L-shaped prey isocline in the Gause predator–prey experiments with a prey refuge

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HIGHLIGHTS

- Predator and prey isoclines are estimated from classic Gause's experiments with protists feeding on yeast.
- It is shown that an L-shaped function fits prey isocline well.
- Such a shape of prey isocline is in agreement with predator–prey population models with a prey refuge.
- Lotka–Volterra and Rosenzweig–MacArthur models either with or without a prey refuge are parameterized by experimental data.
- Among them the one which fits data best is the Rosenzweig–MacArthur predator–prey model with a prey refuge.

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ABSTRACT

Predator and prey isoclines are estimated from data on yeast–protist population dynamics (Gause et al., 1936). Regression analysis shows that the prey isocline is best fitted by an L-shaped function that has a vertical and a horizontal part. The predator isocline is vertical. This shape of isoclines corresponds with the Lotka–Volterra and the Rosenzweig–MacArthur predator–prey models that assume a prey refuge. These results further support the idea that a prey refuge changes the prey isocline of predator–prey models from a horizontal to an L-shaped curve. Such a shape of the prey isocline effectively bounds amplitude of predator–prey oscillations, thus promotes species coexistence.

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1. Introduction

Isoclines have played an important role to identify mechanisms that regulate predator–prey coexistence (Rosenzweig and MacArthur, 1963). For the Lotka–Volterra predator–prey model, the predator isocline is vertical and the prey isocline is horizontal which leads to neutral oscillations in prey and predator population abundance. More realistic models with prey negative density dependence, predator density dependence, or non-linear functional responses lead to non-linear or sloped isoclines that can either stabilize or destabilize predator–prey population dynamics. In their seminal work, Rosenzweig and MacArthur (1963) analyzed effects of isoclines on predator and prey coexistence. Using graphical analysis they showed that a prey isocline with a vertical segment effectively bounds maximal oscillations in prey population numbers. Similarly, a predator isocline with a horizontal segment bounds maximal oscillations in predator numbers. Theoretical models that predict such isoclines can arise due to optimal prey selection by predators, or prey use of a refuge (e.g., Rosenzweig and MacArthur, 1963; Rosenzweig, 1977; Fryxell and Lundberg, 1994; Křivan, 1998; van Baalen et al., 2001; Brown and Kotler, 2004; Křivan, 2007, 2013).

In an attempt to falsify the Lotka–Volterra predator–prey model Gause experimented with various predator–prey systems (Gause, 1934, 1935a; Gause et al., 1936). Fig. 39 in Gause (1934) (see also Gause, 1935a) shows population dynamics of protist *Paramecium bursaria* feeding on yeast *Schizasaccharomyces pombe*, and protist *Paramecium aurelia* feeding on yeast *Saccharomyces exiguus*. Based on these experiments Gause (1935a, p. 45) concluded that "Quite clearly periodic fluctuations of the Lotka–Volterra type occurred". However, using the same data, Rosenzweig (1977) estimated a hump shaped prey isocline and a vertical predator isocline. Such isoclines are predicted by the Rosenzweig–MacArthur predator–prey model (Rosenzweig and MacArthur, 1963) that assumes a negative density dependent prey population growth and the Holling type II functional response. In this model predator–prey population dynamics can be

destabilized by the "Paradox of Enrichment" when the environmental carrying capacity increases above a critical threshold and predator–prey population densities converge to a limit cycle (Rosenzweig, 1971).

To better understand whether predator–prey oscillations were of the neutral Lotka–Volterra type, Gause with his collaborators (Gause, 1935b; Gause et al., 1936) continued experiments with *P. bursaria* feeding on yeast *S. exiguus*. In contrast to previous experiments, there was no aeration that would prevent yeast to sediment at the bottom of the beaker. The authors observed that below a critical prey threshold density all prey (yeast) sedimented and were unavailable to predators (protists) that lived in the water column. Consequently they developed a predator–prey model with a prey refuge. Graphical analysis of this model predicted, in accordance with their experimental observations, coexistence of prey and predators along a limit cycle. This is perhaps the first example of a limit cycle in the literature on predator–prey population dynamics. Their model was analyzed in detail by Křivan (2011) who showed that large refuges stabilize population dynamics at an equilibrium while smaller refuges lead to periodic oscillation in predator and prey numbers along a limit cycle. One distinguished feature of this model is that the prey isocline is L-shaped.

