

# A Mechanistic Model for Interference and Allee Effect in the Predator Population\*

Yu. V. Tyutyunov<sup>a, b</sup>, L. I. Titova<sup>b</sup>, and S. V. Berdnikov<sup>c</sup>

<sup>a</sup> Institute of Arid Zones, Southern Scientific Center, Russian Academy of Sciences, Rostov-on-Don, 344006 Russia

<sup>b</sup> Vorovich Institute of Mechanics and Applied Mathematics, Southern Federal University, Rostov-on-Don, 344090 Russia

<sup>c</sup> Southern Scientific Center, Russian Academy of Sciences, Rostov-on-Don, 344006 Russia

e-mail: tyutyunov@sfedu.ru

Received July 23, 2012; in final form, August 15, 2012

**Abstract**—We present the results of simulations in an individual-based model describing spatial movement and predator–prey interaction within a closed rectangular habitat. Movement of each individual animal is determined by local conditions only, so any collective behavior emerges owing to self-organization. It is shown that the pursuit of prey by predators entails predator interference, manifesting itself at the population level as the dependency of the trophic function (individual ration) on predator abundance. The stabilizing effect of predator interference on the dynamics of a predator–prey system is discussed. Inclusion of prey evasion induces apparent cooperation of predators and further alters the functional response, giving rise to a strong Allee effect, with extinction of the predator population upon dropping below critical numbers. Thus, we propose a simple mechanistic interpretation of important but still poorly understood behavioral phenomena that underlie the functioning of natural trophic systems.

**Keywords:** mathematical modeling, isoclines, trophic isopleths, spatial behavior, pursuit–evasion, agent-based model, Monte-Carlo method

**DOI:** 10.1134/S000635091302022X

## INTRODUCTION

Predator–prey systems are a class of biological objects extensively studied by mathematical modeling. Sustaining energy transfer in ecosystems, trophic interactions represent a paramount type of interspecies relations. It is not incidental that mathematical ecology started from building and examining a predator–prey model [1–4]. In theoretical biology, partitioning of trophic communities into elementary predator–prey pairs allows efficient use of the methods of matrix and graph theory in studying the dynamic properties of complex ecosystems [5].

Over the many decades that have passed since Lotka and Volterra published their works [1, 2], our understanding of the rules whereby trophic communities live has improved substantially, yet many problems still await solution. A topical problem in model description of trophic systems is validation of the choice of trophic function  $g(N, P)$  to specify the dependence of predator individual ration on the numbers of predators ( $P$ ) and prey ( $N$ ) [6].

Consider a particular case of the Gause–Kolmogorov model with logistic reproduction of prey and a constant predator mortality coefficient  $\mu$ :

$$\begin{cases} \frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - Pg(N, P), \\ \frac{dP}{dt} = ePg(N, P) - \mu P. \end{cases} \quad (1)$$

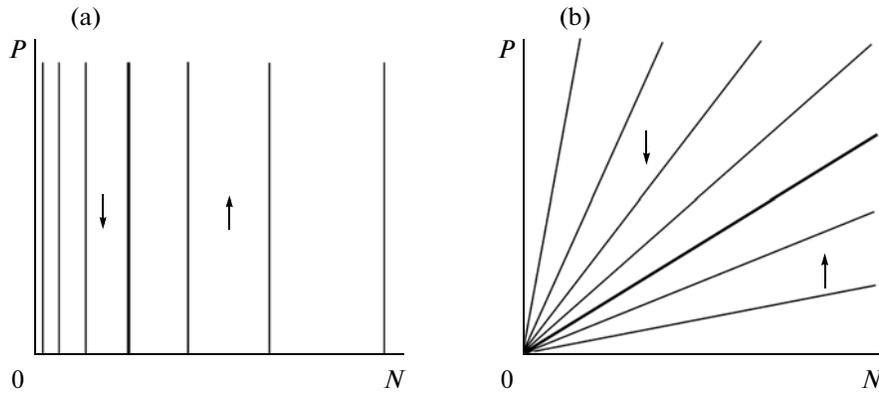
Here  $r$  and  $K$  are the coefficients of reproduction and carrying capacity for the prey,  $e$  is predation efficiency. Even for the two-component set (1), the choice of one or another form of  $g(N, P)$  qualitatively alters the properties of the model and thus its ability to adequately describe the observed dynamics of natural communities [5, 7–9].

