

Risk-sensitivity revisited: from individuals to populations

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Abstract

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 imperatively 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.

Keywords: baseline mortality, density-dependence, foraging, optimal variance, risk-sensitivity

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Introduction

Early models of optimal foraging theory (OFT) 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, soon evidence 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, i.e. 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 is to lie 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 not only be based on an animal's need to survive but also on reproductive constraints. Then it is immediately clear that this additional assumption, i.e. 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 will neither take into account 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, i.e. density-dependence, into behavioural models. A similar notion can be found in Trainor & Caraco (2006): these authors analyse the influence of foraging group sizes on population dynamics.

Up to now, most models of risk-sensitive foraging have focused on the influence the environment has on the behaviour of individuals and 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 a behaviour is under intense selective 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 will 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 equal 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, i.e. 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 (see e.g. Kuznar 2002; Nevai et al. 2007, for recent examples):

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

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, i.e. a certain amount of resources is needed in order 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 will be discussed in detail below.

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

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

Later on we will 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 values for sigma 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), i.e. that the resource dependent specific rate of population increase is zero.

If the population's risk-sensitive foraging strategy was $\sigma = 0$, i.e. absolute risk-proneness, 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. In order 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 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 ($\tilde{x} = \tilde{x}(\sigma)$), i.e. — 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 $\sigma = 0$.

The influence of the risk-sensitive foraging strategy (σ) on the mean amount of resources available per individual at equilibrium (\tilde{x}) can thus easily be calculated by solving equation 5 for \tilde{x} . This was done numerically, see e.g. figure 1.

Of course, the assumption of a simplified bimodal resource distribution as implied in equation 5 is unrealistic. Yet, this allows us to derive model results in a much more accessible manner. The incorporation of continuous probability density functions in equation 5 to achieve a more realistic results will be discussed below.

Optimal risk-sensitive foraging strategies

If — in an evolutionary game — we introduce a mutant with strategy σ_m this strategy will be able to invade and, eventually, out-compete a resident population with strategy σ_r if the invator has a positive specific rate of increase (using equation 5; see equation 6) in an environment determined by the resident, i.e. for a mean resource supply of $x = \tilde{x}(\sigma_r)$:

$$r_m(\tilde{x}(\sigma_r), \sigma_m) > 0. \quad (6)$$

This condition is fulfilled whenever $\tilde{x}(\sigma_m) < \tilde{x}(\sigma_r)$. It is clear that at the individual level the quantity to maximize is the specific rate of population increase (equation 1). As we point out above (equation 2) at population equilibrium this quantity must equal zero. Then the appropriate approach usually is an invasion analysis. Yet, since our model does not include frequency-dependent effects an optimization approach — maximizing population size at equilibrium, i.e. K (Roff 2002) — is sufficient.

Thus, for our model, an alternative approach to invasion analysis is a maximization of the strategy specific carrying capacity or, as an equivalent, a minimization of the mean amount of resources required at population equilibrium ($\tilde{x}(\sigma)$). Note that a maximization of K (i.e. K-Selection, see MacArthur 1962; MacArthur & Wilson 1967) is not universally appropriate. This is especially true when the focal population has an age structure (for a detailed discussion see e.g. Roff 2002). As Charlesworth (1972) points out the decisive quantity to maximize is the size of the so called critical age group, i.e. the age group affected by density dependence (see also Caswell et al. 2004; Benton & Grant 2000). Recently, Lande et al. (2009) showed that an increase in carrying capacity is favoured by natural selection in constant environments. Since we assume a constant environment and no age structure it is admissible to maximize K , i.e. minimize $\tilde{x}(\sigma)$. In order to validate the results obtained from the optimization approach, we performed an equivalent evolutionary invasion analysis as sketched above (see equation 6). All calculations were performed using R 2.9.2 (R Development Core Team 2009).

First results: the effect of resource independent mortality

For our simple model (equations 3, 4 and 5) with resource independent mortality we can easily show that the optimal strategy depends on the curvature $r''(\hat{x})$ at the intersection point ($r(\hat{x}) = 0$) of the fertility and mortality functions (for a detailed deduction see Appendix: Derivation of results).

