



Hunting cooperation and Allee effects in predators



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ABSTRACT

Cooperation is a ubiquitous behavior in many biological systems and is well-known for promoting Allee effects. However, few studies have paid attention to mechanisms inducing Allee effects in predators. Here, we focus on hunting cooperation and use a classical predator–prey system for identifying the impact of this mechanism. We add a cooperation term to the attack rate of the predator population, and investigate the equilibrium stability in phase plane and bifurcation diagrams. We show that hunting cooperation can be beneficial to the predator population by increasing the attack rate. We identify a scenario in which hunting cooperation produces Allee effects in predators and allows the latter to persist when the prey population does not sustain them in the absence of hunting cooperation. However, hunting cooperation can turn detrimental to predators when prey density drastically decreases because of increased predation pressure, which in turn decreases the predator intake. Hunting cooperation can also destabilize the system and promote a sudden collapse of the predator population. We generalize the model and prove that demographic Allee effects always occur when (1) the attack rate increases with the predator density, and (2) the functional response increases with the attack rate. We conclude that Allee effects in predators might be more widespread than expected. Mechanisms inducing such effects may strongly influence not only predators, but also the fate of ecosystems involving predators as in biological control programs.

1. Introduction

Social interactions between individuals are an integral part of life history traits for many species (Courchamp et al., 2008). In particular, cooperative behavior within a population is a widespread and important phenomenon in biological systems (Dugatkin, 1997). It can induce a positive relationship between the per capita growth rate and population density, which is called a demographic Allee effect (Stephens et al., 1999; Courchamp et al., 2008). This effect can potentially lead to population extinction, which has recently seen renewed interest in both theoretical and empirical studies of biological conservation in endangered or exploited ecosystems (Courchamp et al., 1999; Stephens and Sutherland, 1999; Kramer et al., 2009; Gregory et al., 2010; Lidicker, 2010).

Populations rarely exist in isolation, but interact with other species. Ecologists have recognized many mechanisms for inducing Allee effects in prey, such as reproductive facilitation, cooperative breeding, anti-predator behavior, foraging efficiency, and environmental conditioning. Allee effects can equally exist in predators. Yet, theory has largely

focused on Allee effects in prey (e.g. Bazykin, 1998; Courchamp et al., 2000; Liermann and Hilborn, 2001; Boukal and Berec, 2002; Kent et al., 2003; Gascoigne and Lipcius, 2004; Zhou et al., 2005; Jang, 2006; Boukal et al., 2007). Allee effects in predators have been considered as resulting from size-selective predation (de Roos and Persson, 2002; de Roos et al., 2003), mate-limitation (Bazykin, 1998; Zhou et al., 2005; Verdy, 2010; Bompard et al., 2013), positive feedbacks of top predators on nutrient cycling (Brown et al., 2004), or foraging facilitation among predators (Berec, 2010).

Foraging facilitation appears a particularly interesting phenomenon in predator populations. Many living organisms cooperate for hunting, especially carnivores (Macdonald, 1983), including lions (Packer et al., 1990; Scheel and Packer, 1991), wolves (Schmidt and Mech, 1997), African wild dogs (Creel and Creel, 1995), and chimpanzees (Boesch, 1994), but also aquatic organisms (Bshary et al., 2006), birds (Hector, 1986), ants (Moffett, 1988), and spiders (Uetz, 1992). As individuals work toward finding and attacking prey, they can provide more resources to the population and thus positively affect life-history traits. However, we are aware of only two studies that address hunting

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cooperation in predator–prey models. Cosner et al. (1999) derive a functional response for predators that forage in a spatially linear formation and aggregate when they encounter a cluster of prey. Berec (2010) analyzes a predator–prey model that he generalizes to cooperative hunting. He finds that hunting cooperation has a destabilizing effect on predator–prey dynamics, by extending the parameter range that allows limit cycle oscillations.

Here, we study how different intensities of hunting cooperation affect predator density, predator survival, and the stability of the ecological community. In our model, we assume that, due to hunting cooperation, the predator attack rate increases with predator density. While this approach is similar to the one in Berec (2010), there are two important differences. First, we focus on the ecological scenario in which predators are unable to survive without hunting cooperation. It is in this scenario that cooperation is of essence, and we show that it can mediate survival of the predators that would go extinct otherwise. The second difference is that the model used by Berec (2010) assumes a type II functional response, which can generate sustained predator–prey oscillations even in the absence of cooperative effects. Our model assumes a linear functional response. That is, there are no sustained predator–prey oscillations possible in the absence of hunting cooperation. The oscillations that we observe in the presence of hunting cooperation are therefore clearly generated by the cooperative behavior.

2. Hunting cooperation in a classical predator–prey model

2.1. Model description

We extend the classical Lotka–Volterra model with logistic growth of the prey by including hunting cooperation. Predator–prey models can be written in the form

$$\begin{cases} \frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) - \Phi(N, P), \\ \frac{dP}{dt} = e\Phi(N, P) - mP, \end{cases} \quad (1)$$

where N and P are prey and predator densities respectively, r is the per capita intrinsic growth rate of prey, K is the carrying capacity of prey, e is the conversion efficiency, and m is the per capita mortality rate of predators. All parameters are positive. Function $\Phi(N, P)$ is the functional response of predators on prey, i.e. the rate at which individual predators kill prey. It is often presumed to depend only on prey density, and in the case of the Lotka–Volterra model this dependence is linear, i.e. $\Phi(N, P) = \lambda N$, where $\lambda > 0$ is the attack rate per predator and prey.

In the case of hunting cooperation, the functional response depends on both prey and predator densities. We assume that cooperative predators benefit from their behavior, so that the success of attacks on prey increases with predator density. We represent this assumption in the model by replacing the constant attack rate λ by a density-dependent term:

$$\Phi(N, P) = (\lambda + aP)N, \quad (2)$$

where $a > 0$ is a parameter describing predator cooperation in hunting. In what follows, we will refer to aP as the *cooperation term*. If $a=0$, we retain a predator–prey model without hunting cooperation. If we allowed $a < 0$, this would correspond to predator interference, but we would need to floor the term $\lambda + aP$ at zero to prevent negative values.

For better comparison with the hunting cooperation model by Berec (2010), we briefly outline his approach which assumes a type II-like functional response of the form

$$\Phi(N, P) = \frac{\rho(P)N}{1 + h(P)\rho(P)N}$$

that saturates with increasing prey density. If hunting cooperation is

“encounter-driven”, the encounter rate between predators and prey (synonymous with attack rate) is generalized to

$$\rho(P) = \frac{\rho_0}{(b + P)^w}, \quad b \geq 0, \quad (3)$$

and if hunting cooperation is handling-driven, the predator handling time of prey is generalized to $h(P) = h_0(b + P)^w$, $b \geq 0$. In both cases, values of $w > 0$ yield foraging facilitation (i.e., hunting cooperation), $w=0$ retains a functional response of Holling type II, and $w < 0$ yields predator interference.

