

Representing mortality risk in mechanistic models

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Abstract

Mortality risk is a critical and complex component of individual fitness and individual-based ecology, especially when risk-avoidance behaviors are considered. Organisms are subject to multiple kinds of risk that can vary with habitat, time, individual state, individual activity and behavior, and population status. Yet risk is often represented very simply in models and there is little literature on practical ways to model its variation. In our experience, desirable characteristics of risk models include: (a) survival probability can vary with multiple variables of individuals, habitat, and other entities; (b) relations between survival and specific variables can be added or removed or modified without re-fitting the entire model; (c) relations between variables and survival can take different forms, including continuous and nonlinear functions and discrete values; (d) relations between variables and survival are easy to understand and fit to many kinds of data or assumptions; and (e) they can be calibrated by adjusting only one parameter. We review the terminology and conventions that ecologists often use to model risk, and provide a mathematical framework for modeling risk. For complex risks, we describe and illustrate a method with “survival increase functions” that each relate survival probability to one variable. These functions can have a different form for each variable and can each be based on different information. The multiple functions are combined into a single survival probability value that is easily calibrated. We discuss methods for evaluating survival increase functions, ranging from general field observations to controlled field experiments, knowledge and data on mechanisms driving survival, and even conceptual models of those mechanisms. This approach has proven practical for representing complex effects of multiple variables on survival probability in models that represent how individual behavior and fitness depend on risk.

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Introduction

Importance of risk to individual-based ecology

One of the greatest promises of individual-based ecology is the ability to incorporate more realistic mechanisms in our models, thereby making them more general and more capable. Mortality is, of course, an extremely important mechanism in ecology. Mortality is important not only because it is a fundamental driver of population dynamics but also because, as ecologists now widely acknowledge (e.g., Peacor and Werner 2001; Preisser et al. 2005; Verdolin

2006), it is a strong driver of behaviors that trade off risk and other elements of individual fitness such as growth and reproduction. The most general and non-controversial “first-principles” assumptions on which we can base models include that individual traits, including inherent behaviors, have evolved because they convey fitness, and that survival to reproduction is critical to fitness.

Representing how mortality risks vary (over space or time, or among individuals) is important for at least two kinds of model. First are models of the effects of changes that strongly affect risk; examples include land use changes and reintroduction of predators (both illustrated by Ganz et al. 2024). Second are models that include risk-avoidance behavior. If we want models to implement the assumption that behavior acts to increase fitness by avoiding mortality, the models must represent variation in mortality risk: model individuals cannot reduce risk if risk is the same in all places and at all times. Further, risk needs to vary at spatial and temporal scales relevant to behavior. If we model how animals select among habitat patches and how habitat selection varies seasonally, with patch selection dependent in part on predation risk, then we need to represent how risk varies among patch types and over seasons. If we want to model how animal behavior changes diurnally, then we need to represent how risk varies over the daily light cycle.

To address such purposes, individual-based ecology has the challenge of developing methods for quantifying how risk varies and for representing that variation in our models.

Conventional approaches to variation in risk

How individual-based models (IBMs) can represent behavior as fitness-seeking tradeoffs among risk, growth, and other elements of fitness has been addressed to some extent (e.g., chapter 5 of Grimm and Railsback 2005; Railsback and Harvey 2020), but there is little existing literature on general, mechanistic models of how risk varies with characteristics of habitat, time, and the individuals at risk. To get a general idea of how IBMs typically represent risk, we reviewed the IBMs in three recent volumes (499–501) of the journal *Ecological Modelling*, including the older models (published before 2009) described in the supplemental materials of Grimm et al. (2025). Of the 15 IBMs that included mortality, almost all represented multiple causes of mortality, e.g., unspecified “background” mortality and starvation when growth was low. However, only one (Anders et al. 2025) represented one cause of mortality that depended on multiple drivers: tree death from stress related to multiple climate variables, modeled via logistic regression on field data. We conclude that many IBMs represent mortality as multiple risks that each vary with a single variable, but few models explicitly represent how a risk such as predation depends on multiple variables.

While little of it addresses general, mechanistic modeling, there is extensive empirical literature on spatial and temporal variation in predation mortality and risk, especially in wildlife and livestock subject to predation by large carnivores (reviewed, e.g., by Prugh et al. 2019). Much of this literature uses statistical methods such as logistic regression on habitat variables observed where predation did and did not occur, to model how the probability of mortality varies (reviewed by Miller 2015). Other observational approaches are to (a) use tracking data on prey individuals and estimates of when they were killed to estimate predation risk in different habitat types (Ganz et al. 2024), (b) track the predators and observe predation

events (Gervasi et al. 2013), and (c) develop resource selection functions for both predators and prey to estimate how the probability of predators encountering prey varies with habitat (Hebblewhite et al. 2005; Hebblewhite and Merrill 2007).

Such observational study methods and literature have limited value for the individual-based modeler. Studies that examine only mortality events cannot distinguish risk (as we define it below) from the confounding effect of prey exposure (the number of prey killed by predators is a function of both risk and number of prey). The literature and methods are generally limited to large terrestrial predators and prey, which are particularly easy to observe. Because these studies are purely empirical, their results are of questionable value for modeling other systems or novel future conditions. Observational studies also tend to have limited temporal resolution because it is generally difficult to determine precisely (e.g., between day, night, or twilight) when a predation event occurred. And these studies are of course expensive and time-consuming. However, observational studies provide valuable clues about general mechanisms (e.g., differences between wolves and cougars in predation success in dense vs. open habitat, and in willingness to hunt near humans; Atwood et al. 2009; Ganz et al. 2024).