For this scenario only the two cases of either risk-prone ($r''(\hat{x}) > 0$; figures 1 a, b, c) or risk-averse behaviour ($r''(\hat{x}) < 0$; figures 1 d, e, f) are evolutionarily stable. This is true for all parameter combinations (see Appendix). For our choice of fertility and mortality functions a resident strategy (σ_r) that avoids any variance in resource supply ($\sigma_r = 0$) can only be out-competed by a mutant strategy σ_m with $\sigma_m > \sigma_r$ when baseline mortality is low ($M_b < \frac{1}{2}F_{max}$; for an example see figure 1 a, b, c). On the other hand, a resident risk-prone strategy (σ_r) will be out-competed by any other mutant strategy with $\sigma_m < \sigma_r$ when baseline mortality is high ($M_b > \frac{1}{2}F_{max}$; e.g. see figure 1 d, e, f).

Note that these results conform with the energy-budget rule using Jensen's inequality (e.g. Bednekoff 1996; Smallwood 1996). The risk-sensitive foraging strategy depends on the curvature of the fitness

function, a concave-up run ($r''(\hat{x}) > 0$) leading to risk-prone and a concave-down run ($r''(\hat{x}) < 0$) leading to risk-averse behaviour. The central difference between our model and the energy-budget rule is that we do not have to assume a certain energy state. Here, the mean amount of resources available per individual is implicitly defined by the population's strategy σ since we assume population equilibrium (equation 5).

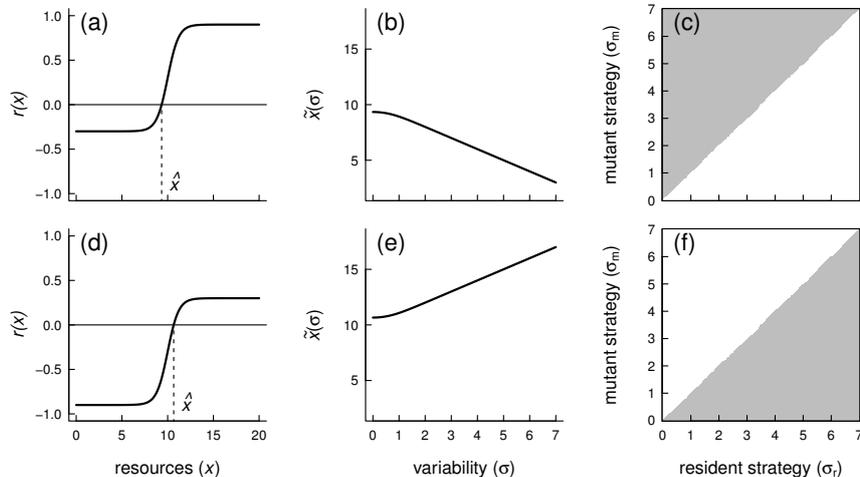


Figure 1: Relation between the amount of resources x acquired by an individual during a reproductive period and the specific rate of population increase $r(x)$ (a, d; see equation 1) and the influence of variation in resource supply (σ) on the mean amount of resources available per individual for a population at equilibrium ($\tilde{x}(\sigma)$; b, e). Results for a numeric solution of equation 5 with parameters $M_b = 0.3$ (a, b, c) or 0.9 (d, e, f); other parameters: $F_{max} = 1.2$, $o_F = 10$, $s_F = 0.5$. Panels c and f show pairwise invasibility plots (PIPs) for the same parameter combinations as panels b and e. Shaded areas indicate positive invader growth (see equation 6). Note that the results are identical: panel b suggests that the optimal strategy for $M_b = 0.3$ is risk-prone. This is confirmed by the PIP (panel c) which indicates that only high values of σ_r cannot be invaded. The opposite is true for $M_b = 0.9$, i.e. risk-aversion is evolutionarily stable (panels e and f).