Our model (2) is similar to Berec's encounter-driven functional response. In particular, for $w = -1$ and $h(P) = 0$, the Berec functional response (3) reduces to Eq. (2), with λ corresponding to $\rho_0 b$ and a corresponding to ρ_0 . In a later Section, we will generalize the relationship between attack rate and predator density in model (2), beyond the form (3) used by Berec (2010).

In the following, we will consider a non-dimensionalized version of model (1) with the functional response (2). Introducing the dimensionless variables

$$n = \frac{e\lambda}{m}N; \quad p = \frac{\lambda}{m}P; \quad \tau = mt,$$

and the dimensionless parameters

$$\sigma = \frac{r}{m}; \quad \kappa = \frac{e\lambda K}{m}; \quad \alpha = \frac{am}{\lambda^2} \quad (4)$$

model (1), (2) becomes

$$\begin{cases} \frac{dn}{d\tau} = n \left[\sigma \left(1 - \frac{1}{\kappa}n \right) - (1 + \alpha p)p \right], \\ \frac{dp}{d\tau} = p[(1 + \alpha p)n - 1], \end{cases} \quad (5)$$

which depends on three parameters only. This is the model we will analyze in the following.

2.2. Equilibria and phase plane analysis

The predator population can persist in the system if the prey population is large enough to sustain the predators. This situation occurs when the carrying capacity of prey is larger than a critical prey density defined by the nontrivial predator nullcline

$$n = \frac{1}{1 + \alpha p}. \quad (6)$$

The prey population can only increase if it withstands the predation pressure. As the predation pressure depends on the predator density, prey population growth is restrained at the critical prey density defined by the nontrivial prey nullcline

$$n = \kappa \left[1 - \frac{(1 + \alpha p)p}{\sigma} \right]. \quad (7)$$

Taken together, these nullclines give information about the number of nontrivial equilibria, and their representation in the phase plane provides clues about equilibrium stability (Fig. 1). In particular, the dynamics of model (5) are well-known in the absence of cooperation, i.e. when $\alpha = 0$. In this case, the predator nullcline equals $n=1$, which is the non-dimensionalized critical prey density for the predator survival in the absence of cooperation. The value of κ compared to this critical prey density is of great importance for equilibrium stability. When the prey carrying capacity is above this critical prey density, both nullclines (6) and (7) intersect exactly once for all other parameter values (Fig. 1D). The system thus reaches a coexistence equilibrium that is globally asymptotically stable (e.g. (Kot, 2001)). However, when the prey carrying capacity is below this density (Fig. 1A), the nullclines (6) and (7) do not cross: because the prey population cannot sustain the predator population, the latter goes extinct, while the prey population

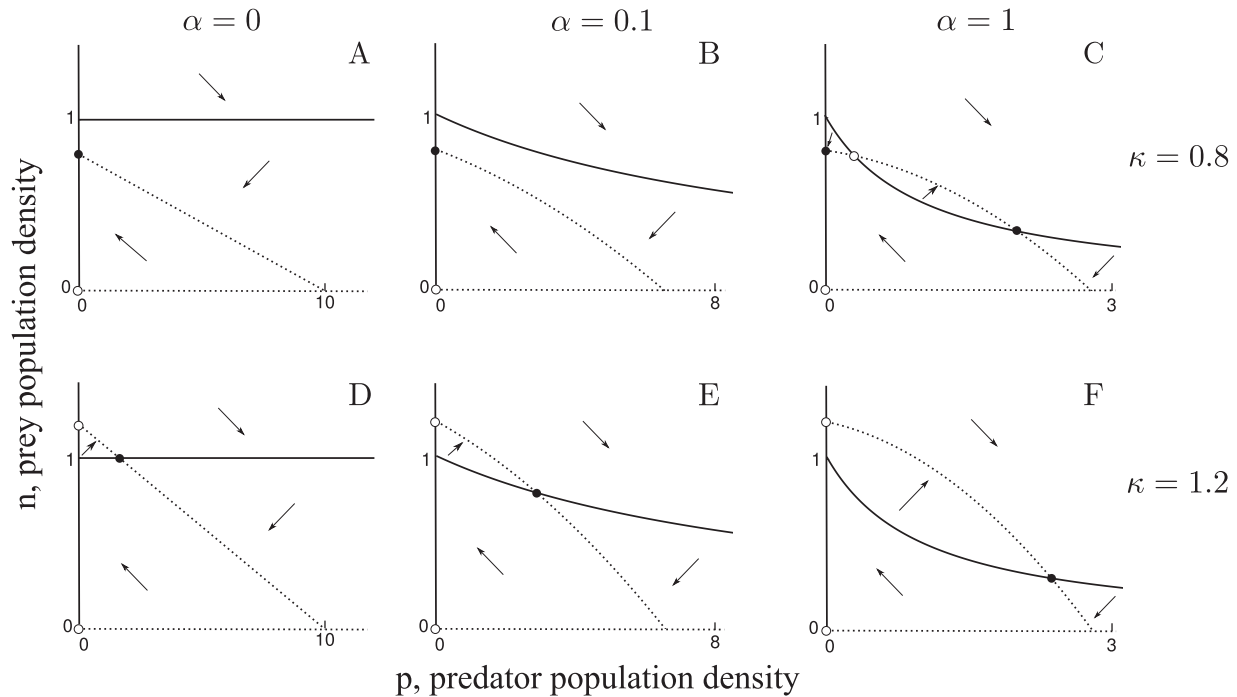


Fig. 1. Phase plane diagrams for the hunting cooperation model (5). Solid lines represent the predator nullclines and dotted lines represent the prey nullclines. Filled circles correspond to stable stationary states and empty circles to unstable stationary states. Arrows indicate the direction of the vector fields. Note the different scales of the horizontal axes. $\alpha = 0, 0.1, \text{ and } 1$ from the left to the right column, $\sigma = 10, \kappa = 0.8$ (A–C), $\kappa = 1.2$ (D–F).

reaches its carrying capacity.