In this paper we are interested in verifying whether the data on protists feeding on yeast from Gause et al. (1936) predict an L-shaped prey isocline. First, we estimate the shape of isoclines directly from the experimental data. Second, we fit several predator–prey models to the experimental data and compare the predicted and estimated predator and prey isoclines.

2. Direct isocline estimation from data

In this paper we use data on population dynamics of protists (*P. bursaria*, squares in Fig. 1) feeding on yeast (*S. exiguus*, dots in Fig. 1) from Table 3 in Gause et al. (1936). The data represent 19 population experiments that differ in the initial predator [number of individuals/ 0.5 cm^3] and prey [number of individuals/0.1 mm^3] densities. Each time series consists of triples (t_i, x_i, y_i), $i = 1, ..., N$ where t_i denotes day, and x_i (y_i) is the prey (predator) density at time t_i. The longest time series 9 lasted 7 consecutive days, but other time series were shorter. Most of the population censuses were taken in consecutive days, but in some cases there were one or two-day gaps. Using these data we estimate predator and prey isoclines.

Isoclines are, by definition, curves in the prey–predator phase space, along which either prey, or predator population neither grows nor declines (i.e., the per capita population growth rate vanishes, Rosenzweig and MacArthur, 1963). We use this definition to estimate isoclines directly from data by identifying predator and prey population densities where either prey or predator derivative changes its sign. Thus, the points on the prey isocline are estimated as those prey–predator pairs (x_i, y_i) (see open and solid dots in Fig. 2A) such that either $x_{i-1} < x_i$ and $x_i > x_{i+1}$ (in which case x_i is a local maximum), or $x_{i-1} > x_i$ and $x_i < x_{i+1}$ (in which case x_i is a local minimum). For example, prey population achieves its local maximum at time 3 in series 2 (Fig. 1, panel 2) and the corresponding prey–predator data point is identified to lie on the prey isocline. We cluster the estimated points for the prey isocline to two groups that we call the horizontal (solid dots in Fig. 2A that correspond to prey–predator pairs $(20, 6.5)$, $(27, 6)$, $(14, 10.2)$) and the vertical group (open dots in Fig. 2A that correspond to prey–predator pairs $(0.8, 13.5)$, $(1.5, 9)$, $(0.8, 9)$, $(2, 36)$, $(0.3, 17)$, $(1.2, 12.5)$, $(0.8, 20)$). The vertical group contains those data points where predator population abundance decreases while horizontal group contains those data points where predator abundance increases. For example, the second point $(27, 6)$ in series 3 (Fig. 1, panel 3) belongs to the horizontal group because at time 2 the predator population increases in abundance. The predator isocline was estimated analogously (but without grouping the data). The estimated data points $((7, 3)$, $(10.5, 2)$, $(1.2, 6)$, $(1.5, 9.2)$, $(3.1, 19)$, $(1.5, 22.5)$,

$(2.5, 16)$, $(1.5, 10.5)$, $(1.2, 8.5)$, $(1, 10)$, $(2, 16)$, $(3, 43)$, $(6, 44.5)$, $(5, 38)$, $(5, 35)$, $(0.8, 31))$ for the predator isocline are shown as squares in Fig. 2A.

The prey isocline data (solid and open dots in Fig. 2A) suggest a piece-wise linear approximation corresponding to the vertical and horizontal data points. For each of these two groups we use the linear regression function `LinearModelFit` of Mathematica 10.0 software package. For the vertical group we estimate prey density (x) as a function of predator density (y). The resulting linear fit $x = 0.56 + 0.03y$ is insignificant (F-stat $= 1.7$, P-value $= 0.25$), so we assume zero trend and we estimate the intercept with x axes to be $x = 1.1$ (t-stat $= 5.00$, P-value $= 0.002$). The residual sum of squares of the fit is 1.9. Similarly, the linear fit for the horizontal group $y = 13.9 - 0.32x$ is insignificant (F-stat $= 4.1$, P-value $= 0.3$), so we assume zero trend and we obtain the best fit $y = 7.6$ (t-stat $= 5.7$, P-value $= 0.03$). The residual sum of squares of the fit is 10.5. Thus, our estimates suggest L-shaped prey isocline with the vertex at the prey–predator point $(x, y) = (1.1, 7.6)$ (solid line in Fig. 2A). The total residual sum of squares obtained as the sum of the residual sum of squares for the horizontal and vertical fit is approx. 12 (the first row of Table 2).