Objectives and scope

Our objectives are to review concepts and mathematical methods that can be used to model how mortality risks vary over multiple dimensions in IBMs and other mechanistic ecological models. We specifically address models that treat one or more risks as explicit functions of multiple characteristics of habitat, individuals, or time. However, we do not address models in which mortality emerges from direct interactions among individuals, e.g., by representing adaptive predators or contagious disease spread.

We also discuss ways in which such methods can be supported by multiple kinds of information, from natural history knowledge, mechanistic understanding, and empirical experiments of several kinds. Our methods are especially applicable to systems and species for which reliable empirical information on risks is difficult to obtain, and for models that benefit from being more mechanistic and general because those characteristics make them useful for predicting responses to novel conditions under which strictly empirical representation of risk would be unreliable.

We focus, but not exclusively, on predation risk to mobile animals that use risk avoidance behaviors such as selecting when and where to feed. Our experience is primarily with modeling salmonid fish, specifically the “InSTREAM” family of IBMs for predicting effects of river management on trout and salmon populations (e.g., Railsback and Harvey 2002; Railsback et al. 2023). These models represent multiple kinds of mortality that are affected by managed variables such as flow and temperature. Simulated risks include two kinds of predation, starvation and disease, and extreme temperatures. Reliably modeling how such risks vary with habitat and among individuals is essential for understanding how management affects individual behavior and fitness and, therefore, population dynamics. InSTREAM assumes individual fish select when and where to feed (or hide) as an adaptive tradeoff between risk and growth (Railsback et al. 2020). However, the methods we present are also applicable to other kinds of risk such as disease, human harvest, and extreme weather or habitat conditions.

The methods also seem useful for modeling such risks to plants as herbivory, lack of resources (water, light, nutrients), pest infestation, and disease.

Concepts

We begin by reviewing concepts we find important for understanding and modeling risk.

Terminology and mathematical conventions

Traditional equation-based ecological models (e.g., the Lotka-Volterra equations) represent mortality via a rate parameter d , the fraction of a population that dies within a specified unit of time (Haefner 2012). However, in an IBM mortality is not a population-level rate but an individual-level event: every time step, each individual either survives or dies. A very simple way to model mortality as an event is using the variable “risk” R as a probability of mortality within a specific time period. We can set the value of R by assuming it equal to an observed mortality rate, but it is important to remember that when we model mortality of individuals in this way, R is a probability, not a rate.

(Here, we generally assume 1 day as the time period. We also use “risk” as a general term for mechanisms that could cause mortality, e.g., the risk of heart attack. The context should make it clear when “risk” is used in this general sense or specifically as a probability of death, R .)

The term “mortality” also has general meanings—the phenomenon or rate of death among individuals—and a specific meaning, the death of an individual. Mortality of an individual is typically represented in IBMs as an event that occurs randomly with probability R of occurring within one time period.

Studies and models that explicitly represent both predators and prey often follow the convention (e.g., Holling 1959) of decomposing R into separate probabilities of (a) a prey individual encountering a predator and (b) the predator successfully killing the prey when an encounter occurs. Similar decomposition can be applicable to other kinds of mortality; disease, for example, is often represented via separate probabilities of exposure to, infection by, and succumbing to a pathogen. While such decomposition is helpful for understanding and quantifying some risks, here we do not include it when discussing predation because it is unnecessary when predators are not represented as explicit individuals.

Models can be simpler to describe and implement when mortality is represented via survival S , the probability of surviving a specific time period, so $S = 1.0 - R$. Under the very common (yet often unstated) assumption that mortality risk in any time period is independent of risk in adjacent periods, the probability of surviving any t time periods is simply S^t , which is especially convenient for models with time steps of variable lengths. Our trout model simulates four time steps representing the light phases of each day (Railsback et al. 2021); the length t (fraction of 1 day) of each phase varies with date. On each time step we model survival of each kind of mortality as a daily probability S_x , and then determine mortality each time step using S_x^t as the probability of surviving.

Modeling risk as a survival probability is also convenient because the probability of surviving multiple, independent, kinds of mortality (discussed below) is calculated simply as the product of the survival probabilities for each mortality type.

The importance of time in understanding risk

Even though we typically evaluate risk and survival as daily probabilities, understanding and making good modeling decisions requires thinking about risk over longer time periods. Seemingly minor differences in daily survival result in large differences over meaningful future periods.

The widespread misuse of the so-called “ μ/f rule” (or “ μ/g ”) provides a good example of the importance of time for understanding risk. Gilliam and Fraser (1987) derived, for a highly simplified system, that long-term fitness for an individual is maximized by selecting the behavior that minimizes the ratio of risk to food intake. Presumably because of its simplicity, this “rule” has been used to represent tradeoff decisions in a variety of models. When we think of daily probabilities and rates, the “rule” may seem reasonable—a small increase in risk, say 10%, is the price for a corresponding increase in food intake. However, when we think about future survival this tradeoff seems less reasonable. If risk is low, e.g., daily S is 0.998 so the probability of surviving for 30 days is 94%, a 10% increase in daily risk reduces the probability of surviving for a year by only 7%. But if risk is already high, e.g., $S = 0.98$, a 10% increase in risk reduces the probability of surviving for a year by 50%. The tradeoff of 10% gain in food for 10% increase in risk is a bad one when risk is already high and behavior should instead emphasize reducing risk. Looking at the long-term consequences of changes in risk makes it clear that the “ μ/f rule” cannot provide good tradeoff decisions across wide ranges of risk.