When predators cooperate, i.e. when $\alpha > 0$, dynamics are more complex because the nullclines are not linear anymore. As previously, two main cases can be distinguished depending on κ values. Recall that κ is a non-dimensionalized parameter and comprises the dimensional carrying capacity, the conversion efficiency as well as the per-capita predator mortality and attack rate, cf. Eq. (4). In fact, κ can be also interpreted as the predator basic reproduction number, defined as the average number of offspring generated by a single predator during its lifetime when introduced into a prey population at carrying capacity. If the basic reproduction number is greater than one, predators can survive and coexist with prey, whereas they go extinct if $\kappa < 1$.

In the coexistence case ($\kappa > 1$), the corresponding nontrivial equilibrium is unique as the nullclines always cross once. The occurrence of coexistence is not affected by the intensity of hunting cooperation (Fig. 1E–F). We however notice that cooperation affects the equilibrium values. The prey density at equilibrium decreases with increasing α , because the success of attacks on prey, and as a consequence the predation pressure, increase as predators cooperate (Fig. 1E–F). For the predator density at equilibrium, there is a hump-shaped relationship with the hunting cooperation. The predator population increases with small values of α , because predators better forage on prey (Fig. 1E), but decreases with large values of α as a consequence of the decrease in prey density (Fig. 1F; note the scale on the horizontal axis).

In the predator extinction case ($\kappa < 1$), two different situations can occur. First, for small values of α , the prey population remains too small to sustain the predator population even if there is hunting cooperation. Consequently, predators go extinct for all initial conditions (Fig. 1B). Second, for larger values of α , the cooperative behavior in predators is large enough to make their survival possible. The nullclines intersect twice (Fig. 1C), and the vector fields of the system indicate that the coexistence equilibrium with the larger predator density is stable, while the other coexistence equilibrium is unstable. The system is bistable: the predator population can still go extinct for low initial predator densities, which is a characteristic of strong Allee effects. Hence, cooperation allows large predator populations to

survive, whereas all predator populations are doomed to extinction without cooperation. In what follows, we will focus on the cooperation-mediated coexistence in the extinction case ($\kappa < 1$).

2.3. Allee thresholds

If the cooperation is strong enough to mediate coexistence, there is a strong Allee effect in the predator population. The so-called Allee threshold is the critical predator density below which predators go extinct and above which predators survive. This critical predator density can be found as the boundary between the basin of attraction of the coexistence state on the one hand and the basin of attraction of the predator-extinction state on the other hand (Fig. 2). Obviously, the Allee threshold varies with the prey population density. The higher the prey population density, the smaller the Allee threshold.

Fig. 2 suggests that increasing hunting cooperation leads to smaller Allee thresholds. This has the effect of reducing the risk of predator extinction. Moreover, increasing hunting cooperation strengthens the resilience of the coexistence state, as its basin of attraction becomes larger with increasing values of α and can therefore absorb greater perturbations. Correspondingly, the basin of attraction to the prey-only state becomes smaller for increased levels of cooperation.

2.4. Bifurcation behavior

We now investigate the bifurcation behavior in the case of cooperation-mediated coexistence ($\kappa < 1$). We begin by varying the cooperation rate α (Fig. 3). The predator–extinction equilibrium ($n = \kappa, p = 0$) is always stable for all values of α (solid gray lines). If a predator population cooperates weakly ($0 \leq \alpha < 0.44$), it does not persist and goes extinct for all initial conditions in the positive quadrant. The prey population thus reaches its carrying capacity. We find a limit point bifurcation at $\alpha = 0.44$, where two branches of coexistence equilibria emerge. One of them is stable and the other one is unstable. The system therefore becomes bistable when predators cooperate more strongly. That is, predators can either go extinct because of strong Allee effects or persist depending on the initial

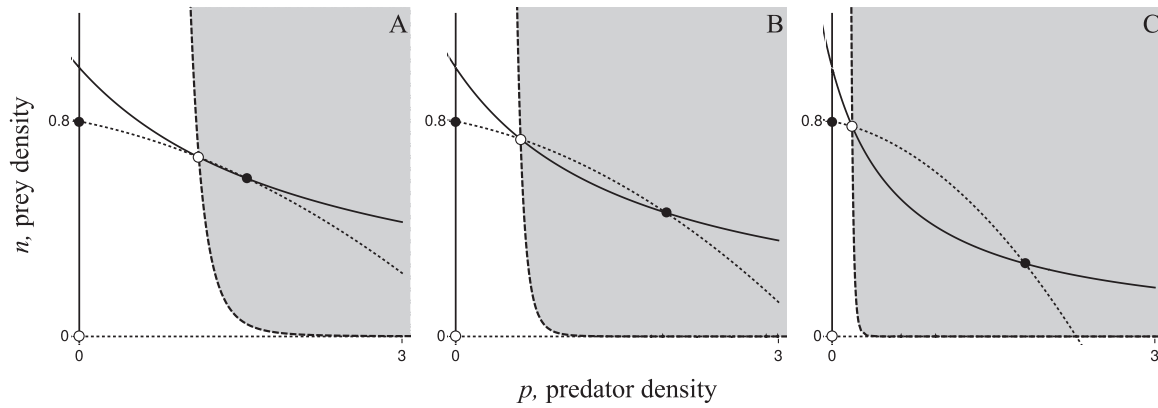


Fig. 2. The Allee threshold of the predator population and the basins of attraction for different cooperation levels, (A) $\alpha = 0.45$, (B) $\alpha = 0.6$, (C) $\alpha = 1.5$. The Allee threshold depends on the prey density and is given by the separatrix curve (thick dashed) between the basins of attraction to the coexistence state (gray area) and to the prey-only state (white area). The thinner lines represent the predator (solid) and prey (dotted) nullclines. Filled circles correspond to stable stationary states and empty circles to unstable stationary states. The separatrix has been computed numerically by running system (5) and checking whether the solution at the end of the simulation is close to one of the two attractors. Other parameter values: $\sigma = 10$, $\kappa = 0.8$ and $\alpha = 0.45$ (A), $\alpha = 0.6$ (B), $\alpha = 1.5$ (C).

