to consider two subcases. If $m_2 > \overline{m}_2$, then $F_{03}(0) = b_0 < 0$, and Lemma 2.1 implies that $F_{03}(x)$ has a unique positive zero. If $m_2 \leq \overline{m}_2$, then $F_{03}(0) = b_0 \geq 0$. Moreover, $r_2 < \gamma$ and $F_{03}'(0) = b_1 > 0$. By Lemma 2.1, $F_{03}(x)$ has no positive zero. This ends the proof. $\qquad\square$

We now investigate the existence of GA-BA-BT equilibrium $E_{30} = (\tilde{G}_A, \tilde{B}_A, \tilde{B}_T, 0)$, which satisfies the following equilibrium equations

$$\tilde{G}_A = 1 - \alpha\tilde{B}_A > 0, \quad \tilde{B}_A = \frac{\theta\tilde{B}_T}{m_1}\left(r_2\tilde{B}_T - \tilde{r}_2\right) > 0,$$

where

$$\tilde{r}_2 = r_2 - m_2, \tag{2.5}$$

and $\tilde{B}_T$ is a positive zero of the polynomial

$$\begin{aligned} F_{30}(x) = \theta r_2^2(r_1 - \alpha\beta)x^3 - 2\theta r_2\tilde{r}_2(r_1 - \alpha\beta)x^2 \\ + [\theta(r_1 - \alpha\beta)\tilde{r}_2^2 + m_1 r_2(\beta + m_1 - r_1)]x + m_1\tilde{r}_0 \end{aligned} \tag{2.6}$$

with

$$\tilde{r}_0 = (\beta + m_1 - r_1)(m_2 - r_2) - m_1 m_2. \tag{2.7}$$

Substituting the expression of $\tilde{B}_A$ into $\tilde{G}_A$, we obtain

$$\tilde{G}_A = -\frac{\alpha\theta r_2}{m_1}\tilde{B}_T^2 + \frac{\alpha\theta\tilde{r}_2}{m_1}\tilde{B}_T + 1. \tag{2.8}$$

The positive zeros of $\tilde{B}_A$ and $\tilde{G}_A$ with respect to $\tilde{B}_T$ are $\tilde{x}_1$ and $\tilde{x}_2$, respectively, where

$$\tilde{x}_1 = \frac{\tilde{r}_2}{r_2}, \quad \tilde{x}_2 = \frac{\tilde{r}_2 + \sqrt{\tilde{r}_2^2 + 4m_1 r_2/(\alpha\theta)}}{2r_2} > \max\{0, \tilde{x}_1\}. \tag{2.9}$$

Hence, $\tilde{G}_A > 0$ and $\tilde{B}_A > 0$ if and only if $\tilde{x}_1 < \tilde{B}_T < \tilde{x}_2$. Note that $F_{30}(x)$ can be rewritten as

$$F_{30}(x) = \theta(r_1 - \alpha\beta)(r_2 x - \tilde{r}_2)^2 x + m_1(\beta + m_1 - r_1)(r_2 x - \tilde{r}_2) - m_1^2 m_2.$$

By the expression of $\tilde{x}_1$, we obtain $F_{30}(\tilde{x}_1) = -m_1^2 m_2 < 0$. It follows from (2.8) that $r_2 \tilde{x}_2 - \tilde{r}_2 = m_1/(\alpha\theta\tilde{x}_2)$, then

$$F_{30}(\tilde{x}_2) = \frac{m_1^2(r_1 + \alpha(m_1 - r_1))}{\alpha^2 \theta \tilde{x}_2} - m_1^2 m_2 = m_1^2 m_2(\tilde{x}_3/\tilde{x}_2 - 1),$$

where

$$\tilde{x}_3 = \frac{r_1 + \alpha(m_1 - r_1)}{\alpha^2 \theta m_2}. \tag{2.10}$$

Note that $F_{30}(\tilde{x}_2) > 0$ if and only if $\tilde{x}_3 > \tilde{x}_2$. For convenience, we also denote

$$\tilde{x}_4 = \frac{2\tilde{r}_2}{3r_2} = \frac{2}{3}\tilde{x}_1$$

as the turning point such that $F_{30}''(\tilde{x}_4) = 0$. For convenience, we denote by $\wedge$ and $\vee$ the conjunction and disjunction, respectively. A statement $P \wedge Q$ means both P and Q are true; a statement $P \vee Q$ means either P or Q is true. We will consider three cases to investigate the existence of the GA-BA-BT equilibrium E_{30} respectively.

Case I (weak GA-BA competition): $r_1 > \alpha\beta$.

Theorem 2.4 *Assume the competition between GA and BA is weak, that is, $r_1 > \alpha\beta$. System (1.2) admits at most one GA-BA-BT equilibrium $E_{30} = (\tilde{G}_A, \tilde{B}_A, \tilde{B}_T, 0)$. Let $\tilde{r}_2, \tilde{r}_0, \tilde{x}_2,$ and $\tilde{x}_3$ be defined as in (2.5), (2.7), (2.9), and (2.10), respectively.*

(a) If $((\tilde{r}_2 < 0) \wedge (\tilde{r}_0 \geq 0)) \vee (\tilde{x}_3 \leq \tilde{x}_2)$, then system (1.2) has no GA-BA-BT equilibrium.

(b) If $((\tilde{r}_2 \geq 0) \vee (\tilde{r}_0 < 0)) \wedge (\tilde{x}_3 > \tilde{x}_2)$, then system (1.2) admits a unique GA-BA-BT equilibrium.

Proof Note that $F_{30}(x)$ is a cubic polynomial with a positive leading coefficient when $r_1 > \alpha\beta$. If $\tilde{r}_2 \geq 0$, then $\tilde{x}_1 \geq \tilde{x}_4 \geq 0$. Recall that $F_{30}(\tilde{x}_1) < 0$. It follows from Lemma 2.1 that $F_{30}(x)$ has a unique zero in $(\tilde{x}_1, \infty)$. This zero is less than $\tilde{x}_2$ if and only if $F_{30}(\tilde{x}_2) > 0$ (i.e., $\tilde{x}_3 > \tilde{x}_2$).

If $\tilde{r}_2 < 0$, then $\tilde{x}_1 < \tilde{x}_4 < 0$. If $\tilde{r}_0 < 0$, then $F_{30}(0) < 0$ and Lemma 2.1 implies that $F_{30}(x)$ has a unique positive zero. This positive zero is less than $\tilde{x}_2$ if and only if $F_{30}(\tilde{x}_2) > 0$ (i.e., $\tilde{x}_3 > \tilde{x}_2$). If $\tilde{r}_0 \geq 0$, then $F_{30}(0) \geq 0$ and $\beta + m_1 - r_1 > 0$. Hence, we have $F_{30}'(0) > 0$. By Lemma 2.1, $F_{30}(x)$ has no positive zero. The proof is completed. $\square$

Case II (strong GA-BA competition): $r_1 < \alpha\beta$.

In this case, $F_{30}(x)$ is a cubic polynomial with a negative leading coefficient. We first consider the quadratic polynomial

$$F'_{30}(x) = 3\theta r_2^2 (r_1 - \alpha\beta) x^2 - 4\theta r_2 \tilde{r}_2 (r_1 - \alpha\beta) x + [\theta(r_1 - \alpha\beta)\tilde{r}_2^2 + m_1 r_2 (\beta + m_1 - r_1)]$$
$$= \frac{1}{3}\theta(r_1 - \alpha\beta)[9r_2^2(x - \tilde{x}_4)^2 - \tilde{\Delta}],$$

where

$$\tilde{\Delta} = \tilde{r}_2^2 + \frac{3m_1 r_2 (\beta + m_1 - r_1)}{\theta(\alpha\beta - r_1)}. \tag{2.11}$$

Denote

$$\tilde{x}_5 = \tilde{x}_4 + \frac{\sqrt{\tilde{\Delta}}}{3r_2} = \frac{2\tilde{r}_2 + \sqrt{\tilde{r}_2^2 + \frac{3m_1 r_2 (\beta + m_1 - r_1)}{\theta(\alpha\beta - r_1)}}}{3r_2} > \tilde{x}_4. \tag{2.12}$$

Theorem 2.5 *Assume the competition between GA and BA is strong, that is, $r_1 < \alpha\beta$. System (1.2) admits at most two GA-BA-BT equilibria. Let $\tilde{r}_2$, $\tilde{x}_1$, $\tilde{x}_2$, $\tilde{x}_3$, $\tilde{\Delta}$, and $\tilde{x}_5$ be defined as in (2.5), (2.9), (2.10), (2.11), and (2.12), respectively.*

(a) System (1.2) has no GA-BA-BT equilibrium if and only if one of the following conditions is satisfied.

(a1) $\tilde{\Delta} > 0 \geq -\tilde{r}_2$ and $(\tilde{x}_5 \leq \tilde{x}_1) \vee (F_{30}(\tilde{x}_5) < 0) \vee ((\tilde{x}_5 \geq \tilde{x}_2) \wedge (F_{30}(\tilde{x}_2) \leq 0))$;
(a2) $\tilde{\Delta} > 0 > \tilde{r}_2$ and

$(\min\{F_{30}(0), F_{30}(\tilde{x}_2)\} \geq 0) \vee (\max\{F_{30}(0), F_{30}(\tilde{x}_2), \tilde{x}_5(\tilde{x}_2 - \tilde{x}_5)\} \leq 0) \vee (F_{30}(\tilde{x}_5) < 0)$;

(a3) $\tilde{\Delta} \leq 0$.

(b) System (1.2) has a unique GA-BA-BT equilibrium if and only if one of the following conditions is satisfied.

(b1) $\tilde{\Delta} > 0 \geq -\tilde{r}_2$ and $(F_{30}(\tilde{x}_2) > 0) \vee ((\tilde{x}_1 < \tilde{x}_5 < \tilde{x}_2) \wedge (F_{30}(\tilde{x}_2) F_{30}(\tilde{x}_5) = 0))$;
(b2) $\tilde{\Delta} > 0 > \tilde{r}_2$, $\min\{F_{30}(0), F_{30}(\tilde{x}_2)\} < 0$, and

$((0 < \tilde{x}_5 < \tilde{x}_2) \wedge (F_{30}(\tilde{x}_5) F_{30}(0) F_{30}(\tilde{x}_2) = 0)) \vee (F_{30}(0) F_{30}(\tilde{x}_2) < 0)$.

(c) System (1.2) has two GA-BA-BT equilibria if and only if one of the following conditions is satisfied.

(c1) $\tilde{\Delta} > 0 \geq -\tilde{r}_2$ and $(\tilde{x}_1 < \tilde{x}_5 < \tilde{x}_2) \wedge (F_{30}(\tilde{x}_2) F_{30}(\tilde{x}_5) < 0)$;
(c2) $\tilde{\Delta} > 0 > \tilde{r}_2$ and $(0 < \tilde{x}_5 < \tilde{x}_2) \wedge (F_{30}(\tilde{x}_5) \cdot \max\{F_{30}(0), F_{30}(\tilde{x}_2)\} < 0)$.