We also perform linear regression analysis for the predator isocline assuming that the prey abundance is a function of predator abundance. The linear regression $x = 3.2 + 0.004y$ is insignificant (F-stat $= 0.006$, P-value $= 0.9$), so we assume zero slope and estimate the predator isocline as $x = 3.3$ (t-stat $= 4.8$, P-value $= 0.0002$, dashed line in Fig. 2A). The residual sum of squares for the fit is approx. 111 (the first row of Table 2).

3. Models

Gause et al. (1936) generalized the Lotka–Volterra predator–prey model by replacing the linear functional response by a non-linear functional response, i.e.,

$$\frac{dx}{dt} = rx - yf(x)$$
$$\frac{dy}{dt} = (ef(x) - m)y. \tag{1}$$

Here x (y) denotes the prey (predator) density, r is the per capita intrinsic prey population growth rate, e is the efficiency rate with which the captured prey are converted to new predators, and m is the predator mortality rate. In particular, Gause et al. (1936) assumed that (i) f is a saturating function, and (ii) there exists a prey refuge that protects x_c prey. Thus, the functional response f is zero for prey population densities that are smaller than x_c (Gause et al., 1936, Fig. 5). A prototype of such a functional response is

$$f(x) = \frac{x^k}{x^k + x_c^k} \frac{\lambda x}{1 + \lambda h x} \tag{2}$$

where h is the handling time, λ is the predator search rate, and parameter k models steepness of the functional response at x_c (Fig. 3). As k increases, functional response (2) tends to

$$f(x) = \begin{cases} 0 & \text{if } x < x_c \\ \frac{\lambda x}{1 + \lambda h x} & \text{if } x > x_c \end{cases} \tag{3}$$

that qualitatively agrees with the functional response shown in Fig. 5, panel 1 in Gause et al. (1936). For positive handling times the sigmoidal functional response (2) is of the Holling type III. When handling time $h = 0$ model (1) with (3) becomes the classical Lotka–Volterra predator–prey model either with a refuge when $x_c > 0$ or without a refuge when $x_c = 0$.

Model (1) assumes prey grow exponentially. We also consider the case where prey growth is logistic, i.e.,