A more complex model: resource dependent mortality

The results shown in figure 1 strongly depend on the symmetry of our fitness function (point-symmetry around the offset). With other fitness functions a broad spectrum of possible relations may result. To explore potential situations systematically we introduce a mortality function ($\mu(x)$) that is dependent on both, foraging success (x) and baseline mortality (M_b):

$$\mu(x) = \frac{1 - M_b}{1 + e^{a_M \cdot x + b_M}} + M_b \quad (7)$$

with $a_M = \frac{-4 \cdot s_M}{1 - M_b}$ and $b_M = -a_M \cdot o_M$. For $x \rightarrow 0$ this function approaches one, i.e. animals with a very low foraging success will die of starvation. For increasing x , mortality decreases in a sigmoid manner approaching a lower limit, the baseline mortality (M_b). In analogy to $\phi(x)$ the mortality function is completely described by its slope (s_M) in the inflection point, its offset (o_M) for the x-shift of the inflection point, and the baseline mortality (M_b).

As in our simplified setting presented above, we can derive $\tilde{x}(\sigma)$ for any point in parameter space (following equations A6a to A6c and A7a to A7c). Here again, we supplemented the results obtained through the optimization approach with with an equivalent evolutionary invasion analysis (see figure 2).

A systematic analysis revealed that only six qualitatively different relations exist between the risk-sensitive foraging strategy (σ) and the mean amount of resources ($\tilde{x}(\sigma)$) available per capita at population equilibrium (see figure 3). For any set of parameters the behaviour of the function $\tilde{x}(\sigma)$ can be completely described by its behaviour for vanishing variance ($\sigma \rightarrow 0$), intermediate (in the order of the difference $\sigma \sim (o_F - o_M)$) and very high variance ($\sigma \rightarrow \infty$) in resource supply. In these intervals $\tilde{x}(\sigma)$ can

