



Risk sensitivity revisited: from individuals to populations

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ARTICLE INFO

Article history:

Received 10 March 2011

Initial acceptance 21 April 2011

Final acceptance 7 July 2011

Available online 19 August 2011

MS. number: 11-00198R

Keywords:

baseline mortality
density dependence
foraging
optimal variance
risk sensitivity

Risk-sensitive foraging theory is central to behavioural ecology. It relates individual fitness to variance in foraging success (risk) and predicts which foraging strategy maximizes fitness under applicable constraints. Fitness usually comprises survival and reproduction. Yet, most models of risk-sensitive foraging have focused on only one of these two factors. Consequently, such models cannot account for the interaction between resource availability and population size, i.e. density dependence.

Here, we incorporate both mortality and reproduction as functions of an individual's risk-sensitive foraging strategy. In our model the individual strategy thus determines the mean availability of resources per capita and consequently the equilibrium population size. From a continuum of possible strategies we are able to pinpoint the exact risk-sensitive strategies that are favoured by natural selection in saturated habitats and demonstrate that, in addition to risk proneness and risk aversion, a number of optimal intermediate variances can be selected for.

In contrast to predictions based on models that ignore the interaction between behaviour, population density and resource availability, our results show that high baseline mortality (e.g. predation risk) does not necessarily lead to risk proneness. In addition to this novel finding, our model confirms the crucial importance of resource-independent (baseline) mortality for optimal risk-sensitive behaviour.

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Early models of optimal foraging theory often only account for mean values of, for example, energy content (Stephens & Charnov 1982; Pyke 1984). Variance and its effects on a forager's decisions were not incorporated. Yet, evidence soon began to accumulate that resource variance (often termed risk) influences foraging decisions in a majority of species (e.g. Caraco 1980; Kacelnik & Bateson 1996; Hurly & Oseen 1999; Mathot et al. 2009). This led to the development of risk-sensitive foraging theory (RSFT). A large number of RSFT models focus completely on foraging for survival, that is, include only one so-called starvation threshold above which an animal is able to survive (e.g. Charnov 1976; Real 1981; Stephens 1981; Stephens & Charnov 1982; Houston & McNamara 1985). Animals are predicted to choose a high variance food option (risk-prone behaviour) when mean foraging success lies below the survival threshold. In the opposite situation, risk aversion (choice of the low variance food source) is predicted. As a further development, the internal state (i.e. energy reserves) of an animal was

taken into account (state-dependent models, e.g. McNamara et al. 1991; Merad & McNamara 1994). Depending on energy reserves and the time remaining to forage these models usually predict risk-prone or risk-averse behaviour.

Evidently, foraging for survival is an important component of animal behaviour. This is especially obvious in seasonal environments with high winter mortality. Yet, foraging decisions should be based not only on an animal's need to survive but also on reproductive constraints. Then it is immediately clear that this additional assumption, that is, a reproductive energetic threshold, can completely change predictions of foraging behaviour (e.g. McNamara et al. 1991). Subsequently, Hurly & Oseen (1999) introduced the idea of a twin threshold model (presented in Hurly 2003). Of course, species living in seasonal environments may adapt their foraging strategy accordingly (i.e. context dependence). Note that here, we take into account neither seasonality nor context dependence. The influence of foraging strategies on population dynamics and vice versa has been largely ignored both theoretically and experimentally. Recently Pen & Weissing (2000) underlined the importance of including this aspect, that is, density dependence, into behavioural models. A similar notion can be found in Trainor & Caraco (2006): these authors analysed the influence of foraging group sizes on population dynamics.

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Up to now, most models of risk-sensitive foraging have focused on the influence the environment has on the behaviour of individuals and have completely ignored the influence of individual behaviour on the environment and the resulting feedback on the individual. It is reasonable to assume that the amount of available resources in a habitat is finite. Therefore, the size of a population is restricted to a certain carrying capacity. When a population has reached a steady state the amount of resources available per capita will be exactly sufficient to balance reproductive output and mortality. Whenever an individual foraging behaviour has an influence on the amount of resources required at population equilibrium, this behaviour will modify the species' carrying capacity. Such behaviour is under intense selection pressure since an increase in carrying capacity is favoured by natural selection in constant environments, as Lande et al. (2009) recently confirmed. Traditionally, this is known as *K* selection (see MacArthur 1962; MacArthur & Wilson 1967; Boyce 1984).

In the following, we present a model of a population foraging in an environment with limited resources. We assume a fixed individual foraging strategy, which determines the variance in foraging success, while the population size determines the mean foraging success. Individual foraging success, on the other hand, determines the individual mortality and the reproductive output. Our model enables us to make predictions about the evolutionarily stable risk-sensitive foraging strategy at the population level.

