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Theoretical Population Biology 64 (2003) 221–231

**Theoretical
Population
Biology**

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Population dynamics of prey exhibiting inducible defenses: the role of associated costs and density-dependence

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Received 16 May 2003; accepted 16 May 2003

Abstract

The effect of antipredator behavior on the dynamics of a resource–consumer model was analyzed in relation to the magnitude of associated costs, and the strength of density-dependence. For this purpose, I present a deterministic continuous resource–consumer model that exhibits biomass conversion, structural homogeneity, and competition for renewable and fixed resources as separate processes. Antipredator behavior is incorporated as an inducible response to consumer density, and has metabolic and feeding costs. By means of numerical methods, I show: (1) that antipredator behavior is stabilizing for certain parameter ranges, where other stabilizing forces do not dominate the dynamics; (2) intraspecific competition for both fixed and renewable resources have a stabilizing role; (3) metabolic cost is always stabilizing, and feeding cost can be stabilizing or destabilizing, depending on the relative strength of the two competition forces.

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Keywords: Antipredator behavior; Predation; Stability; Bifurcation; Intraspecific competition

1. Introduction

Population dynamic consequences of antipredator behavior (APB) have been theoretically addressed in several works. Early works focused on refuge use by prey (either as a constant number or as a constant proportion of the population being protected against predation), including this process in predator–prey models by modifying the functional response of the Lotka–Volterra model (Maynard-Smith, 1974; Murdoch and Oaten, 1975; Harrison, 1979). From these studies a robust prediction emerged indicating a stabilizing effect of prey refuge on system dynamics, particularly when a fixed number of hidden prey was considered. More recently, some authors have confirmed this general stabilizing pattern in the framework of more complex lumped models (Sih, 1987a; Ives and Dobson, 1987; Ruxton, 1995).

Antipredator models have also been presented considering spatial structure, specifically in a two-patch environment with differences in predation risk. Thus, Scheffer and De Boer (1995) explore the dynamic consequences of a predator–prey system in which there are a safe patch for prey (free of predators), a risky patch (occupied by predators), and a passive flow of prey between patches. The effect of the refuge size (antipredator trait) is stabilizing on that system. Nonetheless, since the model of Scheffer and De Boer (1995) does not have costs of using refuges and it is not allowed an active movement of prey to the protected area, this system represents constitutive instead of inducible defenses. On the other hand, Krivan (1997) studied the population dynamics of a two-patch system in which fitness-maximizing predators moves freely between two patches or both prey and predators are free to move and maximize their fitness. The population dynamics consequences are explored under different scenarios of predator mortality risk and prey growth potential. The case where only prey optimize their choice between patches with different protectiveness and growth conditions is analyzed in Krivan (1998). The effect of the optimal behavior on population dynamics was shown to

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be stabilizing. Inducible defenses are implicitly considered in these models since the populations move between patches maximizing their per capita intrinsic growth rate.

Nevertheless, other results, in the context of different models, do not show such a clear pattern, and both stabilization and destabilization arise as a consequence of APB (McNair, 1986; Collings, 1995; Ramos-Jiliberto and González-Olivares, 2000; Ramos-Jiliberto et al., 2002). These different, and sometimes opposing, conclusions regarding the effect of antipredator traits on system dynamics are most likely a consequence of the different models being used. Different models imply different ecological assumptions, which are not always made explicit by the authors. Thus, biomass conversion, self-limited growth, saturating functional response, costs of APB, predator-dependency of APB, and other processes, are components which can be found in one antipredator model or another, in a somewhat arbitrary way. Therefore, the dynamic effects of antipredator responses should be evaluated in relation to other population parameters; otherwise conclusions will be obscured by the different assumptions unique to each model.

Antipredator defenses can be broadly classified into prey traits which prevent the encounter with predators and traits which prevent consumption after encounter (Sih, 1987). Moreover, defenses can be constitutive, i.e. fixed traits, or inducible by cues released by predators. Inducible defenses are expected when predation pressure is variable, there are costs of the defensive strategy and there are reliable cues for detecting predators (Harvell and Tollrian, 1999). In this work I focus on APB that belongs to the category of inducible and encounter-avoidance defenses. Although inducible defenses are found in many taxa and ecosystems (Tollrian and Harvell, 1999), few theoretical papers have incorporated inducible antipredator responses as an essential ingredient in modeling trophic interactions.

Therefore, the purpose of this study is to analyze the population dynamic consequences of APB in a resource-consumer (predator-prey) system, under different costs and density-dependence regimes.

In a previous work (Ramos-Jiliberto et al., 2002) we presented a more restrictive and complex model that differs in some important points from the one presented here: (a) the old model did not include competition for fixed resources; (b) feeding cost was assumed to affect the maximal food intake instead of affecting the consumer-resource encounter rate; (c) metabolic cost was incorporated into a special metabolic function, whereas in this work that cost simply adjusts the maintenance requirement inside the conversion function. But more important, in our 2002 work we did not address the effect of density-dependence on the system dynamics, neither in isolation nor in conjunction with other processes.