Still the most popular one is the Holling function of type II [10]:

$$g(N) = aN/(1 + ahN), \quad (2)$$

despite that in this case model (1)—the MacArthur–Rosenzweig model [11]—demonstrates such absurd, reality-defying properties as the “paradox of enrichment” [12] and the closely related “paradox of biological control” [13–15]. The paradox of enrichment consists in that increased primary production entails destabilization of the model dynamics, with increased amplitudes of oscillation in numbers and elevated risk of extinction either of predators or of both popula-

\* The text and presentation have been additionally amended for the English version. A.G.



**Fig. 1.** Characteristic patterns of isopleths on the  $(N, P)$  plane for trophic functions: (a) Holling type II, (b) Arditi–Ginzburg–Contois.

tions, whereas there is no convincing evidence of any such effect in natural conditions [6, 16, 17]. The paradox of biological control consists in that with the generally accepted MacArthur–Rosenzweig model it is impossible to reproduce any stable dynamics with a low pest level, which corresponds to successful pest suppression with a biocontrol agent [15, 18]. The use of the same trophic function in modeling a food chain leads to another striking inconsistency of the mathematical model with the observations in natural trophic communities: the model predicts unrealistic, oppositely directed reaction of “trophic cascade” levels to bottom-level biomanipulations (“enrichment response” [6, 17]). Namely, if we take a chain model with levels enumerated top-down (solely for demonstration) and increase the productivity at the lowest level, then the abundance at the topmost level 1 would increase, that of level 2 remain constant, while the reaction of the other levels would depend on their parity (!): odd-numbered levels (3, 5, ...) show an increase, while even-numbered ones (4, 6, ...) show a decrease, or preservation at  $h = 0$  [6]. Jensen and Ginzburg [17] have pointed out that a four-level model would “suffer from this prediction of decreasing [producer] abundance with increasing enrichment” [a bizarre situation indeed], while all the known attempts at presenting natural observations of such dynamics involve either inaccurate processing or erroneous interpretation of the data (see also [6, 19]).

The same problems arise upon using any other trophic function depending only on the prey population numbers,  $g(N)$  (*prey-dependent function* [16]). The graphic reflection of the cause of all three contradictions is the verticality of the null isocline of the second equation in set (1) (see Fig. 1a below), and this cause is abolished if the conventional theory is modified by including into the model the predator interference effect, seen at the population level as the dependency of the trophic function on  $P$  [6, 7, 20–23]. The term *mutual interference* was introduced in 1954 by Park [24], who noted the importance of animal

intraspecies behavioral interactions. Yet earlier, in 1947, Ivlev [25, 26] disclosed a phenomenon of “complicated relations of competition”, consisting in reduction of the ration in joint foraging of consumers, and proposed an original trophic function:

$$g(N/P) = g_{\max}(1 - \exp(-kN/P)). \quad (3)$$

Years later, Hassell and Varley in the now classical work [27] proposed their dependence including interference:  $g(N, P) = N/P^m$ . Then came the papers of Beddington [28], DeAngelis et al. [21], and many other results of theoretical and experimental studies on predator interference. In systems of form (1), the use of trophic functions with interference,  $g(N, P)$  (*predator-dependent function* [16]) allows taking into account the time of predator interaction with competitors, implicitly including into a point model the diverse effects of inhomogeneous environs and spatial behavior of animals [23]. Formally, interference stabilizes the dynamics of system (1) owing to that the null isocline of the predator equation with a predator-dependent function  $g(N, P)$  proves to be not vertical but slanted (see Fig. 1b). The latter, in particular, removes the paradox of enrichment: an initially stable equilibrium of (1) remains stable upon increasing the prey population productivity [6].