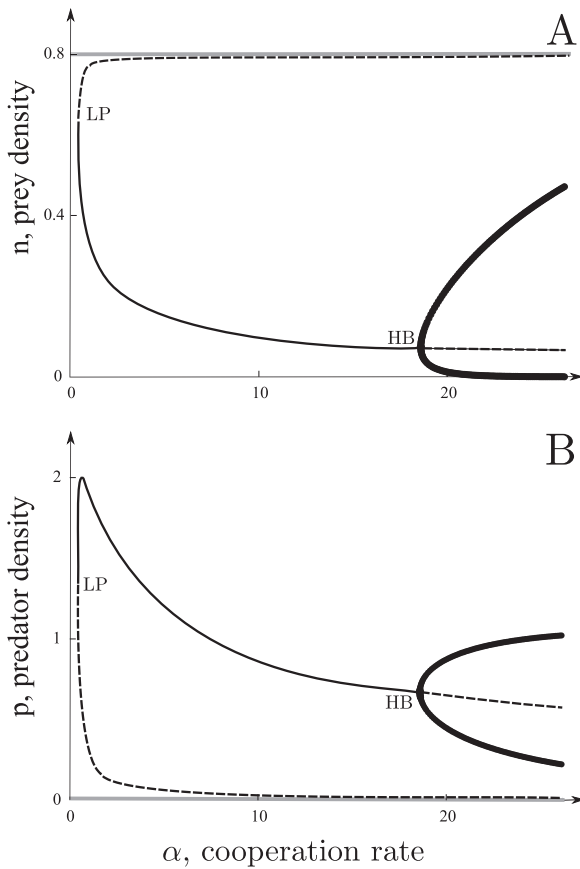


Fig. 3. Bifurcation diagram of prey (A) and predators (B) for model (5) when varying α . Solid gray lines indicate the predator–extinction equilibrium, which is always stable. Solid black lines indicate stable coexistence equilibria and dashed black lines indicate unstable coexistence equilibria. Bold black lines indicate the maxima and the minima of periodic oscillations. Limit points are denoted by LP, and Hopf bifurcations are denoted by HB. $\sigma = 10$ and $\kappa = 0.8$.

condition. For even larger values of α , a Hopf bifurcation occurs ($\alpha = 18.6$): the stable coexistence equilibrium loses stability so that stable limit cycle oscillations emerge, and their amplitudes quickly increase with α .

When the prey population is foraged by a cooperative predator population in the predator extinction scenario ($\kappa < 1$), it can either reach its carrying capacity or a smaller density at equilibrium, so that predator cooperation has a neutral or a negative effect on prey,

respectively (Fig. 3A). By contrast, predators can benefit from their hunting cooperation because it may facilitate their survival. However, this is true only when the cooperation rate and the predator density are large enough. Predator density at the stable coexistence equilibrium shows a hump-shaped relationship with cooperation rate (Fig. 3B), something we already observed for the case $\kappa > 1$ (Fig. 1E,F).

Because prey life-history traits can also strongly influence dynamics, we continue the exploration of the equilibrium stability by varying the per capita growth rate of prey σ and fixing α at 10 (Fig. 4).

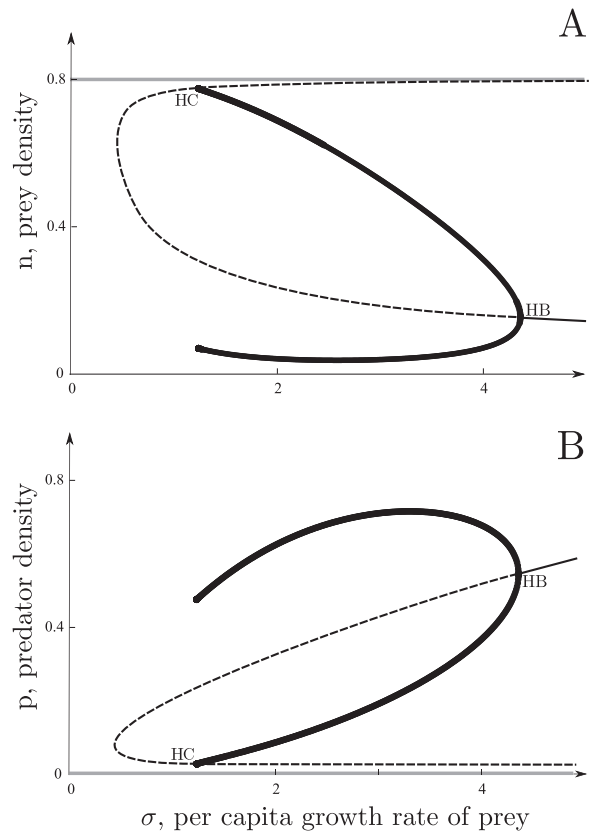


Fig. 4. Bifurcation diagram of prey (A) and predators (B) for model (5) when varying σ . Solid gray lines indicate the predator–extinction equilibrium. Solid black lines indicate stable stationary states and dashed black lines indicate unstable stationary states. Bold black lines indicate the maxima and the minima of periodic oscillations. Homoclinic bifurcations are denoted by HC, and Hopf bifurcations are denoted by HB. $\alpha = 10$ and $\kappa = 0.8$.

For σ values larger than 4.36, the system is bistable, with either stable coexistence or predator extinction. A Hopf bifurcation occurs at $\sigma = 4.36$, and the coexistence equilibrium loses stability for σ values smaller than 4.36. The system remains bistable, but coexistence is now oscillatory due to the limit cycle that emerges in the Hopf bifurcation. The limit cycle can, however, collide with one of the unstable coexistence equilibria in a homoclinic bifurcation ($\sigma = 1.2$). The predator–extinction equilibrium thus becomes the only stable state when $\sigma = 1.2$, which renders the system monostable.

Additional simulations of the equilibrium stability when varying σ show that dynamics can in fact be more complex than in Fig. 4 (Appendix A). In particular, the system can exhibit two Hopf bifurcations, and the oscillations emerging from each of these bifurcation points form a bubble (Fig. A.1) (cf. examples of bubbling in Oliveira and Hilker (2010), Liz and Ruiz-Herrera (2012)). A counter-intuitive impact of the prey growth rate on dynamics is highlighted by these bifurcation diagrams (Fig. 4A and Fig. A.1). We notice that the prey density at equilibrium decreases with increasing growth rate, which may appear paradoxical. In the Lotka–Volterra model without cooperation ($\alpha = 0$), the prey density at equilibrium actually remains constant when varying σ . Here, the seemingly paradoxical observation is an indirect consequence of hunting cooperation that promotes large densities for predators that forage on fast growing prey. This increases the predation pressure on prey, which density at equilibrium decreases in turn.