Proof If $\tilde{\Delta} \leq 0$, we obtain that $F_{30}(x)$ is a decreasing function and has exactly one real zero. Since $F_{30}(\tilde{x}_1) < 0$, the zero is always less than $\tilde{x}_1$. Now, we assume $\tilde{\Delta} > 0$, then the largest zero of $F'_{30}(x)$ is $\tilde{x}_5$. Hence, the maximum of $F_{30}(x)$ in $(\tilde{x}_4, \infty)$ is achieved at $x = \tilde{x}_5$. Moreover, the cubic polynomial $F_{30}(x)$ is concave down (i.e.,

$F_{30}''(x) < 0$) and it has at most two zeros in $(\tilde{x}_4, \infty)$. If $\tilde{r}_2 \geq 0$, then $\tilde{x}_1 \geq \tilde{x}_4 \geq 0$. Recall that $F_{30}(\tilde{x}_1) < 0$. It follows from intermediate value theorem that $F_{30}(x)$ has no zero in $(\tilde{x}_1, \tilde{x}_2)$ if and only if

$$(\tilde{x}_5 \leq \tilde{x}_1) \vee (F_{30}(\tilde{x}_5) < 0) \vee ((\tilde{x}_5 \geq \tilde{x}_2) \wedge (F_{30}(\tilde{x}_2) \leq 0)),$$

one zero in $(\tilde{x}_1, \tilde{x}_2)$ if and only if $(F_{30}(\tilde{x}_2) > 0) \vee ((\tilde{x}_1 < \tilde{x}_5 < \tilde{x}_2) \wedge (F_{30}(\tilde{x}_2)F_{30}(\tilde{x}_5) = 0))$, and two zeros in $(\tilde{x}_1, \tilde{x}_2)$ if and only if $(\tilde{x}_1 < \tilde{x}_5 < \tilde{x}_2) \wedge (F_{30}(\tilde{x}_2)F_{30}(\tilde{x}_5) < 0)$.

If $\tilde{r}_2 < 0$, then $\tilde{x}_1 < \tilde{x}_4 < \min\{0, \tilde{x}_5\}$. We obtain from $F_{30}(\tilde{x}_1) < 0$ that $F_{30}(x)$ has at least one zero in $(-\infty, \tilde{x}_1)$. It follows from intermediate value theorem that $F_{30}(x)$ has no zero in $(0, \tilde{x}_2)$ if and only if

$$(\min\{F_{30}(0), F_{30}(\tilde{x}_2)\} \geq 0) \vee (\max\{F_{30}(0), F_{30}(\tilde{x}_2), \tilde{x}_5(\tilde{x}_2 - \tilde{x}_5)\} \leq 0) \vee (F_{30}(\tilde{x}_5) < 0),$$

one zero in $(0, \tilde{x}_2)$ if and only if

$$((0 < \tilde{x}_5 < \tilde{x}_2) \wedge (F_{30}(\tilde{x}_5)F_{30}(0)F_{30}(\tilde{x}_2) = 0 > \min\{F_{30}(0), F_{30}(\tilde{x}_2)\})) \vee (F_{30}(0)F_{30}(\tilde{x}_2) < 0),$$

and two zeros in $(0, \tilde{x}_2)$ if and only if $(0 < \tilde{x}_5 < \tilde{x}_2) \wedge (F_{30}(\tilde{x}_5) \cdot \max\{F_{30}(0), F_{30}(\tilde{x}_2)\} < 0)$. $\square$

Case III (critical GA-BA competition): $r_1 = \alpha\beta$.
Denote

$$\tilde{x}_6 = \frac{\tilde{r}_0}{r_2(r_1 - m_1 - \beta)}. \tag{2.13}$$

Theorem 2.6 *Assume the competition between GA and BA is critical, that is, $r_1 = \alpha\beta$. System (1.2) admits at most one GA-BA-BT equilibrium. Let $\tilde{x}_1$, $\tilde{x}_2$, and $\tilde{x}_6$ be defined as in (2.9) and (2.13), respectively.*

(a) If $(r_1 = \beta + m_1) \vee (\tilde{x}_6 \leq \tilde{x}_1) \vee (\tilde{x}_6 \leq 0) \vee (\tilde{x}_6 \geq \tilde{x}_2)$, then system (1.2) has no GA-BA-BT equilibrium.
(b) If $(r_1 \neq \beta + m_1) \wedge (\max\{0, \tilde{x}_1\} < \tilde{x}_6 < \tilde{x}_2)$, then system (1.2) admits a unique GA-BA-BT equilibrium.

Proof In this case, we have

$$F_{30}(x) = m_1[r_2(\beta + m_1 - r_1)x - \tilde{r}_2(\beta - r_1) - m_1 r_2].$$

If $r_1 = \beta + m_1$, then $F_{30}(x) = -m_1^2 m_2$ is a negative constant, which implies that no GA-BA-BT equilibrium exists. If $r_1 \neq \beta + m_1$, then $F_{30}(x)$ has the unique zero $\tilde{x}_6$. Hence, a unique GA-BA-BT equilibrium exists provided that $\max\{0, \tilde{x}_1\} < \tilde{x}_6 < \tilde{x}_2$. $\square$

Finally, we investigate the existence of the positive (GA-BA-BT-CT) equilibrium $E^* = (G_A^*, B_A^*, B_T^*, C_T^*)$, where

$$G_A^* = 1 - \alpha B_A^* > 0, \quad C_T^* = 1 + \frac{\sigma B_T^*}{r_3}, \quad B_A^* = \frac{\theta B_T^*}{m_1}(r_2^* B_T^* - \hat{r}_2) > 0, \tag{2.14}$$

and B_T^* is a positive zero of the polynomial

$$F_4(x) = \theta(r_2^*)^2(r_1 - \alpha\beta)x^3 - 2\theta r_2^* \hat{r}_2(r_1 - \alpha\beta)x^2$$
$$+ [\theta(r_1 - \alpha\beta)\hat{r}_2^2 + m_1 r_2^*(\beta + m_1 - r_1)]x + m_1\hat{r}_0 \qquad (2.15)$$

with

$$r_2^* = r_2 + \gamma\sigma/r_3, \;\; \hat{r}_2 = r_2 - m_2 - \gamma, \;\; \hat{r}_1 = r_1 - m_1 - \beta, \;\; \hat{r}_0 = \hat{r}_1\hat{r}_2 - m_1 m_2. \qquad (2.16)$$

The polynomial $F_4(x)$ is an extension of the polynomial $F_{30}(x)$ in (2.6) with r_2 and $\tilde{r}_2$ replaced with r_2^* and $\hat{r}_2$, respectively. In particular, if $\gamma = 0$, then r_2^*, $\hat{r}_2$, and $F_4(x)$ reduce to r_2, $\tilde{r}_2$, and $F_{30}(x)$, respectively. Using a similar argument as in the study of GA-BA-BT equilibrium, we may introduce

$$\hat{x}_1 = \frac{\hat{r}_2}{r_2^*}, \;\; \hat{x}_2 = \frac{\hat{r}_2 + \sqrt{\hat{r}_2^2 + 4m_1 r_2^*/(\alpha\theta)}}{2r_2^*} > \max\{0, \hat{x}_1\}, \qquad (2.17)$$

$$\hat{x}_3 = \frac{r_1 + \alpha(m_1 - r_1)}{\alpha^2\theta m_2}, \;\; \hat{x}_4 = \frac{2\hat{r}_2}{3r_2^*} = \frac{2}{3}\hat{x}_1. \qquad (2.18)$$

For the strong GA-BA competition case (i.e., $r_1 < \alpha\beta$), we define

$$\hat{\Delta} = \hat{r}_2^2 + \frac{3m_1 r_2^*(\beta + m_1 - r_1)}{\theta(\alpha\beta - r_1)}. \qquad (2.19)$$

If $\hat{\Delta} > 0$, we shall denote the largest zero of $F_4'(x)$ as

$$\hat{x}_5 = \hat{x}_4 + \frac{\sqrt{\hat{\Delta}}}{3r_2^*} = \frac{2\hat{r}_2 + \sqrt{\hat{r}_2^2 + \frac{3m_1 r_2^*(\beta + m_1 - r_1)}{\theta(\alpha\beta - r_1)}}}{3r_2^*} > \hat{x}_4. \qquad (2.20)$$

For the critical GA-BA competition case (i.e., $r_1 = \alpha\beta$), we define

$$\hat{x}_6 = \frac{\hat{r}_0}{r_2^* \hat{r}_1}, \qquad (2.21)$$

provide $\hat{r}_1 \neq 0$. The existence theory of the positive equilibrium in strong, weak, and critical GA-BA competition cases is given in the following theorem.

Theorem 2.7 *Let $\hat{r}_0$, $\hat{r}_2$, $\hat{x}_1$, $\hat{x}_2$, $\hat{x}_3$, $\hat{\Delta}$, $\hat{x}_5$, and $\hat{x}_6$ be defined as in (2.16), (2.17), (2.18), (2.19), (2.20), and (2.21), respectively.*

Case I. Assume the competition between GA and BA is weak, that is, $r_1 > \alpha\beta$. System (1.2) admits at most one GA-BA-BT-CT equilibrium.

(a) *If $((\hat{r}_2 < 0) \wedge (\hat{r}_0 \geq 0)) \vee (\hat{x}_3 \leq \hat{x}_2)$, then system (1.2) has no GA-BA-BT-CT equilibrium.*

(b) *If $((\hat{r}_2 \geq 0) \vee (\hat{r}_0 < 0)) \wedge (\hat{x}_3 > \hat{x}_2)$, then system (1.2) admits a unique GA-BA-BT-CT equilibrium.*

Case II. Assume the competition between GA and BA is strong, that is, $r_1 < \alpha\beta$. System (1.2) admits at most two GA-BA-BT-CT equilibria.

(a) *System (1.2) has no GA-BA-BT-CT equilibrium if and only if one of the following conditions is satisfied.*

(a1) *$\hat{\Delta} > 0 \geq -\hat{r}_2$ and $(\hat{x}_5 \leq \hat{x}_1) \vee (F_4(\hat{x}_5) < 0) \vee ((\hat{x}_5 \geq \hat{x}_2) \wedge (F_4(\hat{x}_2) \leq 0))$;*
(a2) *$\hat{\Delta} > 0 > \hat{r}_2$ and*

$$(\min\{F_4(0), F_4(\hat{x}_2)\} \geq 0) \vee (\max\{F_4(0), F_4(\hat{x}_2), \hat{x}_5(\hat{x}_2 - \hat{x}_5)\} \leq 0) \vee (F_4(\hat{x}_5) < 0);$$

(a3) *$\hat{\Delta} \leq 0$.*

(b) *System (1.2) has a unique GA-BA-BT-CT equilibrium if and only if one of the following conditions is satisfied.*

(b1) *$\hat{\Delta} > 0 \geq -\hat{r}_2$ and $(F_4(\hat{x}_2) > 0) \vee ((\hat{x}_1 < \hat{x}_5 < \hat{x}_2) \wedge (F_4(\hat{x}_2)F_4(\hat{x}_5) = 0))$;*
(b2) *$\hat{\Delta} > 0 > \hat{r}_2$, $\min\{F_4(0), F_4(\hat{x}_2)\} < 0$, and*

$$((0 < \hat{x}_5 < \hat{x}_2) \wedge (F_4(\hat{x}_5)F_4(0)F_4(\hat{x}_2) = 0)) \vee (F_4(0)F_4(\hat{x}_2) < 0).$$

(c) *System (1.2) has two GA-BA-BT-CT equilibria if and only if one of the following conditions is satisfied.*

(c1) *$\hat{\Delta} > 0 \geq -\hat{r}_2$ and $(\hat{x}_1 < \hat{x}_5 < \hat{x}_2) \wedge (F_4(\hat{x}_2)F_4(\hat{x}_5) < 0)$;*
(c2) *$\hat{\Delta} > 0 > \hat{r}_2$ and $(0 < \hat{x}_5 < \hat{x}_2) \wedge (F_4(\hat{x}_5) \cdot \max\{F_4(0), F_4(\hat{x}_2)\} < 0)$.*

Case III. Assume the competition between GA and BA is critical, that is, $r_1 = \alpha\beta$. System (1.2) admits at most one GA-BA-BT-CT equilibrium.