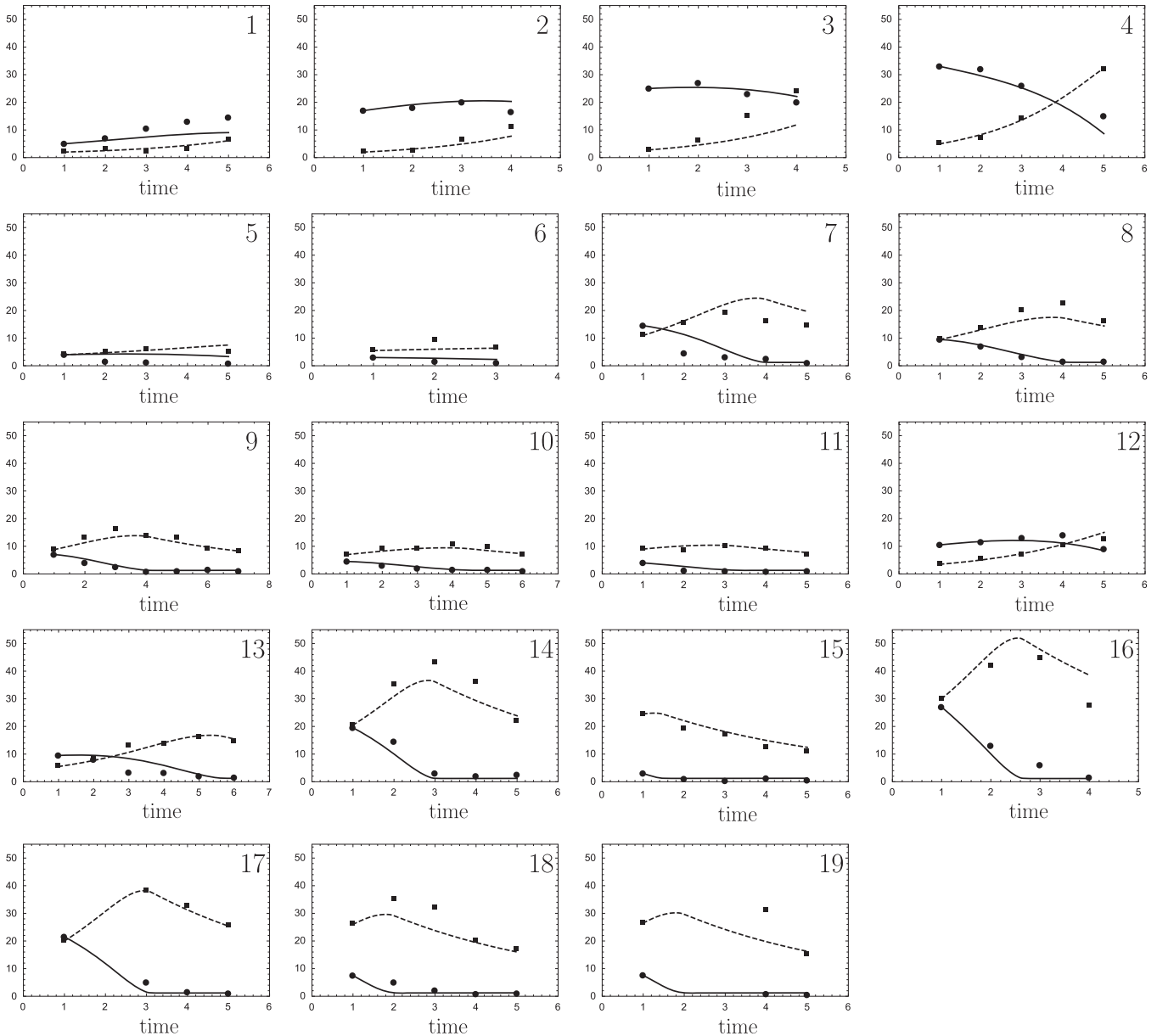$$\frac{dx}{dt} = rx\left(1 - \frac{x}{K}\right) - yf(x)$$

Fig. 1. Fit between the Rosenzweig–MacArthure model (4) with a prey refuge and experimental data on population dynamics of protists *P. bursaria* (squres) and yeast *S. exiguus* (dots). Simulated population dynamics for protists (dashed line) and yeast (solid line) use the best fit parameters given in Table 1 (Model 5).

$$\frac{dy}{dt} = (ef(x) - m)y. \qquad (4)$$

When there is no refuge ($x_c = 0$), model (4) is the Rosenzweig–MacArthur predator–prey model.

In what follows we estimate parameters for the Lotka–Volterra model (1) and the Rosenzweig–MacArthur model (4) assuming either that a prey refuge exists or it does not. This will allow us to compare our estimates of prey and predator isoclines from Section 2 with these new estimates.

4. Results

Parameters for models were estimated using function `NonlinearModelFit` of Mathematica 10. The results are summarized in Table 1.

We consider five models. Models 1 and 2 are the classical Lotka–Volterra predator–prey models (1) without any refuge and zero handling times (i.e., we set $x_c = h = 0$ in functional response (2)). In Model 1 we set $r = 0.5$ and $m = 0.4$ that are the estimates for the per capita intrinsic prey population growth rate and the predator mortality rate taken from Gause et al. (1936, p. 10). Thus, only parameters λ and e are estimated in this case. These estimates lead to prey isocline $y = r/\lambda = 8.3$ and predator isocline $x = m/(e\lambda) = 6.9$ (Fig. 2B, black lines). Model 2 estimates all four parameters including r and m. These estimates lead to prey isocline $y = r/\lambda = 6.0$ and predator isocline $x = m/(e\lambda) = 3.7$ (Fig. 2B, gray lines). The resulting fit is better as the residual sum of squares (SS in Table 1) for Model 2 is much smaller than for Model 1. Because the number of estimated parameters for these two models is not the same, we also calculate the Akaike Information Criterion (AIC) which is again smaller for Model 2.

