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Cooperative hunting in a predator–prey system with Allee effects in the prey

Sophia R.-J. Jang* | **Wenjing Zhang** | **Victoria Larriva**

Department of Mathematics and Statistics, Texas Tech University, Lubbock, Texas

Correspondence
Sophia R.-J. Jang, Department of Mathematics and Statistics, Texas Tech University, 2500 Broadway, Lubbock, TX 79409-1042.
Email: sophia.jang@ttu.edu

Abstract

We propose a continuous-time predator–prey model with Allee effects in the prey and cooperative hunting in predators to explore their effects on population interactions. If the predator's reproductive number exceeds one when prey is at its Allee threshold, then although both populations eventually go extinct, the time that it takes to become extinct may be different between cooperation and no cooperation. If the predator's maximum reproductive number is larger than one, then coexistence occurs for the model of no Allee effect, whereas dynamics of the other model also depend on Allee threshold. There always exists a region of initial population distributions, for which both populations become extinct. When the predator's maximum reproductive number is smaller than one, then predators go extinct if predators do not engage in cooperative hunting or if the degree of cooperation is small. With intense cooperation, predators may persist. However, the region of initial populations for coexistence is smaller for the model with Allee effects than the model of no Allee effects.

Recommendations for Resource Managers

- If predators are specialists and engage in cooperative hunting on a prey population that is subject to Allee effects, then estimate the degree of predator cooperation along with the predator's reproductive numbers when the prey is at its carrying capacity (termed the

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*Dedicated to Professor Suzanne Lenhart on the occasion of her 65th birthday.

predator's maximum reproductive number) and at Allee threshold.

- If both reproductive numbers are larger than one or if the predator's maximum reproductive number is larger than one, while the other reproductive number is smaller than one, then one should cull predators to avoid prey extinction. The number of predators to be removed will depend on the sizes of the two populations.
- If the maximum reproductive number of predators is smaller than one, then the recommended management plan will depend on the degree of hunting cooperation. If the degree is small, then culling predators can avoid prey extinction. If cooperation is intense, then culling a large number of predators will likely cause predator extinction while removing a small number of predators will yield coexistence.

KEYWORDS
Allee effects, cooperative hunting, optimal control, pest

AMS SUBJECT CLASSIFICATION
92B05, 92D25

1 | INTRODUCTION

Cooperation between individuals of social animals is frequently observed and widespread in biological systems (Alves & Hilker, 2017). For example, carnivores, such as wolves, wild dogs, and lions, often work together to capture and kill their preys (Alves & Hilker, 2017; Scheel & Packer, 1991). Other organisms, such as ants, spiders, and birds, also seek and attack their prey collaboratively (Alves & Hilker, 2017; Uetz, 1992). Although there are many cooperative predators in nature, there are only a few mathematical models incorporating such a biological mechanism.

Earlier mathematical models investigating cooperative hunting includes Berec (2010), who uses ordinary differential equations to model predator–prey interactions with a Holling type II functional response. Due to this functional response, Berec studies the effects of cooperative hunting relative to population oscillations and concludes that cooperation can change stability of the coexisting steady states. Cosner, DeAngelis, Ault, and Olson (1999), in contrast, propose models of partial differential equations to explore the effects of predator aggregation when predators encounter a cluster of prey.

More recently, Alves and Hilker (2017) construct models of ordinary differential equations of predator–prey interactions with cooperative hunting in predators to investigate impacts of cooperative hunting upon the two trophic-level interactions. They conclude that cooperative hunting can improve persistence of the predator but may also promote a sudden collapse of the predator. In addition, Alves and Hilker (2017) suggest that cooperative hunting is a mechanism for inducing Allee effects in predators. The Allee effect, referring to the reduced fitness or the decline in population growth at low-population densities, was first observed by Allee (1938). It has significant impact on population survival when the population is at low level. There has been a rebound of interest in Allee effects in recent years due to an increasing fragmentation of habitats, invasions of exotic species, biological control of pests, and so forth.

Motivated by the research of Alves and Hilker (2017) and the importance of Allee (1938) effects, we propose a predator–prey model with Allee effects in the prey and cooperative hunting in the predator to investigate population interactions. We first present the asymptotic dynamics of the model when there is no cooperative hunting and then move on to study the system when there is cooperation. With hunting cooperation, we derive a critical degree of cooperation based on the other model parameters, for which the interaction has no coexisting steady state if the degree of cooperation is smaller than this critical value and there are two coexisting steady states when predator cooperation exceeds this critical magnitude. Further, we compare our results with those of Alves and Hilker (2017).

There are many endangered natural resource prey species that are subject to Allee effects and are also preyed upon by predators that engage in cooperative hunting. According to Gascoigne and Lipcius (2004), there are several heavily fished species in the marine system that are subject to Allee effects. In contrast, it is known that bottlenose dolphins hunt cooperatively (Gazda et al., 2005) for fish and it is expected that some of the fish species may be subject to Allee effects and are human resources as suggested by Gascoigne and Lipcius (2004). To prevent such a prey population from extinction, we adopt the control method of culling or harvesting predators. To manage this control scheme more effectively, we apply optimal control theory explored by Lenhart and Workman (2007) to provide optimal culling strategies based on the parameter regimes and initial population distributions given. From our numerical simulations, we see that culling of the predators can stabilize the interaction and remove the predators within a short period of time. The optimal outcomes of maximizing prey and minimizing predator can be easier to achieve if the costs associated with implementing the control are smaller.

The remainder of this manuscript is organized as follows. We present the model and its analysis in Section 2. Specifically, no cooperation is given in Section 2.1 and Section 2.2 deals with cooperation. The optimal control problem is presented in Section 3.1 with numerical simulations given in Section 3.2. Section 4 provides a brief summary and conclusion.

2 | THE MODEL AND ITS DYNAMICS

In this section, we first present the ordinary differential equation model and rescale the model to a dimensionless system. Subsequently, dynamics of the scaled system are studied in Sections 2.1 and 2.2. In particular, existence and stability of the steady states are derived and impacts of cooperative hunting are explored.

Let $x(t)$ and $y(t)$ denote, respectively, the prey and predator populations at time t. The parameter r is the prey's per capita intrinsic growth rate and K denotes its carrying capacity, whereas a, $a < K$, is the Allee threshold of the prey population. In the absence of predator, the prey population is governed by $x' = rx(1 - \frac{x}{K})(x - a)$. Such an equation has been adopted by Amarasekare (1998), Courchamp, Berec, and Gascoigne (2008), De Silva and Jang (2015), Keitt, Lewis, and Holt (2001), and Lewis and Keitt (1993) to model Allee effects. There are other ways to incorporate the mechanism of Allee effects into a population. For example, G. Wang, Liang, and Wang (1999) use the equation $N' = N(k(1 - \frac{N}{R})(\frac{N}{C+N}) - D)$ to model a single population N subject to Allee effects, where all of the parameters $k, \ R, \ C,$ and D are positive with $k > D$ and C is the Allee constant. The larger C indicates stronger Allee effects.

Our model derivation is based on the classical Lotka–Volterra predator–prey model (Allen, 2006), in which a linear functional response is adopted. Similar to the work of Alves and Hilker (2017), we model cooperation of predator through its attack rate with the degree of cooperation denoted by c. That is, the functional response of the predator becomes $(b + cy)xy$, where $c \geq 0$ and $b > 0$ is the attack rate per predator and prey. If $c = 0$, then there is no cooperation among predators. Let d be the prey conversion to predator and m be the per capita death rate of predator. The interaction between the two populations is given by

$$\begin{aligned} x' &= rx\left(1 - \frac{x}{K}\right)(x - a) - (b + cy)xy, \\ y' &= d(b + cy)xy - my, \end{aligned} \tag{2.1}$$

with nonnegative initial conditions. We nondimensionalize the model by letting

$$\hat{x} = \frac{bd}{m}x, \quad \hat{y} = \frac{b}{m}y, \quad \tau = mt, \quad \hat{c} = \frac{m}{b^2}c, \quad \hat{r} = \frac{1}{bd}r, \quad \hat{K} = \frac{bd}{m}K, \quad \hat{a} = \frac{bd}{m}a. \tag{2.2}$$

Without writing out the hats, we obtain the following dimensionless system:

$$\begin{aligned} x' &= rx\left(1 - \frac{x}{K}\right)(x - a) - (1 + cy)xy, \\ y' &= (1 + cy)xy - y. \end{aligned} \tag{2.3}$$

Dynamics of the prey population in the absence of predator are simple, namely $x(t)$ converges to 0 if $x(0) < a$ and $x(t)$ converges to K if $x(0) > a$. It is clear that solutions of (2.3) exist, remain nonnegative, and are bounded for $t > 0$. Moreover, all solutions of (2.3) with $x(0) \leq a$ and $y(0) > 0$ converge to the extinction steady state $E_0 = (0, 0)$. In contrast, if $x(0) \geq K$ and $y(0) > 0$, then $y(t) > 0$ for $t > 0$ and $x'(0) < 0$. Consequently, $x(t) < K$ for all t large. In what follows, we assume initial conditions of (2.3) satisfying

$$a < x(0) < K \quad \text{and} \quad y(0) > 0. \tag{2.4}$$

The system (2.3) has three boundary steady states $E_0 = (0, 0)$, $E_{11} = (a, 0)$, and $E_{12} = (K, 0)$. Their stability can be determined by using the Jacobian matrix of (2.3) and is summarized in Table 1.