(a) *If $(\hat{r}_1 = 0) \vee (\hat{x}_6 \leq \hat{x}_1) \vee (\hat{x}_6 \leq 0) \vee (\hat{x}_6 \geq \hat{x}_2)$, then system (1.2) has no GA-BA-BT-CT equilibrium.*
(b) *If $(\hat{r}_1 \neq 0) \wedge (\max\{0, \hat{x}_1\} < \hat{x}_6 < \hat{x}_2)$, then system (1.2) admits a unique GA-BA-BT-CT equilibrium.*

Proof The results can be proved via a similar argument as in the proof of Theorems 2.4, 2.5, and 2.6. □

3 Stability analysis

In this section, we investigate the local asymptotic stability of each equilibrium of model (1.2). We are also interested in the multi-stability of equilibria of (1.2), where the final population size of lizard species is determined by the initial conditions.

First, we observe from the last equation of (1.2) that $C_T'(t) \geq r_3 C_T(1 - C_T)$. If $C_T(0) > 0$, then we obtain from the comparison principle

$$\liminf_{t \to \infty} C_T(t) \geq 1.$$

Hence, the trivial equilibrium $E_0 = (0, 0, 0, 0)$, the GA equilibrium $E_{10} = (1, 0, 0, 0)$, the BA-BT equilibrium $E_{02} = (0, \hat{B}_A, \hat{B}_T, 0)$, and the GA-BA-BT equilibrium $E_{30} = (\tilde{G}_A, \tilde{B}_A, \tilde{B}_T, 0)$ (if exists) are always unstable.

Next, we calculate the Jacobian matrix of (1.2) about the CT equilibrium $E_{01} = (0, 0, 0, 1)$ as

$$
J_{01} = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & r_1 - m_1 & m_2\theta & 0 \\ 0 & m_1/\theta & r_2 - m_2 - \gamma & 0 \\ 0 & 0 & \sigma & -r_3 \end{pmatrix}.
$$

Since 1 is an eigenvalue of J_{01}, E_{01} is always unstable.

Theorem 3.1 *Let $\hat{r}_2$, $\hat{r}_1$ and $\hat{r}_0$ be defined in (2.16). The unique GA-CT equilibrium $E_{20} = (1, 0, 0, 1)$ of system (1.2) is locally asymptotically stable if $\hat{r}_1 + \hat{r}_2 < 0 < \hat{r}_0$ and unstable if either $\hat{r}_1 + \hat{r}_2 > 0$ or $\hat{r}_0 < 0$.*

Proof The Jacobian matrix of (1.2) about the GA-CT equilibrium $E_{20} = (1, 0, 0, 1)$ is given by

$$
J_{20} = \begin{pmatrix} -1 & -\alpha & 0 & 0 \\ 0 & r_1 - m_1 - \beta & m_2\theta & 0 \\ 0 & m_1/\theta & r_2 - m_2 - \gamma & 0 \\ 0 & 0 & \sigma & -r_3 \end{pmatrix}.
$$

Note that J_{20} is a block lower tridiagonal matrix and it has two negative eigenvalues -1 and $-r_3$. Recall the definitions of $\hat{r}_2, \hat{r}_1$ and $\hat{r}_0$ in (2.16). The other two eigenvalues of J_{20} are the eigenvalues of the two-dimensional matrix

$$
\begin{pmatrix} \hat{r}_1 & m_2\theta \\ m_1/\theta & \hat{r}_2 \end{pmatrix}.
$$

The trace and the determinant of the above matrix are $\hat{r}_1 + \hat{r}_2$ and $\hat{r}_0$, respectively. Hence, E_{20} is locally asymptotically stable if $\hat{r}_1 + \hat{r}_2 < 0 < \hat{r}_0$ and unstable if either $\hat{r}_1 + \hat{r}_2 > 0$ or $\hat{r}_0 < 0$. $\square$

Now, we assume that the BA-BT-CT equilibrium $E_{03} = (0, \bar{B}_A, \bar{B}_T, \bar{C}_T)$ exists and calculate the Jacobian matrix of (1.2) about E_{03} as follows.

$$
J_{03} = \begin{pmatrix} 1 - \alpha\bar{B}_A & 0 & 0 & 0 \\ -\beta\bar{B}_A & -r_1\bar{B}_A - m_2\theta\bar{B}_T/\bar{B}_A & m_2\theta & 0 \\ 0 & m_1/\theta & -r_2\bar{B}_T - m_1\bar{B}_A/(\theta\bar{B}_T) & -\gamma\bar{B}_T \\ 0 & 0 & \sigma\bar{C}_T & -r_3\bar{C}_T \end{pmatrix}.
$$

We shall make use of the following lemma.

Lemma 3.1 *Let A be a real square matrix of dimension three such that $A_{ii} < 0$ for $i = 1, 2, 3$. Let (i_1, i_2, i_3) be any given permutation of the indices $(1, 2, 3)$. If $A_{i_1 i_3} = A_{i_3 i_1} = 0$ and $A_{i_1 i_1} A_{i_2 i_2} > A_{i_1 i_2} A_{i_2 i_1} > 0 > A_{i_2 i_3} A_{i_3 i_2}$, then all eigenvalues of A have negative real parts.*

Proof Because of symmetry, we only need to consider the first case when $(i_1, i_2, i_3) = (1, 2, 3)$. By assumption, we have $A_{11} A_{22} > A_{12} A_{21} > 0 > A_{23} A_{32}$. Denote $\rho_{12} := A_{11} A_{22} - A_{12} A_{21} > 0$. Then the characteristic polynomial of A is

$$
\begin{aligned}
\det(\lambda I - A) &= \det \begin{pmatrix} \lambda - A_{11} & -A_{12} & 0 \\ -A_{21} & \lambda - A_{22} & -A_{23} \\ 0 & -A_{32} & \lambda - A_{33} \end{pmatrix} \\
&= (\lambda - A_{11})((\lambda - A_{22})(\lambda - A_{33}) - A_{23} A_{32}) - A_{12} A_{21} (\lambda - A_{33}) \\
&= \lambda^3 + a_2 \lambda^2 + a_1 \lambda + a_0,
\end{aligned}
$$

where

$$
\begin{aligned}
a_2 &= -A_{11} - A_{22} - A_{33} > -A_{11} - A_{33} > 0, \\
a_1 &= A_{11} A_{22} + A_{22} A_{33} + A_{33} A_{11} - A_{12} A_{21} - A_{23} A_{32} > \rho_{12} - A_{23} A_{32} > 0, \\
a_0 &= -A_{33} \rho_{12} + A_{11} A_{23} A_{32} > 0.
\end{aligned}
$$

Since $a_2 a_1 - a_0 > (-A_{11} - A_{33})(\rho_{12} - A_{23} A_{32}) - (-A_{33} \rho_{12} + A_{11} A_{23} A_{32}) > 0$, we obtain from the Routh-Hurwitz criterion that all eigenvalues of A have negative real parts. $\qquad\square$

Theorem 3.2 *Assume that the BA-BT-CT equilibrium $E_{03} = (0, \bar{B}_A, \bar{B}_T, \bar{C}_T)$ exists. If $\alpha \bar{B}_A > 1$, then E_{03} is locally asymptotically stable. If $\alpha \bar{B}_A < 1$, then E_{03} is unstable.*

Proof It follows from Lemma 3.1 that the Jacobian matrix J_{03} has an eigenvalue $1 - \alpha \bar{B}_A$ and three additional eigenvalues with negative real parts. Hence, E_{03} is locally asymptotically stable if $\alpha \bar{B}_A > 1$ and unstable if $\alpha \bar{B}_A < 1$. $\qquad\square$

Finally, we assume that the positive (GA-BA-BT-CT) equilibrium exists and calculate the Jacobian matrix of (1.2) about the positive equilibrium as follows.

$$
J_4 = \begin{pmatrix} -G_A & -\alpha G_A & 0 & 0 \\ -\beta B_A & -r_1 B_A - m_2 \theta B_T / B_A & m_2 \theta & 0 \\ 0 & m_1/\theta & -r_2 B_T - m_1 B_A/(\theta B_T) & -\gamma B_T \\ 0 & 0 & \sigma C_T & -r_3 C_T \end{pmatrix} \tag{3.1}
$$

Lemma 3.2 *Given an open set $\Omega \subset \mathbb{R}^n$ and $f = (f_1, \cdots, f_n)^T \in C^1(\Omega, \mathbb{R}^n)$ such that $f(u^*) = 0$ for some $u^* \in \Omega$. Fix $k \in \{1, \cdots, n\}$. Assume that there exists a parametric curve $u \in C^1((x_1, x_2), \Omega)$ such that $u(x^*) = u^*$ for some $x^* \in (x_1, x_2)$ and $f_i(u(x)) = 0$ for all $x \in (x_1, x_2)$ and $i \neq k$. Let $J \in C(\mathbb{R}^n, \mathbb{R}^{n \times n})$ be the derivative of f; namely, $J_{ij} = \partial f_i / \partial u_j \in C(\mathbb{R}^n, \mathbb{R})$ for $1 \leq i, j \leq n$. Denote by*

$J^{(k)} \in C(\mathbb{R}^n, \mathbb{R}^{(n-1)\times(n-1)})$ *the submatrix of J obtained by removing the k-th row and k-th column of J. If $J^{(k)}(u^*)$ is invertible and $u'_k(x^*) \neq 0$, then*

$$\det(J(u^*)) = \det(J^{(k)}(u^*))g_k(x^*)/u'_k(x^*),$$

where

$$g_k(x) = \frac{d}{dx} f_k(u(x)) = \sum_{i=1}^{n} J_{ki}(u(x))u'_i(x).$$

Proof By permutation, we may assume without loss of generality $k = n$. Denote $\mathbf{A} = J^{(n)}(u^*)$. We can use block matrices to express

$$J(u^*) = \begin{pmatrix} \mathbf{A} & \mathbf{w} \\ \mathbf{v}^T & J_{nn} \end{pmatrix},$$

where $\mathbf{v} = (v_1, \cdots, v_{n-1}) \in \mathbb{R}^{n-1}$ and $\mathbf{w} = (w_1, \cdots, w_{n-1}) \in \mathbb{R}^{n-1}$ are column vectors such that $v_j = J_{nj}$ and $w_j = J_{jn}$ for $j = 1, \cdots, n-1$. Since $f_i(u(x)) = 0$ for all $x \in (x_1, x_2)$ and $i \neq n$, we have

$$\sum_{j=1}^{n} J_{ij}(u^*)u'_j(x^*) = \frac{d}{dx} f_i(u(x^*)) = 0, \quad i = 1, \cdots, n-1.$$