Here I present a continuous, deterministic resource-consumer model that obeys the principle of biomass conversion (Ginzburg, 1998) and includes competition for fixed and renewable resources as separate processes; while APB will be treated as a process that primarily interferes with the biomass flow between trophic levels. The assumptions implicit in this model consider APB as an instantaneous and reversible response to predator density; and this response translates to a change in vulnerability of the prey population as predator density varies. These assumptions are realistic for cases of behavioral avoidance triggered by predator cues, such as diel vertical migration of zooplankters in response to fish (Zaret and Suffern, 1976; Lampert, 1989; De Meester et al., 1999), hiding behavior of small mammals as a response to raptors (see Ramos-Jiliberto et al., 2002 and references therein), and activity shifts of tadpoles in response to larval dragonflies (Anholt and Werner, 1999). Morphological defenses exhibited by prey soon after the predator cues are released to the environment could also fit my model system, e.g. ciliates which alter their cell shape in response to protozoan and metazoan predators (Kusch, 1998), and rotifers which develop spines in response to predatory rotifers (Gilbert, 1999). Nevertheless, a more rigorous approach to this kind of defenses may deserve a different strategy. Other morphological or physiological defenses which develop slowly in the prey population should be addressed through including an additional state variable or time delays.

In general the model presented here is a reasonable approximation to those systems for which the prey develops avoidance defenses shortly after predator risk increases and lowers back the defenses shortly after predator risk decreases, relative to the timing of population dynamics. The translation of individual defensive traits to the population level is solved by measuring the dimension of state variables as biomass instead numbers, and by the definition of vulnerability which is expressed here as a continuous smooth function that does not require distinction between, for example, having a half of the population exhibiting the full defensive trait and a half not exhibiting defenses, versus the whole population exhibiting defenses at a half of its effectiveness.

The gain in survival will have two types of costs: a metabolic cost, which translates into an increase in the maintenance requirement of the prey population; and a feeding cost, which translates into a decrease in the encounter rate between the prey and its food resource. The role of costs of APB is unclear since different kinds of costs have been shown to exert different effects on the stability properties of a resource-consumer system (Ramos-Jiliberto et al., 2002). Density dependency, on the other hand, is recognized as a stabilizing factor in population dynamics (see Berryman, 1992), and it has

been suggested that the intraspecific competition for fixed resources (e.g. space) and the intraspecific competition for renewable resources (e.g. food) should be distinguished as separate mechanisms which generate density-dependence (Berryman et al., 1995a).

2. Methods

2.1. The model

2.1.1. Baseline

Here I use the following model (1) for any population of size N and trophic level i :

$$\frac{dN_i}{dt} = N_i[f_i(\phi_i) - b_i N_i] - \phi_{i+1}(N_i, N_{i+1})N_{i+1}. \quad (1)$$

This model accounts for intraspecific competition for fixed resources, measured through the coefficient b_i . The extraction rate, through consumption (predation) by the upper trophic level, is described by the function ϕ_{i+1} . Function f_i denotes the conversion rate of consumed resources from the lower trophic level (ϕ_i), to biomass of level i . Setting $N_i = X$ for a prey population, and $N_{i+1} = Y$ for the top, exclusive and specialist predator of that prey, the structurally homogeneous resource–consumer system is

$$\frac{dX}{dt} = X[f_X(\phi_X) - b_X X] - \phi_Y(X, Y)Y \quad (2a)$$

$$\frac{dY}{dt} = Y[f_Y(\phi_Y) - b_Y Y]. \quad (2b)$$

2.1.2. Antipredator behavior

Prey APB is considered to be an instantaneous and reversible response to predator density (Ramos-Jiliberto and González-Olivares, 2000; Ramos-Jiliberto et al., 2002). The primary effect of such a response is a decrease in predation success through lowering the vulnerability of the average prey to be consumed. This effect is, thus, advantageous for the prey (increasing survival), and detrimental for the predator (decreasing biomass income). The vulnerability function, V , should decrease with predator density, but it is also convenient that $0 < V \leq 1$.

Eq. (3) defines prey vulnerability as a decreasing function of predator biomass (Y), and its shape is either hyperbolic ($z = 1$), sigmoid ($z > 1$), or constant ($z = 0$):

$$V = V(Y) = \frac{1 - v}{1 + Y^z u^{-z}} + v. \quad (3)$$

The maximum of V is equal to one (i.e. no decrease in prey vulnerability) and the minimum is v , which is attained at high predator densities. The value of z (if greater than 1) defines the abruptness of the curve, which should be large if an on/off response takes place;

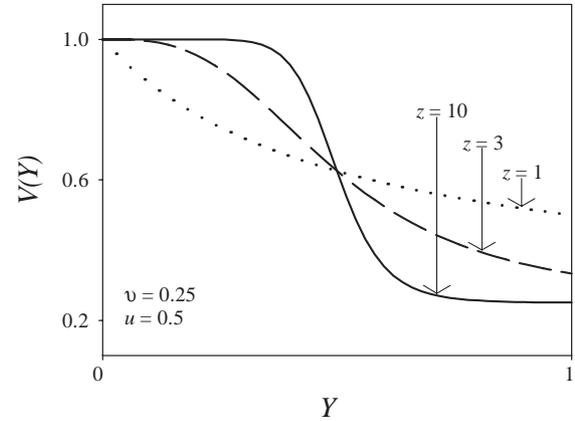


Fig. 1. Graphical representation of prey vulnerability (Eq. (3)) as a function of predator abundance. Three curves are shown for different values of the parameter z . The inflexion point (with $z > 1$) is located at $Y = u$. Parameter v sets the vulnerability level when predator abundance is very high, thus being a measure of the effectiveness of the antipredator behavior.

u indicates the critical region of Y where the anti-predator response is induced (Fig. 1).