When estimating survival parameters for models, it helps to think about survival over a meaningful time period and then calculate the corresponding daily probabilities. For example, we might estimate that an animal in a particularly risky habitat has a 20% chance of surviving for a month. The corresponding daily survival is: $S = 0.2^{(\frac{1}{30})} = 0.948$. Another approach is to estimate a median survival time (t_m) and calculate daily survival probability from it: $S = 0.5^{(\frac{1}{t_m})}$.

Perceived vs. unperceived risks

In some models it is important to distinguish among risks that individuals do vs. do not perceive and respond to. Human harvest, vehicle collisions, disease, natural toxins, pollutants, and introduced predators are example risks that a modeler might assume animals are naïve about and do not avoid via behavior. Such risks can be represented by modeling them exactly as the other risks while assuming that the individuals do not consider them in risk-driven behaviors. For example, Ayllón et al. (2018) added angler harvest to a trout IBM in which individual trout select habitat to trade off growth and predation risk. The risk of mortality via angling was assumed to vary with trout size, season, and angling regulations, but that variation was not considered by model trout in their behavior.

Axes of variation in risk

Here we list some of the “dimensions” in which mortality risks can vary, ending with a summary of those dimensions in our salmonid models. These dimensions are variables or groups of variables that risks often vary over.

Type of risk

Risk types can include predation (including multiple types of predator, as considered below), disease, extreme weather or other habitat conditions, starvation or dehydration, and human-induced risks such as harvest.

Habitat

Many risks are affected by habitat conditions at various scales. For example, risk of wolf and cougar predation on ungulates can differ between open and forested areas (Atwood et al. 2009; Gervasi et al. 2013), and the availability of escape and concealment cover is important for many prey species. Some risks, such as extreme temperature, can be driven entirely by habitat variables.

Time

Some risks vary over time cycles from daily to seasonal and even multi-year. Temporal variation in risks is generally driven by lower-level mechanisms such as predator physiology and life cycles, and daily and seasonal light cycles, but it can be convenient to model such variation as time-driven.

Individual state

Risks commonly vary dramatically with characteristics of the model individuals. If classical ecological models address variation in risk, they typically do so by assuming predation risk decreases as prey size increases. In many real systems, however, the kinds of predators and risk change as prey proceed through their life cycles, and the relations between size and risk may not be simple. Often, different life stages are subject to quite different risks, in which case life stage can be the individual state variable with the most effect on risk.

Individual activity or behavior

Models that represent risk-avoidance behavior must represent the effects of behavior on risk. For example, a model that represents how individuals choose between feeding during day vs. night as an adaptive tradeoff between risk and food intake must represent how risk differs between feeding and alternative activities, during both day and night. (Ellsworth et al. 2024 provides an example empirical study of activity effects, showing that deer survival varied with the percentage of time devoted to vigilance behavior.)

Population status

Some risks can be subject to direct feedbacks from the local or global population status. Mechanisms of such feedbacks include (1) competition for predator avoidance habitat (hiding places), (2) attraction or prey switching by predators, and (3) cannibalism.

We illustrate these axes of variation in risk via Table 1, which lists the types of risk represented in our trout model for its two distinct life stages: eggs, and

Table 1. Axes of risk variation in the trout model of Railsback et al. (2023). For each of the model's two life stages, the types of risk simulated and the variables causing variation in risk are identified.

Life stage	Type of risk	Risk dimensions and variables
Eggs	Thermal stress and disease	Habitat: temperature
	Dewatering	Habitat: water depth
	Scour	Habitat: river flow
	Superimposition (displacement by another spawning female)	Habitat: area of spawning habitat Population status: number of spawners
Juvenile and adult trout	Thermal stress	Habitat: temperature
	Stranding	Habitat: water depth
	Starvation and disease	Individual state: length, weight
	Predation by terrestrial animals	Habitat: depth, velocity, light intensity ^a , distance to escape cover
		Time: light intensity ^a
		Individual state: length
		Individual activity: feeding vs. hiding
		Population status: availability of hiding cover
	Predation by fish	Habitat: depth, temperature, light intensity ^a
		Time: light intensity ^a
		Individual state: length
		Individual activity: feeding vs. hiding Population status: density of piscivorous adult trout

^aLight intensity depends on time of day (dawn, day, dusk, night) and water depth.

swimming juvenile and adult trout. We list the dimensions that each type of risk varies across and the variables used to represent that variation. The abundant literature on stream salmonid ecology provides empirical evidence for how each risk varies with each variable.

A mathematical framework for modeling risk variation

In this section we present one general framework for modeling variation in risk. It includes the steps of (1) identifying types of risk; (2) for each type, representing how survival depends on each of multiple variables; and (3) combining the effects of multiple variables into one survival probability value.

This framework differs from conventional approaches by letting us develop models of risk that are realistically complex, general instead of specific to a site or time, and supported by multiple kinds of information.