The above system can be written in matrix form as

$$\mathbf{A} \begin{pmatrix} u'_1(x^*) \\ \cdots \\ u'_{n-1}(x^*) \end{pmatrix} = -\mathbf{w}u'_n(x^*).$$

By assumption, $\mathbf{A}$ is invertible. Consequently,

$$g_n(x^*) = J_{nn}u'_n(x^*) + \mathbf{v}^T \begin{pmatrix} u'_1(x^*) \\ \cdots \\ u'_{n-1}(x^*) \end{pmatrix} = [J_{nn} - \mathbf{v}^T \mathbf{A}^{-1} \mathbf{w}]u'_n(x^*).$$

The desired formula can be obtained by taking determinants on both sides of the following identity

$$\begin{pmatrix} \mathbf{A} & \mathbf{w} \\ \mathbf{v}^T & J_{nn} \end{pmatrix} \begin{pmatrix} \mathbf{I} & -\mathbf{A}^{-1}\mathbf{w} \\ \mathbf{0} & 1 \end{pmatrix} = \begin{pmatrix} \mathbf{A} & 0 \\ \mathbf{v}^T & J_{nn} - \mathbf{v}^T \mathbf{A}^{-1} \mathbf{w} \end{pmatrix}.$$

The proof is complete. □

In view of (2.14), we can choose a parametric curve as

$$B_T = x, \quad C_T = 1 + \frac{\sigma x}{r_3}, \quad B_A = \frac{\theta x}{m_1}(r_2^* x - \hat{r}_2), \quad G_A = 1 - \frac{\alpha \theta x}{m_1}(r_2^* x - \hat{r}_2).$$

Along this parametric curve, the right-hand sides of the first, third, and fourth equations in (1.2) vanish, while the right-hand side of the second equation becomes

$$f(x) = -\frac{\theta}{m_1^2} x F_4(x),$$

where $F_4(x)$ is given in (2.15). If $E^* = (G_A^*, B_A^*, B_T^*, C_T^*)$ is a positive equilibrium, then we obtain $F_4(B_T^*) = 0$, $f'(B_T^*) = -\theta B_T^* F_4'(B_T^*)/m_1^2$, and $B_A'(B_T^*) = \theta(2r_2^* B_T^* - \hat{r}_2)/m_1$. It then follows from (3.1) and Lemma 3.2 that the determinant of the Jacobian about E^* is

$$\det(J_4^*) = \det(J_4^{(2)}(E^*)) f'(B_T^*)/B_A'(B_T^*)$$
$$= G_A^* \left[(r_2 r_3 + \sigma \gamma) B_T^* C_T^* + \frac{m_1 r_3 B_A^* C_T^*}{\theta B_T^*} \right] \frac{B_T^* F_4'(B_T^*)}{m_1(2r_2^* B_T^* - \hat{r}_2)}.$$

By the last term of (2.14), we have $r_2^* B_T^* - \hat{r}_2 = m_1 B_A^*/(\theta B_T^*)$, thus

$$2r_2^* B_T^* - \hat{r}_2 = r_2^* B_T^* + \frac{m_1 B_A^*}{\theta B_T^*}.$$

Hence, we obtain from $r_2 r_3 + \sigma \gamma = r_3 r_2^*$ and the above two equalities that

$$\det(J_4^*) = \frac{r_3}{m_1} G_A^* B_T^* C_T^* F_4'(B_T^*). \tag{3.2}$$

The following theorem shows that the bistability of two positive equilibria or bistability of E_{20} and E^* cannot occur.

Theorem 3.3 *If there exist two positive equilibria $E^* = (G_A^*, B_A^*, B_T^*, C_T^*)$ and $E^{**} = (G_A^{**}, B_A^{**}, B_T^{**}, C_T^{**})$ with $B_T^{**} > B_T^*$, then E^{**} is unstable. If the GA-CT equilibrium E_{20} exists and is locally asymptotically stable, then either there exists no positive equilibrium or there exists a unique positive equilibrium that is unstable.*

Proof Let $E^* = (G_A^*, B_A^*, B_T^*, C_T^*)$ and $E^{**} = (G_A^{**}, B_A^{**}, B_T^{**}, C_T^{**})$ be two positive equilibria with $B_T^{**} > B_T^*$. We obtain from Theorem 2.7 that $r_1 < \alpha\beta$ and $F_4'(B_T^{**}) < 0$. Let J_4^{**} be the Jacobian matrix corresponding to E^{**}. By (3.2), we have $\det(J_4^{**}) < 0$, and hence, J_4^{**} has at least one positive eigenvalue. This proves that E^{**} is unstable.

If the GA-CT equilibrium E_{20} exists and is locally asymptotically stable, then we obtain from Theorem 3.1 and (2.16) that $\hat{r}_0 \geq 0$, $\hat{r}_1 < 0$, and $\hat{r}_2 < 0$. For the weak GA-BA competition case ($r_1 > \alpha\beta$), we obtain from Theorem 2.7 that no positive equilibrium exists. For the critical GA-BA competition case ($r_1 = \alpha\beta$), we obtain

from (2.21) that $\hat{x}_6 < 0$, and again there exists no positive equilibrium. For the strong GA-BA competition case ($r_1 < \alpha\beta$), we obtain from (2.15) that $F_4(0) = m_1\hat{r}_0 > 0$ and the leading coefficient of $F_4(x)$ is negative. Moreover, it follows from (2.17) and (2.18) that $\hat{x}_1 < \hat{x}_4 < 0$. Note that $\hat{x}_4$ is the turning point of $F_4(x)$. We conclude that either $F_4(x)$ has no zero in $(0, \hat{x}_2)$ or a unique zero in $(0, \hat{x}_2)$ with a negative slope. That is, if a positive equilibrium $E^* = (G_A^*, B_A^*, B_T^*, C_T^*)$ exists, then it is unique and $F_4'(B_T^*) < 0$. By (3.2), we have $\det(J_4^*) < 0$, and hence, J_4^* has at least one positive eigenvalue. This proves that E^* is unstable. $\qquad\square$

Now, we provide a sufficient condition for a general tri-diagonal matrix of the fourth dimension to be Hurwitz (i.e., all eigenvalues have negative real parts).

Lemma 3.3 *Let $A \in \mathbb{R}^{4\times 4}$ be a tri-diagonal matrix such that $A_{ij} = 0$ for $|i - j| > 1$. We write*

$$A = \begin{pmatrix} -a_1 & A_{12} & 0 & 0 \\ A_{21} & -a_2 - a_3 & A_{23} & 0 \\ 0 & A_{32} & -a_4 & A_{34} \\ 0 & 0 & A_{43} & -a_5 \end{pmatrix},$$

and assume a_1, a_2, a_3, a_4, and a_5 are positive. Furthermore, we assume $A_{12}A_{21} > 0$, $\mu = a_1a_2 - A_{12}A_{21} \geq 0$, $\nu = a_3a_4 - A_{23}A_{32} \geq 0$, and $\xi = -A_{34}A_{43} > 0$. Then A is a Hurwitz matrix; namely, all eigenvalues of A have negative real parts.

Proof The characteristic polynomial of A is

$$\det(\lambda I - A) = \det\begin{pmatrix} \lambda + a_1 & -A_{12} & 0 & 0 \\ -A_{21} & \lambda + a_2 + a_3 & -A_{23} & 0 \\ 0 & -A_{32} & \lambda + a_4 & -A_{34} \\ 0 & 0 & -A_{43} & \lambda + a_5 \end{pmatrix}$$

$$= (\lambda + a_1)(\lambda + a_2 + a_3)((\lambda + a_4)(\lambda + a_5) - A_{34}A_{43}) - A_{23}A_{32}$$
$$(\lambda + a_1)(\lambda + a_5) - A_{12}A_{21}((\lambda + a_4)(\lambda + a_5) - A_{34}A_{43})$$
$$= \lambda^4 + c_3\lambda^3 + c_2\lambda^2 + c_1\lambda + c_0,$$

where

$c_3 = a_1 + a_2 + a_3 + a_4 + a_5,$
$c_2 = \mu + \nu + \xi + a_1a_3 + a_1a_4 + a_2a_4 + (a_1 + a_2 + a_3 + a_4)a_5,$
$c_1 = \mu(a_4 + a_5) + \nu(a_1 + a_5) + \xi(a_1 + a_2 + a_3) + (a_1a_3 + a_1a_4 + a_2a_4)a_5,$
$c_0 = \mu a_4a_5 + \nu a_1a_5 + \xi a_1a_3 + \mu\xi.$

It follows from the above expressions that c_3, c_2, c_1, and c_0 are positive. Now, we compute

$$c_3c_2 - c_1 = \mu(a_1 + a_2 + a_3) + \nu(a_2 + a_3 + a_4) + \xi(a_4 + a_5)$$

$$+ (a_1 + a_2 + a_3 + a_4)(a_1a_3 + a_1a_4 + a_2a_4 + a_5c_3),$$

which is also positive. Next, we obtain

$$
\begin{aligned}
c_1(c_3c_2 - c_1) &> \mu(a_4 + a_5)(a_1 + a_2 + a_3 + a_4)a_5c_3 \\
&\quad + \nu(a_1 + a_5)(a_1 + a_2 + a_3 + a_4)a_5c_3 \\
&\quad + \xi(a_1 + a_2 + a_3)(a_1 + a_2 + a_3 + a_4)(a_1a_3 + a_1a_4 + a_2a_4 + a_5c_3) \\
&\quad + \mu\xi[(a_1 + a_2 + a_3)^2 + (a_4 + a_5)^2].
\end{aligned}
$$

Note that

$$
\begin{aligned}
(a_4 + a_5)(a_1 + a_2 + a_3 + a_4)a_5 &> a_4a_5(a_1 + a_2 + a_3 + a_4) + a_5a_4a_5 = a_4a_5c_3, \\
(a_1 + a_5)(a_1 + a_2 + a_3 + a_4)a_5 &> a_1a_5(a_1 + a_2 + a_3 + a_4) + a_5a_1a_5 = a_1a_5c_3,
\end{aligned}
$$

and

$$
\begin{aligned}
&(a_1 + a_2 + a_3)(a_1 + a_2 + a_3 + a_4)(a_1a_3 + a_1a_4 + a_2a_4 + a_5c_3) \\
&\quad > (a_1 + a_2 + a_3)(a_1 + a_2 + a_3 + a_4)a_1a_3 + a_3(a_1 + a_2 + a_3 + a_4)a_1a_4 \\
&\quad\quad + (a_1 + a_2)(a_1 + a_2 + a_3 + a_4)(a_1a_4 + a_2a_4) + (2a_1a_3 + 2a_1a_2)a_5c_3 \\
&\quad > a_1a_3(a_1 + a_2 + a_3 + a_4)^2 + 2a_1a_2a_4(a_1 + a_2 + a_3) + 2a_1a_3a_5c_3 + 2a_1a_2a_5c_3 \\
&\quad > a_1a_3c_3^2 + 2a_1a_2(a_4 + a_5)(a_1 + a_2 + a_3),
\end{aligned}
$$

where in the last inequality, we have made use of the fact $c_3 = a_1 + a_2 + a_3 + a_4 + a_5$. Since $\mu = a_1a_2 - A_{12}A_{21} < a_1a_2$, we obtain from the above inequalities that

$$
\begin{aligned}
c_1(c_3c_2 - c_1) &> \mu a_4a_5c_3^2 + \nu a_1a_5c_3^2 + \xi a_1a_3c_3^2 + 2\xi\mu(a_4 + a_5)(a_1 + a_2 + a_3) \\
&\quad + \mu\xi[(a_1 + a_2 + a_3)^2 + (a_4 + a_5)^2] = c_0c_3^2.
\end{aligned}
$$

It then follows from the Routh-Hurwitz criterion that all eigenvalues of A have negative real parts. This completes the proof. $\qquad\square$

As a direct application of Lemma 3.3, we obtain the local asymptotic stability of the positive (GA-BA-BT-CT) equilibrium when the GA-BA competition is weak or critical.