TABLE 1 Stability of boundary steady states of (2.3)

Steady state	Stability
$E_0 = (0, 0)$	Asymptotically stable
$E_{11} = (a, 0)$	Repeller if $a > 1$, saddle point if $a < 1$
$E_{12} = (K, 0)$	Asymptotically stable if $K < 1$, saddle point if $K > 1$

In particular, both populations go extinct if initial prey population is small due to the fact that the prey population is subject to Allee effects. We next study asymptotic dynamics of (2.3). We separate our discussion into $c = 0$ and $c > 0$.

2.1 | Dynamics of the model when $c = 0$

When the predator population does not engage in cooperative hunting, $c = 0$, the dynamics of (2.3) are easy to understand and are given by the following theorem. The proof is provided in Appendix A. In fact, the y-isocline is given by the vertical line $x = 1$ and thus there exists a unique interior steady state if and only if $a < 1 < K$.

Theorem 2.1 *Let* $c = 0$. *Then* $E_0 = (0, 0)$ *is globally asymptotically stable if* $a > 1$. *If* $K < 1$, *then (2.3) has no interior steady state and the stable manifold* M_{11}^{+} *of* $E_{11} = (a, 0)$ *separates* $\mathbb{R}_{+}^{2}$ *into two positively invariant regions* R_1 *and* R_2 *such that* E_0 *and* $E_{12} = (K, 0)$ *are globally asymptotically stable in* R_1 *and* R_2, *respectively. If* $a < 1 < K$, *then (2.3) has a unique interior steady state* $E^* = (1, y^*)$, $y^* = r(1 - 1/K)(1 - a)$, *where* E^* *is a repeller if* $a + K > 2$ *and asymptotically stable if* $a + K < 2$. *The interior steady state* E^* *undergoes a Hopf bifurcation when* $a + K = 2$.

Notice that our system (2.3) when $c = 0$ is a special case of the following model studied by J. Wang, Shi, and Wei (2011) with $\delta = 1$:

$$\begin{aligned} u' &= g(u)(f(u) - v), \\ v' &= v(g(u) - \delta), \end{aligned}$$

where $\delta > 0$ is the predator's per capita death rate. The function $f(u)$ is C^1 with $f(1) = 0 = f(\beta)$, $0 < \beta < 1$, and $f(u)$ is positive for $u \in (\beta, 1)$ and negative on $(0, \beta) \cup (1, \infty)$. Consequently, parameter β is the prey's Allee threshold. The functional response $g(u)$ is strictly increasing with $g(0) = 0$ and there exists a unique $\lambda > 0$ such that $g(\lambda) = \delta$. In Wang et al. (2011), λ is used as a bifurcation parameter and global bifurcation analysis is provided. In our study of the model (2.3) with $c = 0$, parameter K is used as the bifurcation parameter and we only address local bifurcation. Further, the asymptotic dynamics obtained in Theorem 2.1 are the same as the corresponding dynamics of the model explored by J. Wang et al. (2011).

When $c = 0$ and $a < 1 < K$, both E_{11} and E_{12} are saddle points and the stable manifold of E_{12} lies on the positive x-axis. The stable manifold M_{11}^{+} of E_{11} separates $\mathbb{R}_{+}^{2}$ into two positively invariant regions A_1 and A_2 with $E_0 \in A_1$. We can conclude that $E^* \in A_2$ and E_0 is globally asymptotically stable in A_1. We suspect that E^* is globally asymptotically stable in A_2 when E^* is asymptotically stable.

Recall that a and K are dimensionless and from (2.2) we can interpret a and K as the reproductive numbers of the predator when the prey is at its Allee threshold and carrying capacity, respectively. Therefore, if a exceeds one, then the predator drives the prey to below its Allee threshold since the predator's reproductive is greater than one, and, as a result, both populations go extinct. The parameter K may be interpreted as the maximum reproductive number of the predators since it is the predator's reproductive number when the prey is at its carrying capacity. Consequently, if K is smaller than one, then the predator population goes extinct since each individual predator cannot replace itself by an offspring over its lifetime at the optimal environment. In this circumstance, the prey population may become extinct or eventually stabilize at K depending on initial populations.

2.2 | Dynamics of the model when $c > 0$

In this subsection, we investigate the impacts of cooperative hunting upon dynamics of the predator–prey interactions. We shall separate the discussion into three cases, namely $a > 1$, $a < 1 < K$, and $K < 1$. For the case of $a < 1 < K$, a unique interior steady state exists and we study the effect of c upon local stability and magnitude of the steady state. In particular, we prove that predator cooperation is destabilizing. Here, "destabilizing" means that the steady state changes from stability to instability. For $K < 1$, we derive a critical degree of cooperative hunting, c_T, such that the interaction has no interior steady state if $c < c_T$ and there are two coexisting steady states if $c > c_T$.

To this end, we let $c > 0$. The nontrivial y-isocline is given by $y = \frac{1}{c}(\frac{1}{x} - 1)$, $x > 0$, and the nontrivial x-isocline satisfies $r(1 - x/K)(x - a) - (1 + cy)y = 0$. It follows that the x-component of an interior steady state is a solution of

$$r(1 - x/K)(x - a) = \frac{1 - x}{cx^2}, \quad x > 0. \tag{2.5}$$

The left-hand side of (2.5) is a concave parabola going through $E_{11} = (a, 0)$ and $E_{12} = (K, 0)$. The right-hand side of (2.5) approaches ∞ as $x \to 0^+$, passes through the point $(1, 0)$, and is strictly decreasing for $x \in (0, 1)$. As a result, (2.3) has no interior steady state when $a > 1$ and there exists a unique interior steady state if $a < 1 < K$. The existence and the number of interior steady states will depend on other parameters when $K < 1$.

2.2.1 | The case of $a > 1$

Recall that the dimensionless parameter a is the predator's reproductive number when the prey population is at its Allee threshold. The condition $a > 1$ implies that each individual predator can reproduce more than one predator over its lifetime when the prey population is at its Allee threshold, which in turn drives the prey population to below the threshold. Therefore, the prey population goes extinct and so does the predator. Consequently, the extinction steady state is globally asymptotically stable. The case of no predator cooperation is presented in Theorem 2.1. In the following, we show that both populations also go extinct when predators cooperate. The proof is similar to that of Theorem 2.1 and is therefore omitted.