MODEL DESCRIPTION AND RESULTS

A Simple Model

Our considerations are based on a discrete time model of population dynamics. During one time step (reproductive period) an individual may die with a certain probability (μ) and produces a certain number of offspring (ϕ , fertility). Thus, population growth (r) is determined by the specific rate of population increase

$$r(x) = \phi(x) - \mu(x). \quad (1)$$

We assume that mortality and reproduction are both dependent on the amount of resources (x) acquired by an individual. In an environment of constant, limited productivity, food supply (x) per individual will decrease with increasing population size and the population will eventually reach equilibrium when the number of births equals the number of deaths and the specific rate of population increase (equation (1)) approaches zero

$$r(\hat{x}) = \phi(\hat{x}) - \mu(\hat{x}) = 0. \quad (2)$$

This implicitly determines the amount of resources available to an individual at equilibrium (\hat{x}) in a constant, spatially homogeneous environment. Note that since we suppose a steady state, that is, population equilibrium, it is irrelevant whether we assume the specific rate of population increase (r) to be zero or the basic reproductive number (R_0) to be one (Mylius & Diekmann 1995). Although our reflections are based on a dynamic model of population growth in discrete time we are exclusively interested in the stationary state when reproduction balances mortality (equation (2)). We thus assume a population (of stable size) that has reached its carrying capacity. Our focus lies exclusively on resources and on evolutionarily stable optimal foraging strategies at the population level.

Fertility and Mortality

We assume a sigmoid relation between the number of offspring produced (fertility, $\phi(x)$) and individual resource intake (x). Such

a functional relationship is a simple description of the fact that, on the one hand, below a certain amount of resources no significant reproduction is possible and that, on the other hand, the number of offspring produced by an individual cannot increase infinitely. This is plausible for a wide range of animal life histories and is a common assumption in models of risk sensitivity (for recent examples see e.g. Kuznar 2002; Nevai et al. 2007):

$$\phi(x) = \frac{F_{\max}}{1 + e^{a_F \cdot x + b_F}} \quad (3)$$

with $a_F = \frac{-4 \cdot s_F}{F_{\max}}$ and $b_F = -a_F \cdot o_F$. This transformation allows us to use readily interpretable biological terms instead of a_F and b_F to describe the sigmoid fertility function. This function is completely described by the maximum fertility (F_{\max}), the slope (s_F) in the inflection point and the X axis offset (o_F) of the inflection point. For $x \rightarrow 0$ fertility approaches zero, that is, a certain amount of resources is needed to produce offspring. With increasing resources (x) fertility increases until an upper limit, the maximum fertility (F_{\max}), is reached. s_F is inversely related to the costs of offspring production. The influence of this specific implementation is discussed in detail below.

For the sake of simplicity we first assume a constant, resource-independent mortality (e.g. predation):

$$\mu(x) = M_b. \quad (4)$$

Later on we relax this assumption and incorporate resource-dependent mortality.

Variability in Foraging Success

We assume a fixed individual feeding strategy (σ) which determines the individual variance (risk) in resource intake. Thus, individuals with a high value of σ are risk-prone and individuals with a low value are risk-averse.

As pointed out above, the acquired individual resource mean across all individuals in the population (\bar{x}) is determined by the environment (i.e. amount of all available resources) and, since we assume that resources are limited, influenced by the population size. Evidently, this introduces density dependence in the amount of resources available per capita. In addition, we assume that the focal population has reached its equilibrium size. This is captured in our equilibrium assumption (equation (2)), that is, that the resource-dependent specific rate of population increase is zero.

If the population's risk-sensitive foraging strategy was $\sigma = 0$, that is, absolute risk aversion every individual would receive exactly \hat{x} resources (equation (2)). Yet, as soon as $\sigma \neq 0$ we have to introduce a distribution of resources. To simplify, we do not assume a probability density function with mean \bar{x} and variance σ , but just two possible outcomes of foraging activity. An individual either finds more food than the average ($\bar{x} + \sigma$) or, with equal probability, finds less than the average ($\bar{x} - \sigma$). The variance in foraging success is determined by the individual feeding strategy (σ). This does not change the fact that higher values of σ indicate more risk-prone foraging strategies. For this simplified type of a risk-sensitive foraging strategy the equilibrium condition (equation (2)) becomes

$$r(\tilde{x}, \sigma) = \phi(\tilde{x} + \sigma) + \phi(\tilde{x} - \sigma) - \mu(\tilde{x} + \sigma) - \mu(\tilde{x} - \sigma) = 0. \quad (5)$$

From equation (5) it becomes clear that actually the mean amount of resources available to an individual at population equilibrium (\tilde{x}) is a function of the foraging strategy ($\tilde{x} = \tilde{x}(\sigma)$), that is, as pointed out in the Introduction, the foraging strategy feeds back on resource availability. Note that \hat{x} is a special case of \tilde{x} for $\sigma = 0$.

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