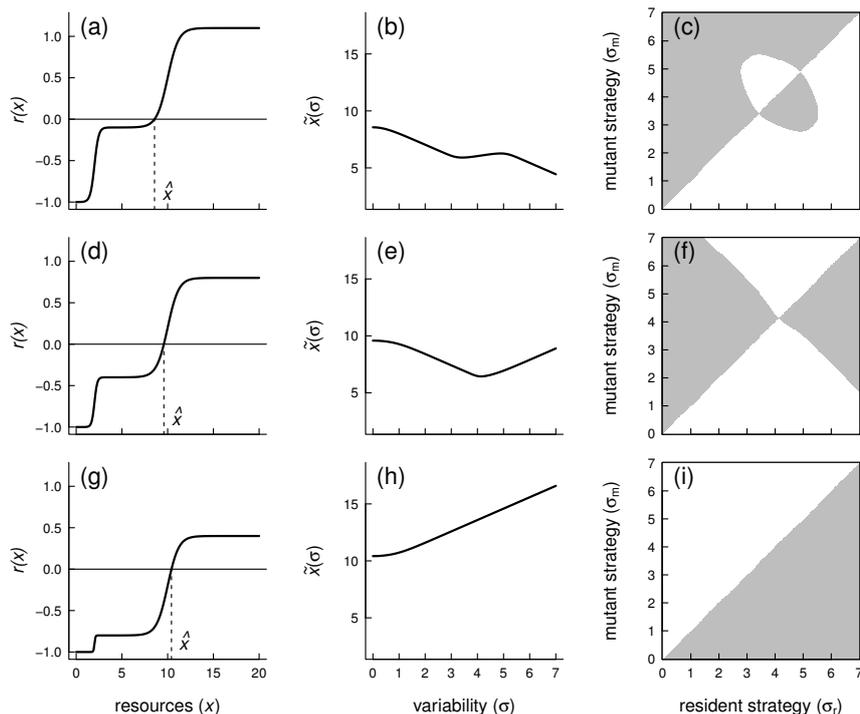


Figure 2: Relation between the amount of resources x acquired by an individual during a reproductive period and the specific rate of population increase $r(x)$ (a, d, g; see equation 1) and the influence of variation in resource supply (σ) on the mean amount of resources available per individual for a population at equilibrium ($\hat{x}(\sigma)$; b, e, h) for three different baseline mortalities (a, b, c: $M_b = 0.1$; d, e, f: $M_b = 0.4$; g, h, i: $M_b = 0.8$) while all other parameters are kept constant. Results for a numeric solution of equation 5 using equation 7 as mortality function: $F_{max} = 1.2$, $o_F = 10$, $s_F = 0.5$, $o_M = 2$, $s_M = -1$. Panels c, f and i show pairwise invasibility plots (PIPs) for the same parameter combinations as panels b, e and h. Shaded areas indicate positive invader growth (see equation 6). Note that as in figure 1 the results are identical. Panel b ($M_b = 0.1$) suggests a local intermediate optimum while the global optimum is risk-proneness. The PIP (panel c) confirms the global ESS to be risk-proneness and the existence of a local ESS with a corresponding repeller. Both panels e and f indicate the convergence stable ESS to be risk-intermediate for $M_b = 0.4$. Selection for risk-averse behaviour in panel h ($M_b = 0.8$) is confirmed by the corresponding PIP (panel i).

either increase or decrease (ignoring the limiting case of no change which does not change the biological interpretation of our results). Note that from our model derivation (see Appendix) it becomes immediately clear that a similar spectrum of results can already be obtained using a simple model with fixed mortality but an asymmetric fertility function, or with the symmetric fertility function given in equation 3 but a skewed probability distribution of resources.

A key result of our model is that the relation between the strategy-specific variance in foraging success (σ) and the resulting mean amount of energy available at equilibrium ($\hat{x}(\sigma)$) is dominantly influenced by baseline mortality (M_b) and maximum fertility (F_{max}). Whenever baseline mortality is high (compared to maximum fertility) strategies that increase variance in resource acquisition result in an increase in the mean amount of resources needed. Thus, high baseline mortalities favour the evolution of risk-averse behaviour (see figure 2 g, h, i and figure 3 row 4).

However, as figure 3 shows this is not universally true and has to be analysed in more detail: For low variance (σ) the mean amount of resources available in equilibrium ($\hat{x}(\sigma)$) will be an increasing function of σ whenever the condition $r''(\hat{x}) < 0$ holds, i.e. $r(\hat{x})$ has a concave-down run (figure 3 rows 4 to 6). When the offset (o_F) of reproduction is sufficiently larger than that of mortality (o_M) this condition can be simplified to $M_b > \frac{1}{2}F_{max}$. For high variance, on the other hand, the condition $M_b > F_{max} - 1$ must be fulfilled to support risk-averse behaviour (figure 3 row 4).

$r''(\hat{x})$	$r'(\tilde{x}-\sigma) - r'(\tilde{x}+\sigma)$	$F_{max} - M_b$	qualitative shape of $\tilde{x}(\sigma)$
> 0	< 0	> 1	
> 0	< 0 (solid) > 0 (dashed)	< 1	
> 0	> 0	> 1	
< 0	> 0	< 1	
< 0	> 0 (solid) < 0 (dashed)	> 1	
< 0	< 0	< 1	