Note that among the various dependences proposed (some are given in [29, 30]) the simplest one is the Arditi–Ginzburg–Contois function:

$$g(N/P) = \alpha N / (P + \alpha h N), \quad (4)$$

a generalization of the Holling type II function that does not require additional parameters [6, 7, 16, 31, 32]. In (4),  $\alpha$  specifies search efficacy, and  $h$  is “handling time” (i.e., the time in which a predator deals with one prey item) in the absence of competitors. However, as distinct from (2) where parameter  $a$  is the area searched by predator per unit time, in (4) this area in fact depends on the number of predators,  $a = \alpha/P$ . Note also that, like the Ivlev function (3), the Arditi–Ginzburg–Contois formula (4) belongs to the class of

trophic functions the argument of which is the ratio of prey to predator numbers (*ratio-dependent function* [16]).

Which of the multitude of proposed  $g(N, P)$  forms would be most adequate to modeling a particular system? The choice of trophic function and its substantiation cannot rely solely on speculative schemes and reasoning [7, 17]. Along with observations on natural [33, 34] and laboratory trophic systems [30, 35], theory demands models explaining the very mechanism whereby predator interference does emerge [23, 29, 36, 37].

## MODEL OF ANIMAL SPATIAL BEHAVIOR

We propose a simple mechanistic model of the spatial behavior of individuals in a predator–prey system, which allows direct estimation of the form of  $g(N, P)$  dependence under various hypotheses concerning movement of  $N$  prey individuals and  $P$  predators in a rectangular space  $L_x \times L_y$ . Namely, we will be interested in how the trophic function is influenced by the ability of individuals to make not only random but also directed movements evoked by a non-uniform spatial distribution of an antagonistic population.

### Model Description

Let every individual release a specific scent—a substance (pheromone, exometabolite) that spreads and decays much faster than the animal moves from place to place. Then the distribution of individual scent can be taken to be normal, centered at the individual location point with rmsd  $\sigma_N$  for the prey and  $\sigma_P$  for the predator. The smell of the whole population in every point of the model space is determined by summation of the scents coming from all individuals. The moves of an  $i$ -th predator are described by equation  $\mathbf{x}_{i,t+1}^P = \mathbf{x}_{i,t}^P + \xi_{i,t}^P + \mathbf{v}_{i,t}^P$ , where  $\mathbf{x}_{i,t}^P$  is a vector specifying the position of the individual in discrete moments  $t = 0, 1, 2, \dots$ ;  $\xi_{i,t}^P$  is a random vector uniformly distributed inside a circle of radius  $\sigma_P$ , modeling random motion; while  $\mathbf{v}_{i,t}^P = \kappa_P \nabla S_N(\mathbf{x}_{i,t}^P) + \theta_P \mathbf{v}_{i,t+1}^P$  is the vector of directed movement of the predator along the gradient of prey scent  $S_N$  in point  $\mathbf{x}_{i,t}^P$ . For prey the formulae are analogous, differing only in that the indices  $N$  and  $P$  swap places. The taxis coefficients  $\kappa_N$  and  $\kappa_P$  specify the intensity of aimed movements;  $\theta_N, \theta_P \in [0, 1]$  set their inertia. The direction is set by the sign:  $\kappa_N \leq 0$ , i.e., predator smell is repellent for prey;  $\kappa_P \geq 0$ , as prey smell is attractant for predators.

In this way, by changing the parameter values, we can model various strategies of motion of predators and their prey inside the rectangle. Here we present

the results obtained under condition of reflection at the boundaries, but imposing a sticking condition does not qualitatively affect the results.

A prey winding up in an  $r$ -vicinity of a predator may evade capture with a probability  $\gamma$ , otherwise it is eaten. To maintain the numbers through the simulation, an eaten prey was replaced with a new one at a random point; this trick was borrowed from real lab experiments [38].