Proposition 2.1 *Let* $c > 0$ *and* $a > 1$. *Then (2.4) has no interior steady state and* $E_0 = (0, 0)$ *is globally asymptotically stable.*

Comparing Proposition 2.1 with Theorem 2.1, we see that global extinction occurs when $a > 1$ independent of whether $c = 0$ or $c > 0$. Although both populations go extinct, however, the time that it takes to becoming extinct may be different between the scenarios of cooperation and of no cooperation. See Figure 1a,b for the illustration, where $a = 1.2 > 1$, $K = 1.3$, and

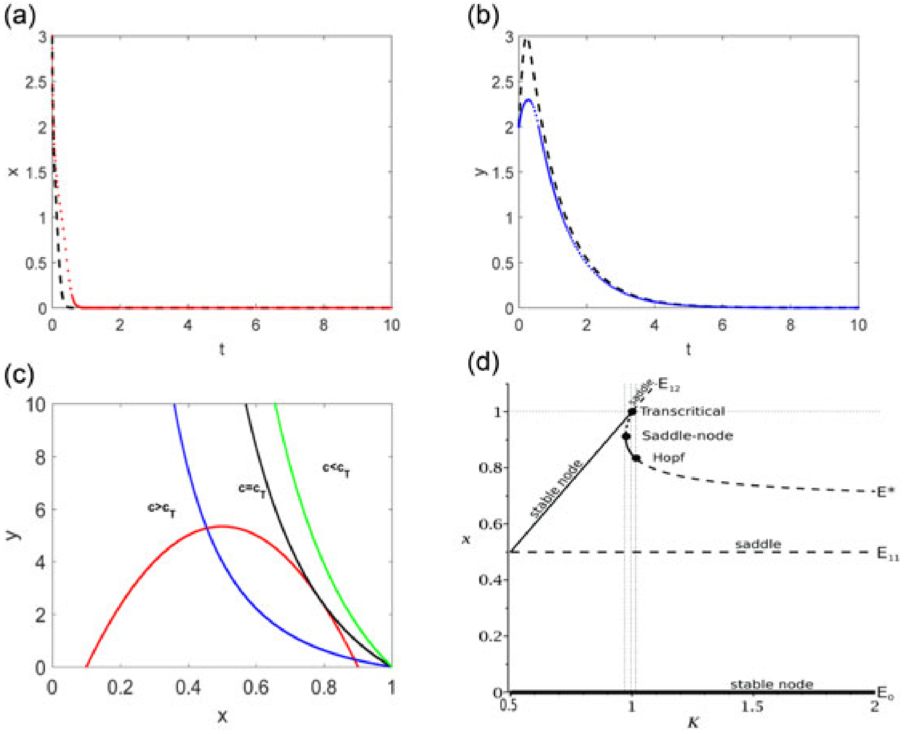

FIGURE 1 Plots (a) and (b) are time evolutions of the prey and predators, respectively, when $a > 1$ with black dashed lines denoting cooperation. (c) Illustrates the isoclines for $c > 0$ and $K = 0.9 < 1$ with $r = 30$ and $a = 0.1$, where the red concave curve represents the left-hand side of (2.5). The critical value $c_{\mathrm{T}} = 0.13287$ is computed, for which the two curves are tangent to each other at the unique interior steady state when $c = c_{\mathrm{T}}$. There is no interior steady state if $c = 0.08 < c_{\mathrm{T}}$ and there are two interior steady states if $c = 0.5 > c_{\mathrm{T}}$. A bifurcation diagram using K as the varying parameter with $c = 4$ is given in (d), where $r = 1$, $a = 0.5$, and the solid and dashed lines indicate stable and unstable steady states, respectively

$r = 10$. The black dashed lines are for $c = 0.5$ and the solid lines are for $c = 0$ using the same initial condition (3, 2). As demonstrated numerically, with cooperation, the prey population goes extinct earlier than the scenario of no cooperation. In contrast, the predator population yields a larger maximum size before extinction if the population cooperates.

2.2.2 | The case of $a < 1 < K$

Let $a < 1 < K$, that is, the reproductive number of the predators is smaller than one when the prey is at its Allee threshold, while this reproductive number is larger than one when the prey is at its carrying capacity. It follows from an earlier discussion that the system has a unique interior steady state, denoted by $E^* = (x^*, y^*)$. Notice $a < x^* < 1$ and $y^* = \frac{1}{c}(\frac{1}{x^*} - 1)$. As a result, the magnitude of the prey population in the unique coexisting steady state is smaller than the corresponding prey density $x^* = 1$ of no cooperation $c = 0$.

We first study the impacts of cooperative hunting upon the size of the components of the interior steady state. The result is summarized in Proposition 2.2, which can be readily seen geometrically from the graphs of (2.5). We give an analytical derivation here for later use.

Proposition 2.2 *Let $c > 0$ and $a < 1 < K$. Then (2.3) has a unique interior steady state $E^* = (x^*, y^*)$, where $a < x^* < 1$ and $\frac{\partial x^*}{\partial c} < 0$. Further, $\frac{\partial y^*}{\partial c} < 0$ if $x^* \in (a, \frac{a+K}{2})$, and $\frac{\partial y^*}{\partial c} > 0$ if $x^* \in (\frac{a+K}{2}, 1)$ and $c > 0$ is not too small.*

Proof Existence and uniqueness of the interior steady state $E^* = (x^*, y^*)$ follow from the above discussion. Differentiating both sides of (2.5) with respect to c and after some calculations, we obtain

$$\frac{\partial x^*}{\partial c} = \frac{x^*(c^2x^*(y^*)^2 - (1 - x^*)(1 + 2cy^*))}{c(1 + 2cy^*) - \frac{rc^2}{K}(x^*)^2(2x^* - a - K)}. \tag{2.6}$$

It is straightforward to verify $c^2x^*(y^*)^2 - (1 - x^*)(1 + 2cy^*) = -\frac{1-x^*}{x^*} < 0$. To study the denominator of (2.6), notice $c(1 + 2cy) - \frac{rc^2}{K}x^2(2x - a - K) = \frac{c}{x}(2 - x - \frac{rcx^3}{K}(2x - a - K))$, which is positive if $a + K \geq 2$ or if $a + K < 2$ and $1 \geq \frac{rc}{K}(2 - a - K)$. If $a + K < 2$ and $1 < \frac{rc}{K}(2 - a - K)$, then there exists a unique positive $x_\mathrm{d} < 1$ such that the denominator of (2.6) is zero at $x = x_\mathrm{d}$, positive on $(0, x_\mathrm{d})$ and negative on $(x_\mathrm{d}, 1)$, that is, x_d is the unique solution of $2 - x = \frac{rcx^3}{K}(2x - a - K)$ in $(0, 1)$. However, since the x component of the unique interior steady state satisfies $1 - x = \frac{rc}{K}x^2(K - x)(x - a)$ and $1 - x < 2 - x$, we conclude that $x^* < x_\mathrm{d}$. It follows that $\frac{\partial x^*}{\partial c} < 0$. In contrast, since

$$\frac{\partial y^*}{\partial c} = \frac{(x^*)^2 - x^* - c\frac{\partial x^*}{\partial c}}{c^2(x^*)^2} \tag{2.7}$$

and $\frac{\partial x^*}{\partial c} < 0$, the effect of cooperative hunting on the magnitude of y component of the interior steady state is therefore not monotone. In fact, since the left-hand side of (2.5) is a concave function independent of c and the right-hand side of (2.5) is strictly decreasing with respect to c, we have $\frac{\partial y^*}{\partial c} < 0$ if $x^* \in (a, \frac{a+K}{2})$, and $\frac{\partial y^*}{\partial c} > 0$ if $x^* \in (\frac{a+K}{2}, 1)$ and $c > 0$ is not too small. □

It follows from Proposition 2.2 that cooperative hunting of the predator decreases the prey density in the coexisting steady state, while its impact on the predator density depends on the prey density and also on the strength of cooperation. We next move on to explore the impact of predator cooperation upon the stability of the interior steady state.

Toward this end, the stability of E^* is determined by the Jacobian matrix at E^*,

$$J(E^*) = \begin{pmatrix} \frac{rx^*}{K}(a + K - 2x^*) & -cx^*y^* - 1 \\ y^*/x^* & cx^*y^* \end{pmatrix}, \tag{2.8}$$

where $J(E^*)$ given in (2.8) reduces to (A.1) when $c = 0$. Consequently, cooperative hunting may change stability of the unique interior steady state. In particular, E^* is a repeller if $x^* \leq (a + K)/2$ by (2.8), where x^* depends on c. Since x^* decreases as c increases by Proposition 2.2, we can conclude that cooperative hunting in general is destabilizing. In particular, E^* is more likely to be unstable since $x^* \leq (a + K)/2$ is more likely to occur as x^*

decreases with increasing c. This conclusion is consistent with the result obtained by Berec (2010) where destabilizing also occurs as hunting cooperation increases. In the following, we prove analytically that predator cooperation is destabilizing.