2.5. Two-parameter bifurcation

At this point, we have considered the effects of α and σ separately. Now we complement the bifurcation analysis by varying σ with α simultaneously (Fig. 5A). The two-parameter bifurcation diagram shows that for small values of α and σ , the predator–extinction equilibrium is the only stable state of the system (white area). Above the solid line, which corresponds to the limit point bifurcation, the system is bistable. On the one hand, the prey and the predator populations can reach either the coexistence equilibrium or the predator–extinction equilibrium (gray area). On the other hand, for larger values of α , the coexistence equilibrium loses stability due to a Hopf bifurcation. On the right-hand side of the dotted line corresponding to the Hopf bifurcation curve, the system is bistable between the predator–extinction equilibrium and cyclic coexistence (dotted area). Moreover, the curves of the limit point bifurcation and Hopf bifurcation tangentially touch in a Bogdanov–Takens bifurcation point. This is also where a homoclinic bifurcation curve emerges. As a consequence, the cyclic coexistence can suddenly disappear and cause predator extinction for all initial conditions.

Finally, Fig. 5B shows a two-parameter bifurcation diagram when α and κ are varied simultaneously. This diagram recaps some findings from the phase plane analysis. If $\kappa > 1$, there is a unique coexistence equilibrium. If $\kappa < 1$, the predator population goes extinct unless a large enough value of α induces a strong Allee effect and allows the survival of large predator populations. The gray area in Fig. 5B marks the parameter region of cooperation-mediated coexistence. The necessary level of cooperation is the smaller, the higher the prey carrying capacity.

In addition, Fig. 5B shows that the stable coexistence state becomes unstable when increasing cooperation or enriching the carrying capacity. The destabilization takes place via a Hopf bifurcation and gives rise to sustained predator–prey oscillations. The oscillations occur for both cases $\kappa < 1$ and $\kappa > 1$. We do not observe homoclinic bifurcations in Fig. 5B, because of the large value of σ . For smaller values of σ , we have found homoclinic bifurcations for $\kappa < 1$ (not shown here).

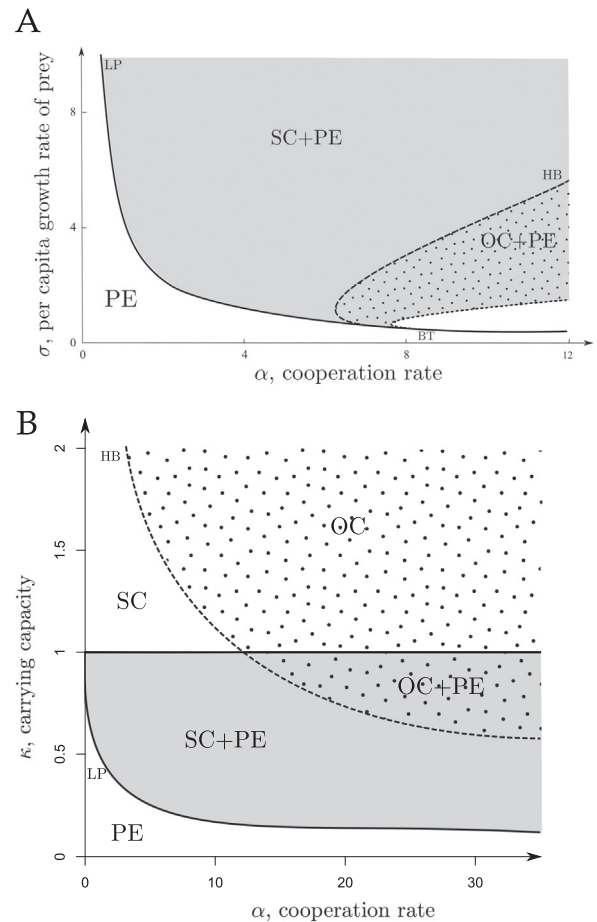


Fig. 5. Two-parameter bifurcation diagrams of model (5) for varying α and (A) σ , (B) κ . The solid line represents limit point bifurcations (LP), the dashed line Hopf bifurcations (HB), and the dotted line homoclinic bifurcations (HC). In the white area, the predator population goes extinct (predator extinction – PE) or coexists with the prey (stable coexistence – SC, oscillatory coexistence – OC). In the gray area, a strong demographic Allee effect occurs. The system is bistable and approaches either predator extinction or a coexistence attractor, which can be stable or oscillating. In (A), the curves of the limit point bifurcation and Hopf bifurcation tangentially touch in a Bogdanov–Takens point denoted by BT. This is where the homoclinic bifurcation curve emerges that renders the system monostable. Parameter values: (A) $\kappa = 0.8$, (B) $\sigma = 10$.

3. Generalization

3.1. Generalized model

So far, our results are based on model (5) with the two assumptions that (i) the functional response increases linearly with prey density and (ii) the cooperation term increases linearly with predator density. In order to verify that our results are not an artefact of these assumptions, we now analyze a model with a generalized functional response $\Phi(N, \lambda(P), h)$. We assume that the functional response depends on prey density N , on a generalized attack rate with hunting cooperation $\lambda(P)$ which may depend on P , and on a set of parameters h that can represent extra parameters such as predator handling time. We return to dimensional variables and parameters; starting from the dimensional model (1), the generalized model reads

$$\begin{cases} \frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) - \Phi(N, \lambda(P), h)P, \\ \frac{dP}{dt} = e\Phi(N, \lambda(P), h)P - mP, \end{cases} \quad (8)$$

in which parameters remain the same as before.

We now focus on the identification of demographic Allee effects in

predators. We consider the per-capita growth rate F of predators

$$F = \frac{dP}{Pdt} = e\Phi(N, \lambda(P), h) - m,$$

and investigate when it is positively correlated with predator density at small predator densities, i.e.

$$\left. \frac{dF}{dP} \right|_{P=0} > 0, \tag{9}$$

which corresponds to the definition of a demographic Allee effect. Note that a *strong* demographic Allee effect can only occur if F is negative for small predator densities. This Section, however, is not restricted to strong Allee effects. We can write inequality (9) as

$$\left. \frac{\partial\Phi(N, \lambda(P), h)}{\partial\lambda(P)} \frac{\partial\lambda(P)}{\partial P} \right|_{P=0} > 0. \tag{10}$$

This means that the predator population experiences a demographic Allee effect if, at small predator densities,

Condition (1): $\lambda(P)$ increases with P , and

Condition (2): $\Phi(N, \lambda(P), h)$ increases with $\lambda(P)$.

Alternatively, inequality (10) would be satisfied if $\lambda(P)$ decreases with P , as could happen for predator interference, and if $\Phi(N, \lambda(P), h)$ decreases with $\lambda(P)$. However, since we consider hunting cooperation, we henceforth exclusively assume that the cooperation term $\lambda(P)$ increases with predator density P , i.e. that Condition (1) is always satisfied. Condition (2) implies that the functional response increases with $\lambda(P)$. This seems reasonable and therefore suggests that a demographic Allee effect may be widespread. Note that it is the case for many functional responses commonly used in theoretical ecology, including linear as well as type I, II, III, and IV functional responses.

