Ratio-dependent functional response emerges from optimal foraging on a complex landscape

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ABSTRACT

A spatially implicit consumer–resource model, having the form of the Rosenzweig–MacArthur equations except for density-dependent loss on the consumer, is analyzed. Both the rates of resource intake and of mortality of the consumer are assumed to be proportional to the amount of risk it takes during foraging, and the consumer is assumed to take an amount of risk that maximizes its fitness as a tradeoff between growth and predation. Given these conditions, it is shown that a ratio-dependent functional response for the consumer–resource interaction emerges and that the system is highly stable.

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1. Introduction

A general model of consumer–resource interaction (commonly called predator–prey, but referred to here as consumer–resource for generality, as the resource is plant biomass in this case) is frequently written in the form

$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - F(R, H)H \tag{1}$$

$$\frac{dH}{dt} = \beta F(R, H)H - dH - \mu H^2 \tag{2}$$

where R is the resource biomass with logistic growth, r is the intrinsic growth rate of the resource and K is its carrying capacity, H is consumer biomass, d is the consumer mortality rate, and $F(R, H)$ is the so-called functional response, representing the per capita rate of consumption by the consumers. A commonly used functional response is the Holling Type 2 (HT2):

$$F = \frac{aR}{1 + ahR} \tag{3}$$

where a is the maximum rate of consumption per unit consumer per unit resource, and h is the handling time of the consumer per unit resource. The HT2 functional response depends only on resource density and has the property that the rate of feeding saturates as R approaches large values. β is the conversion rate from resource biomass to consumer biomass and d is the death rate of consumer. The term μH^2 represents density-dependent mortality of the consumer. Often in modeling consumer–resource interactions it is assumed that consumer mortality is density independent, so μ is set to zero, and in that case the pair of Eqs. (1) and (2) is the well known Rosenzweig–MacArthur (RM) model, which is widely used for describing such interactions. In the state plane diagram for the RM model the consumer zero-isocline is a vertical line and the resource zero-isocline is typically hump-shaped (Fig. 1) and their intersection is the equilibrium point. The equilibrium is unstable when the consumer zero-isocline is to the left of the peak of the resource zero-isocline and gives rise to a stable limit cycle.

Although the HT2 is perhaps the most widely used functional response, a number of arguments, synthesized recently by Arditi and Ginzburg (2012), have been made in support of ratio-dependent functional responses, in which $F = F(R/H)$ rather than $F(R)$. A particular example of a ratio-dependent (RD) response is

$$F = \frac{aR/H}{1 + ahR/H} \tag{4}$$

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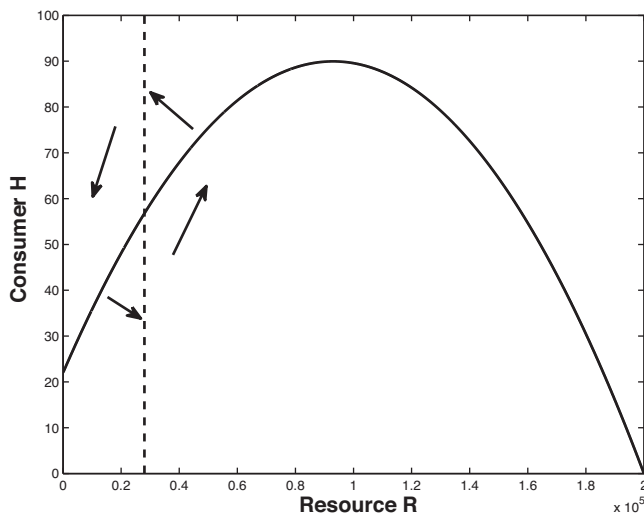   *E-mail address:* rliu1@uwyo.edu (R. Liu).

Fig. 1. Typical state plane diagram of Rosenzweig–MacArthur model. Parameter values are $r = 1.1$, $K = 200,000$, $d = 2.0$, $h = 0.0014$, $\beta = 0.0043$, $a = 0.05$.

In this response the feeding rate is determined by the ratio of resource biomass to consumer biomass. As those authors point out, the popularity of the HT2 may be due to that fact that it is found from a formal derivation. Derivation of the HT2 is based on simple assumptions of instantaneous mass balance, following assumptions similar to those in formulating enzyme kinetic equations of chemistry; i.e., of molecules moving in homogeneous space and interacting with each other (e.g., Case, 2000). Although the straightforward derivation of the HT2 is appealing, its use as basis for consumer–resource interaction in the RM model leads to system dynamics that are not typically observed empirically in consumer–resource systems. One of these predictions is the 'paradox of enrichment', in which increasing values of resource carrying capacity, K, destabilize an initially stable system. Another is that an increase in K does not lead to an increase is resource abundance at equilibrium, but only in consumer abundance, another deviation from what is usually observed empirically (Arditi and Ginzburg, 2012).