Estimates of the expected individual ration  $g$  for  $N, P = 1, \dots, 25$  pairs were computed by the Monte-Carlo method. In the end of each run, the  $g$  value was determined as the total number of prey eaten by all predators in the experiment divided by its duration and by the number of predators. Under constancy of population numbers, this calculation corresponds to the laboratory methods and is perfectly correct. Running 500 replicates of stochastic iteration over time ( $t = 1, 2, \dots, 200$ ) ensured convergence and high enough accuracy at  $L_x = 5, L_y = 3; r = 0.1; \gamma = 0.001; \sigma_N = 0.5; \delta_N = 0.1; \theta_N = 0.25; \sigma_P = 0.5; \delta_P = 0.25; \theta_P = 0.5$ . The error in calculating individual rations did not exceed 0.0001. We observed no qualitative changes in the results upon varying the parameter values in additional simulations.

### Simulation Results

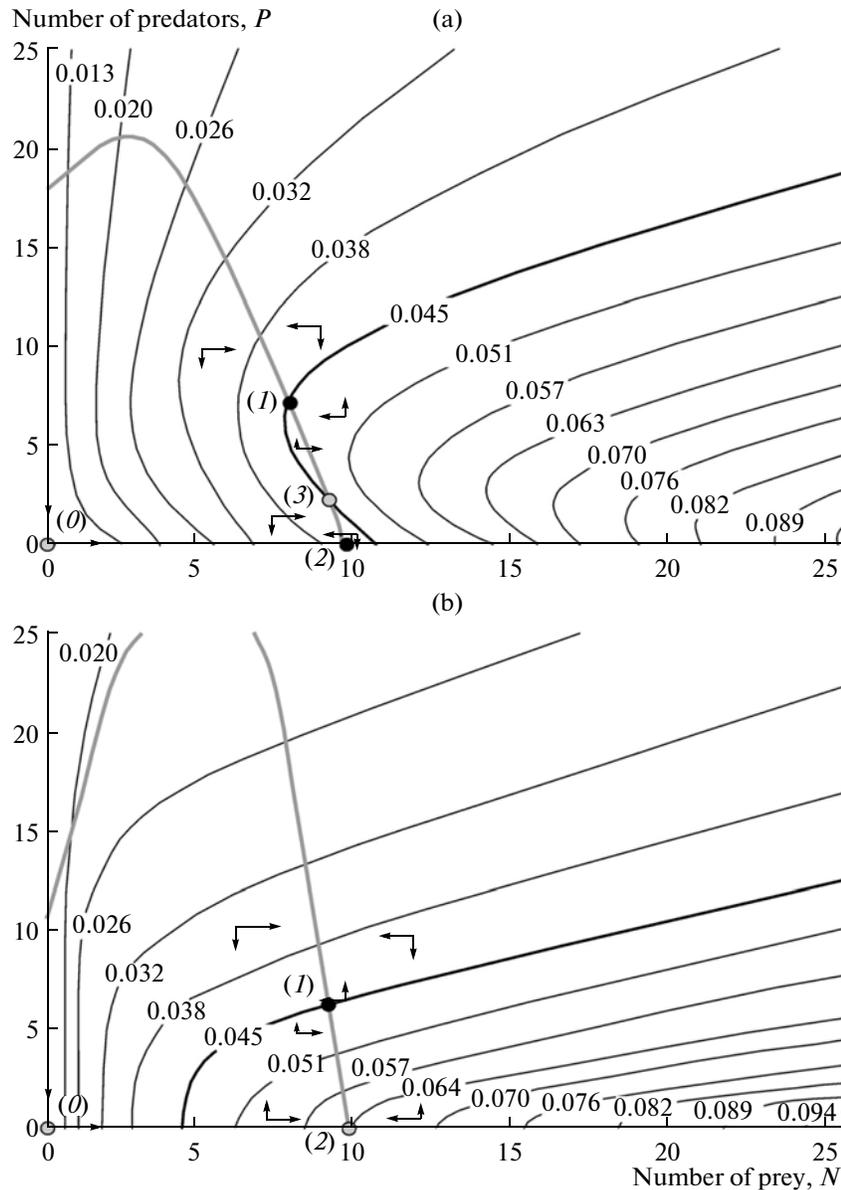
Plotting the lines of  $g(N, P) = \text{const}$  (isopleths) on the  $(N, P)$  plane provides a graphic demonstration of the essential consequence of predator interference and of the changes in the latter with varying numbers of either population.