3.2. Simulations

We verify the conclusions from the generalized model by numerical simulations, for which we consider different functional responses that increase with the attack rate. Here, we choose type II, type III, and type IV functional responses. The corresponding model equations and their non-dimensionalized versions are given in Appendix B. Fig. 6 shows the two-parameter bifurcation diagrams when varying the cooperation rate α and prey growth rate σ . We again focus on the case in which the predator population cannot survive when they do not cooperate, by choosing $\kappa = 0.8 < 1$. The models contain extra handling time parameters, which we keep all fixed at the same value.

The model based on a type II functional response shows a bifurcation behavior (Fig. 6A) quite similar to the one in Fig. 5. The major difference is that the parameter region leading to limit cycle oscillations is considerably expanded, mostly because the Hopf bifurcation curve turned counter-clockwise and is now almost vertical. Moreover, the homoclinic bifurcation curve moved slightly such that the parameter region of essential extinction shrank. Overall, the type II function response promotes the possibility of sustained oscillation, which is consistent with standard expectation.

The bifurcation diagram of the type IV based model (Fig. 6C) differs from the one of the type II based model (Fig. 6A) in two aspects. First, the Hopf bifurcation curve turned even further counter-clockwise. Consequently, there is increased tendency for destabilization. Second, the parameter region of essential extinction has markedly expanded, which makes sense as a type IV functional response is known to induce homoclinic bifurcations.

Surprisingly, the type III based model shows a significantly different behavior (Fig. 6B). It is difficult to compare to the bifurcation diagrams in Figs. 6A and C, because the non-dimensional model uses some other dimensionless variables (Appendix B). Nevertheless, the Hopf bifurcation curve notably does not touch the limit point curve. As a consequence, there is neither a Bogdanov–Takens bifurcation point

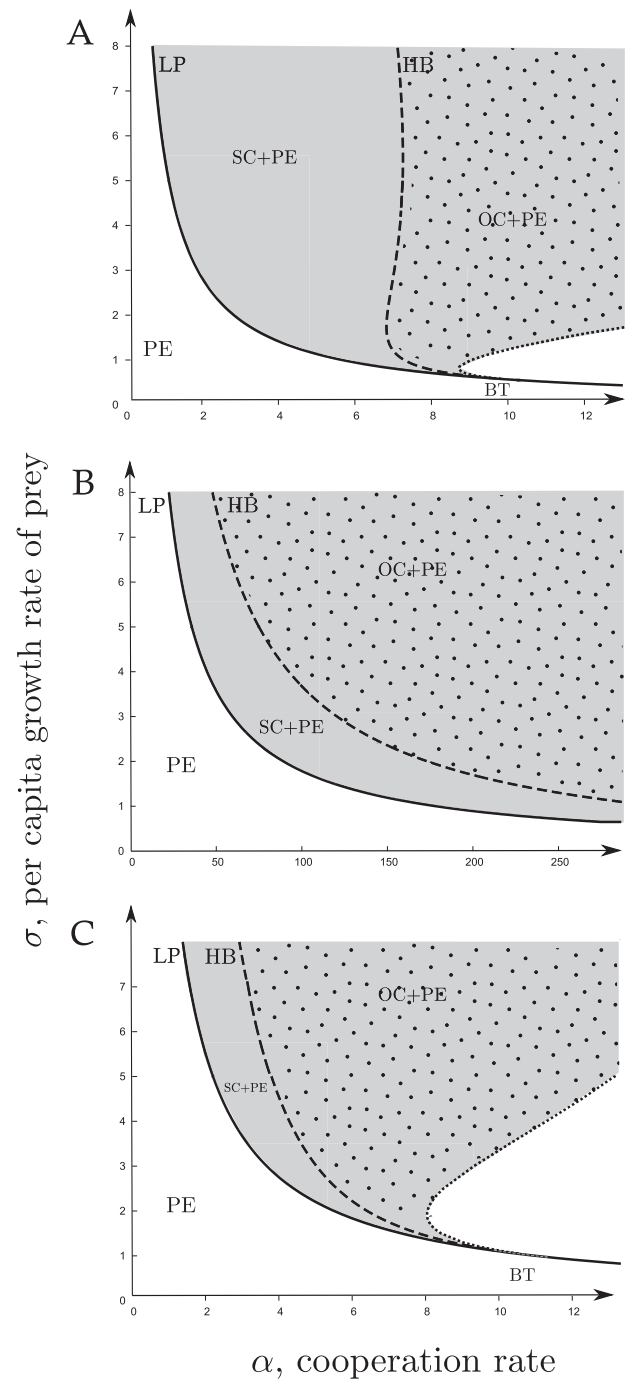


Fig. 6. Two-parameter bifurcation diagrams of the hunting cooperation models based on functional responses of (A) type II, (B) type III, and (C) type IV. The meaning of lines, shadings, and abbreviations are as in Fig. 5. Model equations used are (14)– (16), respectively, with parameter values $h_1 = 0.1, h_2 = 0.9, h_3 = 0.1, h_4 = 0.5$, and $\kappa = 0.8$. Note the different axes ranges.

nor a homoclinic bifurcation curve. We also tested other parameter values (e.g. $h_2=0.2$ and smaller), for which there are not even Hopf bifurcations. In that case, the stable coexistence equilibrium does not become destabilized by foraging facilitation. Type III functional responses are known to have stabilizing effects.

4. Discussion

Social interactions within a population are an integral part of life history traits for many species (Courchamp et al., 2008). They are

known to deeply affect dynamics and densities in the entire ecosystem. Current knowledge predicts that Allee effects in predators tend to be destabilizing if they are caused by mate finding (Zhou et al., 2005; Verdy, 2010) or hunting cooperation (Berec, 2010). This paper confirms these findings, both in the case when predators go extinct or persist in the absence of cooperation. In addition, this paper adds three novel impacts of predator cooperation beyond destabilization, namely (i) cooperation-mediated coexistence, (ii) overexploitation with increasing predator density, and (iii) catastrophic cycle collapse if the level of cooperation is too high.

4.1. Cooperation-mediated coexistence: a positive consequence of the Allee effect

Hunting cooperation can ensure the persistence of the predator population when predators would go extinct in the absence of hunting cooperation. This extinction is described by the condition $\kappa < 1$ and could be caused, for instance, by a lack of prey or too high mortality and hunting pressure. Cooperation can therefore allow predators to persist in degrading environments and less favorable climatic conditions, extend their range shifts to less productive ecosystems, or invade habitats in which prey have better cover.

