TAKING FEAR BACK INTO THE MARGINAL VALUE THEOREM: THE RISK-MVT AND OPTIMAL BOLDNESS

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ABSTRACT

Foragers exploiting heterogeneous habitats must make strategic movement decisions in order to maximize fitness. Foraging theory has produced very general and insightful formalizations of the optimal patch-leaving decisions rational individuals should make. One is the Marginal Value Theorem (MVT), which models the sequential visit of habitat patches and their spatial distribution, as encapsulated in the travel time, i.e. the average time it takes to move from one patch to another. The MVT has a simple intuitive graphical interpretation in terms of gain functions and travel times. However, it considers only energy gains, and the effect of predation risk on the time allocation strategy is notoriously lacking. An important development that includes predation risk was Brown's (1988) economic treatment of optimal patch leaving decisions, often cited as an extension of the MVT, and forming the basis of GUD theory. However, it is a more abstract result that does not have the specificities or graphical appeal of the MVT. Although both successful, the two theories are seldom connected; textbook presentations of the MVT typically do not cover Brown's developments, and reciprocally. Here we formally introduce the risk-MVT (rMVT), showing how the systematic introduction of the different possible types of risk into the original MVT yields generalized rMVT equations. Much of the graphical simplicity of the MVT is retained, provided one uses the appropriate risk-relative timescale, such as the micromort units used in decision analysis. Optimal strategies under the risk-MVT can be used to define the "optimal boldness" in a habitat. We show that Brown's GUD-theory is equivalent to a rMVT, but only for one particular possible definition of fitness. Reconciling the two theories could help behavioral ecologists take the best of two worlds.

INTRODUCTION

Optimal foraging theory has provided a rich framework to assess the behavior of individuals in the light of natural selection and adaptive evolution (Stephens and Krebs 1986; Begon et al. 1996; Mangel 2006). One very popular theory is the Marginal Value Theorem (MVT)(Charnov 1976). The latter applies to a broad range of situations where individuals must decide between exploiting further their current patch of resources, or leaving the patch in search of another one (Calcagno 2018). The MVT models an explicit dynamics of sequential patch visits, whereby movement bouts and patch finding are a prerequisite to patch exploitation. The process of finding a new patch necessitates some amount of time, called the travel time. Patch exploitation also takes time, and the accumulation of gains in a patch is captured by the so-called gain function. This function can have various shapes, but generally describes diminishing returns, caused for instance by the gradual depletion of local resources . From a set of constraints imposed by habitat characteristics (spatial distribution and intrinsic values of resource patches), the MVT predicts the optimal time individuals should exploit a patch before leaving in search for another one (or giving-up time; GUT), and the fitness would be achieved in this habitat. The MVT thus connects local instantaneous decisions (when to leave a patch) to global properties of the habitat that can, at least in principle, be independently measured and manipulated. This coupling is best captured by the famous graphical solution of the homogeneous MVT, often presented in articles and textbooks (Parker and Stuart 1976; Stephens and Krebs 1986; Mangel 2006).

Although the MVT makes many simplifying assumptions, whose implications have been extensively discussed, its great simplicity probably underlies its sustained appeal. Nonetheless, a major limitation of the MVT is that it considers resource acquisition only, omitting the potential risks inherent to foraging, such as predation risk (McNamara and Houston 1987; Calcagno 2018). This is quite problematic as for many taxa predation risk is a fundamental aspect of foraging: individuals can suffer attacks from predators and be perturbed by them in several ways, including death (Brown et al. 1999; Preisser et al. 2005). Foragers are sometimes better off disregarding resource-replete patches if these are too risky, or conversely tolerate predation risk in order to satisfy energy requirements McNamara and Houston (1987).

To address this shortcoming, another popular theory addressing patch-leaving decisions, usually called GUD-theory, was introduced by Brown (1988). Just like the MVT, GUD theory considers patchy habitats and predicts when individuals should leave a patch, based on marginal rates. Because of this similarity, the two theories are sometimes used more or less interchangeably regarding optimal patch leaving decisions. Still, they have significant differences. In particular, Brown's theory characterizes an instantaneous decision at a particular point in time: at any time, the individual is seen as choosing between alternative activities, characterized by marginal gains or costs, with no need to specify what the activities are or imposing that some must be performed sequentially. It does not explicit how the different marginal rates arise from global habitat characteristics. In this respect, Brown's theory is more general, and more abstract, than the MVT: it is a general description of the (local) mathematical properties of an optimal strategy. Regardless, the recognition that risk plays a role in shaping patch utilization patterns, and the possibility to include predation risk in foraging theory, was a major improvement brought forth by Brown's (1988) theory, and the cause of its popularity.