2.1.3. Extraction function

For the purposes of this work, I use a type II extraction function, with self-interference among consumers (Beddington, 1975; Huisman and DeBoer, 1997):

$$\phi_i(N_{i-1}, N_i) = \frac{q_i N_{i-1}}{q_i/\alpha_i + N_{i-1} + s_i N_i}, \quad (4)$$

where N_{i-1} is the resource availability for the consumer population of size N_i ; α_i the encounter rate between the consumer and its resource; q_i is the inverse of the handling time per resource item, and defines the limit of the extraction function when resources are most abundant; s_i is a self-interference coefficient that accounts for intraspecific competition for food. The half-saturation term in this function is given by $(q_i/\alpha_i + s_i N_i)$. By adding Eqs. (3) and (4) and rearranging terms we obtain

$$\phi_X(X) = \frac{q_X}{1 + ((q_X/\alpha_X) + s_X X)R^{-1}} \quad (5)$$

and

$$\phi_Y(X, Y) = \frac{q_Y}{1 + ((q_Y/\alpha_Y) + s_Y Y)[V(Y)X]^{-1}}. \quad (6)$$

2.1.4. APB feeding cost

Assuming that APB involves some behavioral change that diminishes the encounter rate between a prey and its food, one can specify a simple, linear equation that describes a decrease in α_X , of relative magnitude C_F , as vulnerability decreases (Fig. 2):

$$\alpha_X = \alpha_X(V) = a[1 - C_F(1 - V)] \quad (7)$$

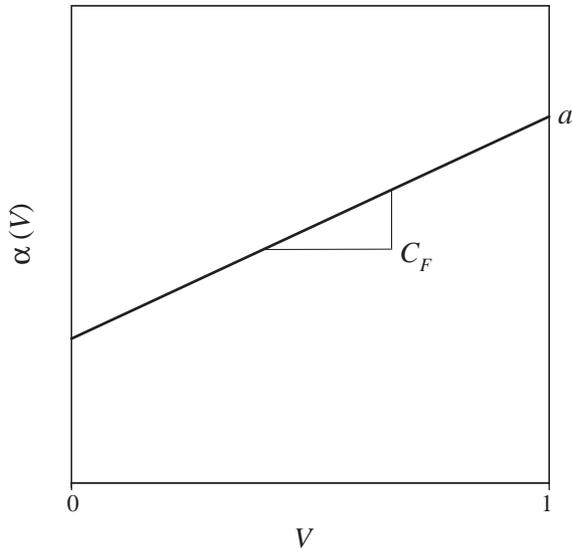


Fig. 2. Feeding cost of APB. As prey vulnerability decreases, the parameter α decreases from its maximal value, a , at a rate C_F .

where a is the encounter rate when the consumer does not exhibit APB. The feeding cost $C_F \in \{0, 1\}$ represents the difference between the encounter rate of invulnerable consumers and that of fully vulnerable consumers. For example, $C_F = 0.5$ means that hypothetically invulnerable consumers ($V = 0$) possess an encounter rate 50% lower than vulnerable ($V = 1$) ones.

2.1.5. Conversion function

For simplicity, I use a linear conversion function, which is the form most commonly found in ecological literature:

$$f_i(\phi_i) = k_i + m_i\phi_i. \quad (8)$$

Usually the intercept k_i (i.e. the rate of biomass gain with no consumption), is set to be negative, and is interpreted as the background mortality rate. On the other hand, the product of the consumption rate ϕ_i and the slope m_i is interpreted as birth rate; m_i being the conversion efficiency (e.g. Yodzis, 1989; Berryman and Gutierrez, 1999). Defining an amount of ingestion ϕ^0 needed for zero growth (i.e. a maintenance requirement), setting $f_i^1 \rightarrow 0$ as $\phi \rightarrow \phi^0$ gives:

$$f_i(\phi_i) = m_i(\phi_i - \phi_i^0). \quad (9)$$

2.1.6. APB metabolic cost

The maintenance requirement can be affected either directly or inversely by APB. This is accomplished through changes in metabolic expenditure. Some animals avoid predation by minimizing their movements (Werner and Anholt, 1993), others by shifting their feeding and vigilance behavior (e.g. Sih, 1987b; Lima and Dill, 1990; Vásquez, 1994, 1996; Vásquez et al., 2002), or by shifting their spatial location (Lampert,