A great deal of effort has been expended in trying to remedy the lack of realism of the RM model (e.g., Jansen, 1995; Roy and Chattopadhyay, 2007). Real ecological systems are more complex than the simple chemical kinetics analog of the HT2, so many possible elaborations to the RM model reflecting that complexity have been advanced in the literature to produce more realistic consumer–resource behavior. For example, inclusion of spatial extent and inhomogeneity, spatial refuges for resources, or density-dependent mortality of consumers can often eliminate such phenomena as the paradox of enrichment and lead to increases in resources with increasing carrying capacity. However, Arditi and Ginzburg (2012) pointed out that the RD functional response, without any elaboration, avoids some of the problems of the simple RM model. When the RD functional response (4) is substituted into Eqs. (1) and (2), the new model, called the Arditi–Ginzburg model, does not have the above-mentioned difficulties of the RM model. In addition, they argue that although the RD functional response is not derivable in the straightforward manner of the HT2, it can be shown to be an emergent property of taking into account spatial and temporal complexity. They described a few specific ways in which an RD response could emerge for interacting consumers and resources. The RD response could emerge due to temporal variability in populations and spatial heterogeneity in their environment. For example, Poggiale et al. (1998) consider a two-patch system, one patch of which is a refuge, while on the

other patch a high rate of predation is experienced. The resources (animal prey in this case) move back and forth between the patches randomly but on a much slower time scale than dynamics within the patch in which predation is occurring. To a good approximation, the predator–prey dynamics on the slow time scale can be described with a donor-dependent functional response, with $F(R, H)H$ being reduced to $a(R/H)H$, a simple case of an RD response. In another hypothesized mechanism, the spatial structure of consumer home ranges as a function of consumer density, leads to an RD response. A number of consumers are assumed to have home ranges in a given region, and where these home ranges overlap the consumers are assumed to share the prey equally. As consumer density increases, there is increasing overlap of home ranges and each consumer obtains a smaller fraction of the total resource. The intake of resource per consumer varies as function $F(R/H)$. Again, this depends on a fast time scale for predation, and slower for population growth (Arditi and Ginzburg, 2012).

Although we believe both of these proposals represent plausible explanations for the emergence of ratio-dependence in relatively common situations, we propose a mechanism for emergence of RD that has relevance to a great many situations in nature and does not require assumptions about time scales. It is based on three assumptions.

The first assumption is that the risk of predation is related to the rate of consumption, a. Consumers must obtain resources for growth and reproduction and, at the same time, avoid being preyed on or being victims of other forms of accidental mortality that are entailed by foraging (Lima, 1998; Kie, 1999). The goal of encountering and obtaining resources necessarily involves risky behavior, such as leaving the vicinity of areas that are relatively safe from predation or other accidental forms of mortality and foraging in areas where such mortality is a greater risk (Brown and Cotler, 2004; Cowlinshaw, 1997). Therefore, there is a tradeoff, such that higher possible rates of consumption are associated with higher rates of mortality. The simplest assumption for the model is that risk of predation or other accidental mortality during foraging is proportional to the coefficient that represents the maximum rate of consumption per unit resource density, which is exactly the parameter a in Eq. (3).

The second assumption is that predation and other foraging risks will increase with density of the consumer population. This is motivated by the likelihood that when the consumer density is higher, individual consumers need to forage farther away from areas that are relatively safe from predation to avoid conflict and competition with other consumers. Therefore we assume $\mu > 0$ in Eq. (2) and assume that the final term in the equation represents mortality during foraging. Although the assumption of density-dependent mortality is used less often in the literature than the assumption that $\mu = 0$, $\mu > 0$ is still a fairly common textbook assumption (e.g., Case, 2000) and has substantial literature support (Anderson, 2001; Bonenfant et al., 2009; Hixon and Carr, 1997; Forrester, 1995; McPeek et al., 2001; McPeek, 2012; Schmitt and Holbrook, 1999). This consideration of possible predation and other accidental mortality proportional to H^2 rather than H (as assumption of an earlier paper, Liu et al., submitted for publication) parallels a similar consideration of two variations, 'fixed cost' and 'variable cost' models by Tien and Ellner (2012), in their analysis of predator–prey coevolution, with the H^2 assumption being similar to tradeoff cost that increases non-linearly. Unlike the models of Tien and Ellner (2012), our models are not based on evolutionary changes, but simply on the ability of the consumers to change their strategies in response to changes in environmental conditions.

The third assumption is that individuals in the population of consumers pursue a strategy that involves a tradeoff between food intake and risk of predation that results in optimal fitness.