Theorem 3.4 *If $r_1 \geq \alpha\beta$, then the positive equilibrium $E^* = (G_A^*, B_A^*, B_T^*, C_T^*)$ (if exists) is always locally asymptotically stable.*

Proof The Jacobian matrix in (3.1) satisfies all the conditions of the tri-diagonal matrix in Lemma 3.3. In particular, we choose $a_2 = r_1 B_A^*$ and $a_3 = m_2\theta B_T^*/B_A^*$. Consequently, $\mu = (r_1 - \alpha\beta)G_A^* B_A^* \geq 0$, $\nu = r_2 m_2 \theta (B_T^*)^2/B_A^* > 0$ and $\xi = \gamma\sigma B_T^* C_T^* > 0$. Hence, Lemma 3.3 implies that all eigenvalues of J_4^* have negative real parts and the positive equilibrium E^* is locally asymptotically stable. $\qquad\square$

In conclusion, the trivial equilibrium $E_0 = (0, 0, 0, 0)$, the GA equilibrium $E_{10} = (1, 0, 0, 0)$, the CT equilibrium $E_{01} = (0, 0, 0, 1)$, the BA-BT equilibrium $E_{02} = (0, \hat{B}_A, \hat{B}_T, 0)$, and the GA-BA-BT equilibrium $E_{30} = (\tilde{G}_A, \tilde{B}_A, \tilde{B}_T, 0)$ (if exists) are always unstable. Theorems 3.1, 3.2 and 3.4 provide some sufficient conditions for the stability of the GA-CT equilibrium $E_{20} = (1, 0, 0, 1)$, the BA-BT-CT equilibrium $E_{03} = (0, \bar{B}_A, \bar{B}_T, \bar{C}_T)$, and the positive (GA-BA-BT-CT) equilibrium $E^* = (G_A^*, B_A^*, B_T^*, C_T^*)$. Theorem 3.3 excludes the bistability of two positive equilibria and bistability of E_{20} and E^*. There are only two possibilities of bistability: the bistability of E_{03} and E^*, and the bistability of E_{20} and E_{03}. These results are presented in Table 2 and will be used in the next section for numerical explorations.

4 Numerical simulations

In this section, we use numerical simulations to reveal rich dynamics of system (1.2). It has been demonstrated in (Ji et al. 2022) that the dispersal activity of brown anoles has a significant impact on the coexistence of lizard species. Hence, we choose m_2, the migration rate of brown anoles from the ground to the tree, as a bifurcation parameter. We fix the parameter values as $r_3 = 1.2$, $\beta = 2$, $\gamma = 1.3$, $\sigma = 0.54$, $m_1 = 0.6$, $\theta = 0.42$.

In the first scenario, we choose $r_1 = 3.5$, $r_2 = 3.2$, and $\alpha = 0.9$. From (2.16), we find two constants $m_2^{a_1} < m_2^{a_2}$ such that $\hat{r}_0 > 0$ if and only if $m_2 < m_2^{a_1}$, and $\hat{r}_2 > 0$ if and only if $m_2 < m_2^{a_2}$. Hence, the conditions for Case I.(b) in Theorem 2.7 are satisfied for all $m_2 > 0$. No bifurcation exists in this scenario; see Fig. 2a.

In the second scenario, we choose $r_1 = 1.6$, $r_2 = 2.3$, and $\alpha = 0.9$. There exist $m_2^b < m_2^{b,BP}$ such that if $m_2 < m_2^b$, then the conditions for Case II.(b1) in Theorem 2.7 are satisfied, and if $m_2 \in (m_2^b, m_2^{b,BP})$, then the conditions for Case II.(b2) in Theorem 2.7 are satisfied. In either case, there exists a unique positive equilibrium that is stable. The value $m_2^{b,BP}$ corresponds to the branch point. When $m_2 > m_2^{b,BP}$, the conditions for Case II.(a2) in Theorem 2.7 are satisfied and hence no positive equilibrium exists; see Fig. 2b. In this case, the GA-CT equilibrium E_{20} is the unique stable equilibrium.

In the third scenario, we choose $r_1 = 1.4$, $r_2 = 2.3$, and $\alpha = 1.6$. There exist three threshold values $m_2^{c_1,BP} < m_2^{c_2} < m_2^{c_3,BP}$. If $m_2 < m_2^{c_1,BP}$, then the conditions for Case II.(b1) in Theorem 2.7 are satisfied, and there exists a unique positive equilibrium that is stable. If $m_2 \in (m_2^{c_1,BP}, m_2^{c_2})$, then the conditions for Case II.(c1) in Theorem 2.7 are satisfied, and there exist two positive equilibria; one is stable and the other is unstable. The value $m_2^{c_1,BP}$ corresponds to a branch point. If $m_2 \in (m_2^{c_2}, m_2^{c_3,BP})$, then the conditions for Case II.(c2) in Theorem 2.7 are satisfied, and there also exist two positive equilibria; one is stable and the other is unstable. If $m_2 > m_2^{c_3,BP}$, then the conditions for Case II.(b2) in Theorem 2.7 are satisfied, and there exists a unique positive equilibrium that is unstable. Moreover, the GA-CT equilibrium E_{20} and BA-BT-CT equilibrium E_{03} are bistable for model (1.2). The value $m_2^{c_3,BP}$ corresponds to another branch point; see Fig. 2c.

Table 2 The biological meaning, existence and stability conditions of equilibria of (1.2)

Equilibrium	Biological meaning	Existence condition	Stability condition
$E_0 = (0, 0, 0, 0)$	No species survive	Always exists and is unique	Unstable
$E_{01} = (0, 0, 0, 1)$	Only CT lizards survive	Always exists and is unique	Unstable
$E_{10} = (1, 0, 0, 0)$	Only GA lizards survive	Always exists and is unique	Unstable
$E_{02} = (0, \hat{B}_A, \hat{B}_T, 0)$	Exclusion of GA and CT lizards	Always exists and is unique	Unstable
$E_{20} = (1, 0, 0, 1)$	Exclusion of BA and BT lizards	Always exists and is unique	Theorem 3.1
$E_{03} = (0, \bar{B}_A, \bar{B}_T, \bar{C}_T)$	Exclusion of GA lizards	Theorem 2.3	Theorem 3.2
$E_{30} = (\tilde{G}_A, \tilde{B}_A, \tilde{B}_T, 0)$	Exclusion of CT lizards	Theorems 2.4-2.6	Unstable
$E^* = (G_A^*, B_A^*, B_T^*, C_T^*)$	All species coexist	Theorem 2.7	Theorem 3.4
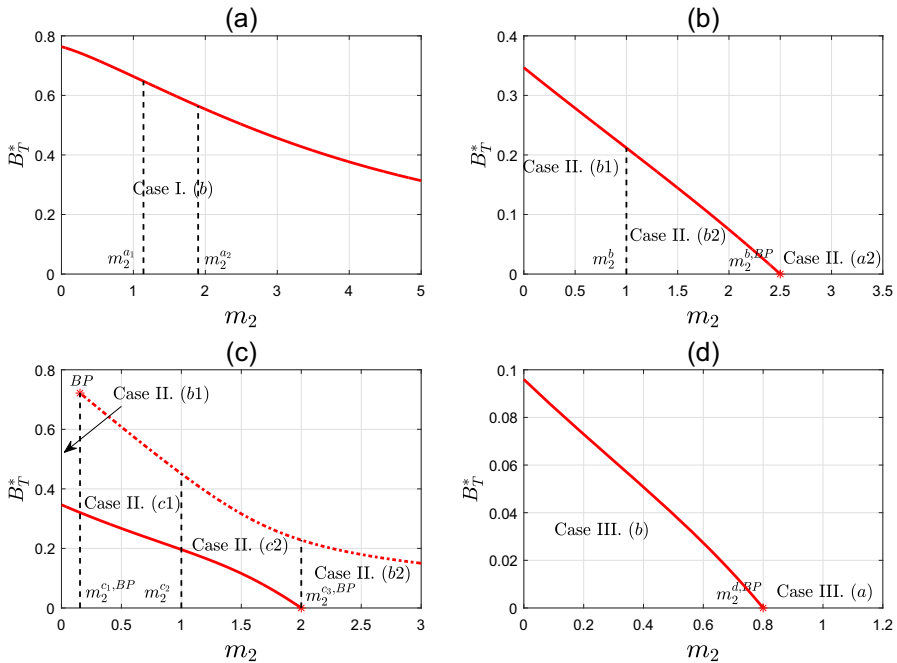
Fig. 2 Illustration of equilibrium BT populations B_T^* versus the bifurcation parameter m_2. The solid (dotted) curve means the positive equilibrium $E^* = (G_A^*, B_A^*, B_T^*, C_T^*)$ is stable (unstable), and the asterisk stands for the branch point (BP). The parameters are chosen as $r_3 = 1.2$, $\beta = 2$, $\gamma = 1.3$, $\sigma = 0.54$, $m_1 = 0.6$, and $\theta = 0.42$. The other parameter values in the four panels are given as follows: **a** $r_1 = 3.5$, $r_2 = 3.2$, $\alpha = 0.9$; **b** $r_1 = 1.6$, $r_2 = 2.3$, $\alpha = 0.9$; **c** $r_1 = 1.4$, $r_2 = 2.3$, $\alpha = 1.6$ and **d** $r_1 = 1.8$, $r_2 = 1.5$, $\alpha = 0.9$

In the fourth scenario, we choose $r_1 = 1.8$, $r_2 = 1.5$, and $\alpha = 0.9$. There exists one branch point at $m_2 = m_2^{d,BP}$. If $m_2 < m_2^{d,BP}$, then the conditions for Case III.(b) in Theorem 2.7 are satisfied, and there exists a unique positive equilibrium that is stable. If $m_2 > m_2^{d,BP}$, then the conditions for Case III.(a) in Theorem 2.7 are satisfied, and system (1.2) has no positive equilibrium; see Fig. 2d. In this case, the GA-CT equilibrium E_{20} is the unique stable equilibrium.