In random motion ( $\kappa_N = \kappa_P = 0$ ) there is no interference, the isopleths are parallel vertical lines as in Fig. 1a, i.e., the trophic function does not depend on predator numbers,  $g = g(N)$ .

However, in the more realistic case of pursuit–evasion ( $\kappa_N = -0.3, \kappa_P = 0.2$ ) the pattern is qualitatively altered (Fig. 2a): with growing  $N$  and  $P$  the isopleths deviate from the vertical, in evidence of interference—decreasing rate of prey consumption by a predator with increasing number of competitors. Moreover, the dependence of ration on  $P$  in Fig. 2a is obviously nonmonotonic: both growth and excessive reduction in predator numbers entail a drop in hunting efficacy; i.e., for any fixed amount of prey there is some optimal size of the predator population that ensures maximal individual consumption.

If the prey do not evade the predators ( $\kappa_N = 0$ ), the dependence of ration on  $P$  is only monotonic (Fig. 2b).

However, these results give us more than just an idea of how the trophic function behaves with varying population numbers under particular hypotheses concerning individual behavior. It is not difficult to see that the null isocline for the predator equation in set (1),  $g(N, P) = \mu/e$ , is also an isopleth. Moreover, from



**Fig. 2.** Isoleths of trophic function  $g(N, P)$  computed with predator–prey spatial behavior simulations and the resulting phase diagrams for the Gause–Kolmogorov model (1): (a) pursuit–evasion, (b) no evasion. Bold lines denote the null isoclines of (black) predator and (gray) prey equations. Black circles mark stable and gray ones mark unstable equilibria.

the  $g(N, P)$  values calculated at particular parameters values (e.g.  $\mu = 0.045$ ;  $e = 1$ ;  $r = 0.19$  and  $K = 10$ ) we can approximately reconstruct in the same  $(N, P)$  plane the null isocline for the prey population (gray line in Fig. 2) by numerically solving the equation  $r(1 - N/K) - Pg(N, P)/N = 0$ . Thus, we can fully envision the possible solutions of set (1), its equilibria and their stability.

**Main Findings**

1. For highly specialized animal species capable of purposeful spatial movement, the predator–prey

dynamics can not be described by model (1) unless the trophic function involves interference.

2. Predator interference may result from active pursuit of prey.

3. The slanted disposition of isopleths in the phase plane  $(N, P)$  is evidence of a stabilizing influence of predator interference on the system dynamics, which helps lifting the paradoxes of conventional theory.

4. Evasion of predator by the prey further modifies the null isocline so that a nontrivial saddle-type equilibrium appears (point 3 in Fig. 2a), while the equilibrium corresponding to extinction of predators

(point 2) becomes stable. The latter in fact is a realization of a strong Allee effect [40, 41].

5. A concurrent effect (and counterintuitive as it may seem) is that a population of predator-evading prey proves to be more vulnerable than a non-evading one.

6. At high enough population numbers, the arrangement of isopleths on the  $(N, P)$  plane is close to the characteristic pattern of the Arditi–Ginzburg–Contois function [6, 16], which is another argument in favor of using this simplest dependence (see also [19, 29, 30]).

## DISCUSSION

The main goal of this work was to demonstrate—with a simple and easily implemented model of animal spatial behavior—the emergence of interference, seen as the dependency of the mean ration of predators (trophic function) on their numbers. In our opinion, the simplicity of the model is its clear advantage. Let us discuss some additional aspects of the results thus obtained.

First of all, a brief comment on terminology. Before “interference” came into use, Ivlev [25] wrote about “complicated competition”, and some works, e.g. a study of Bazykin et al. [39] on models with a  $g(N, P)$  trophic function, also speak of competition—but “competition” and “interference” should not be confused or used interchangeably. Competition for a common food resource within a predator population can be envisaged in models with interference but as well in those without interference, i.e.  $g = g(N)$ . Using “competition” to mean interference is incorrect for one more reason: predator interference (dependency of ration on  $P$ ) may involve both competition and cooperation [20], which is also evident from our results.