Cooperation-mediated survival is clearly a positive consequence of the Allee effect induced by foraging facilitation. The Allee effect is often associated with problems of rarity, which result in population decline and extinction (e.g. (Courchamp et al., 1999; Berec et al., 2007)). In applied ecology, species preservation, wildlife management and resource exploitation, Allee effects are consequently considered as something dangerous and therefore undesirable (see Dennis (1989)).

Given that the Allee effect goes back to animal sociality and cooperative behavior (Allee, 1931; Stephens and Sutherland, 1999), it is somewhat surprising that the inherently positive aspect of Allee effects seems to be little appreciated in the literature. Here we have shown that cooperation can be clearly beneficial for population persistence and promotes ecosystem diversity. Moreover, our simulations suggest that cooperation promotes the resilience of the predator–prey coexistence state. There are some other modeling studies that demonstrate a positive consequence of the Allee effect on the coexistence of competing species in a spatial context (Levin, 1974; Ferdy and Molofsky, 2002; Molofsky and Bever, 2002; M'Gonigle and Greenspoon, 2014). The current paper therefore extends the amount of ecological situations in which Allee effects are actually friends, not foes.

4.2. Overexploitation by large predator groups: negative consequences of cooperation

Hunting cooperation can have not only positive, but also negative effects for predators. If cooperation is too strong, then predator equilibrium density declines with further increasing cooperation rate. The beneficial impact of cooperation on predators is then overcompensated by the decrease in prey density since a scarcer prey implies a smaller predator density in turn. This happens in both ecological scenarios of predator extinction and coexistence (cf. Figs. 3B and Fig. 1E,F, respectively). This result is consistent with the assumptions by Schmidt and Mech (1997) about wolf packs and the decrease of food acquisition when the pack increases, for example.

Predators might not benefit from foraging indefinitely, which is why at some point the attack could not increase with predator density anymore. Instead, predator interference could dominate over foraging facilitation at larger densities such that there is a hump-shaped relationship between attack rate and density (Berec, 2010). In that case, there is a regulation of predator densities, which could prevent overexploitation of prey, depending on how exactly interference and foraging facilitation interact.

4.3. Population cycles and their sudden disappearance

We surprisingly find sustained oscillations in the model based on a linear functional response. This reveals that hunting cooperation alone (without a saturating functional response) can induce limit cycles. The oscillations are probably caused by the foraging facilitation introducing a delay in the predator response to the decrease in the prey density.

The generalized models based on type II, III, and IV functional responses are known to produce predator–prey cycles even without hunting cooperation (cf. respectively (Rosenzweig and MacArthur, 1963; Oaten and Murdoch, 1975; Freedman and Wolkowicz, 1986)). In the presence of foraging facilitation, we found that all of these three functional responses tend to have a destabilizing effect on the coexistence equilibrium. An exception is the type III functional response, as it had no destabilizing effect at all in many of the numerical experiments performed. This conforms that the impact of type III responses is not clear-cut (Uszko et al., 2015).

The oscillations can however have a dramatic impact on the system, as limit cycles can disappear through homoclinic bifurcations. In that case, essential extinction of predators occurs for almost all initial conditions. This situation occurs when the trough of a cycle drops below the minimum viable population density set by the Allee effect. It is particularly widespread in the model based on a type IV functional response. The essential extinction scenario is typical for bistable system with oscillations (Bazykin, 1998; Schreiber, 2003; Hilker et al., 2009; Segura et al., 2016). An exception is again the type III response, as we did not observe essential extinctions in the simulations performed with this functional response.

Verdy (2010) also found homoclinic bifurcations, but they varied only the carrying capacity. Here we have shown that cooperation itself can cause cycle disappearance and ultimately predator extinction.

4.4. Conditions for Allee effects in generalized models

In addition to the introduction of the positive density-dependent cooperation term to the predator–prey system, we also directly analyze the per capita rate of the predator population, and conceptualize Allee effects in predators. This allows us to formalize the conditions that promote demographic Allee effects, independently from the exact expression of the positive density dependent term we add in the predator–prey system.

Generalization of the model reveals that hunting cooperation always induces Allee effects in predators when both (1) the attack term is positively correlated with the predator density, and (2) the functional response increases with the attack rate. The first condition is always satisfied in this work, because we exclusively consider foraging facilitation. We note that it does not hold for predator interference, or for hump-shaped attack rates that first increase with predator density but then decrease when predator density becomes too large and interference may dominate the positive effects of cooperation (Berec, 2010). The second condition is satisfied by many functional responses, including linear, type II, III, and IV functional responses. We however exclude functional responses which directly depend on the predator density. The positive impact of cooperation on the attack rate can indeed be counterbalanced by predator-density dependence, so that demographic Allee effects cannot occur, and the predator population does not benefit from their cooperation when hunting (Kramer et al., 2009). As a consequence, in this study we do not consider ratio-dependent functional responses, in which consumption depends on the prey density per predator capita (Arditi and Ginzburg, 1989). We also do not consider functional responses with predator interference (Beddington, 1975; DeAngelis et al., 1975; Berec, 2010; Příbylová and Berec, 2015). Moreover, we ignore predator–prey models that do not conform to the Lotka–Volterra framework based on functional and numerical responses, such as the Holling–Tanner model (Tanner, 1975).

4.5. Biological control implications, ecosystem consequences, and population structure

This result can have important applications in biological control using predators. Allee effects have been indeed discussed as one of the potential causes of biological control failure, as they can alter predator establishment and efficiency when controlling target pests (Freckleton, 2000). Our work however shows that Allee effects can turn positive for cooperative predators, which benefit from an increased attack rate, and can thus persist.

The increase in the attack rate with the predator density can also be interpreted as an increase in the costs of anti-predator defense for the prey (Skelly, 1992), so that the prey population becomes less efficient against predator attacks when the density of the latter increases. Anti-predator behavior, such as habitat selection, vigilance, and crypsis (Ruxton et al., 2004), is well-known to induce Allee effects in prey (Mooring et al., 2004; Courchamp et al., 2008). Here we reveal that such behavior can also induce Allee effects at a higher trophic level. As a consequence, we suppose that mechanisms leading to Allee effects or promoting emergence of such effects through trophic cascades may be more exhaustive than expected.