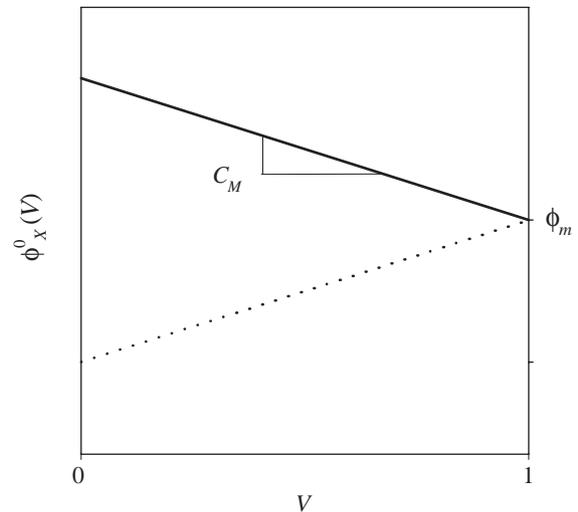


Fig. 3. Metabolic cost of APB. As prey vulnerability decreases, the parameter ϕ_X^0 changes from a value ϕ_m , at a rate C_M .

1989). These responses drive either an increase or decrease in metabolic losses. These relationships can be formalized in the following equation, and is graphically represented in Fig. 3:

$$\phi_X^0 = \phi_X^0(V) = \phi_m[1 - C_M(V - 1)], \quad (10)$$

where ϕ_m represents the maintenance requirement for zero growth when prey are in the fully vulnerable state (i.e. when $V = 1$). $C_M \in \{-1, \infty\}$ is the metabolic cost of APB for prey; it represents the maximal increase in the maintenance requirement as a consequence of APB. Under some circumstances, the metabolic cost could be negative (i.e. a benefit) since APB can reduce activity metabolism. Nevertheless, in this model metabolic cost is considered to be positive (i.e. an actual cost).

2.2. Numerical analyses

Stability analyses and continuation routines were run using the software XPPAUT version 5.5 (Ermentrout, 2002). The implicit, adaptive step-size integrator CVODE was used to find the numerical solutions of the differential equations. One and two-parameter bifurcation diagrams were obtained by continuation of fixed points and Hopf bifurcation points, using the AUTO package (Doedel, 1984) included in XPPAUT. The control parameters were: magnitude of prey vulnerability decrease under high predator density, intraspecific competition for fixed resources, intraspecific competition for renewable resources, feeding cost, and metabolic cost of APB.

3. Results

For analysis, the model parameters were initially set to those values shown in Table 1. When changes were

Table 1
Initial parameter values used in the analyses

Parameter	Value
b_X	0.003
b_Y	0.002
m_X	0.6
m_Y	0.5
ϕ_Y^0	0.5
R	1000
q_X	3
q_Y	5
α_Y	0.05
s_X	0
s_Y	0
ν	1
z	10
u	20
C_F	1
C_M	1
a	0.05
ϕ_m	0.6

made for stability analyses, they are indicated in the corresponding section.

The survival gain of prey as a result of APB is measured by the parameter ν . The effect of the value of ν on the prey equilibrium density and local stability is shown in Fig. 4. Parameter ν is an inverse measure of the effectiveness of APB, since lower ν values imply that prey greatly reduces its vulnerability under the presence of high predator density. Fig. 4 shows six bifurcation diagrams with varying degrees of competition and APB costs. The left plots show the results for high-cost conditions and the right plots show the results for zero-cost conditions. Top, middle and bottom plots show, respectively, the results for increasing levels of food competition. It can be seen that in all cases the effect of increasing ν is destabilizing and lowers the equilibrium density of prey (i.e. lowering prey vulnerability as a result of APB stabilizes the community non-trivial equilibrium and increases the prey equilibrium density). Competition levels affect the position of the Hopf bifurcation on the abscissa and, consequently, the size of stability basins. With weaker competition, the prey density stabilizes at lower vulnerability levels, and the amplitudes of the limit cycles are larger at any value of ν . With stronger levels of competition, the dynamics can be unstable only if APB produces very small survival gains.