We have found that when the prey evades the predator, i.e., at negative taxis ( $\kappa_N = -0.3$ ), conditions are created for collective behavior: an increase in the number of predators (to a certain limit) results in an increase in individual ration (see Fig. 2a). The mechanism of this phenomenon in the model is easy to understand: a buildup in predator smell makes the prey aggregate in predator-free spaces, but the ensuing accumulation of smell from crowding prey stimulates the attacks of predators and enhances their efficiency. However, with a further increase in  $P$  the true competition starts to prevail over such cooperation, whereby the predator ration declines (though it remains somewhat higher than in hunting passive, non-evading prey). Ostensibly, the model actualizes a scenario of collective hunting, but this collective behavior is a result of self-organization—the behavior of each individual predator in the model is set by a simple algorithm and exclusively local information. In other words, the model does not include or imply any social “mutual aid” mechanisms; every organism behaves as

an autonomous (and absolutely egoistic) individual. Yet in the final analysis it is such cooperation that gives rise to an Allee effect in the pursuit–evasion model.

Let us recall that the Allee principle in population ecology is understood as any mechanism whereby increased population density improves the fitness of individuals [40, 41]; there is no such effect in the orthodox representation of logistic population growth. The other side of a strong Allee effect is that a population having dwindled in numbers below some threshold is doomed to extinction. Mechanisms whereby Allee effects may arise in a population system include defensive behavior of prey, spatial behavior of predators enforcing aggregation, modification of the environment by the animals, difficulty in finding mates, genetic degeneration, etc. [41]. Our model does not explicitly include all these features, yet it enables us to assess the behavioral mechanisms of emergence of interference, (quasi)cooperation, and Allee effect in a predator population. In particular, it is shown that evasive behavior of the prey may lead to predator extinction.

Thus, our results support the expedience of considering predator interference as an implicit way of taking into account the spatial and behavioral effects in a point model [6, 21, 23, 27, 28]. One more reason to use type  $g(N, P)$  trophic functions in model (1) is that thereby we obviate the notorious paradoxes of the standard theory [12–15, 17].

We should note that an alternative to the Gause–Kolmogorov model considered here is the Leslie–Gower model [42, 43] where not the reproduction but the mortality of predators depends on the ratio of  $P$  and  $N$ :

$$\begin{cases} \frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - aNP, \\ \frac{dP}{dt} = s\left(1 - \frac{P}{kN}\right)P. \end{cases} \quad (5)$$

Inasmuch as the null isocline of the predator equation in (5) is a slanted straight line from the origin, this model might also lift the “paradox of enrichment.” However, the Leslie–Gower system itself suffers a serious fault, neglecting energy conservation (predator feeding and reproduction are not related in any way) [6, 44]. Besides, today we have numerous experimental data in evidence of the dependency of the ration of predators on their numbers, but there has been no convincing evidence in favor of the Leslie–Gower hypothesis. For this reason, here we have restricted ourselves to the logically consistent framework of the Gause–Kolmogorov model.

In principle, the Gause–Kolmogorov model can also accommodate a mortality coefficient growing with population numbers, e.g.,  $\mu(P) = mP$  [45, 46]. Though this does stabilize the predator–prey dynam-

ics (to lift the “paradox of enrichment”), there remain the problems with discrepant responses in the trophic chain [44]. To add, it would obviously be hard to substantiate the dependency of predator mortality on predator abundance. Putative competition for a resource other than prey, as proposed by Bazykin [46], is not a very good idea, inasmuch as this “other resource” does not anyhow influence the reproduction of predators. A more plausible interpretation proposed by Steele and Henderson [45] implies that  $\mu(P)$  is predator mortality caused by some top predator not envisioned in the model. Admittedly, in an earlier work of Berdnikov et al. [22] predator fish mortality was taken to depend on its numbers, but indirectly and realistically, through shortage of food.