Step 1: Select types of risk

The first step is determining which types of risk to model separately. We assume that the modeler has carefully determined what risks need to be in a model to meet its intended purpose. "Pattern-oriented modeling" is a powerful strategy for doing so, thoroughly illustrated by Grimm and Railsback (2005, 2012). As Table 1 illustrates, we need to model risks separately if they are driven by different variables (e.g., thermal stress is driven by temperature while starvation and

disease are driven by an individual's weight relative to its length), or if they are driven by the same variables but in different directions (e.g., increasing depth makes a small trout less vulnerable to terrestrial predators but more vulnerable to fish predators). Another reason to separate risks into different types is to allow model results to indicate how much mortality was caused by each risk: if we want to observe how many simulated elk are killed by wolves vs. cougars, then we need to model these two predators separately.

There are of course costs of using more types of risk: more assumptions and parameters, and more computations. While traditional modelers associate more parameters with higher uncertainty, a more-resolved representation of risk could reduce uncertainty by supporting more realistic behavior and results and by making more empirical evidence useful for representing risk.

Step 2: Model survival of each risk

Next, for each type of risk we need to model how survival probability S varies with one or more selected variables. Selecting the variables that drive each risk is similar and related to the process of selecting types of risk: variables should be included if they are considered essential to the model's purpose or—via pattern-oriented modeling—essential for establishing the model's credibility. But a variable might be considered essential for a model only because it is a critical driver of risk.

We discuss four ways to model how S depends on selected variables, but focus on the third and fourth, which we find most useful and novel.

Statistical models

Above (**Conventional approaches to variation in risk**) we identify examples of studies that modeled risk statistically, from several kinds of data, and discuss limitations of such approaches. Logistic regression is an appealing analysis framework because it estimates how the probability of an event—mortality—depends on multiple variables. However, modelers must be aware of differences between observed mortality rates and the survival probability variables in their models, especially for models containing risk-avoidance behavior. A model parameter representing S in the absence of risk avoidance behavior might be poorly estimated by data on actual mortality events, because actual mortality rates depend on prey abundance and behavior as well as the underlying survival probability.

Estimated S for risk categories

If there are few types of risk and they vary over few variables that can all be treated categorically, variation in S can be modeled as a matrix (Table 2). The matrix simply contains values of S for each combination of risk and variable value. Those values are essentially model parameters that must be evaluated by the modeler. In cases where sufficient observations are available, values for such survival parameters can be estimated via calibration. For example, the parameters in Table 2 could be calibrated by running an elk IBM iteratively to find the values that cause the model to best reproduce observed rates of predation by wolves and cougars in the two habitat types.

Table 2. Example survival probability matrix. This simple example contains values of S for two kinds of risk (two predators) for prey (e.g., elk) in two habitat categories.

Predator \ Habitat	Forest	Meadow
Wolf	$S_{W \times F} = 0.98$	$S_{W \times M} = 0.985$
Cougar	$S_{C \times F} = 0.99$	$S_{C \times M} = 0.95$

Continuous univariate models of S

Risks assumed to depend on only one variable can be modeled as continuous functions that are either estimated from observations (as in Option 1) or designed by considering a variety of information. Such univariate functions could have any shape as long as they produce values between 0.0 and 1.0. We find two forms especially useful.

Logistic curves are useful for representing nonlinear effects of a variable on survival (Fig. 1), for several reasons. First, they produce S values (the Y axis) ranging from 0.0 to 1.0 as the driving variable (X axis) varies over its entire range. They are also good at representing variables that produce high and low survival over wide ranges but sharp changes in survival between those ranges, which are quite common. Finally, when the right kind of observations are available, logistic curves are readily fit to data via logistic regression.

The equation for a logistic function is:

$$Y = \frac{\exp(Z)}{1.0 + \exp(Z)} \quad \text{Eq. 1}$$

where Z is a function of the X value:

$$Z = A + (B \times X). \quad \text{Eq. 2}$$

We find it convenient to define A and B , and therefore the shape of the logistic curve, via two model parameters, $X_{0.1}$ and $X_{0.9}$, which are the X values that produce Y values of 0.1 and 0.9 (Fig. 1): $B = -4.3944 / (X_{0.1} - X_{0.9})$ and $A = -2.1972 - (B \times X_{0.1})$.

Because of the $\exp$ functions in equations 1 and 2, logistic functions are particularly vulnerable to variable overflow/underflow errors, which occur when the computer tries to produce a floating-point number larger or smaller than it can handle. The ranges of values causing errors depend on the software platform and sometimes the hardware. These errors can be avoided while providing the ability to evaluate logistic functions over wide ranges by adding code that sets Y to 1.0 when Z is greater than (e.g.) 35 (corresponding to $Y = 0.999999999999999$ in 64-bit Excel) and to 0.0 when Z is less than -200 (corresponding to $Y = 1.4\text{E-}87$).