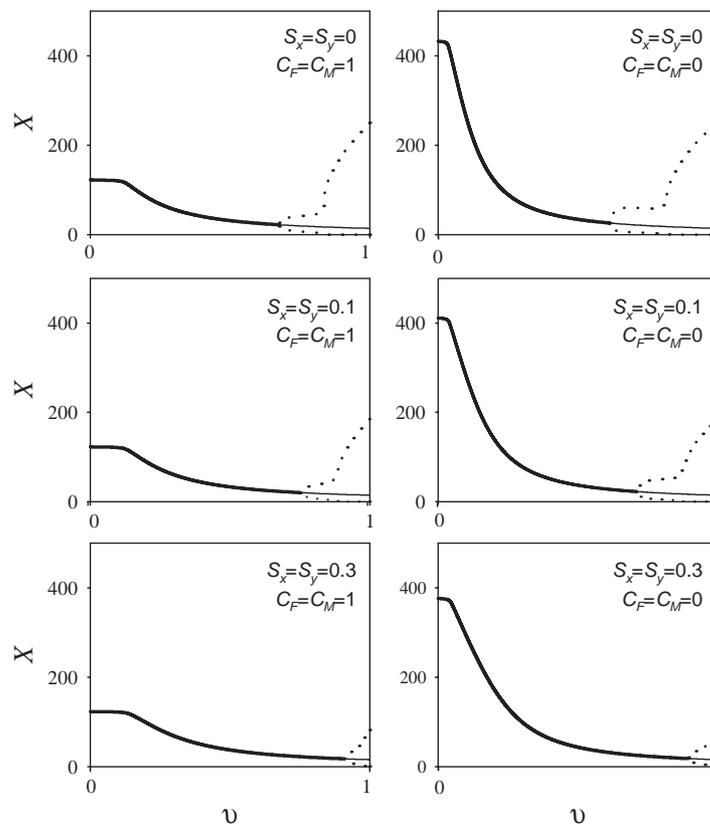


Fig. 4. Bifurcation diagrams of prey equilibria with parameter ν , representing APB effectiveness, as the control parameter. Thick continuous lines represent stable fixed points, thin continuous lines represent unstable fixed points, dotted lines show the maxima and minima of stable orbits.

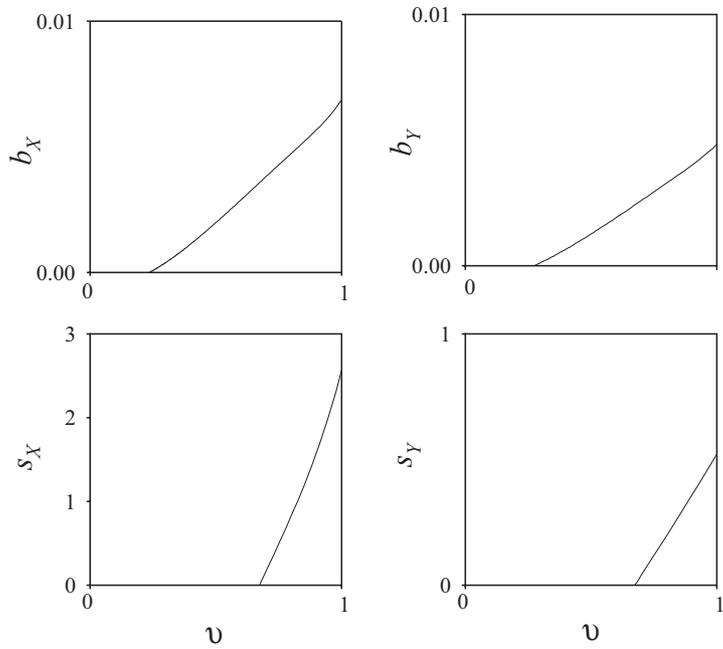


Fig. 5. Two-parameter bifurcation diagrams for v versus intraspecific competition parameters. The line shows the continuation of the Hopf bifurcation, and separates two stability basins: stable points occur on the upper-left side, and limit cycles on the lower-right side. APB costs are set to zero.

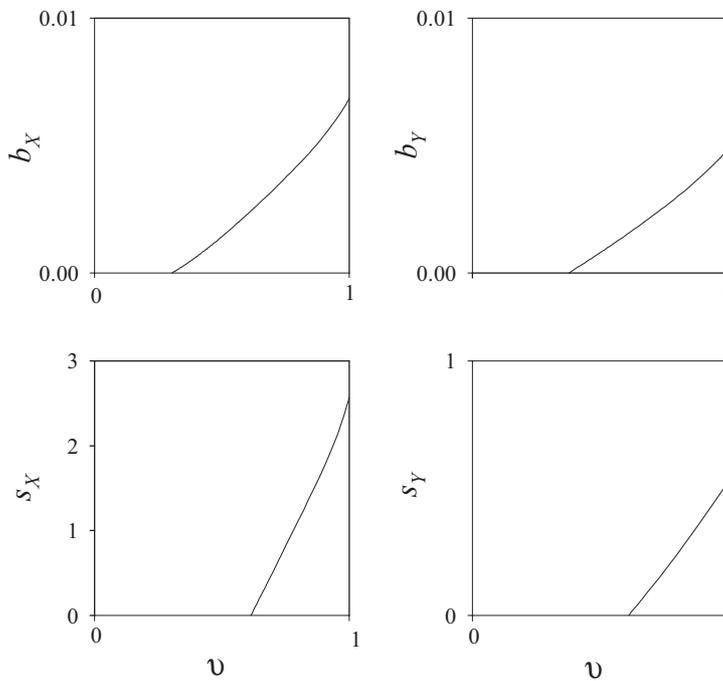


Fig. 6. Two-parameter bifurcation diagrams for v versus intraspecific competition parameters. The line shows the continuation of the Hopf bifurcation, and separates two stability basins: stable points occur on the upper-left side, and limit cycles on the lower-right side. APB costs are set to one.

On the other hand, a higher APB cost determines a decreased prey equilibrium density, since APB is more effective (lowest values of v).