Figure 3: Typical examples of the relation between the foraging strategy (σ) and the mean amount of resources available in equilibrium ($\tilde{x}(\sigma)$). Note that the evolutionarily stable strategy is the foraging strategy (σ) found at the minimum of $\tilde{x}(\sigma)$. Depending on the specific shape of the fitness function ($r(x)$) this relation may exhibit the six qualitatively different forms shown in the right column. a) The second derivative $r''(\hat{x})$ of the fitness function at the equilibrium point (\hat{x} , defined by equation 2) determines the slope of this relation for small variances in resource supply (first column; see also equations A7a to A7c). For concave-up fitness functions ($r''(\hat{x}) > 0$) the mean amount of resources required ($\tilde{x}(\sigma)$) will decrease with increasing variance, while it will increase with increasing variance when the fitness function is concave-down ($r''(\hat{x}) < 0$). b) For intermediate values of σ , the slope of $\tilde{x}(\sigma)$ is determined by the difference of the slopes of $r'(x)$ at $x = \tilde{x} + \sigma$ and $x = \tilde{x} - \sigma$ (second column; equations A6a to A6c). If the difference is positive ($\tilde{x} - \sigma > 0$) the mean amount of resources needed in population equilibrium ($\tilde{x}(\sigma)$) will increase with increasing variance in resource supply (σ); if it is negative ($\tilde{x} - \sigma < 0$) the opposite will hold. c) For sufficiently large variances in resource supply (σ) the slope of ($\tilde{x}(\sigma)$) is solely determined by the difference between maximum fertility (F_{max}) and baseline mortality (M_b) (third column; equations A8a to A8c). The difference determines whether mortality or fertility is limiting in population equilibrium. If the difference is small ($F_{max} - M_b < 1$) fertility is limiting and the mean amount of resources needed in population equilibrium ($\tilde{x}(\sigma)$) will increase with increasing variance in resource supply (σ); if it is large ($F_{max} - M_b > 1$) the opposite will hold.

An example for the strong influence of baseline mortality (M_b) on the relation between variance, i.e. foraging strategy (σ), and the mean amount of resources available in equilibrium (\tilde{x}) is shown in figure 2. For low baseline mortality ($M_b = 0.1$) our model predicts risk-prone behaviour while it predicts risk-averse behaviour for high baseline mortality ($M_b = 0.8$). With intermediate baseline mortality ($M_b = 0.4$) an optimum is predicted for intermediate values of the variance (σ) in resource supply. Note that in the low mortality case we found an intermediate optimum which is only locally evolutionarily stable, but not globally (figure 2 a, b, c). The general conditions under which such local optima may occur are defined in figure 3.

Continuous resource distributions

The results presented in figure 2 are based on our very simple model with variance in resource supply (σ) resulting from a simplified bimodal resource distribution yielding either $\tilde{x} + \sigma$ or $\tilde{x} - \sigma$. Using a more plausible continuous resource distribution (i.e. gamma distribution) we tested whether or not the above described six possible functional shapes of $\tilde{x}(\sigma)$ are dependent on a specific type of distribution (for the derivation see Appendix). These tests revealed that the choice of probability distribution did not qualitatively change the predictions of our model (see figure 4).

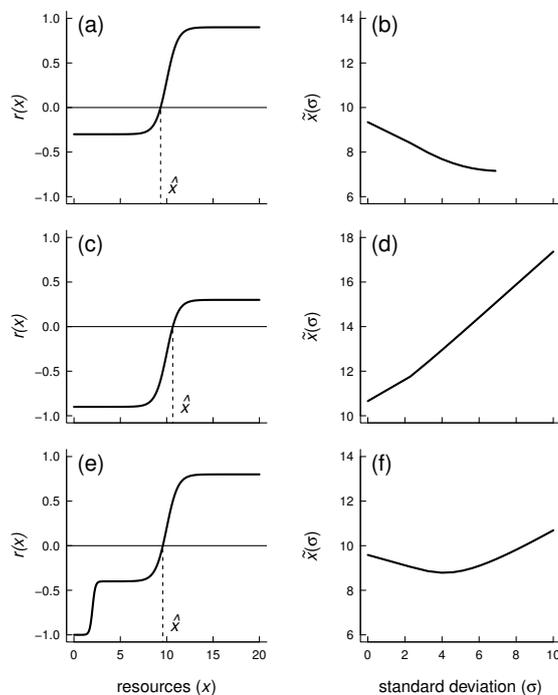


Figure 4: Relation between the amount of resources x acquired by an individual during a reproductive period and the specific rate of population increase $r(x)$ (a, c, e). Panels b, d and f show the influence of variation in resource supply (σ) on the mean amount of resources available per individual for a population at equilibrium ($\tilde{x}(\sigma)$) assuming a continuous resource distribution. Here, we use a gamma probability density function (see Appendix for the exact derivation). Panels a, b, c and d replicate the results from figure 1 (only resource independent mortality a: $M_b = 0.3$ and b: $M_b = 0.9$; $F_{max} = 1.2$, $o_F = 10$, $s_F = 0.5$). Panels e and f show results for the same parameters as used in figure 2 d and e (same as above except: $M_b = 0.4$, $o_M = 2$, $s_M = -1$).