Linear models of survival can be useful for chronic risks that persist over long times and cannot be alleviated rapidly. We use a linear model of how survival of starvation and disease depends on an individual's energy reserves, in models in which energy reserves can change relatively little in one time step. If we define an individual variable *energy-deficit* as the fraction by which energy reserves are below those of a healthy individual (so, e.g., *energy-deficit* = 0.2 means the individual's energy is 20% below a healthy value), we can model the

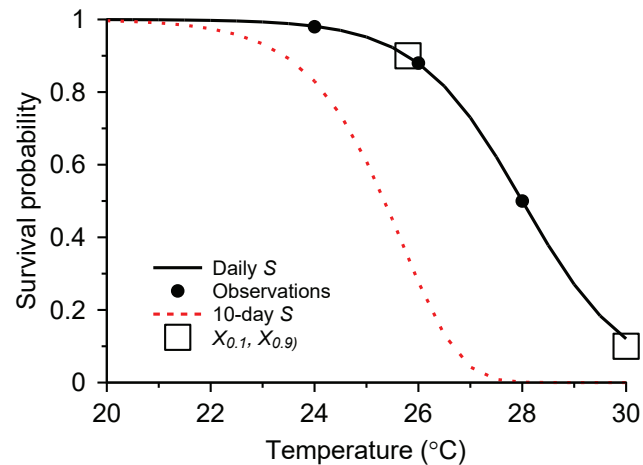


Figure 1. Example logistic curve for S , representing trout survival of high-temperature stress. The round symbols represent observations from two laboratory studies of daily survival at temperatures of 24, 26, and 28 °C. The solid curve is a logistic function fit to the three observations, the model of daily S . The square symbols indicate the two parameters that define the logistic curve: $X_{0.1}$ and $X_{0.9}$ are 30.2 and 25.8 °C. The dotted curve shows 10-day survival probability, equal to S^{10} .

daily probability of not starving S_s as linear: $S_s = 1.0 - (P_s \times \text{energy-deficit})$ where P_s is a parameter. Higher values of P_s cause survival to decrease more rapidly as energy decreases.

This kind of linear model produces a gradually decreasing probability of surviving prolonged periods of risk, e.g., when *energy-deficit* is constantly positive or increasing steadily due to constant weight loss (Fig. 2).

Univariate models can be fit to data, including data from multiple sources, or even to a set of assumed values. Both linear and logistic functions can be fit via regression when suitable data are available, and via other techniques when data are not suitable for regression. For example, the logistic parameters $X_{0.1}$ and $X_{0.9}$ illustrated in Fig. 1 were fit to the three observed survival rates by using Excel's Solver to minimize the sum of squared differences between observed and logistic-curve values.

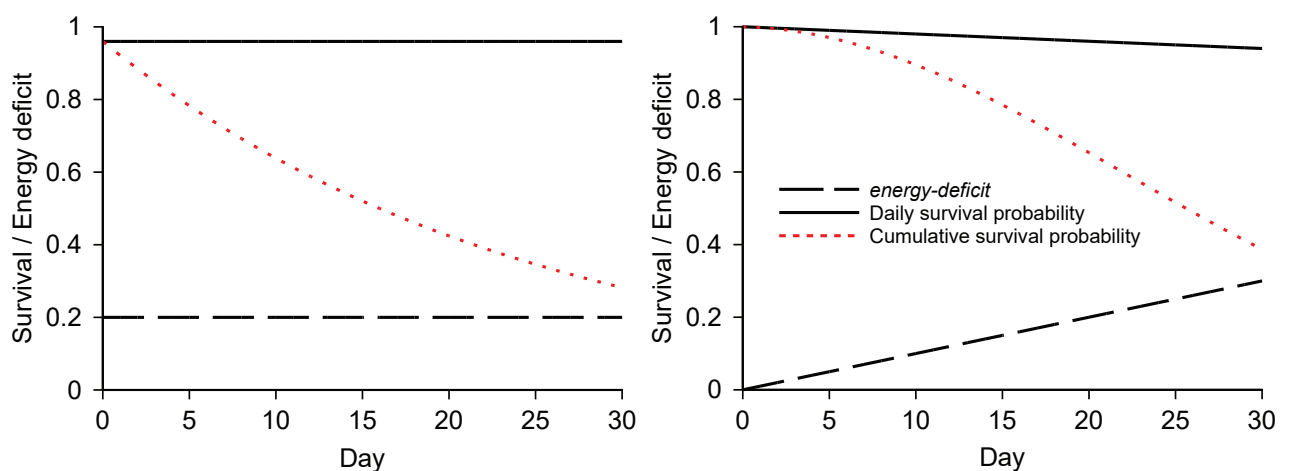


Figure 2. Example linear survival model, representing survival of starvation and disease S_s as a function of energy deficit. The solid lines indicate the value of S_s when P_s is 0.2, when *energy-deficit* (left) is constant at 0.2, and (right) starts at 0.0 and increases by 0.01 on each of 30 days. The dotted lines indicate the cumulative probability of surviving from day 0.

Multivariate models using “survival increase functions”

None of the previous three methods for modeling S have all of the following characteristics that we find essential for modeling some kinds of risk, especially predation:

- S can be modeled as a function of multiple variables (e.g., how a fish’s survival of predation by birds varies with fish size, depth, and light intensity);
- Variables can be added to the model, or the relation between one variable and S can be modified, without having to re-fit or re-calibrate the entire model of S ;
- The relations between variables and S can take different forms, including continuous and discrete relations (e.g., the effects of fish size and depth on predation risk are continuous functions but the effect of light intensity is represented as discrete values for day, night, and twilight);
- The value of S (i.e., the overall intensity of predation) can be calibrated easily by changing one parameter; and
- The relations between each variable and S are easy to see, understand, and fit to data or assumptions.