Figs. 5 and 6 show stability diagrams in the parameter space of v and the competition parameters S_X , S_Y , b_X

and b_Y . Analyses reveal that competition for both fixed and renewable resources interact with APB effectiveness to produce similar qualitative effects on the stability of the non-trivial community equilibrium. This is true when APB has no associated costs (Fig. 5), as well as

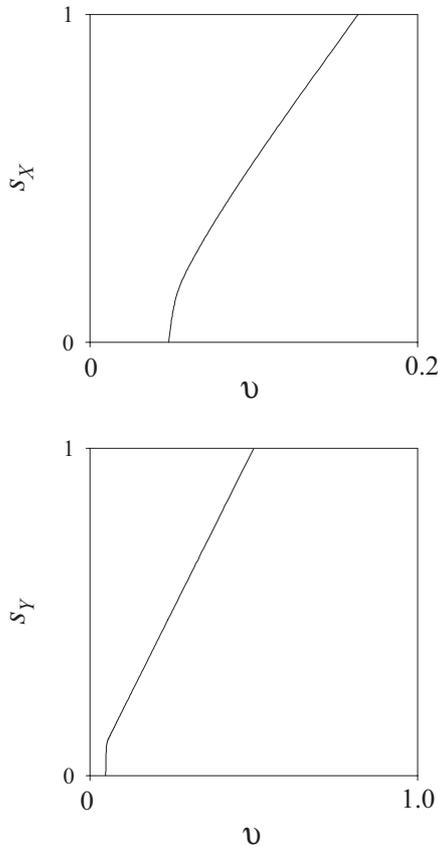


Fig. 7. Two-parameter bifurcation diagrams for v versus S_X and S_Y , representing competition for renewable resources. The line shows the continuation of the Hopf bifurcation, and separates two stability basins: stable points occur on the upper-left side, and limit cycles on the lower-right side. APB costs are set to one, and the competition parameters for fixed resources are set to zero.

when APB is costly (Fig. 6). The main effect is that both kinds of intraspecific competition exert a stabilizing effect. Therefore, the equilibrium point is locally unstable at low APB effectiveness and low levels of competition. From Figs. 5 and 6 it is possible to note some differences between the effects of the four competition parameters, stability being more sensitive to b_X and b_Y than to S_X and S_Y . Expressing this effect in numbers, when b_Y or b_X is greater than 0.01 this is sufficient condition for local stability of the equilibrium, but a value of S_X or S_Y greater than 3 and 0.5, respectively, is needed in order to assure stability. Nevertheless, in the limiting case $b_Y = b_X = 0$ (Fig. 7), the stability basin of the stable point is reduced to the region of large APB effectiveness and/or strong competition for renewable resources. However, competition among prey is a slightly stronger stabilizing factor than competition among predators, in the sense that the stability basins of the fixed points are comparatively larger in the b_X and S_X versus v planes (Figs. 5 and 6).

Fig. 8 shows the interacting effect of competition and metabolic cost of APB on the local stability of the resource–consumer system. In this example, APB effectiveness was set to a moderate level of 0.65. The two upper plots show the effects of competition for fixed resources and metabolic cost; the lower plots show the effects of food competition and C_M . In the left-hand plots the competition is among prey, whereas the right-hand plots show competition among consumers. These analyses reveal that the effect of metabolic cost on system dynamics is strongly dependent on the competition strength. At high levels of competition (either

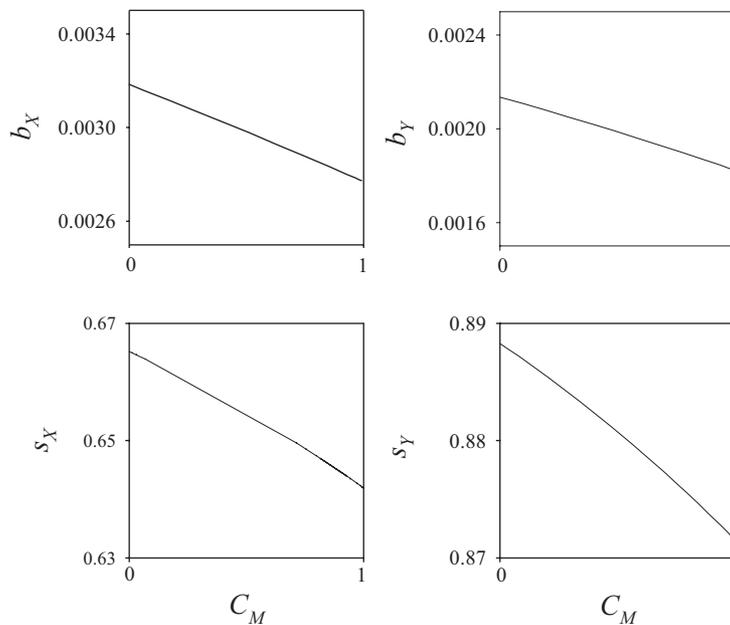


Fig. 8. Two-parameter bifurcation diagrams for metabolic cost versus intraspecific competition parameters. The line shows the continuation of the Hopf bifurcation, and separates two stability basins: stable points occur on the upper-right side, and limit cycles on the lower-left side. $C_F = 1$, and $v = 0.65$.