Model 3 is the Lotka–Volterra predator–prey model with a prey refuge and the refuge size x_c is an additional parameter that is estimated from data. Functional response (2) requires to set parameter value for steepness k. We tested several values of this parameter and our estimates show that the residual sum of squares decreases with
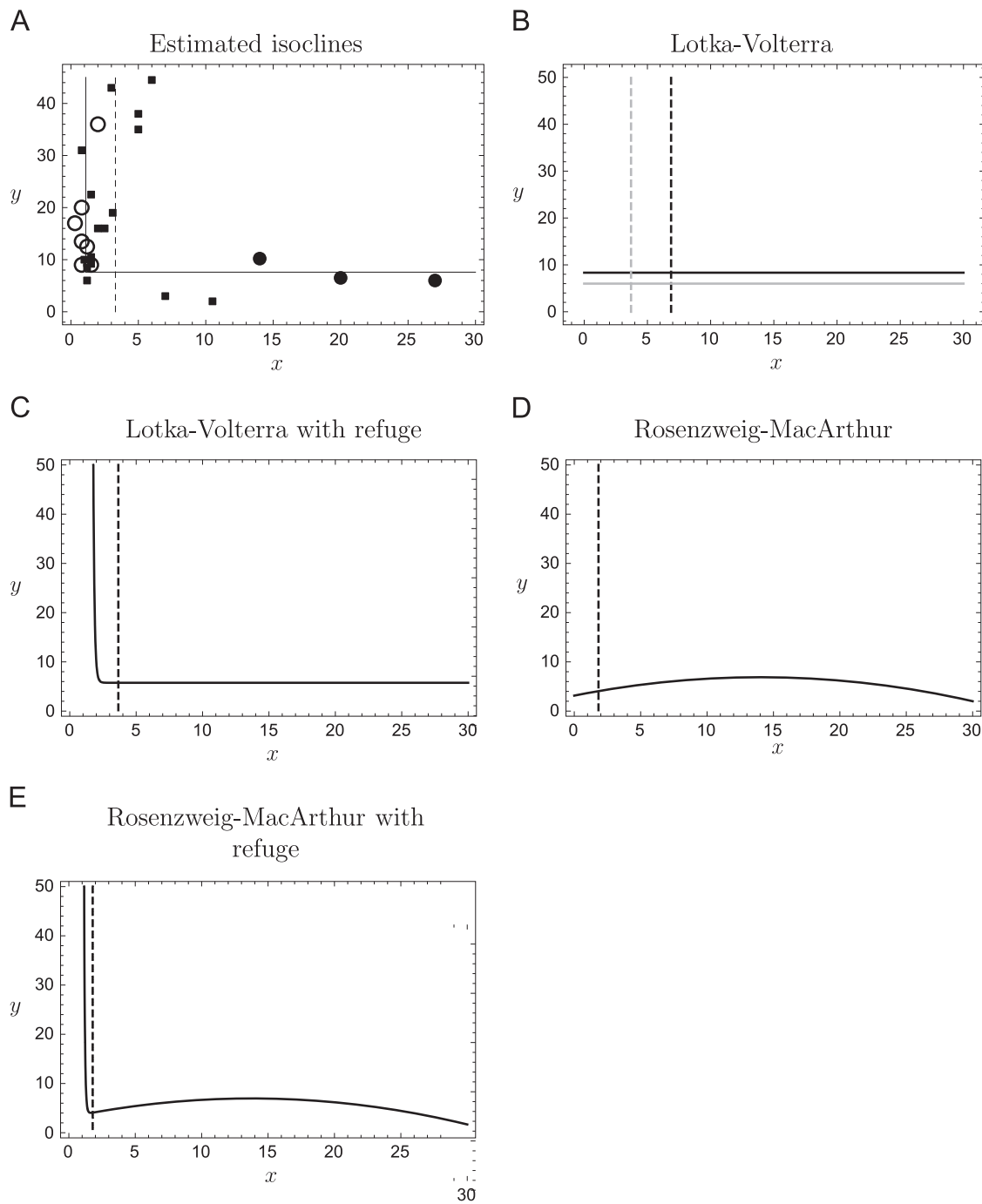
Fig. 2. Estimates of prey (solid line) and predator (dashed line) isoclines. In panel A the solid dots and the open dots are estimates of the prey isocline, and the solid squares are estimates of the predator isocline from experimental data. The open dots correspond to those data points where predator density is decreasing, while at the solid dots the predator density is increasing. Panels B and C show predator and prey isoclines estimated from the Lotka–Volterra model (1) without a refuge and with a refuge, respectively. Black lines in Panel B correspond to parameters of Model 1 in Table 1 while gray lines correspond to parameters of Model 2. Panels D and E show predator and prey isoclines estimated from the Rosenzweig–MacArthur model (4) without and with a refuge, respectively. Parameters are those given in Table 1.