As pointed out above, the decisive difference between our simple model with only resource independent mortality and the more complex model is the difference in symmetry of the resulting fitness function ($r(\tilde{x})$). This led to the occurrence of risk-intermediate strategies (see figure 2). Note that the asymmetry resulting from including resource dependent mortality (equation 7) could also be obtained by an asymmetric resource distribution. Every non-uniform probability density function would have this effect (see Appendix: Continuous resource distributions). This explains why a skewed distribution like the gamma

distribution may shift resulting risk-sensitive strategies quantitatively. Yet, figure 3 still holds for all unimodal resource distributions.

Discussion

To take into account the interaction between evolutionary dynamics and density-dependent population growth we combined survival and reproduction in a single model. Although it is clear that individual foraging strategies feed back on population dynamics and thus — in a world with limited resources — on resource availability, animal behaviour is rarely viewed in a population context. Most models only including either mortality (see e.g. Charnov 1976; Stephens & Charnov 1982; Houston & McNamara 1985) or fertility (Bednekoff 1996; Poethke & Liebig 2008) and thus have to explicitly specify either resource availability or the internal energy-state of the focal individual. Our model is based on the assumption of a steady environment and population equilibrium. Thus, resource availability is an emergent property and the behaviour modelled is not context-dependent. Since the environment (i.e. resource availability) is assumed to be constant the behaviour modelled here is not flexible but a fixed life-time strategy. In addition to this and in contrast to the threshold models of Schmitz & Ritchie (1991) and Hurly (2003) we use continuous functions to describe mortality and fertility which makes our model general enough to be applied to wide range of possible life-histories.

The results of our model analysis clearly demonstrate that risk-sensitive foraging strategies cannot exclusively be classified as risk-averse or risk-prone (Caraco 1980; Stephens 1981; Young et al. 1990). Already our rather simple sigmoid mortality and fertility functions lead to a spectrum of behavioural rules represented by six qualitatively different functional relationships between variance in resource supply (σ) and the mean per capita amount of resources available in equilibrium (\bar{x}). Beside risk-averse and risk-prone behaviour, optimal risk-intermediate behaviours can be explained with our model.

With their model of diet choice Schmitz & Ritchie (1991) reached a rather similar result. However, these authors ignored population size — and therefore density-dependence — but assumed a specific relationship between the mean and variance in energy intake as a function of diet breadth. By contrast, our model does not make any assumptions concerning the mechanism of variance manipulation. It would be valid for the case of diet choice as well as for variance manipulation achieved through group formation. In the latter case, forming an egalitarian group would reduce variance (among many others Caraco 1981; Caraco et al. 1995; Clark & Mangel 1986) while forming a group with reproductive skew would raise variance for each single group member (e.g. Poethke & Liebig 2008), respectively.

Risk-intermediate behaviour as predicted by our model has been observed in free living hummingbirds (Hurly & Oseen 1999). In a two threshold model Hurly (2003) attempted an explanation which resulted in a quite complex model that mainly suffers from a rather arbitrary fitness model.

McNamara et al. (1991) outlined the immense importance of baseline mortality for predicting foraging strategies. Our results confirm their assessment. As shown in figure 2, different baseline mortalities may completely change the predicted optimal risk-sensitive foraging strategy even when all other parameters are kept constant. It would be interesting to test this prediction by comparing whether or not animals with comparable life-histories, but adapted to different baseline mortalities (e.g. predation pressure), exhibit the predicted foraging strategies. However, in contrast to the findings of McNamara et al. (1991), we found that high baseline mortalities do not necessarily increase the range of risk-prone behaviour. For most life-history parameters, high baseline mortality leads to risk-averse behaviour or to the choice of a strategy yielding an optimal intermediate variance in resource supply. Quite contrary to the prediction of McNamara et al. (1991), our model shows that animals should never be risk-prone if baseline mortality (M_b) surpasses a critical value ($M_b > F_{max} - 1$). As summarized in figure 3 risk-prone behaviour cannot be evolutionarily stable in these cases because such a behaviour would lead to an increase in the amount of resources needed to balance mortality and reproduction, i.e. a decrease in carrying capacity, so that risk-averse or intermediate strategies can invade.