Simply fitting a multivariate equation for S would not provide these characteristics, so we developed the following method for modeling complex survival probabilities. It uses separate functions to represent the effect of each variable, with those effects then combined into a survival probability. As we discuss below, this approach assumes that variables driving S have independent effects.

First, we identify a minimum survival probability S_{min} , which is a model parameter. The value of S_{min} represents survival under the least-safe conditions.

Second, we estimate “survival increase functions” (SIFs) for each variable (of model individuals, their habitat, or anything else) that affects survival. The SIFs produce “survival increase” values that range from 0.0 to 1.0 and represent the degree to which the variable increases survival probability: a SIF value of 0.0 provides no increase in survival and a value of 1.0 makes the individual completely safe ($S = 1.0$). However, SIFs have no other limitations on their form or origin: each can be a different function type developed from different information.

The function types described above as univariate models of S are also useful as SIFs. Most of the SIFs we use are logistic curves, but we also use discrete functions to represent the effects of boolean (true-false) or categorical variables. For example, a SIF for use of hiding behavior can simply be: survival increase is 0.8 if the individual is hiding and 0.0 if not. A SIF for the effect of light on risk could simply be: survival increase is 0.0 in daytime, 0.6 during twilight, and 0.9 at night.

A SIF can also be modified so that its value never reaches 1.0—no values of its variable make individuals completely safe. For example, a model of predation survival could include a variable representing vegetation density, and assume that survival probability is higher when vegetation is denser but some predators can be successful in even the densest vegetation. We can model that effect with a SIF that uses a logistic curve limited to values less than 1.0; such a curve only requires one additional parameter for the maximum survival increase, which all logistic curve values are multiplied by.

Example SIFs (for the risk of terrestrial predators on trout) are illustrated in Fig. 3. The function for depth (panel A) is a logistic curve with $X_{0.1}$ and $X_{0.9}$ equal to 20 and 150 cm and a maximum value of 0.8: even trout in the deepest water are still vulnerable to diving predators such as otters and mergansers. Panel B is the length function, a logistic curve with $X_{0.1}$ and $X_{0.9}$ equal to 6 and 3 cm: very small trout are less visible and less valuable to predators, and the largest trout are still vulnerable to many predators. The light function is also a logistic curve, with $X_{0.1}$ and $X_{0.9}$ equal to 50 and -10 W/m²: only light levels at or below those characteristic of twilight reduce risk. The SIF for use of hiding cover (Panel D) is a discrete function: the survival increase value is 0.8 if a trout is hiding in concealment cover, and otherwise 0.0.