increasing k (Fig. 4). Thus, we set arbitrarily $k=20$, for which the functional response (2) is shown in Fig. 3. For Model 3 the estimate of the refuge size $x_c = 1.97$ is only marginally significant (*P*-value$=0.06$). When compared with Model 2 without a refuge, both the residual sum of squares and the AIC are smaller. The corresponding isoclines are shown in Fig. 2C.

Models 4 and 5 are for the Rosenzweig–MacArthur model (4) either without or with a refuge. Both of these models fit data better when compared with the Lotka–Volterra models (Table 1). Model

5 with a refuge fits data slightly better when compared with Model 4 without a refuge. Isoclines for Models 4 and 5 are shown in Fig. 2D and E, respectively. Fig. 1 shows the fit between Model 5 and all 19 time series.

We also compare how isoclines for Models 1–5 fit the estimated isoclines (i.e., the dots for the prey isocline and the squares for the predator isocline in Fig. 2A). The predator isocline in Models 1–5 is a vertical line expressed as $x = $ const. Thus, we calculate the residual sum of squares between the estimated data (squares in Fig. 2A) and

this line as $\sum (x_i - \text{const})^2$ where x_i is the prey density. For models that do not assume prey refuge we calculate the residual sum of squares between estimated points (solid and open dots in Fig. 2A) and the prey isocline $y(x)$ (expressed as a function of prey density x) as $\sum (y_i - y(x_i))^2$. For models with a prey refuge, we calculate the residual sum of errors separately for horizontal and vertical group of points. For the horizontal group (i.e., when $x > x_c$) we calculate $\sum (y_i - y(x_i))^2$ while for the vertical group (when $x < x_c$) we calculate $\sum (x_i - x(y_i))^2$ (i.e., assuming the vertical part of the prey isocline $x(y)$ is a function of predator abundance) and we add both these sums. Thus, the residual sum of squares is calculated exactly the same way as in Section 2. Our results (Table 2) clearly show that models that consider a prey refuge fit the estimated prey isocline much better than models without a prey refuge.
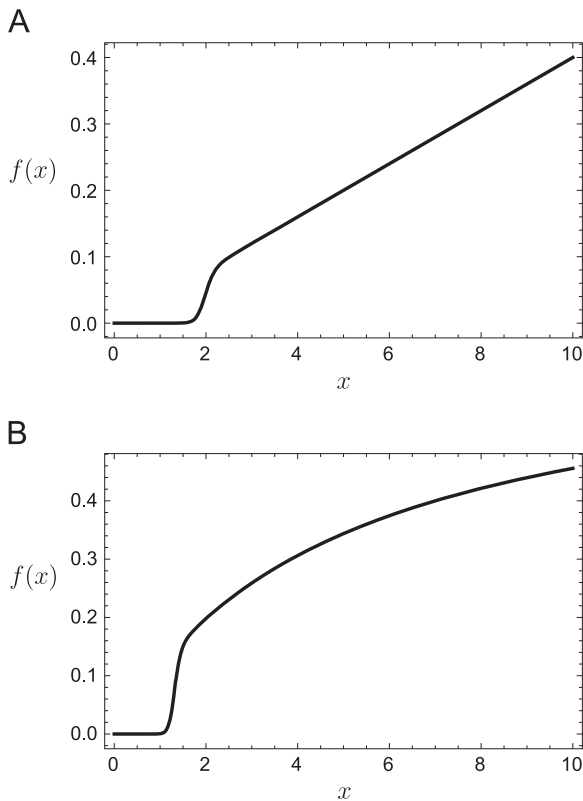
5. Discussion