Next, we use Fig. 3 to illustrate the stability regions in the $\sigma - m_2$ plane while fixing the other parameter values as $r_1 = 1.48$, $r_2 = 7.4$, $r_3 = 1.2$, $\alpha = 0.9$, $\beta = 2$, $\gamma = 1.3$, $m_1 = 0.43$, and $\theta = 0.25$. The positive equilibrium E^*, the BA-BT-CT equilibrium E_{03} and the GA-CT equilibrium E_{20} are the unique stable equilibria of (1.2) in the parameter regions D_1, D_2 and D_5, respectively. Both E_{03} and E^* are locally asymptotically stable in D_3, and bistability of E_{20} and E_{03} occurs in the region D_4. The phase orbits of (1.2) in each domain D_i, $i = 1, 2, 3, 4, 5$ are illustrated in Fig. 4.

We now fix $\sigma = 3$ and choose m_2 as the bifurcation parameter to illustrate the stability dynamics in Fig. 5. For convenience, we denote the abscissa of BP_1, LP_1, LP_2, BP_2 and BP_3 by m_2^{b1}, m_2^{l1}, m_2^{l2}, m_2^{b2}, and m_2^{b3}, respectively. There exist two unstable equilibria E_{20} and E_{03} and a unique stable equilibrium E^* when $m_2 \in [0, m_2^{b1})$. As m_2 increases and crosses the branch point m_2^{b1}, another unstable positive equilibrium
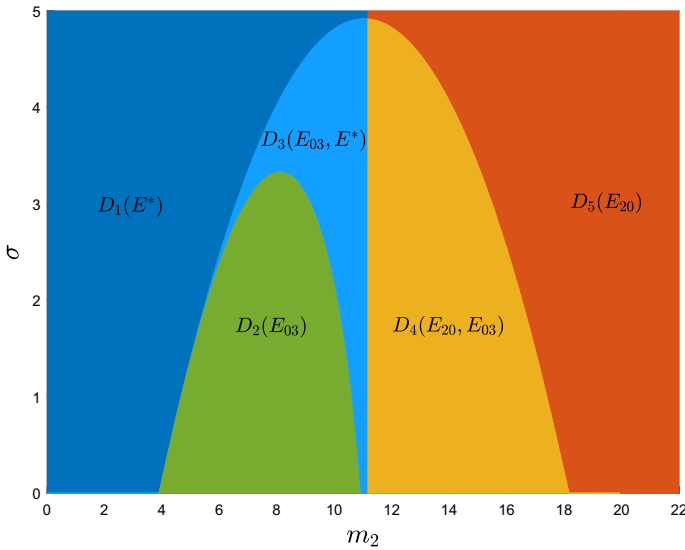
Fig. 3 Stability regions of the equilibria E_{20}, E_{03} and E^* in the plane of m_2 and σ. The other parameters are chosen as $r_1 = 1.48$, $r_2 = 7.4$, $r_3 = 1.2$, $\alpha = 0.9$, $\beta = 2$, $\gamma = 1.3$, $m_1 = 0.43$, and $\theta = 0.25$. The equilibria listed in the brackets are locally asymptotically stable in the corresponding parameter region. The biological meanings of these five regions are listed as follows. D_1: coexistence of all four species; D_2: exclusion of GA lizards; D_3: either coexistence of all four species or exclusion of GA lizards; D_4: either exclusion of GA lizards or exclusion of BA and BT lizards; D_5: exclusion of BA and BT lizards. In particular, bistability dynamics of equilibria occurs when the parameters lie in D_3 or D_4

appears and E_{03} becomes stable for $m_2 \in (m_2^{b1}, m_2^{l1})$. Two positive equilibria coincide at $m_2 = m_2^{l1}$ and $m_2 = m_2^{l2}$. Hence, there does not exist any positive equilibrium when $m_2 \in (m_2^{l1}, m_2^{l2})$. Meanwhile, E_{03} is the unique stable equilibrium in this interval. Note that E_{03} and E^* are bistable for $m_2 \in (m_2^{l2}, m_2^{b2})$. If $m_2 > m_2^{b2}$, E_{20} becomes stable and E_{03} losses its stability at $m_2 = m_2^{b3}$. Hence, E_{20} and E_{03} are bistable for $m_2 \in (m_2^{b2}, m_2^{b3})$ and E_{20} is the unique stable equilibrium of (1.2) for $m_2 > m_2^{b3}$. Moreover, there exists no positive equilibrium when $m_2 > m_2^{b3}$. This agrees with the bifurcation results in Fig. 3.

Inspired by the experimental results in (Pringle et al. 2019), we choose the parameters in domain D_3 of Fig. 3 where E_{03} and E^* are bistable for model (1.2). The basins of attractions for E_{03} and E^* are plotted in Fig. 6. It is observed from Fig. 6a-6c that the basins of attractions are non-monotone in the migration rate m_2. However, it is monotone in the intraguild predation rate σ; see Figures 6d-6f. As σ increases, the basin of attraction for E_{03} is shrinking while the basin of attraction for E^* is enlarging. This coincides with the idea in the keystone-predation model that a larger intraguild predation rate makes it easier to stabilize species coexistence.
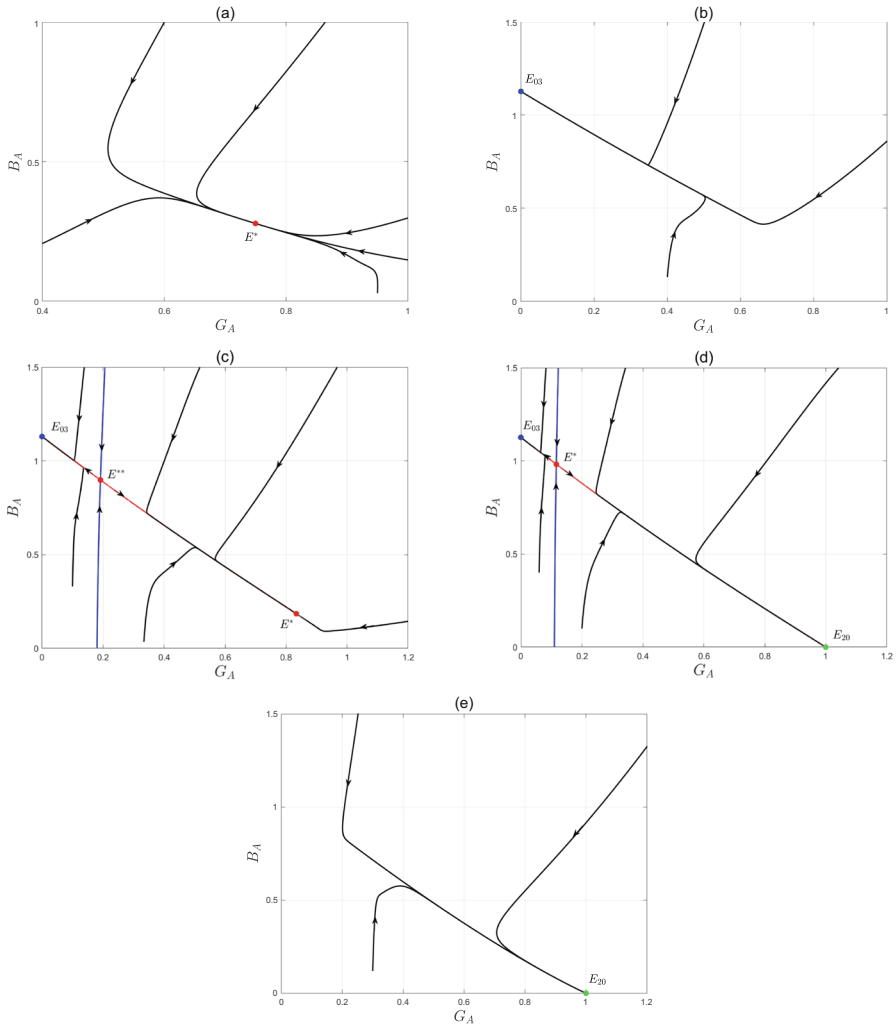
Fig. 4 Phase orbits of system (1.2) projected on the $G_A - B_A$ plane. The panels (a)-(e) correspond to the parameters in the regions D_1-D_5, respectively. In particular, we fix $\sigma = 3$ and choose m_2 to be the following values: (a) $m_2 = 2$; (b) $m_2 = 8$; (c) $m_2 = 10.5$; (d) $m_2 = 12$ and (e) $m_2 = 20$. The red (resp. blue) curves in panels (c) and (d) denote the unstable (resp. stable) manifolds of the saddle equilibria E^{**} and E^*, respectively

5 Data fitting

In this section, we fit model (1.1) to the experimental data from 2011 to 2016, as collected in Supplementary Data 3 (Pringle et al. 2019).
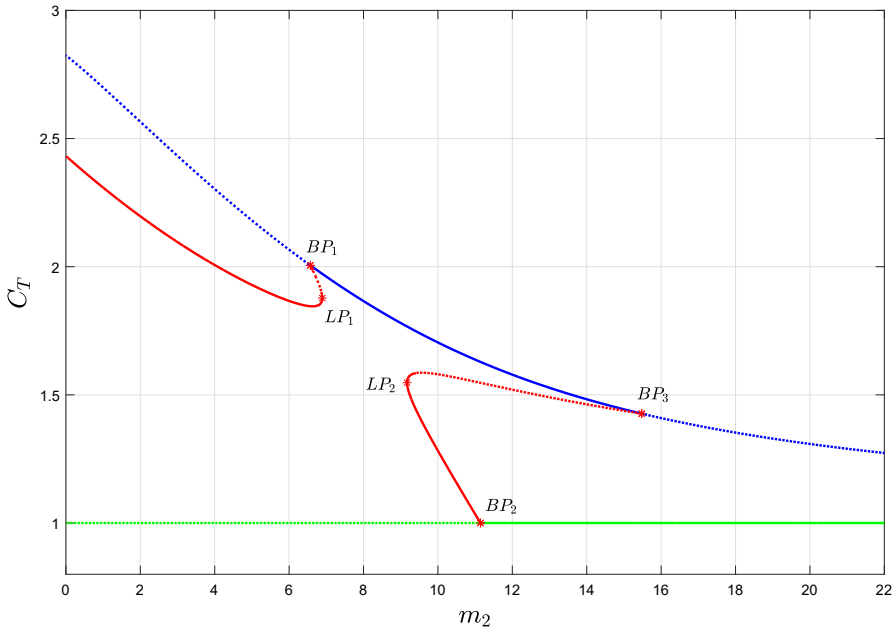
Fig. 5 Bifurcation diagram of CT lizards with m_2 as the bifurcation parameter. The red solid (resp. dotted) curve denotes the stable (resp. unstable) E^*; the blue solid (resp. dotted) curve represents the stable (resp. unstable) E_{03}; the green solid (resp. dotted) curve stands for the stable (resp. unstable) E_{20}. Here, LP_i, $i = 1, 2$, and BP_j, $j = 1, 2, 3$ are the limit points and branch points, respectively. We fix $\sigma = 3$ and choose other parameters as given in Fig. 3. The branch points in Figs. 2 and 5 are different as the parameter values are different
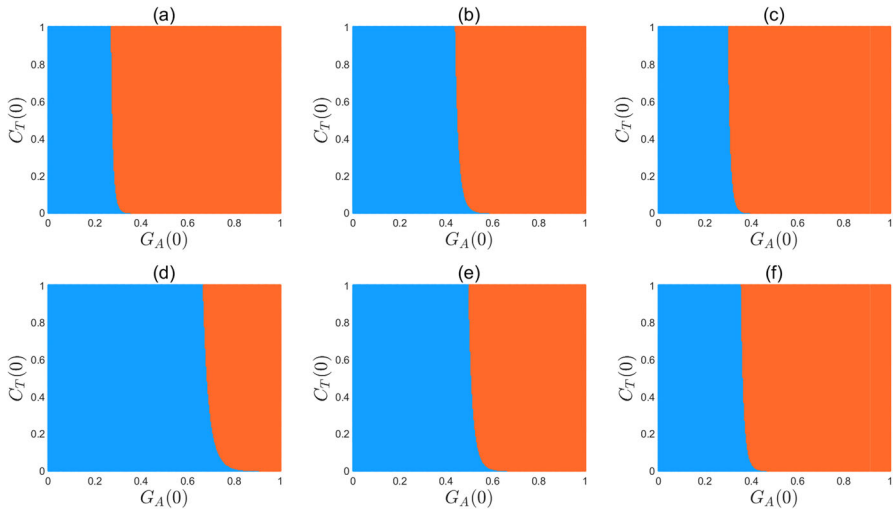
Fig. 6 Basins of attractions of E_{03} and E^* for system (1.2) with initial conditions $B_A(0) = 5$, $B_T(0) = 1$. The blue (resp. red) domain denotes the basin of attraction of E_{03} (resp. E^*). We select **a** $m_2 = 7.8$, $\sigma = 3.5$; **b** $m_2 = 9.4$, $\sigma = 3.5$; **c** $m_2 = 11$, $\sigma = 3.5$; **d** $m_2 = 10.4$, $\sigma = 2.7$; **e** $m_2 = 10.4$, $\sigma = 3.1$ and **f** $m_2 = 10.4$, $\sigma = 3.5$, and other parameters are presented in Fig. 3