Theorem 2.2 *Let $c > 0$ and $a < 1 < K$. Then there exists a unique x_h^* in $(\frac{a+K}{2}, 1)$ such that the unique interior steady state $E^* = (x^*, y^*)$ is asymptotically stable if $x^* \in (x_\mathrm{h}^*, 1)$ and a repeller if $x^* \in (a, x_\mathrm{h}^*)$, and a Hopf bifurcation occurs at $x^* = x_\mathrm{h}^*$. With respect to c, there exists a unique $c_\mathrm{h} > 0$ such that E^* undergoes a Hopf bifurcation at $c = c_\mathrm{h}$ and E^* is asymptotically stable for $c \in (0, c_\mathrm{h})$ and a repeller for $c > c_\mathrm{h}$.*

Proof It is clear that the unique interior steady state E^* is a repeller if $x^* \le (a + K)/2$ by (2.8). Let $x^* > (a + K)/2$. Then, $a + K < 2$ since $x^* < 1$. We study the sign of $\mathrm{tr}(J)$ and $\det(J)$. Observe that $\det(J) = (1 - x^*)(\frac{rx^*}{K}(a + K - 2x^*) + \frac{2 - x^*}{c(x^*)^2})$ and its sign turns out to be the negative sign of $c(1 + 2cy^*) - \frac{rc^2}{K}(x^*)^2(2x^* - a - K)$ that appears in (2.6). Therefore, $\det(J) > 0$ for all feasible interior steady states.
Solving for $\mathrm{tr}(J) = 0$, that is, $\frac{rx^*}{K}(a + K - 2x^*) + 1 - x^* = 0$, we obtain a unique solution x_h^*, $\frac{a+K}{2} < x_\mathrm{h}^* < 1$, such that $\mathrm{tr}(J) > 0$ on $(0, x_\mathrm{h}^*)$ and $\mathrm{tr}(J) < 0$ if $x^* \in (x_\mathrm{h}^*, 1)$. Since $\det(J) > 0$, similar to the proof of Theorem 2.1, we can show that (2.3) undergoes a Hopf bifurcation at $x^* = x_\mathrm{h}^*$. Further, $\frac{\partial x^*}{\partial c} < 0$ by Proposition 2.2, there exists a unique $c_\mathrm{h} > 0$ such that (2.3) exhibits a Hopf bifurcation at $c = c_\mathrm{h}$, and E^* is asymptotically stable for $c \in (0, c_\mathrm{h})$ and it is a repeller if $c > c_\mathrm{h}$. ☐

Under the condition that the predator's reproductive number is smaller than one when the prey population is at its Allee threshold and the predator's maximum reproductive number exceeds one, the interaction also supports only one coexisting steady state in the presence of cooperative hunting. Therefore, hunting cooperation does not change the existence and the number of the coexisting steady states in the parameter regime of $a < 1 < K$. However, cooperation changes stability of the steady state and in general it is destabilizing since predator cooperation decreases prey density x^* in the coexisting steady state and thus x^* is more likely to be in (a, x_h^*).

2.2.3 | The case of $K < 1$

When the maximum reproductive number of the predators is less than one, $K < 1$, the predator population would go extinct without cooperation by Theorem 2.1. With cooperative hunting, we prove in this subsection that (2.3) can have either zero, one, or two interior steady states. Therefore, cooperative hunting of the predator may promote survival of the population when $K < 1$. See Figure 1c for the illustration of these scenarios, where the parameter values are $a = 0.5$, $K = 0.9$, and $r = 30$. The concave red curve is the left-hand side of (2.5), whereas other curves denote the right-hand side of (2.5) with three c values to demonstrate the number of interior steady states. A bifurcation diagram using K as the varying parameter is given in Figure 1d with $r = 1, a = 0.5$, and $c = 4$, where solid and dashed lines denote stable and unstable steady state, respectively.

The number of interior steady states when $K < 1$ is given analytically by the following theorem where c_T is defined in (2.10).

Theorem 2.3 *Let $c > 0$ and $K < 1$. Then system (2.3) has no interior steady state if $c < c_\mathrm{T}$, in which the stable manifold M_{11}^+ of $E_{11} = (a, 0)$ separates $\mathbb{R}_+^2$ into two positively* *invariant regions R_1 and R_2 such that $E_0 = (0, 0)$ and $E_{12} = (K, 0)$ are globally asymptotically stable in R_1 and R_2, respectively. If $c = c_{\mathrm{T}}$, then (2.3) has a unique interior steady state, which is nonhyperbolic. If $c > c_{\mathrm{T}}$, then (2.3) has two interior steady states $E_i^* = (x_i^*, y_i^*)$, $x_1^* < x_2^*$ and $y_1^* > y_2^*$.*

Proof Observe that the two isoclines are tangent to each other at the point of unique interior steady state and the tangency must locate to the right of the vertical line $x = (a + K)/2$. Differentiating both sides of (2.5) and setting them equal, we obtain another equation in addition to (2.5). Using these two equations and after some calculations results in

$$x(1 - x)(a + K - 2x) = (K - x)(x - a)(x - 2). \tag{2.9}$$

It can be easily seen that (2.9) has a unique solution x_{T} in $(\frac{a+K}{2}, K)$, which corresponds to the x component of the unique interior steady state. Solving for the corresponding c yields

$$c_{\mathrm{T}} = \frac{1 - x_{\mathrm{T}}}{r(1 - x_{\mathrm{T}}/K)(x_{\mathrm{T}} - a)x_{\mathrm{T}}^2}. \tag{2.10}$$

We conclude that (2.3) has two interior steady states $E_i^* = (x_i^*, y_i^*)$, $i = 1, 2$, $x_1^* < x_2^*$, and as a result, $y_1^* > y_2^*$, if $c > c_{\mathrm{T}}$, and (2.3) has no interior steady state if $c < c_{\mathrm{T}}$. Therefore, dynamics of the model are similar to the case of $c = 0$ if $c < c_{\mathrm{T}}$ and $K < 1$. Namely that the stable manifold M_{11}^+ of E_{11} separates $\mathbb{R}_+^2$ into two positively invariant regions R_1 and R_2 such that E_0 and E_{12} are globally asymptotically stable in R_1 and R_2, respectively. At $c = c_{\mathrm{T}}$, the Jacobian matrix at the unique tangential steady state has $\det(J) = 0$ and hence the steady state is nonhyperbolic. ☐

Notice that since E_2^* is close to the stable boundary steady state $E_{12} = (K, 0)$, one can conclude that E_2^* is always a saddle point, whereas E_1^* may be stable or unstable depending on parameter regimes. The stable manifold M_{11}^+ of E_{11} along with the stable manifold $M_{2^*}^+$ of E_2^* then separate $\mathbb{R}_+^2$ into three positively invariant regions B_i, $i = 1, 2, 3$, such that $E_0 \in B_1$, $E_1^* \in B_2$, and $E_{12} \in B_3$, and solutions in B_1 and B_3 converge to E_0 and E_{12}, respectively, by the Poincaré–Bendixson theorem (Thieme, 2003).

Recall that the dimensionless parameter K is the maximum reproductive number of the predators. The condition $K < 1$ implies that each individual predator cannot replace itself over its lifespan under the maximum prey size. As a result, predators go extinct when they do not hunt cooperatively as illustrated in Theorem 2.1. We extend this biological conclusion in Theorem 2.3 to the case where predators engage in cooperative hunting but do not cooperate intensively, that is, $c < c_{\mathrm{T}}$. When the degree of cooperation is large, $c > c_{\mathrm{T}}$, then the interaction can support two coexisting steady states and hence cooperative hunting can promote predator persistence.

3 | CULLING PREDATOR

In this section, we consider the scenario where the prey population subject to Allee effects is an endangered natural resource species and is also preyed upon by the predators that engage in cooperation hunting. We seek some biological strategies to prevent prey extinction by harvesting or culling the predator. Optimal control has been applied to many biological systems successfully on controlling either diseases or pests (Lenhart & Workman, 2007; Numfor, Hilker, & Lenhart, 2017; Pantha, Day, & Lenhart, 2016). In this section, we apply optimal control theory given by Lenhart and Workman (2007) to study the biological problem. We devise a best strategy for culling the predator by maximizing the prey population and minimizing the predators along with the costs associated with the control. To this effort, we shall set up the control problem using the original system. This approach is also adopted recently by Numfor et al. (2017) for studying predator–prey interactions. In Section 3.1, we set up the optimal control problem and numerical investigation is presented in Section 3.2.

3.1 | The optimal control problem

Based on the original predator–prey system (2.1), we let $u(t)$ denote the time-dependent harvesting or culling of the predator and the model is as follows:

$$\begin{aligned} x' &= rx(1 - x/K)(x - a) - (b + cy)xy, \\ y' &= d(b + cy)xy - my - u(t)y. \end{aligned} \tag{3.1}$$

The initial condition is positive with $x(0) = x_0 > 0$ and $y(0) = y_0 > 0$. Let $T > 0$ be the fixed time span, for which the control is applied. The admissible control class for our problem is

$$U = \{u : u(t) \text{ is piecewise continuous with } 0 \leq u(t) \leq 1 \text{ on } [0, T]\}. \tag{3.2}$$

The goal is to maximize prey population and minimize predator population along with minimizing the cost associated with controlling the predator over the time interval $[0, T]$. Therefore, the objective functional is given by

$$J(u) = \int_0^T \left(x(t) - y(t) - \frac{A}{2} u^2(t) \right) dt, \tag{3.3}$$

where $A > 0$ is a weighted constant representing the cost associated with implementing the control. The optimal control problem consists of

$$\max_{u \in U} J(u) \tag{3.4}$$

subject to the state equations (3.1). Notice that the form of objective functional given in (3.3) has been used by other researchers, such as Burden, Ernstberger, and Fister (2004), to study optimal immunotherapies. In particular, we assume identical weights for prey and predator in $J(u)$.