In this paper we estimate predator and prey isoclines using classic data on protists feeding on yeast (Gause et al., 1936). First, we estimate isoclines directly from data. These estimates suggest that the prey isocline is an L-shaped piece-wise linear line that has a horizontal and a vertical part (Fig. 2A, solid line) while the predator isocline is a vertical line in the prey–predator phase space (Fig. 2A, dashed line). Second, we parametrize the Lotka–Volterra and the Rosenzweig–MacArthur predator–prey models either with a prey refuge or without it which allows us to estimate the isoclines for these models (Fig. 2B–E). Again, corresponding prey isoclines for models that assume a prey refuge fit the estimated prey isocline much better when compared with models that do not consider a refuge (Table 2). Our results suggest that a prey refuge leads to prey isoclines with a steep part at low prey densities. Such a shape of the prey isocline effectively bounds amplitude of predator–prey oscillations, thus promotes predator and prey coexistence as observed by Rosenzweig and MacArthur (1963).

Gause experimented extensively with various predator–prey systems (Gause, 1934; Gause, 1935a,b; Gause et al., 1936). The data he collected has helped us to understand mechanisms regulating predator–prey coexistence and have been used in many analysis (e.g. Jost and Arditi, 2000, 2001; Jost and Ellner, 2000; Nedorezov, 2012). The difference between Gause (1935a) (these results are also reported in Gause, 1935b) and Gause et al. (1936) experiments is the fact that in the latter experiments there was a prey refuge. Indeed Gause (1935a,p. 45) mentions that "during the course of experiments the yeast was prevented from settling on the bottom of the container by passing air bubbles through the salt solution" while Gause et al. (1936, p. 11) mention "it can be seen that a certain threshold concentration of yeast cells sedimenting on the bottom and elsewhere cannot be destroyed by predators…". Thus, in these latter experiments, prey, when at low densities, were in a refuge and we use these experimental data to test for the effects a refuge has on isoclines.
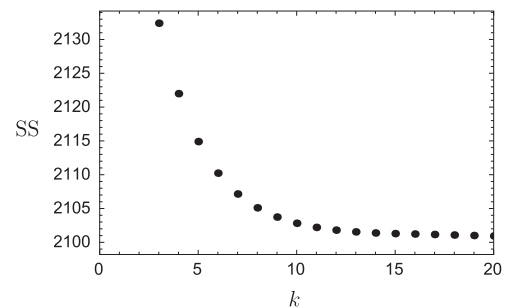

Fig. 3. Functional response (2). Panel A shows the functional response for the Lotka–Volterra model ($h=0$) with a refuge. Parameters are those from Table 1, Model 3. Panel B shows the functional response for the Rosenzweig–MacArthur model with a refuge. Parameters are those from Table 1, Model 5. The steepness of the functional response is in both cases $k=20$.

Fig. 4. Dependence of the residual sum of squares for the Lotka–Volterra predator–prey model with a refuge on parameter k.

Table 1

Estimated parameters and standard errors. SS is the residual sum of squares, AIC is the Akaike Information Criterion. N.e. is not estimated. Numbers typeset in roman are significant (P-value < 0.05), the value in italics is marginally significant (P-value $= 0.06$).

Model	r	m	λ	e	h	K	x_c	SS	AIC
1. The Lotka–Volterra model (1) with $r=0.5$ and $m=0.4$	0.5 (n.e.)	0.4 (n.e.)	0.06 ± 0.003	0.97 ± 0.06	—	—	—	6353	932
2. The Lotka–Volterra model (1)	0.24 ± 0.04	0.12 ± 0.02	0.04 ± 0.004	0.81 ± 0.10	—	—	—	2148	785
3. The Lotka–Volterra model (1) with refuge	0.23 ± 0.04	0.12 ± 0.02	0.04 ± 0.004	0.82 ± 0.1	—	—	*1.97 ± 1.05*	2101	784
4. The Rosenzweig–MacArthur model (4) without refuge	0.44 ± 0.06	0.23 ± 0.03	0.14 ± 0.02	1.23 ± 0.12	1.43 ± 0.13	33.0 ± 3.46	—	1330	722
5. The Rosenzweig–MacArthur model (4) with refuge	0.44 ± 0.06	0.23 ± 0.02	0.14 ± 0.03	1.26 ± 0.11	1.48 ± 0.14	32.4 ± 3.33	1.31 ± 0.31	1291	720

Table 2
Fit between model isoclines and isoclines estimated from data. Models 1–5 are the same as those in Table 1. SS denotes the residual sum of squares.