Here, we consider closed populations and assume homogeneity in the environment and among the individuals. However, age- and size-structured ecosystems are often more complex in nature, due to individual behavior and spatial factors. Such factors can reverse the fate of prey–predator systems. In particular, species that cooperate when hunting are also known for living in groups and occupying a local territory (Packer et al., 1990). The set of groups can be then seen as a metapopulation or a spatially structured population (Hanski, 1999; Fronhofer et al., 2012). Allee effects can occur within each group, but this also affects the entire metapopulation with emerging Allee-like effects that impose a threshold for groups below which the metapopulation goes extinct (Amarasekare, 1998; Zhou and Wang, 2004). In this work, we however suggest that Allee effects can be associated with beneficial impacts of cooperation, and with persistence of endangered species. In such a context, mechanisms leading to Allee effects may turn beneficial for populations at risk of extinction, even in complex structured ecosystems.

4.6. Final remarks

It is worth emphasizing that we obtained all these results from a very basic predator–prey model, in which a simple cooperation term is added to the attack rate for representing the benefits that hunting cooperation brings to the predator population. Our model is a special case of the more general model proposed by Berec (2010). Nevertheless, we find four novel results. First, foraging facilitation can mediate the survival of predators. We were able to obtain this result because we started from the ecological scenario that predators would go extinct without cooperation. By contrast, Berec (2010) focused in simulations on the ecological scenario that predators persist

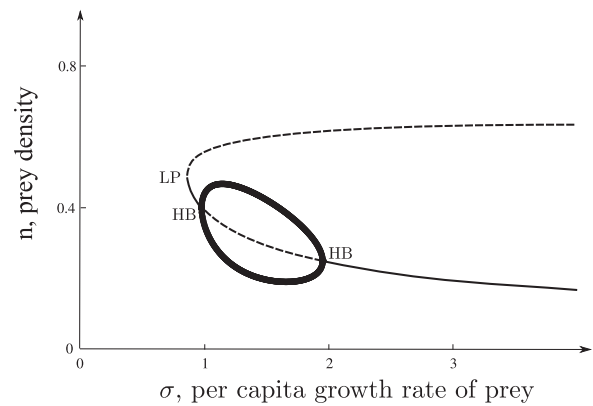


Fig. A.1. Bifurcation diagram of prey for model (5) when varying σ . Solid lines indicate stable stationary states, dashed lines indicate unstable stationary states. Bold lines indicate the maxima and the minima of periodic oscillations. The limit point bifurcation is denoted by LP and Hopf bifurcations are denoted by HB. $\alpha = 10$ and $\kappa = 0.65$.

on the prey in the absence of cooperation. Moreover, we find that predator survival is more resilient (robust to perturbations) for higher levels of cooperation.

Second, we discover that too much cooperation can backfire to predators as they may overexploit their prey. This holds in both scenarios where predators would go extinct or survive without cooperation. This has not been observed in the model by Berec (2010). We speculate that this might be because Berec (2010) varied parameter w that shows up in the exponent of the encounter rate (3), whereas we varied parameter a that describes the proportional relationship (2) between cooperation and predator density.

Third, we find that limit cycle oscillations can be induced by foraging facilitation alone, because our model is based on the linear functional response that does not yield oscillations without hunting cooperation. The model by Berec (2010) is based on a saturating type II functional response and is shown to extend the parameter range of oscillations that already occur without foraging facilitation. Furthermore, fourth, we find homoclinic bifurcations. They imply another detrimental effect of foraging facilitation, because increased cooperation can lead to cycle disappearance and predator extinction. As we have reduced the number of parameters to three in the non-dimensionalized model, we were able to more easily explore the parameter space and model behavior.

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Appendix A. Appendix A

Fig. A.1 shows a bifurcation diagram with two Hopf bifurcations giving rise to a 'bubble'.

Appendix B. Appendix B

Here we give the model equations that are based on functional responses of type II, III, and IV in the absence of hunting cooperation. The models follow system (1) and the respective functional responses

$$\Phi_{II}(N, P) = \frac{\rho(P)N}{1 + H_1\rho(P)N}, \quad (11)$$

$$\Phi_{III}(N, P) = \frac{\rho(P)N^2}{1 + H_2\rho(P)N^2}, \quad (12)$$

$$\Phi_{IV}(N, P) = \frac{\rho(P)N}{1 + H_3\rho(P)N + H_4\rho(P)N^2}, \quad (13)$$

where $H_1, H_2, H_3 > 0$ are handling times, and $H_4 > 0$ describes how handling time increases with prey density due to group defense in the type IV functional response. The attack or encounter rate is $\rho(P) = \lambda + aP$ in all cases and follows the assumptions on foraging facilitation presented in the main text.

We now non-dimensionalize the models. For the type II based model, i.e. (1), (11), we obtain

$$\begin{cases} \frac{dn}{d\tau} = n \left[\sigma \left(1 - \frac{n}{\kappa} \right) - \frac{(1 + \alpha p)p}{1 + h_1(1 + \alpha p)n} \right], \\ \frac{dp}{d\tau} = p \left[\frac{(1 + \alpha p)n}{1 + h_1(1 + \alpha p)n} - 1 \right], \end{cases} \quad (14)$$

where $h_1 = H_1 \frac{m}{e}$, and all the other parameters and variables are as in the main text.

For the type III based model, i.e. (1), (12), we obtain

$$\begin{cases} \frac{dn}{d\tau} = n \left[\sigma \left(1 - \frac{n}{\kappa} \right) - \frac{(1 + \alpha p)np}{1 + h_2(1 + \alpha p)n^2} \right], \\ \frac{dp}{d\tau} = p \left[\frac{(1 + \alpha p)n^2}{1 + h_2(1 + \alpha p)n^2} - 1 \right], \end{cases} \quad (15)$$

where $n = \sqrt{\frac{e\lambda}{m}}N$, $p = \sqrt{\frac{\lambda}{em}}P$, $\tau = mt$, $\kappa = \sqrt{\frac{e\lambda}{m}}K$, $\alpha = \frac{a}{\lambda} \sqrt{\frac{em}{\lambda}}$, $h_2 = H_2 \frac{m}{e}$, and $\sigma = \frac{r}{m}$.

For the type IV based model, i.e. (1), (13), we obtain

$$\begin{cases} \frac{dn}{d\tau} = n \left[\sigma \left(1 - \frac{n}{\kappa} \right) - \frac{(1 + \alpha p)p}{1 + h_3(1 + \alpha p)n + h_4(1 + \alpha p)n^2} \right], \\ \frac{dp}{d\tau} = p \left[\frac{(1 + \alpha p)n}{1 + h_3(1 + \alpha p)n + h_4(1 + \alpha p)n^2} - 1 \right], \end{cases} \quad (16)$$

where $h_3 = H_3 \frac{m}{e}$, $h_4 = H_4 \frac{m^2}{e^2\lambda}$, and all the other parameters and variables are as in the main text.

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