It is clear that the class of all initial conditions with a control $u \in U$ for which the state equations being satisfied on the finite time interval $[0, T]$ is nonempty. Moreover, solutions of (3.1) remain nonnegative on $[0, T]$ by Thieme (2003) and the set of the admissible controls U is closed and convex. The right-hand side of each of the state equations is continuous, bounded above by the sum of the control and the state, and can be written as a linear function of u. Further, for fixed x and y, the integrand of $J(u)$ is convex on U. The integrand of $J(u)$ is concave in u and is bounded above by $C_2 - C_1 u^\gamma$ for some $C_1 > 0$ and $\gamma = 2 > 1$. It follows from Fleming and Rishel (1975) that there exists an optimal control for the problems (3.1)–(3.4).

We now apply the Pontryagin maximum principle to derive necessary conditions. Our derivation is based on the work outlined by Lenhart and Workman (2007). Let (λ_1, λ_2) be the adjoint vector. The Hamiltonian of the optimal problems (3.1)–(3.4) is

$$H(x, y, u, \lambda_1, \lambda_2) = x - y - \frac{A}{2}u^2 + \lambda_1[rx(1 - x/K)(x - a) - (b + cy)xy] + \lambda_2[d(b + cy)xy - my - u(t)y]. \tag{3.5}$$

The adjoint variables satisfy $\lambda_1' = -\frac{\partial H}{\partial x}$ and $\lambda_2' = -\frac{\partial H}{\partial y}$ with the transversality conditions $\lambda_i(T) = 0$, $i = 1, 2$. Applying the optimality condition $\frac{\partial H}{\partial u} = 0$, we obtain $u = -\frac{\lambda_2 y}{A}$. Since $0 \le u(t) \le 1$, the characterization of the optimal control u^* is therefore

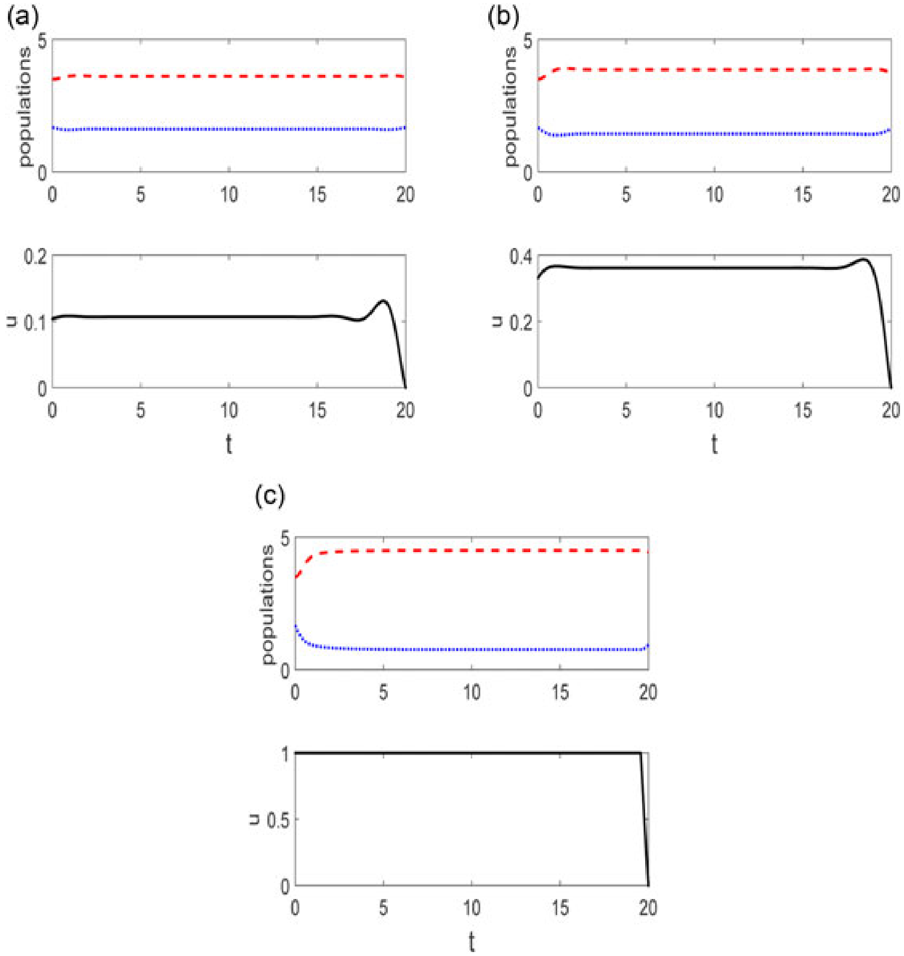

FIGURE 2 Populations and optimal controls over time are plotted in the parameter regime with $c = 0$, for which the interior steady state is asymptotically stable in the absence of control with $A = 15$, 5, and 0.5 in (a)–(c), respectively. The initial condition is $(x^*, y^*) = (3.5, 1.68)$ for all the simulations, where dashed and dotted lines denoted the prey and predator, respectively

$$u^*(t) = \min\left\{\max\left\{0, \frac{-\lambda_2(t)y(t)}{A}\right\}, 1\right\}. \tag{3.6}$$

Once the optimal control is characterized, the optimality system consists of the state and adjoint equations and is given as

$$\begin{aligned} x' &= rx(1 - x/K)(x - a) - (b + cy)xy, \\ y' &= d(b + cy)xy - my - u^*(t)y, \\ \lambda_1' &= -1 - \lambda_1[r/K(x - a)(K - 2x) + r/K(K - x)x - (b + cy)y] - \lambda_2[d(b + cy)y], \\ \lambda_2' &= 1 + \lambda_1[cxy + (b + cy)x] - \lambda_2[cdxy + d(b + cy)x - m - u], \end{aligned} \tag{3.7}$$

with $x(0) = x_0 > 0$, $y(0) = y_0 > 0$, and $\lambda_i(T) = 0, 1 \leq i \leq 2$, where $u^*(t)$ is given in (3.6). The optimality system (3.7) yields a two-point boundary value problem, which will be solved numerically in the following subsection.

3.2 | Numerical simulations

Our numerical scheme for solving the optimal control problem follows the forward–backward sweep method discussed in Lenhart and Workman (2007).

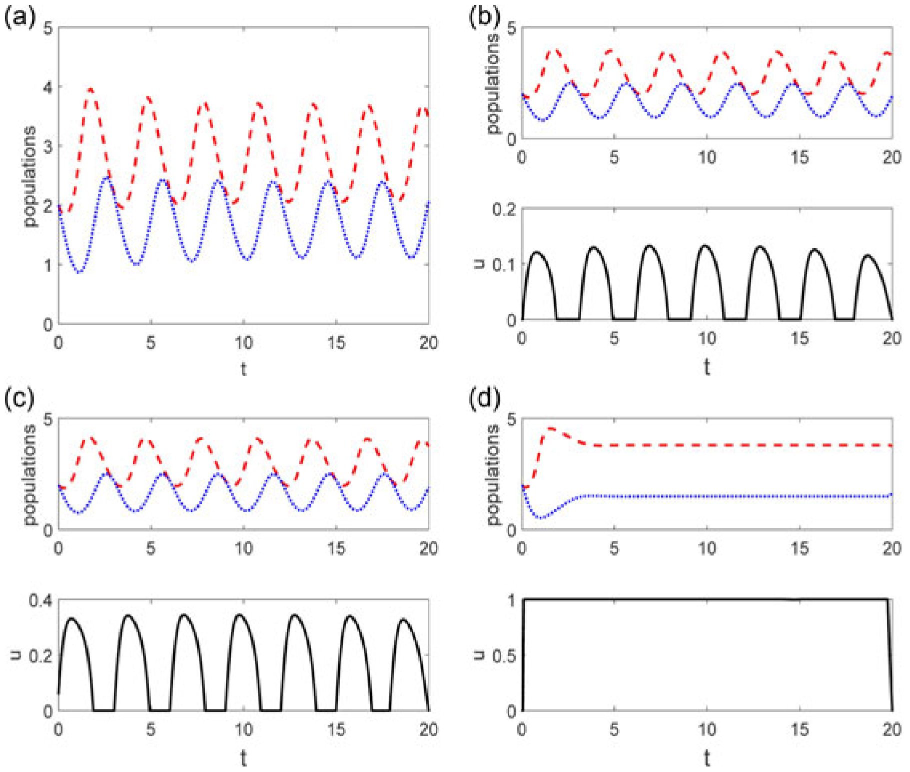

FIGURE 3 Populations and optimal controls over time are plotted in the parameter regime with $c = 0$, for which the populations are oscillating in the absence of control. There is no control in (a), while $A = 15$, 5 and 0.5 in (a)-(d), respectively. Initial condition is (2, 2) for all the simulations. Dashed and dotted lines are denoted for prey and predator, respectively