Model	SS for prey isocline	SS for predator isocline
Isoclines estimated from data	12	111
The Lotka–Volterra Model 1	1038	319
The Lotka–Volterra Model 2	1351	114
The Lotka–Volterra Model 3 with refuge	28	113
The Rosenzweig–MacArthur Model 4 without refuge	211	146
The Rosenzweig–MacArthur Model 5 with refuge	19	148

While the predator isocline is easy to estimate from experimental data because the data suggest that it is a vertical line (see squares in Fig. 2A), estimating the prey isocline is more complicated. The data suggest that the prey isocline can be approximated as an L-shaped function (see dots in Fig. 2A) with a horizontal (solid dots) and a vertical segment (open dots). The problem here is that if the isocline has both horizontal and vertical segments, it cannot be described as a function of a single variable (i.e., either as a function $y(x)$ of prey density only, or as a function $x(y)$ of predator density only). This makes difficult to use software packages for piece-wise linear regression (e.g., package "segmented" in R), as these assume that the estimated object is a function. Here we cluster the estimated data points for the prey isocline into two groups, one that describes the "horizontal" part and the other that describes the "vertical" part of the prey isocline. The linear regression fit of the horizontal part assumes this part of the prey isocline to be a linear function of prey density while the vertical part of the prey isocline is a linear function of predator density. Neither of these two fits shows a significant trend so the resulting best fit of the prey isocline is L-shaped with a vertical and a horizontal part (Fig. 2A). Such a shape agrees with theoretical predictions for the Lotka–Volterra model (1) with a prey refuge (Křivan, 2011, Fig. 2C and D).

Using experimental data on protists feeding on yeast (Gause, 1935a), Rosenzweig (1977) estimated prey and predator isoclines graphically. His analysis predicted a hump shaped prey isocline and vertical predator isocline. Such isoclines agree with the Rosenzweig–MacArthur predator–prey model (Rosenzweig and MacArthur, 1963; Rosenzweig, 1971). In this paper we estimate model parameters for both the Lotka–Volterra model (1) and the Rosenzweig–MacArthur (4) model either with or without a prey refuge. The resulting parameter estimates are given in Table 1 together with the residual sum of squares and the Akaike Information Criterion (AIC). The AIC is often used to compare several models that differ in the number of parameters. Models 1–3 are the Lotka–Volterra models either without refuge (Models 1 and 2), or with a refuge. Model 1 estimates only two parameters while the prey per capita population growth parameter $r=0.5$ and the predator per capita mortality rate $m=0.4$ were taken from Gause et al. (1936). Compared to Model 2 that estimates all four parameter, Model 1 fits experimental data poorly (Table 1). It may be that because the parameters r and m were measured in a single species experiments, these values change when both predators and prey are together. Model 3 estimates also the refuge size x_c. For this we have to define steepness of the functional response k in (2) at the refuge size. Dependence of the residual sum of squares on parameter k (Fig. 4) shows that as the steepness of the functional response increases, the fit gets better. As we could not fit k as another unknown parameter, we chose arbitrarily $k=20$ in this paper.

Our results show that the Rosenzweig–MacArthur model (4) fits data better when compared with the Lotka–Volterra model (Table 1) as both the residual sum of squares as well as the AIC are smaller. The Rosenzweig–MacArthur model with prey refuge (Model 5 in Table 1) fits the experimental data best. Fit between model predictions and experimental data is shown in Fig. 1. Fit between isoclines for models considered in this paper and estimated isoclines is shown in Table 2. These results show anew that models that consider a prey refuge fit the estimated prey isocline much better when compared to models without a refuge.

Our results show that a prey refuge strongly influences the shape of prey isocline estimated from experimental data. Moreover, the observed prey isocline agrees with predictions of theoretical predator–prey models that consider a prey refuge (eg., Rosenzweig and MacArthur, 1963; Křivan, 2011). Because the prey refuge manifests at low prey population densities, it can be difficult to identify effects of prey refuge in experimental predator–prey data unless these contain enough points at low prey densities. Because refuges can be also behavioral (e.g., due to prey switching by predators or changes in prey behavior under predation risk, Brown and Kotler, 2004; Křivan, 2013) prey isoclines with a vertical part should be ubiquitous in nature.

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