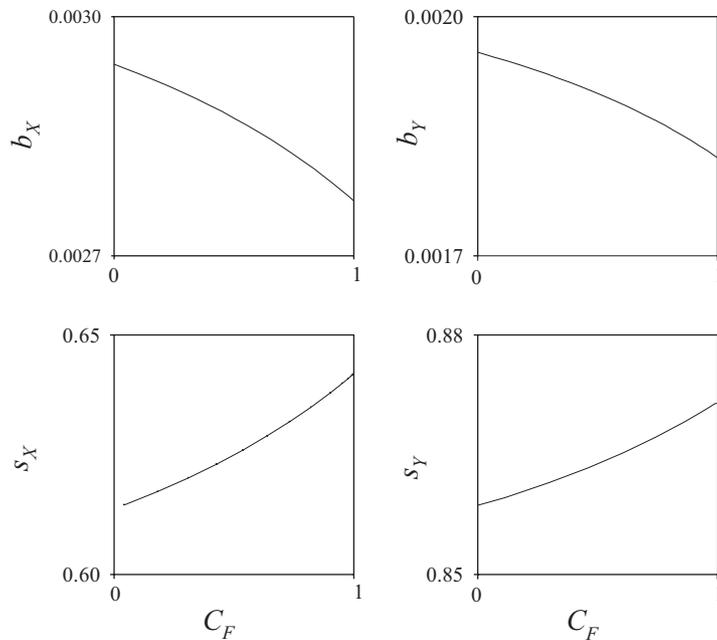


Fig. 9. Two-parameter bifurcation diagrams for feeding cost versus intraspecific competition parameters. The line shows the continuation of the Hopf bifurcation, and separates two stability basins: stable points occur on the upper side, and limit cycles on the lower side. $C_M = 1$, and $v = 0.65$.

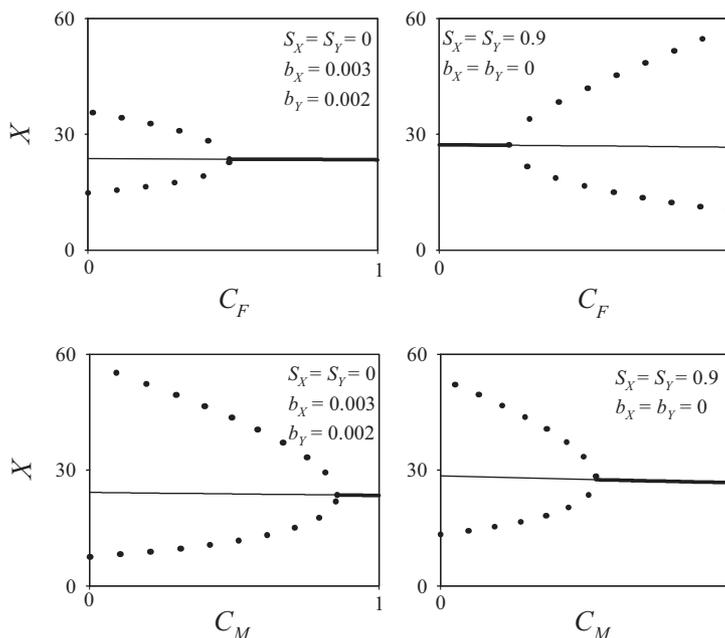


Fig. 10. Bifurcation diagrams of prey equilibria with C_F (upper plots) and C_M (lower plots) as the control parameters. $v = 0.65$. Thick continuous lines represent stable fixed points, thin continuous lines represent unstable fixed points, and dotted lines show maxima and minima of stable orbits.

among prey or among predators, for fixed or renewable resources) the equilibrium is stable, irrespective of the value of C_M . At low levels of competition, the dynamics are unstable, and stable limit cycles surround the equilibrium point. At intermediate competition levels there is a range of values of the competition coefficients where C_M changes the qualitative behavior of the system, transforming an unstable point into a stable point as the cost grows.

An analysis of Fig. 9 reveals that the effect of feeding cost of APB on the stability properties of the system is different to that of the metabolic cost stated above. Here, the effect of the feeding cost of APB is destabilizing at high levels of S_X and S_Y , and low levels of b_X and b_Y . The distinction between the effects of feeding and metabolic costs is more clearly shown in Fig. 10. At high levels of b_X or b_Y the dynamics are always stable, but at moderate levels of these para-

meters, the stability depends on the values of APB costs and the values of S_X and S_Y (Fig. 10). Specifically, when food competition is low the effect of feeding cost is stabilizing (upper left plot), but with a combination of very low competition for fixed resources and strong food competition the effect of feeding cost is destabilizing (upper right plot). On the other hand, the effect of metabolic cost can only be stabilizing (lower plots of Fig. 10).

4. Discussion

The baseline model (1) allows for the inclusion of a range of extraction and conversion functions. For example, when a linear conversion function is used in combination with a prey-dependent linear, non-saturating extraction function, and setting $b_i = 0$, the Lotka–Volterra predator-prey model (Lotka, 1925; Volterra, 1926) is obtained; if a prey-dependent type-II extraction function is used instead of the linear one, the Rosenzweig–McArthur model is obtained (Rosenzweig, 1971). Finally, if a hyperbolic conversion function is used in combination with the Beddington predator-dependent extraction function (4), the metaphysiological model of Getz is obtained (1991). In this work, I used the simplest form of the model that allows for separate analysis of the effect of competition for fixed resources, and competition for renewable resources. Furthermore, structural homogeneity was respected and APB was incorporated as an inducible and costly response (see Ramos-Jiliberto and González-Olivares, 2000; Ramos-Jiliberto et al., 2002).