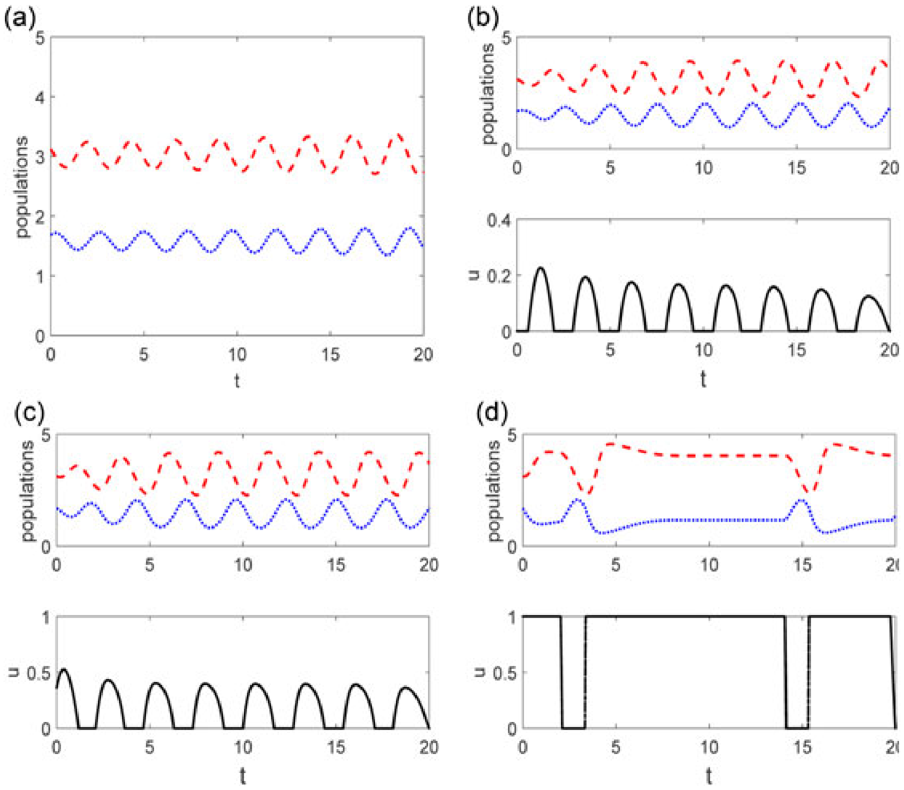

FIGURE 4 Populations and optimal controls over time are plotted in the parameter regime with $c = 0.1$, for which the populations are oscillating in the absence of control. There is no control in (a), while $A = 15$, 5, and 0.5 in (b)-(d), respectively. Initial condition is $E^* + (0.1, 0.1)$ for all the simulations. Dashed and dotted lines are denoted for prey and predator, respectively

The results of $c = 0$ are presented in Figure 2 with $a = 0.7$, $K = 5$, $r = 2$, $b = d = 1$, and $m = 3.5$. Since $a < m/bd < K$, (2.3) has a unique interior steady state $E^* = (3.5, 1.68)$, where $(a + K)/2 < m/bd = x^*$ and E^* is asymptotically stable in the absence of control. The E^* is used as the initial condition in the simulations for the optimal control problems (3.1)–(3.4) by varying the costs with $T = 20$. Specifically, $A = 15$, 5, and 0.5 are given in Figure 2a–c, respectively. One can see that as the cost A associated with the control gets smaller, we are able to increase the control u so that the predator population becomes smaller and the prey population becomes larger over the control period [0, 20].

We next decrease m to 2.8 while keeping all other parameter values as those in Figure 2. With $c = 0$, the unique interior steady state $E^* = (2.8, 1.848)$ is unstable since $2.8 < (a + K)/2$. Figure 3 presents the simulation results using initial condition (2, 2). Figure 3a shows that the populations are oscillating in the absence of control, and Figure 3b–d applies the optimal control with $A = 15$, 5, and 0.5, respectively. We obtain similar conclusions as those of Figure 2. In addition, harvesting or culling of the predator can eliminate oscillatory behavior of the interactions when the cost associated with the control is small.

With the same parameter values as those of Figure 2 but using $c = 0.1$, then the unique interior steady state $E^* = (3.0209, 1.5858)$ is unstable when there is no control. Notice that the prey density in the unique interior steady state is smaller than the corresponding one in Figure 2,

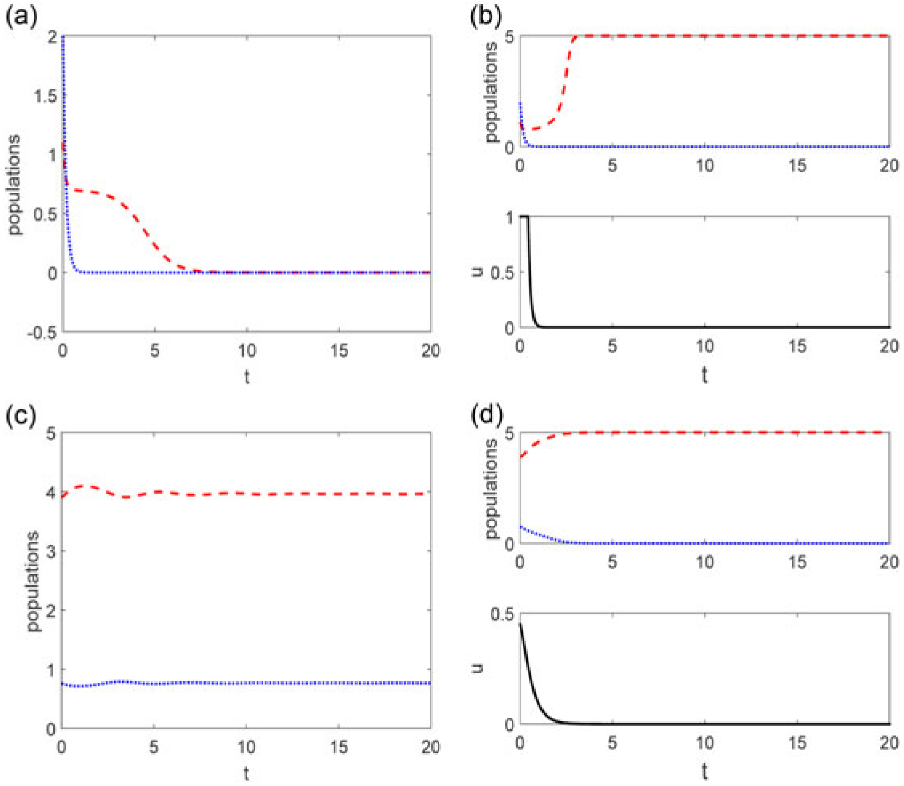

FIGURE 5 Populations and optimal controls over time are plotted in the parameter regime $K < m/bd$ so that the number of interior steady states depends on c. In (a)-(b), $c = 0.5 < c_T$. There is no control in (a), while $A = 0.5$ in (b). In (c)-(d), $c = 1.0 > c_T$ and there are two interior steady states. No control is given in (c), while $A = 15$ in (d). Dashed and dotted lines are denoted for prey and predator, respectively

which confirms Proposition 2.1. We use initial condition (3.1209, 1.6858) close to E^* for all the simulations and the results are presented in Figure 4. There is no control in (a), while (b)-(d) apply $A = 15$, 5, and 0.5, respectively. We see that cooperative hunting in the predator is destabilizing and it is harder to control the populations even when the cost associated with the control $A = 0.5$ is small.