Our model and its predictions could be readily tested e.g. in the context of group formation. Well explored taxa can be found among social spiders (see above). As outlined above risk-sensitivity, in this case group size, could be correlated with e.g. predation pressure. Such an analysis would allow to test our predictions concerning the effect of baseline mortality. Similar correlative studies can be done with other life-history (fertility, costs of offspring production) or environmental parameters (variance in resource supply). For an extension of our model to the formation of egalitarian groups and a more comprehensive

discussion of this issue see Fronhofer et al. (in press).

In our model we did not differentiate between male and female behaviour and implicitly assumed that resource dependent mortality as well as fertility are the same for both sexes. However, it is most probable that particularly the influence of resource supply on the expected number of offspring differs between males and females (for a discussion on the role of males for population dynamics see Rankin & Kokko 2007). In polygynous species the expected offspring production of well fed males may easily surpass that of equally well fed females. In such a situation feeding strategies of males and females may be different. Nevertheless, as population dynamics are only influenced by female behaviour our model will still be valid for females. For males on the other hand mean resource supply will be determined by female behaviour.

Of course, we do not model population dynamics, but assume a steady state with a population at equilibrium. This assumption implies strong K-selection. Evidently, in populations which have not reached their carrying capacity other evolutionary forces may act: in empty habitats individuals usually experience strong r-selection, which is not covered by our model. Since in such cases resources are not limited which leads to high energy budgets risk-averse behaviour should be selected for (Bednekoff 1996; Smallwood 1996). Expanding our model to a metapopulation perspective characteristically including patch turnover and dispersal would allow to take into account both evolutionary forces. Such an approach could lead to a coexistence of two distinct (respectively r- and K-) strategies.

With the approach presented above we introduce density-dependence into a model of risk-sensitive foraging. This allows us to shift the focus from individuals to populations, a step that has never been done before. The results of our optimization approach — validated by an evolutionary invasion analysis — show that density-dependence and therefore population dynamics may drastically change model predictions. This has important implications for our understanding of animal behaviour which is usually observed in the context of a population.

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Appendix

Derivation of results

To decide whether an increase of variability (σ) will increase or decrease the mean amount of resources available at equilibrium (\tilde{x}) we analyse situations with very low and very high variance. Whenever a change in behaviour increases the variability in resource supply (σ) by an infinitesimally small amount $|d\sigma|$, food supply in the bad situation will become

$$\tilde{x} - \sigma - d\sigma_1 \tag{A1}$$

and in the good situation

$$\tilde{x} + \sigma + d\sigma_2. \tag{A2}$$

The total increase in variability (σ) will be

$$d\sigma = d\sigma_1 + d\sigma_2. \tag{A3}$$

To satisfy the equilibrium condition (equation 5) $d\sigma_1$ will not necessarily equal $d\sigma_2$. Thus, restricting our analysis to equilibrium links changes of $d\sigma_1$ to changes of $d\sigma_2$. Both will depend on the steepness $\frac{dr(x)}{dx}$ of the fitness function at $x = \tilde{x} - \sigma$ and $x = \tilde{x} + \sigma$. Based on equation 5 we can write

$$d\sigma_1 \cdot \left. \frac{dr(x)}{dx} \right|_{\tilde{x}-\sigma} = d\sigma_2 \cdot \left. \frac{dr(x)}{dx} \right|_{\tilde{x}+\sigma}. \tag{A4}$$