To my knowledge, there are no previous works where the effects of density-dependence are explicitly examined together with APB and associated costs. Furthermore, the structure of earlier models used to analyze the population effects of APB often contains quite restrictive assumptions. I consider a restrictive assumption to be the lack of structural homogeneity, since in this case the populations of resources and consumers are believed to follow different dynamic rules due only to the fact that they belong to different trophic levels (Getz, 1984; Berryman et al., 1995b). Accepting that most populations in nature are, at the same time, resources and consumers of other populations, structural homogeneity is a parsimonious rule.

Among the first models addressing the population consequences of APB were those which considered that a fixed fraction, or number, of prey was unavailable to predators, but there was no implicit cost (Maynard-Smith, 1974; Murdoch and Oaten, 1975; Harrison, 1979). With time, more realistic models were introduced, which considered that the amount of hidden prey could vary with predator density (Sih, 1987a; Ives and Dobson, 1987; Ruxton, 1995) and that prey APB

imposed some growth cost (McNair, 1986; Sih, 1987a; Ruxton, 1995; Ives and Dobson, 1987). Still, some form of density-dependence was incorporated in the models by McNair (1986), Ruxton (1995), Sheffer and de Boer (1995), Collings (1995), Ramos-Jiliberto and González-Olivares (2000), and Ramos-Jiliberto et al. (2002). Nevertheless, none of these models distinguished between competition for fixed versus renewable resources, as mechanisms generating density-dependence. Under the diversity of assumptions which are explicit or implicit in previous population models of APB, it is difficult to infer, from the published results, the role of cost and density-dependence on system dynamics.

The analyses performed here reveal that predator-induced APB is a stabilizing force (i.e. an increase of antipredator effectiveness can transform an unstable equilibrium into a stable equilibrium). This effect appears if other stabilizing factors do not dominate the dynamics (e.g. if density-dependence is not very low, in which case the dynamics remain unstable; or if density-dependence is very high, in which case the dynamics remain stable irrespective of the realization of APB). This result is in agreement with most previous work (Maynard-Smith, 1974; Murdoch and Oaten, 1975; Harrison, 1979; Sih, 1987a; Ives and Dobson, 1987; Ruxton, 1995; Sheffer and de Boer, 1995), although a more elusive pattern results from the model of McNair (1986). Ramos-Jiliberto and González-Olivares (2000) followed the metaphysiological approach closely based on the model by Getz (1991, 1994). This model lacks competition for fixed resources, and the conversion function is saturating instead of linear (as in the present work). The results of Ramos-Jiliberto and González-Olivares (2000) suggest that APB is destabilizing in some portion of the parameter space, but through a further increase in APB response the unstable equilibrium can be transformed to a stable one in which extinction of one or both populations occur. However, in the model of Ramos-Jiliberto et al. (2002), APB could transform a stable equilibrium into an unstable one, but not vice versa. Nevertheless, in most of the parameter space APB did not change the qualitative stability of the system. In the present work, I have not found any evidence for destabilization of the community equilibrium as a consequence of increasing APB response.

Another result of this work is that at a given level of antipredator effectiveness, density-dependence remains as a strong stabilizing force. However, density-dependence arising from competition for renewable resources appears to have a weaker stabilizing effect, in relation to competition for fixed resources.

Finally, APB metabolic cost can stabilize a system which is initially unstable, and cannot destabilize a system which is initially stable. Conversely, APB feeding cost can stabilize a system which is initially unstable,

and it can also destabilize a system which is initially stable, depending on the competition parameters. At very low levels of competition for renewable resources, and a moderate level of competition for fixed resources, the effect of feeding cost is stabilizing. On the other hand, if competition for renewable resources is strong, and competition for fixed resources is very weak, the effect of feeding cost is destabilizing. These results are different from those previously reported. While Sih (1987a) found a stabilizing effect of APB cost on community equilibrium, Ruxton (1995) showed that APB cost was marginally stabilizing. It is important to note that neither author considered different types of costs. On the other hand, Ramos-Jiliberto et al. (2002) found that feeding and metabolic costs can either exert a stabilizing or a destabilizing effect, depending on the other parameters, particularly on the values of the costs themselves, and APB effectiveness. The patterns shown here are more unambiguous than those of Ramos-Jiliberto et al. (2002), but both studies agree in that the dynamic consequences of APB at the population and community level depend on the interaction of several parameters, particularly APB costs and effectiveness.

The results of this work are amenable to empirical testing, since the parameters representing the different kinds of costs and intraspecific competition are all environment-dependent (e.g. the thermal environment should determine the magnitude of metabolic costs, and the availability of nesting sites should affect the magnitude of the competition among bird for fixed resources).

From a theoretical point-of-view, future research should clarify the robustness of these predictions by studying models with different conversion functions, perhaps more realistic than the linear one used here. Likewise, the addition of non-linear density-dependence, more complex APB functions, population structure, and multitrophic relationships are expected to be considered as an extension of this work, in order to gain a better understanding of trophic interactions in nature.

Acknowledgments

This work was supported by FONDECYT grant 3000051. The author thanks Eduardo González-Olivares for valuable comments and suggestions.

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