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Letter to the Editor

Abstract

Gabriel et al. proposed solutions to two paradoxes raised by Levins and Ginzburg in the logistic equation. The resolution of these two paradoxes lies in the distinguishing of two concepts in ecological studies: carrying capacity and population equilibrium. I focus on the contradiction raised by the first model of Ginzburg's paradox and metapopulation framework with the traditional concept of carrying capacity. By the clarification of these two concepts and defining the carrying capacity as the environment's maximal load, the paradox will not arise.

Keywords: Logistic model; Verhulst equation; Metapopulation; Density-dependent

Carrying capacity, population equilibrium, and environment's maximal load

Gabriel et al. (2005) illustrated two paradoxes in the logistic equation, namely Levins' paradox and Ginzburg's paradox, which I think arise from the confusion in the concept of carrying capacity; therefore, it could not be resolved only through mathematical adjustment of the logistic equation. Moreover, Gabriel et al. did not resolve the problem arisen from the first model of Ginzburg's paradox (Eq. (5) in Gabriel et al., 2005; Ginzburg, 1992), which can also be illustrated by a clarification of carrying capacity in the following.

Levins' paradox disappears in the original Verhulst equation (Verhulst, 1838; Hutchinson, 1978) but incurs a new problem on the meaning of negative carrying capacity ($K < 0$) when population in sink environment (Dias, 1996) or influenced by Allee effect (McCarthy, 1997; Hui and Li, 2003, 2004) and, as a result, has negative intrinsic increasing rate ($r < 0$). [*Note*: Phil Ganter, Tennessee State University, suggested that the negative carrying capacity might be a measure of just how unfavorable the environment is.] Gabriel et al. (2005) resolved this problem by a redefinition of the carrying capacity and let the negative carrying capacity be zero without changing the positive ones (Eq. (4) in their paper). Here, the concept of carrying capacity adopted by Gabriel et al. (2005) is the equilibrium of population and consists of the classical ecological concept of carrying capacity (Vandermeer, 1969).

To illustrate, let us consider a thought experiment in Fig. 1. There are three eggs in a nine-position egg-box (Fig. 1A). If we eat one and then put a new one in it everyday, the size of the egg population will be maintained at three. Now what is the carrying capacity of this egg population, three or nine? This experiment is mechanically similar to Vandermeer's protozoan *Paramecium bursaria* experiment (Vandermeer, 1969). The size of the protozoan population could be about 3000 individuals in a 0.5 ml Petri dish if we stacked them like sardines. The 3001st individual would cause all the animals to be squeezed to death (Vandermeer and Goldberg, 2003). Actually, Vandermeer (1969) found that the real population leveled off at around

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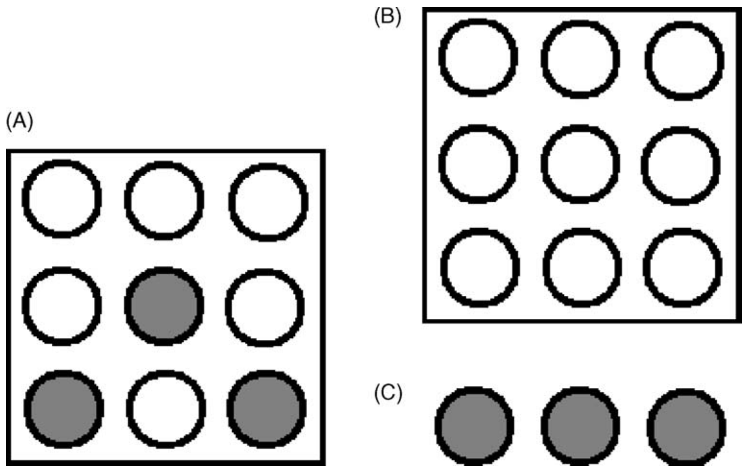

Fig. 1. The carrying capacity of an egg population.

290 individuals and suggested that 290 individuals per 0.5 ml should be the carrying capacity, not 3000 individuals (Vandermeer and Goldberg, 2003). So according to Vandermeer's concept the carrying capacity in the egg-box analogy would not be nine (Fig. 1B) but three (Fig. 1C).

Now, if we eat two eggs per day, the carrying capacity will be $K_\infty = 0$ as shown in Eq. (4) of Gabriel et al. (2005). Obviously, this resolution contradicts our intuition of carrying capacity, which should be the number of positions in the egg-box, i.e. nine. Moreover, this confusion of carrying capacity directly leads to the first model of Ginzburg's paradox, which considers additional mortality in the logistic equation without changing the environment,

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\left(1 - \frac{N}{K}\right) - \mu N. \quad (1)$$

The new equilibrium is $K(r - \mu)/r$. Ginzburg (1992) rejected this approach because it "disagrees with our intuition about unchanging equilibrium." He rejected Eq. (1) due to his confusion of population equilibrium and carrying capacity. Gabriel et al. (2005) suggested that "such a behaviour is ultimately dictated by the model, and not the intuition." Therefore, Gabriel just concentrated on the second model of Ginzburg's, which in fact has a mechanistic problem (Ginzburg, 1992), and uses a mathematical adjustment to avoid this problem (Gabriel et al., 2005).

However, according to our knowledge, Eq. (1) does not have any mechanistic problem. On the contrary, it has been widely used as a theoretical foundation in spatial and metapopulation ecology (such as Hanski and Gilpin, 1997; Tilman and Kareiva, 1997; Hanski, 1998, 1999; Gaston and Blackburn, 2000; McGeoch and Gaston, 2002; Hanski and Gaggiotti, 2004; Hui and Yue, 2005; Hui et al., 2004). In fact, if we let $P = N/K$, Eq. (1) will be transformed into the famous Levins' patch occupant model (Levins, 1969),

$$\frac{\mathrm{d}P}{\mathrm{d}t} = rP(1 - P) - \mu P. \quad (2)$$

Berryman (1992) transformed this equation into a logistic equation and obtained the equilibrium of P, $(r - \mu)/r$. Hanski (1999) called this stable equilibrium the local "carrying capacity" of metapopulation, whereas other scientists call this equilibrium local density (Matsuda et al., 1992; Iwasa, 2000; Sato and Iwasa, 2000). Once again, the concept of equilibrium was confused with carrying capacity. The reason why they called it local density or local carrying capacity is that the average or realistic equilibrium is always smaller than this equilibrium due to demographic stochasticity (Iwasa, 2000; Hui and Li, 2004).

This confusion also appears in other textbook. Begon et al. (1990) combined the carrying capacity with maximal equilibrium and defined that carrying capacity is the maximal population size supported indefinitely by a given environment [part of carrying