5.1 Data

The original data contain population estimates and mean ground proportions for each lizard species, enabling us to calculate the population sizes of GA, BA, BT, and CT lizards on each island annually, as shown in Table 3. Specifically, we calculate the population sizes of BT and CT lizards by multiplying the population estimate by the mean ground proportion. For GA and BA lizards, we subtract the mean ground proportion from one and multiply the result with the population estimate to determine their population sizes.

We use data from the following four islands to fit our model and estimate its parameters.

- Island 5. No GA or CT lizards are present on Island 5. We will estimate the carrying capacities and movement rates of BA and BT lizards, respectively. The estimated parameter values will be used as the baseline values.
- Island White Bay Cay. The CT lizards are introduced to the ecosystem of BA and BT lizards. By comparing the estimated movement rates to baseline values from Island 5, we analyze how the movement behaviors of BA and BT lizards change due to the CT lizards invasion.
- Island 1. Both GA and CT lizards are introduced to the ecosystem of BA and BT lizards. All lizard species persist and coexist.
- Island 926. Similar as on Island 1, both GA and CT lizards are introduced to the biosystem of BA and BT lizards. However, the GA lizards invasion fails, leading to their eventual extinction.

5.2 Intrinsic growth rates

During a breeding season of one year, female green anoles, brown anoles and curly-tailed lizards lay approximately 8-18, 17-62 and 2-6 eggs, respectively (Lovern et al. 2004; Dees et al. 2020; Hall et al. 2018; Smith and Engeman 2004). The average lifespans of green and brown anoles are 8 and 2 years, respectively (Toda et al. 2010; Hall et al. 2018). In addition, the maximum longevity of curly-tailed lizards is 10.8 years (Snider and Bowler 1992). For simplicity, we assume the average lifespan of CT lizards to be 6 years. Based on the information of sex (male or female) and maturation status (adult or juvenile) of each recorded lizard in Supplementary Data 6 of (Pringle et al. 2019), we compute the female adult proportions of green anoles as 0.3861 on Island 1 and 0.3750 on Island 926. The female adult proportion of brown anoles on Islands 5, White Bay Cay, 1 and 926 are 0.3780, 0.3610, 0.4408 and 0.4398, respectively. As there is no information regarding the sex distribution of curly-tailed lizards in Supplementary Data 6 of (Pringle et al. 2019), we assume that the male and female populations are equally distributed. Consequently, the female adult proportions of curly-tailed lizards on Islands White Bay Cay, 1 and 926 are computed as 0.3534, 0.3623, and 0.3568, respectively. The intrinsic growth rate of lizard species can be calculated by $r = NF - 1/L$, where N is the average number of eggs laid by one adult female per year, F is the proportion of adult female, and L is the average lifespan. For green anoles, brown anoles and curly-tailed lizards, we choose N to be 12, 30 and

Table 3 Population sizes of each lizard species on four islands

Year		2011	2012	2013	2014	2015	2016
Population sizes on Island 5	BA	67.2	112.3	163.4	176.7	284.3	174.2
	BT	38.7	57.4	149.7	118.3	80.6	83.4
Population sizes on Island White Bay Cay	BA	121.1	210.0	188.9	211.9	124.3	124.0
	BT	32.2	35.9	37.9	11.9	1.0	3.4
	CT	6.0	9.5	33.4	63.0	63.0	75.0
	GA	10.0	7.7	4.8	15.4	23.2	11.0
Population sizes on Island 1	BA	115.6	73.7	113.8	157.7	108.6	88.7
	BT	133.1	24.6	28.1	6.2	4.3	3.1
	CT	5.0	10.3	24.4	26.3	25.9	30.1
Population sizes on Island 926	GA	11.0	5.0	1.0	1.0	0	0
	BA	146.5	187.9	215.9	328.7	-	-
	BT	186.5	53.3	44.9	54.4	-	-
	CT	7.0	8.4	8.7	19.0	-	-

Green anoles become extinct by 2015 on Island 926, and there are no records on the population sizes of brown anoles and curly-tailed lizards in 2015 and 2016 (Pringle et al. 2019)

4, respectively. Consequently, we have

$r_{BA} = r_{BT} = 10.8400 \text{ year}^{-1}$ on Island 5,

$r_{BA} = r_{BT} = 10.3300 \text{ year}^{-1}, \ r_{CT} = 1.2469 \text{ year}^{-1}$ on Island White Bay Cay,

$r_{GA} = 4.5082 \text{ year}^{-1}, \ r_{BA} = r_{BT} = 12.7240 \text{ year}^{-1}, \ r_{CT} = 1.2825 \text{ year}^{-1}$ on Island 1,

$r_{GA} = 4.3750 \text{ year}^{-1}, \ r_{BA} = r_{BT} = 12.6940 \text{ year}^{-1}, \ r_{CT} = 1.2605 \text{ year}^{-1}$ on Island 926.

5.3 Weighted root mean square error (WRMSE)

For one-dimensional data, we can use the root mean square error (RMSE) as the loss function in our optimization algorithm:

$$RMSE = \left[\frac{1}{n} \sum_{k=1}^{n} (y_k - Y_k)^2 \right]^{1/2},$$

where n represents the number of data points, y_k is the observed data value at point k, and Y_k is the corresponding model-approximated value.

In cases where the data are multidimensional and the components vary in scale, we suggest employing the weighted root mean square error (WRMSE) as the loss function:

$$WRMSE = \sum_{j=1}^{m} w_j \left[\frac{1}{n_j} \sum_{k=1}^{n_j} (y_{jk} - Y_{jk})^2 \right]^{1/2}. \tag{5.1}$$

Here, m denotes the dimension of the data, n_j is the number of data points in the j-th dimension, y_{jk} is the observed value at the k-th point in the j-th dimension, and Y_{jk} is its corresponding model-approximated value. The weights $w_1, \cdots, w_m$ are set to balance the scale of errors across different data dimensions.

Considering the data in Table 3, where the dimension is $m = 4$ and the indices j represent GA, BA, BT, and CT, we note that the population sizes of BA and BT lizards are roughly ten times larger than those of GA and CT lizards. Therefore, we assign the weights as $w_{GA} = w_{CT} = 1$ and $w_{BA} = w_{BT} = 0.1$ to adjust for this disparity in population size scales.

5.4 Overfitting and identifiability

In model (1.1), we describe the intraguild competition and predation between BT and CT lizards using bilinear functions, represented by $q_{BT} u_{BT} u_{CT}$ and $p_{BT} u_{BT} u_{CT}$. However, it is impossible to separately identify the parameters q_{BT} and p_{BT}; changing one while adjusting the other by the same amount does not affect their combined sum $q_{BT} + p_{BT}$. Based on the data in Table 3, our model can only estimate this combined sum. Similarly, the individual values of parameters p_{CT} and q_{CT} cannot

be determined from the data on population sizes. Instead, we focus on estimating the difference $p_{CT} - q_{CT}$ by fitting the model to the available data.

Turning to the data from Island 5 in Table 3, where neither GA nor CT lizards are present, we simplify model (1.1) to a two-dimensional system for BA and BT lizards. We will employ Markov Chain Monte Carlo (MCMC) algorithm (Haario et al. 2001, 2006) and MCMC toolbox for Matlab (Laine 2018) to estimate parameters including the carrying capacities K_{BA} and K_{BT}, and the movement rates m_{BA} and m_{BT}. The data do not provide clear identification for the movement rates m_{BA} and m_{BT}. As shown in Table 4, two different parameter sets fit the Island 5 data well. In these sets, the carrying capacities K_{BA} and K_{BT} are similar, but the movement rates vary significantly. Despite this, the estimated movement rate ratios m_{BA}/m_{BT} in both sets are roughly 0.5. This indicates that, in the absence of predation and competition from other species, brown anoles spend about one-third of their time in terrestrial habitats and two-thirds in arboreal habitats. Considering that intrinsic growth rates are on the order of 10^1 per year, we select movement rates of the order 10^2 per year, reasoning that movement between ground and tree habitats is likely faster than reproduction rates.

5.5 Invasion of CT and BA lizards

We analyze the data from Island White Bay Cay. In the absence of GA lizards, we reduce our model (1.1) to a three-dimensional system of BA, BT, and CT lizards. The estimated parameter values are detailed in Table 4. Notably, the movement rate ratio m_{BA}/m_{BT} is reduced to 0.1, suggesting a significant habitat shift of brown anoles from the ground to the tree follows the invasion of CT lizards.

Further, we apply model (1.1) to the data from Island 1 and Island 926. Here, both GA and CT lizards are introduced into the ecosystem of BA and BT lizards. We compare the estimated parameter values in Table 4. The movement rate ratios m_{BA}/m_{BT} are approximately 0.2 on these islands, higher than on Island White Bay Cay (around 0.1) but lower than on Island 5 (around 0.5). This indicates that both GA and CT lizards affect the movement patterns of brown anoles. The predation and competition of CT lizards drive BT lizards toward arboreal habitats, while GA lizards add competition for arboreal resources, positively influencing the m_{BA}/m_{BT} ratio. This suggests that green anoles have a relatively smaller impact on brown anoles behavior than curly-tailed lizards, consistent with findings in (Losos and Spiller 1999).