In any case, the most natural way of improving the dynamic properties of the Gause–Kolmogorov model is to modify the trophic function by allowing for predator interference.

In conclusion, we would like to say a few words about the place and the role of simple theoretical models in mathematical ecology. Designing simple (minimal, basic) models capable of reproducing complex behaviorally induced effects is an extremely useful occupation [47, 48]. Minimal models allow the researcher to tersely present the essence of theoretical notions on the system under study, to test the alternative concepts and pick out the one that can consistently and most simply explain the empirical observations [49, 50]. Eventually, it is qualitative validation of basic models that ensures the reliability of the more complicated modeling tools built for applied tasks such as natural ecosystems management. Regrettably, mathematical ecology—unlike e.g. mechanics—currently puts in opposition the basic theoretical and the applied simulation models. Theoretical models are at best used only in teaching students, while simulation (“computer-dwelling”) models are often contrived without any regard to theory—and the result is often not even a black box, but a black box with inconceivable properties. Such opposition is unnatural and untenable, and must be overcome: in simulation systems of any complexity, the building blocks must be simple, sensible, and empirically proven basic models. If such a block turns out to be nonworking, we must not complicate the simulation model just to procure a desired result, but rather, we must modify or revise the theory [6, 50].

#### ACKNOWLEDGMENTS

The authors are grateful to A.B. Medvinsky for conceptual discourse on minimal models, and to R. Arditi and L.R. Ginzburg for stimulating discussions.

We also thank A.V. Galkin whose insightful suggestions and corrections made during translation of our

text into English have greatly improved the manuscript.

The work was supported by Federal Target Programs “Cadres” (project code 2012-1.1-12-000-1001-033) and “World Ocean” (project code 2011-16-420-5-007).

#### REFERENCES

1. A. J. Lotka, *Elements of Physical Biology* (Williams and Wilkins, Baltimore, 1925).
2. V. Volterra, *Nature* **188**, 558 (1926).
3. G. F. Gause, *The Struggle for Existence* (Williams and Wilkins, Baltimore, 1934).
4. V. A. Kostitzin, *Biologie Mathématique* (Librairie Armand Colin, Paris, 1937).
5. Yu. M. Svirezhev and D. O. Logofet, *Stability of Biological Communities* (Nauka, Moscow, 1978) [in Russian].
6. R. Arditi and L. R. Ginzburg, *How Species Interact: Altering the Standard View on Trophic Ecology* (Oxford Univ. Press, Oxford, 2012).
7. P. A. Abrams and L. R. Ginzburg, *Trends Ecol. Evol.* **15**, 337 (2000).
8. R. Arditi, J.-M. Callois, Yu. Tyutyunov, and C. Jost, *Compt. Rend. Biol.* **327**, 1037 (2004).
9. Yu. M. Svirezhev, *Ecol. Model.* **216**, 89 (2008).
10. C. S. Holling, *Can. Entomol.* **91** (5), 293 (1959).
11. M. L. Rosenzweig and R. H. MacArthur, *Am. Naturalist* **97**, 217 (1963).
12. M. L. Rosenzweig, *Science* **171**, 385 (1971).
13. R. F. Luck, *Trends Ecol. Evol.* **5**, 196 (1990).
14. A. A. Berryman, in *Theoretical Approaches to Biological Control*, Ed. by B. A. Hawkins and H. V. Cornell (Cambridge Univ. Press, Cambridge, 1999), pp. 3–21.
15. R. Arditi and A. A. Berryman, *Trends Ecol. Evol.* **6**, 32 (1991).
16. R. Arditi and L. R. Ginzburg, *J. Theor. Biol.* **139**, 311 (1989).
17. C. X. J. Jensen and L. R. Ginzburg, *Ecol. Model.* **188**, 3 (2005).
18. N. Sapoukhina, Yu. Tyutyunov, and R. Arditi, *Am. Naturalist* **162**, 61 (2003).
19. H. R. Akçakaya, R. Arditi, and L. R. Ginzburg, *Ecology* **76**, 995 (1995).
20. M. Begon, J. L. Harper, and C. R. Townsend, *Ecology: Individuals, Populations and Communities* (Sinauer Associates, 1986).
21. D. L. DeAngelis, R. A. Goldstein, and R. V. O’Neill, *Ecology* **56**, 881 (1975).
22. S. V. Berdnikov, V. V. Selyutin, V. V. Vasilchenko, and V. V. Caddy, *Fisheries Res.* **42**, 261 (1999).
23. C. Cosner, D. L. DeAngelis, J. S. Ault, and D. B. Olson, *Theor. Popul. Biol.* **56**, 65 (1999).
24. T. Park, *Physiol. Zool.* **27**, 177 (1954).
25. V. S. Ivlev, *Uspekhi Sovr. Biol.* **24**, 417 (1947).
26. V. S. Ivlev, *Experimental Ecology of Fish Nutrition* (Pishchepromizdat, Moscow, 1955) [in Russian].
27. M. P. Hassell and G. C. Varley, *Nature* **223**, 1133 (1969).