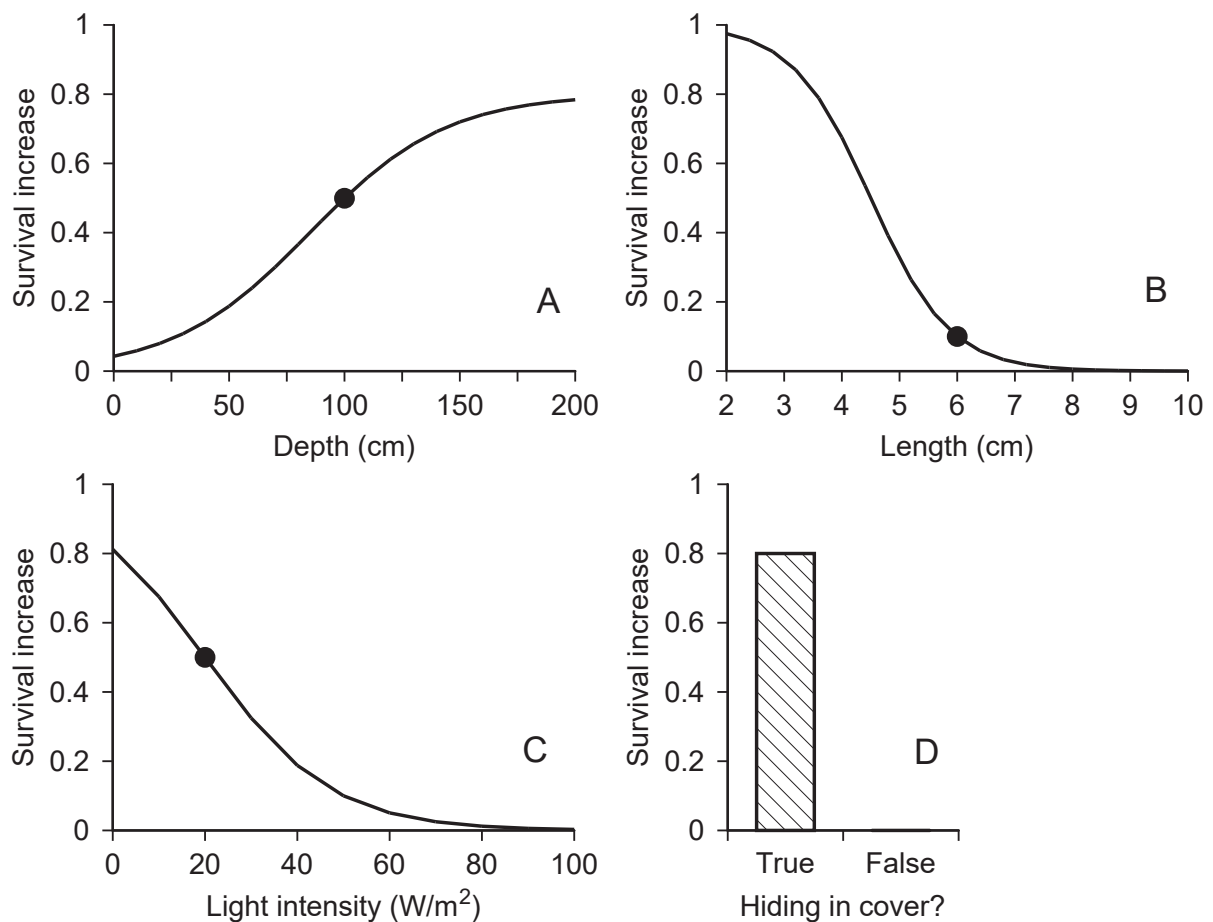


Figure 3. Example survival increase functions, for variables affecting terrestrial predation risk to trout in Table 1. The round symbols indicate survival increase values at (A) depth = 100 cm (survival increase = 0.5), (B) length = 6 cm (0.1), and (C) light intensity = 20 W/m² (0.5). Survival increase for fish hiding in concealment cover (D) is 0.8.

The third step is to combine the SIFs into a value of S , using a method (Railsback et al. 2023) in which each SIF contributes to reducing risk, so survival depends on all such variables. We model the interaction among SIF values (F_i where i indicates the functions, e.g., panels A–D in Fig. 3) by treating each F_i as a probability and calculating the joint probability of surviving all of them:

$$S = S_{min} + (1 - S_{min}) \left(1 - \prod_{i=1}^{i=n} (1 - F_i) \right). \quad \text{Eq. 3}$$

Using the example survival increase values of Fig. 3, the product term in Eq. 3 is: $(1-0.5)(1-0.1)(1-0.5)(1-0.8) = 0.045$. If S_{min} is 0.9, then $S = 0.9955$. Using this method, all the SIFs affect S but S is most sensitive to those with highest values (Fig. 4).

One limitation of this method is that it does not represent interactions among the ecological factors affecting risk, e.g., the relation between depth and S depending on the value of light intensity. Such interactions could of course be added to a model, if the benefits of additional realism appear to outweigh the costs of substantial additional model complexity.

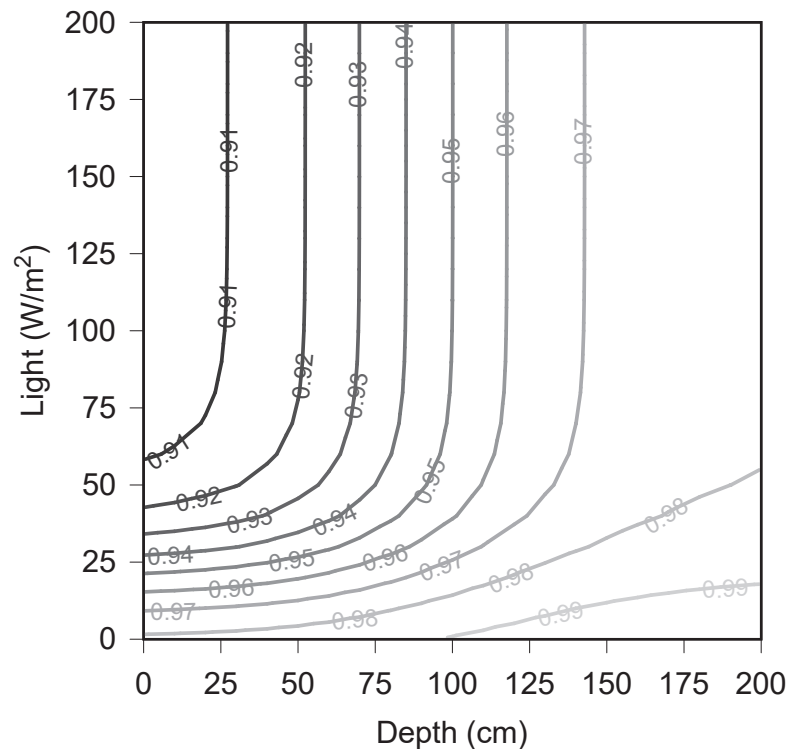


Figure 4. Example values of S from Eq. 3 when it includes the depth and light SIFs of Fig. 3. S_{min} is equal to 0.9. When light intensity is low, S is most sensitive to light; otherwise, S is most sensitive to depth.

The final step in using this method is to estimate a value for S_{min} . We typically do this via calibration of the full model, searching for S_{min} values that produce reasonable model results. In many models, values of such survival parameters are found by fitting results to observed or assumed values of abundance or survival rate. However, models with tradeoff behaviors that relate (e.g.) growth to risk may also produce growth and size results that also respond strongly to S_{min} . For such models, it may be necessary to calibrate S_{min} simultaneously with parameters that drive growth.

If a model includes more than one type of risk that uses this method for S (e.g., predation by terrestrial animals and fish, in Table 1), it may be possible to estimate each value of S_{min} relatively independently, if the two types of risks mainly affect different life stages or sizes of individuals. In our trout model, only juvenile trout are vulnerable to predation by other fish, so we can estimate S_{min} for that risk using observed juvenile survival rates, and then estimate S_{min} for terrestrial predators using overall population abundance.