The fitted curves are illustrated in Figs. 7 and 8. These figures highlight a rapid population shift of brown anoles from terrestrial to arboreal habitats following the introduction of CT lizards, indicating a swift disruption in the balance between BT and BA lizard populations. This observation offers valuable insights for field studies. Even though the curves in Figs. 7 and 8 cannot capture all of the patterns seen in the data, the loss function WRMSE values are relatively small (refer to Table 4). This suggests that our fitting results are reasonable and acceptable. Also, the limited number of data points may have an impact on the fitting results, considering that the experiment mentioned in (Pringle et al. 2019) only records lizard population data once every year. By collecting more frequent time-series data immediately after introducing CT lizards,

Table 4 Estimated parameters of system (1.1) on four islands

Parameters and Variables	Estimated values on Island 5		Estimated values on Island White Bay Cay	Estimated values on Island 1	Estimated values on Island 926
	First	Second			
K_{GA}	–	–	–	30.4293	35.7296
K_{BA}	191.6960	190.4758	230.4655	128.8520	239.3591
K_{BT}	101.9522	102.9046	69.9148	149.6723	249.2029
K_{CT}	–	–	62.1841	23.9830	12.3042
q_{GA}	–	–	–	0.0267	0.0198
q_{BA}	–	–	–	0.0399	0.0554
$p_{BT}+q_{BT}$	–	–	0.7970	1.0608	0.5275
$p_{CT}-q_{CT}$	–	–	0.0096	0.0178	0.0043
m_{BA}	19.8198	126.5216	109.8706	123.5026	120.6575
m_{BT}	36.1181	247.2911	1079.3960	752.4755	660.5162
m_{BA}/m_{BT}	0.5487	0.5116	0.1018	0.1641	0.1827
$WRMSE$	8.1785	8.1931	11.1858	11.6931	10.6067

The biological meanings of parameters are given in Table 1. The WRMSE is defined in (5.1)
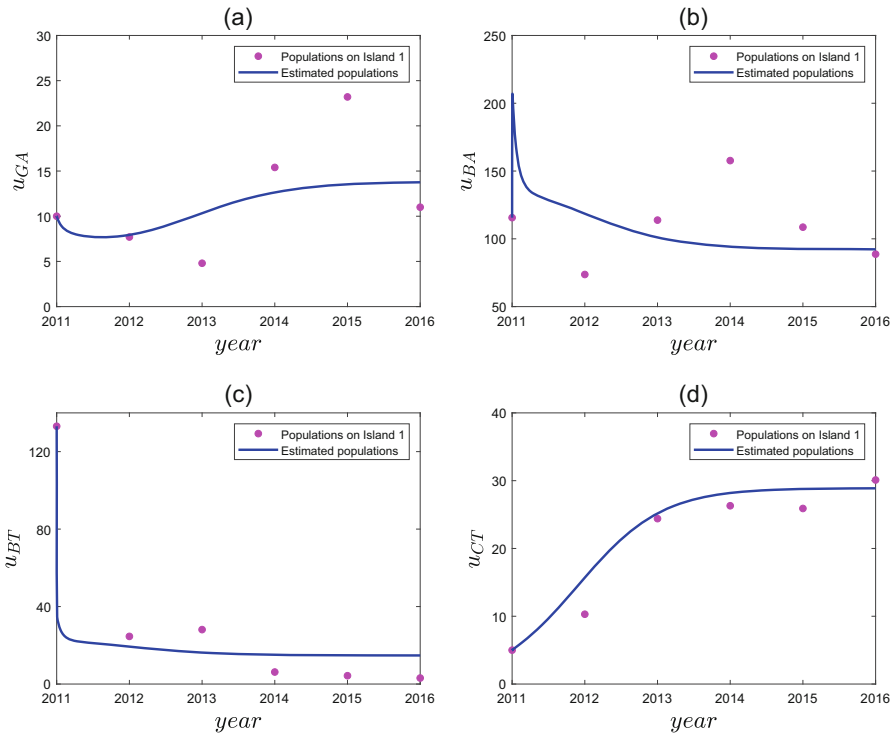
Fig. 7 Fitting results of lizard species on Island 1 for system (1.1). The magenta circles represent observed lizard populations from 2011 to 2016, while the blue curves stand for the fitting curves. The root mean square errors between the observed data and the fitted values for the four lizard species are 4.8213 (GA), 32.8566 (BA), 9.0756 (BT), and 2.6786 (CT)

we could gain a deeper understanding of the rapid dynamics and behavioral shifts in brown anoles when faced with predatory threats.

5.6 Coexistence or extinction

The predation and competition of CT lizards are characterized by the sum $p_{BT} + q_{BT}$, which is estimated as 1.1 on Island 1 and 0.5 on Island 926. Note that the GA lizards persist on Island 1 and become extinct on Island 926. We conclude that the predation rate and the competition rate from CT lizards have a positive indirect impact on the survival of the GA lizards. A strong predation and competition from CT lizards will reduce the population of BT lizards. As the ratio m_{BA}/m_{BT} is not significantly affected by the change in $p_{BT} + q_{BT}$, the population of BA lizards is also reduced. Hence, the competition of BA lizards on GA lizards is weaker and the GA lizards are more likely to survive with higher predation and competition rates of CT lizards on BT lizards.
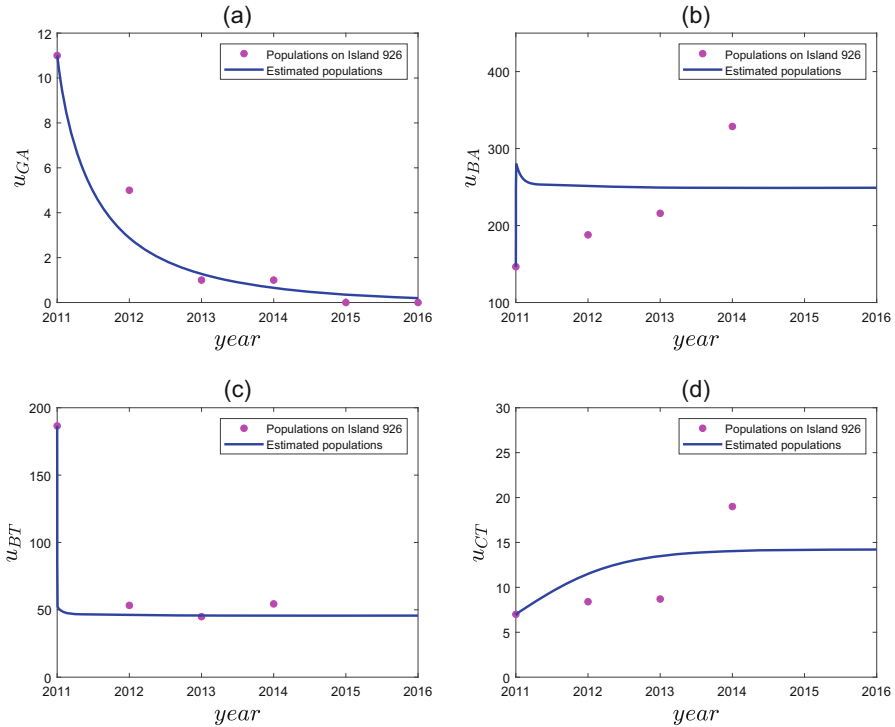
Fig. 8 Fitting results of lizard species on Island 926 for system (1.1). The magenta circles represent observed lizard populations from 2011 to 2016, while the blue curves stand for the fitting curves. The root mean square errors between the observed data and the fitted values for the four lizard species are 0.8984 (GA), 53.6681 (BA), 5.6321 (BT), and 3.7783 (CT)

6 Conclusion and discussion

In this paper, we propose a biological model to examine the interactions among three lizard species: green anoles (GA), brown anoles, and curly-tailed lizards (CT). Given that brown anoles are semi-terrestrial, we divide their population into two groups: BA lizards, living in trees, and BT lizards, residing on the ground. The ground-dwelling CT lizards are top predators which both prey on and compete with brown anoles for ground-based resources (Schoener et al. 1982). This necessitates the inclusion of intraguild predation (IGP) in our model. Additionally, the fear response to these predators may drive BT lizards to arboreal regions, thereby disrupting the niche ecological structure (Pringle et al. 2019).

Our model encompasses various dynamics: competition between GA and BA lizards, as well as between BT and CT lizards; the dispersal behavior of brown anoles; and the intraguild predation of CT lizards on BT lizards. We investigate and determine the stability of eight possible equilibria. Our findings reveal that all but three equilibria are unstable: the GA-CT equilibrium E_{20}, the BA-BT-CT equilibrium E_{03}, and the positive GA-BA-BT-CT equilibrium E^*. Furthermore, we identify five potential stable scenarios resulting from these dynamics: (1) only E_{20} is stable; (2) only E_{03} is

stable; (3) only E^* is stable; (4) both E_{20} and E_{03} are stable; and (5) both E_{03} and E^* are stable.

The dispersal behaviors of brown anoles play a pivotal role in determining the survival or extinction of these lizard species (Ji et al. 2022). The degree of intraguild predation by CT lizards also has a significant effect on local biodiversity (Pringle et al. 2019). To delve deeper, we use the dispersal rate and intraguild predation rate as the bifurcation parameters for a two-dimensional bifurcation analysis. Our numerical results indicate that the positive equilibrium remains stable with a low dispersal rate. However, increased dispersal rates heighten competition between GA and BA lizards, potentially leading to the collapse of the niche structure and the disappearance of GA lizards.

We have also adapted our model to fit the experimental data from (Pringle et al. 2019). This adaptation illustrates how both foraging behavior and predation risk influence the movement rates of brown anoles. In particular, the introduction of CT lizards significantly alters the dynamic between BT and BA lizards, decreasing their movement rate ratio m_{BA}/m_{BT} and causing a swift transition of brown anoles from ground to tree habitats.

Introducing both GA and CT lizards into the ecosystem of BA and BT lizards can reveal complex interactions. Lower predation and competition rates from CT lizards cause a habitat shift in brown anoles, which in turn increases BA lizard populations and intensifies competition for GA lizards, potentially leading to their extinction. This aligns with the refuge-competition model (Persson and Eklov 1995; Orrock et al. 2013). On the other hand, excessive predation on and competition with BT lizards by CT lizards can decrease the populations of both BA and BT lizards, allowing GA lizards to thrive due to less competition, in line with the keystone-predation model (Paine 1966; Leibold 1996).

Data availability statement The data supporting the findings of this study are obtained from the Supplementary Data of (Pringle et al. 2019); see https://doi.org/10.1038/s41586-019-1264-6.

Declarations

Conflict of interest The authors have no Conflict of interest to declare that are relevant to the content of this article.

Ethical statement The paper reflects the authors' original research, which has not been previously published or is currently being considered for publication elsewhere.

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