This allows calculating the change in \tilde{x} resulting from increased resource variability

$$d\tilde{x} = \frac{d\sigma_2 - d\sigma_1}{2}. \quad (\text{A5})$$

Depending on the specific form of the fitness function $r(x)$ three qualitatively different situations may occur:

$$r'(\tilde{x} - \sigma) < r'(\tilde{x} + \sigma) \Rightarrow -d\sigma_1 + d\sigma_2 < 0 \Rightarrow \frac{d\tilde{x}(\sigma)}{d\sigma} < 0, \quad (\text{A6a})$$

$$r'(\tilde{x} - \sigma) = r'(\tilde{x} + \sigma) \Rightarrow -d\sigma_1 + d\sigma_2 = 0 \Rightarrow \frac{d\tilde{x}(\sigma)}{d\sigma} = 0, \quad (\text{A6b})$$

$$r'(\tilde{x} - \sigma) > r'(\tilde{x} + \sigma) \Rightarrow -d\sigma_1 + d\sigma_2 > 0 \Rightarrow \frac{d\tilde{x}(\sigma)}{d\sigma} > 0. \quad (\text{A6c})$$

For a constant resource supply σ approaches 0, \tilde{x} approximately becomes \hat{x} and equations A6a to A6c become

$$r''(\hat{x}) > 0 \Rightarrow \frac{d\tilde{x}(\sigma)}{d\sigma} < 0, \quad (\text{A7a})$$

$$r''(\hat{x}) = 0 \Rightarrow \frac{d\tilde{x}(\sigma)}{d\sigma} = 0, \quad (\text{A7b})$$

$$r''(\hat{x}) < 0 \Rightarrow \frac{d\tilde{x}(\sigma)}{d\sigma} > 0. \quad (\text{A7c})$$

On the other hand when variance (σ) of resources supply is extremely high the specific rate of population increase (r) will be determined by the mean of its minimum value ($r(\tilde{x} - \infty) = -1$) and its maximum value ($r(\tilde{x} + \infty) = F_{max} - M_b$). This yields the conditions for high variance (σ) in resource supply

$$F_{max} - M_b > 1 \Rightarrow \frac{d\tilde{x}(\sigma)}{d\sigma} < 0, \quad (\text{A8a})$$

$$F_{max} - M_b = 1 \Rightarrow \frac{d\tilde{x}(\sigma)}{d\sigma} = 0, \quad (\text{A8b})$$

$$F_{max} - M_b < 1 \Rightarrow \frac{d\tilde{x}(\sigma)}{d\sigma} > 0. \quad (\text{A8c})$$

It should be noted here that in real systems the amount of available resources cannot drop below $x = 0$ and baseline mortality (M_b) — as a probability to die during one reproductive period — cannot surpass a maximum value of $M_b = 1$.

Continuous resource distributions

The probability of collecting a specific amount of resources (x) during a defined time interval (here one reproductive season) can be described by a probability density function $P(x, \bar{x}, \sigma^2)$ with mean foraging success \bar{x} and variance σ^2 . Here, we will relax the assumption of a symmetric bimodal distribution as implied by equation 5. Since resources should always be positive we assume a gamma distribution with shape parameter k and scale parameter θ :

$$P(x, \bar{x}, \sigma^2) = x^{k-1} \frac{e^{-\frac{x}{\theta}}}{\theta^k \gamma(k)} \quad (\text{A9})$$

with $\bar{x} = k\theta$, $\sigma^2 = k\theta^2$ and γ as the gamma function.

In order to include $P(x, \bar{x}, \sigma^2)$ as a resource distribution we must extend equation 5 and integrate the fertility and mortality functions (equations 3 and 7) weighted with the resource distribution:

$$r(\tilde{x}, \sigma^2) = \int_0^\infty P(x, \bar{x}, \sigma^2) \cdot \phi(x) \cdot dx - \int_0^\infty P(x, \bar{x}, \sigma^2) \cdot \mu(x) \cdot dx = 0. \quad (\text{A10})$$

As for the simple bimodal distribution used above this equation can be solved numerically for \tilde{x} . Note that this approach works with any continuous probability density function.

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