Informing survival increase functions

The main advantages of the SIF approach is that it allows models of survival to make use of many kinds of data and mechanistic understanding. Each SIF can be based on the best information available for the relation it represents, whether that information is from field observations, controlled field or laboratory experiments, or only conceptual models. Observations of realized predation, such as those we reference in the Introduction, can inform estimates of habitat effects on predation risk after confounding factors are taken into account. However, here we focus on (a) field experiments designed to evaluate how risk varies along specific gradients and (b) use of information on mechanisms driving risk.

Field observations that contrast survival across relevant gradients in habitat or in the characteristics of individuals—on spatial and temporal scales relevant to the model in use—provide ideal information for building survival increase functions. Such observations are not common in the scientific literature, although the most feasible spatial and temporal scales for field experiments (e.g., a few square meters with trials of one day or less) are likely to align with the scales of many individual-based models. However, animals generally do not voluntarily occupy high-risk habitat, so enclosures or tethering (e.g., Harvey and Nakamoto 2013; Michel et al. 2020) may be necessary to obtain habitat-specific observations, and these methods should be applied with caution. For example, enclosures can affect relative risk across habitat gradients if they attract predators, while tethering experiments may better quantify predator encounter rates rather than risk per se, and also confound the effects of habitat or individual characteristics of prey (Baker and Waltham 2020).

An alternative to directly measuring risk is to quantify the prey's perception of risk or antipredator behavior. For a variety of reasons, the perception of, and responses to, predation risk by prey may not match actual risk (Gaynor et al. 2019). However, for individual-based modeling, the perception of risk may be as, or more, important information than actual risk by virtue of its influence on tradeoff behaviors (especially, habitat selection), while any mismatches between prey perception and reality may be negligible in the context of other uncertainties in model formulation. Prey responses to perceived predation risk are often complicated by trade-offs between risk and the need to obtain food. However, measurement of giving-up food densities (Brown 1988) exploits the risk:food trade-off to quantify the perception of risk. The general study design for this method is to create situations in various habitat types where a prey animal's food availability—and therefore, inversely, the risk incurred to feed—can be controlled, and determining the food density at which the prey “gives up” because further feeding is not worth the perceived risk. This method has been widely applied in some taxa, but its application faces a variety of challenges (discussed, e.g., by Bedoya-Perez et al. 2013 and Menezes et al. 2014) and it is not applicable to all taxa and settings. Measurement of giving up densities may be particularly challenging on the spatial and temporal scales relevant to many individual-based models. Use of apparatus to directly measure giving-up harvest rate may work better at smaller spatial and temporal scales (e.g., Harvey and White 2017).

In addition to direct measures of relative survival or the perception of risk by prey, we can use basic life history information and fundamental principles of physiology and ecology to identify specific mechanisms through which variables affect risk and then to evaluate SIFs that represent those mechanisms. This approach is highly dependent on the system being modeled; we illustrate it with examples from the trout predation relations identified in Table 1. Railsback et al. (2023) based the SIF for temperature effect on fish predation in part on laboratory data on how metabolic rates of predator fish (and, presumably, their food intake) vary with temperature. The SIF for prey size effect on fish predation was based on the “gape limitation” concept because fish swallow their prey whole. The SIF for effect of light intensity on fish predation was based in part on literature on how fish vision varies with light intensity but also the understanding that bigger fish have bigger eyes and better night vision, perhaps putting them at an advantage over prey fish in low light.

Conclusions

Survival is clearly a key ecological mechanism, not only because it directly affects abundance but also because risk-avoidance behaviors can have strong indirect effects on individual fitness. IBMs and other mechanistic models designed to address problems driven in part by survival therefore are likely to need realistic representations of how mortality risks vary. This need is especially strong for models that represent behaviors that trade off risk and other elements of fitness. We previously (Railsback and Harvey 2020) addressed modeling such tradeoff behaviors but did not explicitly address how to model variation in risk.

Understanding and modeling risk and its effects are challenging because animals (and plants) are subject to a variety of risks, and each kind of risk can vary with characteristics of the individuals, their habitat, their behavior, and interactions such as competition and cooperation. Risk is also challenging to model because observed mortality rates are not necessarily directly related to intrinsic predation risk. Observed mortality is instead often a complex outcome of intrinsic risk (e.g., predator density), risk reduction behavior, and population status. Disease mortality rates, for example, could be a function of pathogen distributions (the intrinsic risk), the energy available to individuals to fight infection, and the frequency of infectious interactions among individuals. Predation mortality rates can be a function of predator densities, predator avoidance behavior, and prey densities. Consequently, observed mortality rates—even if we know the cause of mortality—do not necessarily provide the information we need to model risk.

In our experience, the criteria for a useful multivariate model of survival probability listed above (**Multivariate models using “survival increase functions”**) are very important: to produce IBMs mechanistic enough to be reliable under diverse and novel conditions, without undue effort, we need approaches that let us model the effects of multiple variables, using different information and function forms for each variable, while the effect of each variable is easy to see and understand. The survival increase function method we propose meets those criteria and we expect it to be generally useful in a variety of models. However, we also expect that other modelers will develop useful alternatives.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

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Data availability

All of the data that support the findings of this study are available in the main text.

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