In Figure 5, we increase m to 7 while keeping all other parameters the same as those in Figure 2 but varying c. Then, $K < m/bd$ so that the number of interior steady states depends on c. The critical c_T given in Theorem 2.2 in the setting of the model (2.1) is computed with $c_T = 0.9865225$ and $x_T = 4.111703$. If $c = 0.5$, then Theorem 2.2 implies that the model of no control has no interior steady state. Using the initial condition (1.1, 2), both populations go extinct without the control as shown in Figure 5a. With the control of $A = 0.5$, the prey population survived as presented in Figure 5b. Let $c = 1 > c_T$. Then, there are two interior steady states $E_1^* = (3.9635, 0.7661)$ and $E_2^* = (4.2467, 0.6483)$ in the absence of control, where E_1^* is asymptotically stable and E_2^* is a saddle point. Figure 5c,d provides the simulation results using initial condition (3.9, 0.76) with $A = 0$ and 15, respectively. We obtain similar results if we decrease A to 5 and 0.5, which are not presented. Notice that the strategy of culling predators can eliminate the predator population and increase prey population to its carrying capacity as shown in Figure 5d.

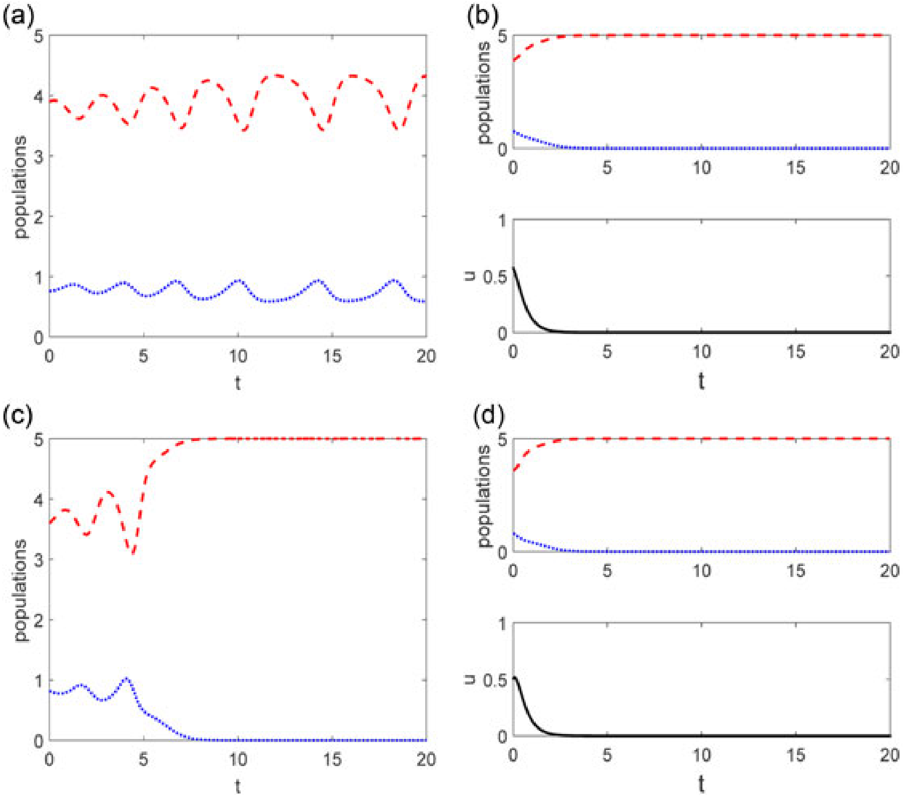

FIGURE 6 Populations and optimal controls over time are plotted in the parameter regime $K < m/bd$ so that the number of interior steady states depends on c. In (a)-(b), $c = 1.05 > c_T$. There is no control in (a) and $A = 15$ in (b). In (c)-(d), $c = 1.1 > c_T$ and there are two interior steady states. No control is given in (c), while $A = 15$ in (d). Dashed and dotted lines are denoted for prey and predator, respectively

Let $c = 1.05 > c_T$. Then, (2.3) has two interior steady states $E_1^* = (3.7787, 0.8119)$ and $E_2^* = (4.3847, 0.5681)$, where E_1^* is a repeller and E_2^* is a saddle point. In the absence of control, populations are oscillating over time as illustrated in Figure 6a. With a control of $A = 15$, the predator population becomes extinct and the prey reaches its carrying capacity $K = 5$ in a short period of time. See Figure 6b. Similar results are obtained but not provided for $A = 5$ and 0.5. Finally, we increase c to $1.1 > c_T$. Then, (2.1) has two interior steady states $E_1^* = (3.6602, 0.8295)$ and $E_2^* = (4.4593, 0.5180)$, where E_1^* is a repeller and E_2^* is a saddle point. We use the initial condition (3.6, 0.82) close to E_1^*. With no control, the solution converges to $E_{12} = (5, 0)$ by time $t = 10$, as shown in Figure 6c. With a control of $A = 15$ and using the same initial condition, the predator is also eliminated as shown in Figure 6d. Comparing the predator population in Figure 6c,d, the predator increases its size before extinction when there is no control. With a small control, the predator decreases monotonically to extinction.

4 | SUMMARY AND CONCLUSION

The Allee effect, referring to the reduced fitness or the decline in population growth at low-population densities observed originally by Allee (1938), has a significant consequence on population survival when the population is at low level. There has been a rebound of interest in Allee effects recently due to fragmentation of habitats, invasions of exotic species, biological control of pests, and so forth, all involved with small populations (Courchamp et al., 2008).

Motivated by a recent work of Alves and Hilker (2017) on cooperative hunting of predators and based on the classical Lotka–Volterra model, we propose a system of predator–prey interactions with Allee effects in the prey and cooperative hunting in the predator to study population interactions. Due to this Allee effect, the resulting model has an extra parameter than the system studied by Alves and Hilker (2017) of no Allee effects in the prey, namely the appearance of the prey's Allee threshold. Our analyses as well as the numerical explorations of Alves and Hilker (2017) are carried out on a scaled system, where the dimensionless parameter K is interpreted as the predator's maximum reproductive number. It is the average number of offsprings an individual predator can reproduce over its lifetime when the predator is introduced into a prey population at its carrying capacity. Analogously, the dimensionless parameter a is the predator's reproductive number when the prey is at its Allee threshold.

If the maximum reproductive number K of predators exceeds one, $K > 1$, then by applying the tool of uniform persistence explored by Butler and Waltman (1986) such as in Jang and Baglama (2003) to the model of Alves and Hilker (2017), we can prove that both populations coexist indefinitely for all positive initial populations. This phenomenon is no longer true for our model with Allee effects in the prey. In fact, if, in addition, the predator's reproductive number when the prey is at its Allee threshold is also greater than one, $a > 1$, then both populations go extinct. In this circumstance, the predator can reproduce more than one offspring when the prey is at the Allee threshold, which drives the prey to below the threshold so that extinctions occur for all population distributions. Although global extinction holds for both models of hunting cooperation and of no cooperation, the time that it takes to becoming extinct is different between the two scenarios as demonstrated in Figure 1a,b. With cooperative hunting, the prey can go extinct earlier than the situation of no cooperative hunting and the predator may yield a larger population size before extinction.

If, in contrast, the predator's reproductive number is less than one when prey is at the Allee threshold, $a < 1 < K$, then similar to the Alves and Hilker (2017) model, the interaction has a unique interior steady state, in which hunting cooperation can destabilize the coexisting steady state. Further, the prey population in the coexisting steady state decreases with increasing degree of cooperation but this is not true for the predator population. These local dynamics are similar between our model and the model of Alves and Hilker (2017). However, while coexistence occurs for the model of Alves and Hilker (2017) as discussed above, extinction happens for our model if initial populations lie above the stable manifold of the predator extinction steady state $(a, 0)$. This extinction is mediated by the predator that drives the prey to below the Allee threshold so that both populations become extinct.