28. J. R. Beddington, *J. Anim. Ecology* **44**, 331 (1975).
29. Yu. Tyutyunov, L. Titova, and R. Arditi, *Ecol. Complexity* **5** (1), 48 (2008).
30. Yu. Tyutyunov, L. Titova, F. A. Surkov, and E. N. Bakaeva, *Zh. Obshch. Biol.* **71**, 52 (2010).
31. D. S. Contois, *J. Gen. Microbiol.* **21**, 40 (1959).
32. L. R. Ginzburg, Yu. I. Gol'dman, and A. I. Railkin, *Zh. Obshch. Biol.* **32**, 724 (1971).
33. C. Jost, G. Devulder, J. A., Vucetich, et al., *J. Anim. Ecol.* **74**, 809 (2005).
34. J. A. Vucetich, R. O. Peterson, and C. L. Schaefer, *Ecology* **83**, 3003 (2002).
35. J. P. DeLong and D. A. Vasseur, *BMC Ecology* **11**, 1 (2011).
36. J.-Ch. Poggiale, J. Michalski, and R. Arditi, *Bull. Math. Biol.* **60**, 1149 (1998).
37. R. Arditi, Yu. Tyutyunov, A. Morgulis, et al., *Theor. Popul. Biol.* **59**, 207 (2001).
38. T. Tully, P. Cassey, and R. Ferriere, *OIKOS* **111**, 479 (2005).
39. A. D. Bazykin, F. S. Berezovskaya, G. A. Denisov, and Yu. A. Kuznetsov, *Ecol. Model.* **14**, 39 (1984).
40. W. C. Allee, *Animal Aggregations: A Study in General Sociology* (Chicago Univ. Press, Chicago, 1931).
41. P. A. Stephens and W. J. Sutherland, *Trends Ecol. Evol.* **14**, 401 (1999).
42. P. H. Leslie, *Biometrika* **35**, 213 (1948).
43. P. H. Leslie and J. C. Gower, *Biometrika* **47**, 219 (1960).
44. C. Jost, *Comparing predator–prey models qualitatively and quantitatively with ecological time-series data: PhD Thesis* (Institute National Agronomique, Paris-Grignon, 1998).
45. J. H. Steele and E. W. Henderson, *Am. Naturalist* **117**, 676 (1981).
46. A. D. Bazykin, *Mathematical Biophysics of Interacting Populations* (Nauka, Moscow, 1985) [in Russian].
47. S. V. Petrovskii and H. Malchow, *Theor. Popul. Biol.* **59**, 157 (2001).
48. A. B. Medvinsky, S. V. Petrovskii, D. A. Tikhonov, et al., *J. Biosci.* **26**, 77 (2001).
49. L. R. Ginzburg and M. Colyvan, *Ecological Orbits: How Planets Move and Populations Grow* (Oxford Univ. Press, Oxford, 2004).
50. L. R. Ginzburg and C. X. J. Jensen, *Trends Ecol. Evol.* **19**, 121 (2004).