When the maximum reproductive number of the predators is less than one, $K < 1$, predators go extinct for both the proposed model and the model of Alves and Hilker (2017) if there is no hunting cooperation. In this circumstance, while the prey population persists in Alves and Hilker (2017), the prey may go extinct in our model due to the Allee effects in prey. With cooperative hunting, we derive a critical degree of cooperation c_{T} in terms of other model parameters, for which the predators may persist only if cooperation exceeds this critical magnitude, $c > c_{\mathrm{T}}$. With intense hunting cooperation, that is, $c > c_{\mathrm{T}}$, our model and the model of Alves and Hilker (2017) possess two coexisting steady states where one of them is always a saddle point. The stable manifold of the saddle point in Alves and Hilker (2017) separates the positive coordinate plane into two positively invariant regions with predator extinction occurs below the stable manifold and persistence above the manifold. For our model, there is an additional saddle point, $(a, 0)$, and, as a result, the stable manifolds of the two saddle points separate the positive quadrant into three positively invariant regions. Predator extinction remains held below the stable manifold of the coexisting steady state but unlike the Alves and Hilker (2017) model coexistence does not occur above this manifold. The predator persistence happens only when the populations are between the two stable manifolds. Both populations go extinct above the stable manifold of the boundary steady state $(a, 0)$ due to Allee effects occurring in the prey population. Consequently, the region of coexistence is smaller in our model than the model of Alves and Hilker (2017) due to Allee effects in the prey population.

In this investigation, we consider the situation when the prey population discussed above is an endangered species and is also a valuable natural resource. To save such a prey population from extinction, we adopt a control strategy by harvesting or culling its predators. To implement this control method effectively, we apply the well-established optimal control theory described by Lenhart and Workman (2007) to provide an optimal management plan. The goal is to maximize the prey population and minimize the predators while also minimizing the costs associated with the control over a fixed finite time period. From our numerical investigations, we see that it is easier to achieve the goal if the costs associated with the control are smaller. This is particularly true if the predators do not engage in cooperation. In addition, culling the predators can stabilize the interaction if there is no cooperative hunting as shown in Figure 3. With cooperative hunting, culling the predators can prevent prey extinction as illustrated in Figure 5 and can also eliminate predators as shown in Figures 5 and 6. The optimal schedules for culling the predators in different scenarios characterized by parameter sets and initial conditions can be obtained numerically by solving the two-point boundary value problem deduced from the optimal control problem. With this control strategy, we are able to rescue the endangered population when its predators are hunting cooperatively.

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ORCID

Sophia R.-J. Jang http://orcid.org/0000-0001-9877-145X

REFERENCES

Allee, W. C. (1938). *The social life of animals*. London: William Heinemann.

Allen, L. J. S. (2006). *An introduction to mathematical biology*. New Jersey: Prentice-Hall.

Alves, M. T., & Hilker, F. M. (2017). Hunting cooperation and Allee effects in predators. *Journal of Theoretical Biology*, *419*, 13–22.

Amarasekare, P. (1998). Allee effects in metapopulation dynamics. *The American Naturalist*, *152*, 298–302. https://doi.org/10.1086/286169

Berec, L. (2010). Impacts of foraging facilitation among predators on predator–prey dynamics. *Bulletin of Mathematical Biology*, *72*, 94–121.

Burden, T., Ernstberger, J., & Fister, K. (2004). Optimal control applied to immunotherapy. *Discrete & Continuous Dynamical Systems—Series B*, *4*, 135–146.

Butler, G. J., & Waltman, P. (1986). Persistence in dynamical systems. *Journal of Differential Equations*, *63*, 255–263.

Cosner, C., DeAngelis, D. I., Ault, J., & Olson, D. (1999). Effects of spatial grouping on the functional response of predators. *Theoretical Population Biology*, *56*, 65–75.

Courchamp, F., Berec, L., & Gascoigne, J. (2008). *Allee effects in ecology and conservation*. New York: Oxford University Press.

De Silva, M., & Jang, S. R.-J. (2015). Competitive exclusion and coexistence in a Lotka–Volterra competition system with Allee effects and stocking. *Letters in Biomathematics*, *2*, 56–66.

Fleming, W., & Rishel, R. (1975). *Deterministic and stochastic optimal control*. New York: Springer.

Gascoigne, J., & Lipcius, R. (2004). Allee effects in marine systems. *Marine Ecology Progress Series*, *269*, 49–59.

Gazda, S., Richard, C., Connor, R., Robert, K., Edgar, R., & Cox, F. (2005). Division of labour with role specialization in group-hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. *Proceedings of the Royal Society B*, *272*, 135–140.

Jang, S. R.-J., & Baglama, J. (2003). Persistence in variable-yield nutrient-plankton models with nutrient recycling. *Mathematical and Computer Modelling*, *38*, 281–298.

Keitt, T., Lewis, M., & Holt, R. (2001). Allee effects, invasion pinning, and species' borders. *The American Naturalist*, *157*, 203–216.

Lenhart, S., & Workman, J. T. (2007). *Optimal control applied to biological models*. New York: Chapman & Hall.

Lewis, M., & Keitt, T. (1993). Allee dynamics and the spread of invading organisms. *Theoretical Population Biology*, *43*, 141–158.

Numfor, E., Hilker, F. M., & Lenhart, S. (2017). Optimal culling and biocontrol in a predator–prey model. *Bulletin of Mathematical Biology*, *79*, 88–116.

Pantha, B., Day, J., & Lenhart, S. (2016). Optimal control applied in an anthrax epizootic model. *Journal of Biological Systems*, *24*, 495–517.

Scheel, D., & Packer, C. (1991). Group hunting behaviour of lions: A search for cooperation. *Animal Behaviour*, *41*, 697–709.

Thieme, H. R. (2003). *Mathematics in population biology*. New Jersey: Princeton University Press.

Uetz, G. W. (1992). Foraging strategies of spiders. *Trends in Ecology & Evolution*, *7*, 155–159.

Wang, G., Liang, X.-G., & Wang, F.-Z. (1999). The competitive dynamics of populations subject to an Allee effect. *Ecological Modelling*, *124*, 183–192.

Wang, J., Shi, J., & Wei, J. (2011). Predator–prey system with strong Allee effect in prey. *Journal of Mathematical Biology*, *62*, 291–331.

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APPENDIX A

Proof of Theorem 2.1 *Let $a > 1$. Then, E_{11} is a repeller and E_{12} is a saddle point with its stable manifold on the positive x-axis. Let $(x(0), y(0))$ satisfying (2.4) be given. If $x(t) > a$ for $t \geq 0$, then $y'(t) = (x - 1)y > (a - 1)y$ for $t \geq 0$ implies $y(t) \to \infty$ as $t \to \infty$ and we obtain a contradiction. Therefore, $x(t_0) \leq a$ for some $t_0 > 0$ and $y(t) > 0$ for $t \geq 0$, and such a solution converges to E_0. It follows that E_0 is globally asymptotically stable. Let $K < 1$. Then, E_{11} is a saddle point, E_{12} is asymptotically stable, and the system has no interior steady state. The stable manifold M_{11}^{+} of E_{11} lies in $\{(x, y) \in R_{+}^{2} : x > a,\ \ y > 0\}$. As a result, the system has no positive periodic solution and the ω-limit set of every solution is a steady state by the Poincaré–Bendixson theorem (Thieme, 2003). Moreover, M_{11}^{+} separates $\mathbb{R}_{+}^{2}$ into two positively invariant regions R_1 and R_2 with $E_0 \in R_1$ and $E_{12} \in R_2$. Consequently, solutions in R_1 and R_2 converge to E_0 and E_{12}, respectively.*

If $a < 1 < K$, then (2.3) has a unique interior steady state $E^* = (1, y^*)$, where $y^* = r(1 - 1/K)(1 - a)$. The Jacobian matrix evaluated at E^* is given by

$$J(E^*) = \begin{pmatrix} \frac{r}{K}(a + K - 2) & -1 \\ y^* & 0 \end{pmatrix} \tag{A.1}$$

with $\det(J) = y^* > 0$ and $\operatorname{tr}(J) = \frac{r}{K}(a + K - 2)$. It follows that E^* is a repeller if $a + K > 2$ and it is asymptotically stable if $a + K < 2$. To show that E^* undergoes a Hopf bifurcation when $a + K = 2$, we let $\lambda_{\pm}$ denote the eigenvalues of $J(E^*)$. Then, $\lambda_{\pm}|_{a+K=2} = \pm\sqrt{\det(J)}\,i$ and we need to verify that $\lambda_{\pm}$ crosses the imaginary axis transversally at $a + K = 2$, that is, $\frac{\partial(Re\,\lambda_{\pm})}{\partial K}|_{a+K=2} \neq 0$. It is sufficient to verify $\frac{\partial(\operatorname{tr}(J))}{\partial K}|_{a+K=2} \neq 0$, which is trivial since $\frac{\partial(\operatorname{tr}(J))}{\partial K}|_{a+K=2} = \frac{r(2-a)}{K^2}|_{a+K=2} > 0$. Therefore, a Hopf bifurcation occurs at $a + K = 2$. ☐