Both theories have proved very successful, and both continue to serve as bases for further developments (Charnov and Parker 1995; Calcagno et al. 2013, 2014; Pacheco-Cobos et al. 2019; Arehart et al. 2023). As of May 2023, Charnov's 1976 article had been cited 3,485 times and Brown's 1988 article 1,031 times, according the Scopus citation database

(Fig. 1; see Supporting Information). This makes them some of the most cited papers in behavioral ecology and animal behavior ever, a remarkable achievement for theoretical pieces. Charnov's 1976 publication is now regarded as iconic by its publishing journal (Rosenberg 2020). Both articles continue to be abundantly cited, at remarkably similar paces, their relative rate of citations quite stable over the past 20 years (Fig. 1a). The two theories thus appear to have reached some form of steady coexistence, but this coexistence does not imply much coalescence. Indeed, textbook treatments of the MVT often do not cover Brown's developments (Begon et al. 1996; Westneat and Fox 2010), and reciprocally GUD-theory typically regards the MVT as an earlier step no longer to be considered in itself (Morris and Davidson 2000). In the literature, the two theories are generally not cited by the same articles or by the same authors (even though they are cited in similar journals; see Fig. S1). The relative overlap of their citing articles or citing authors, as quantified by Sorensen index, never exceeded a low 15% and are on a downward tendency (Fig. 1b), suggesting some divide in the community.

We seek here to unify these two sister theories of patch-leaving decisions, by introducing the concept of risk into the original MVT. We first show that the MVT can readily accommodate fear effects and mortality risk, while retaining much of its predictive power and graphical appeal, proposing what we call the risk-MVT (rMVT). We then formally highlight the connections between this rMVT and Brown's theory. We conclude with some simple predictions that can be derived from the rMVT. Our purpose is not to comprehensively study the consequences of risk on rMVT predictions, but to suggest a way to have the "resource acquisition" and "fear" perspectives of patch-leaving decisions reconciled in a single framework.

MODELS AND METHODS

Charnov's original MVT

In its general form allowing for heterogeneous patch characteristics in space (e.g. different resource levels; Calcagno et al. (2014)), the MVT can be stated as

$$F_i'(t_i^*) = \frac{\langle F_j(t_j^*)\rangle}{T + \langle t_j^*\rangle} = E_n^* \quad \text{for i in 1...s} \tag{1}$$

where s is the number of different patch types in the habitat, and brackets denote averages over all patches (Calcagno et al. 2013). F_i is the gain function in a patch of type i and T is the average travel time, i.e. the time needed to move from one patch to another. Prime denotes differentiation with respect to time.

The optimal residence times t_i^*, obtained as solutions of eq. (1), maximize the individual fitness, specifically the long-term average rate of gain E_n^* (Charnov 1976). It follows the well-known result that patches should be left when the marginal rate of gain falls to the long term average of gain in the habitat (E_n^*), and the often-used graphical solution involving a tangent line (Parker and Stuart 1976; Stephens and Krebs 1986; Calcagno 2018). The long-term rate of gain is an appropriate fitness proxy provided many patches are visited (Charnov 1976) and, more critically, that the time horizon is independent of individual decisions (Calcagno 2018). The optimal marginal rate of gain in turn controls the optimal level of patch exploitation, as can be assessed by the amount of resource left in the patch, or GUD (Brown 1988; Calcagno et al. 2014).

The many facets of risk

Predation risk can impact foraging in many different ways (Brown et al. 1999; Arehart et al. 2023). In the context of the MVT, three broad categories of risk ought to be distinguished, depending on the scale at which risk disrupts the foraging process. First, risk can impact solely the dynamics of resource acquisition at the local (within patch) level. For instance, the perception of risk can elicit vigilance and/or increase the level of stress while foraging in a patch (Apfelbach et al. 2005; Clinchy et al. 2013). We refer to these as "Disturbance" scenarios. Second, a more severe form of risk causes the premature end of patch visits, forcing the individual to leave the current patch. This applies to individuals that escape when perturbed by a potential predator, and to foragers that can be displaced by competitively dominant individuals or species (Blumstein 2006). We call these "Escape" scenarios. Last, risk can result in the death of the individual, an even more severe and global threat, as it prematurely stops not only the current patch visit but the entire foraging sequence. This puts "Death" scenarios in a league of their own. The three categories of risk have their impact on the MVT illustrated in Figure 2a, and are of course not mutually exclusive (Moll et al. 2017).

An additional distinction must be made, depending on whether the occurrence of risky events cause a direct loss of some, or even all, of the accumulated gains. Interruptions by predators, for instance, obviously reduce the effective foraging time, lowering future gain levels. This only interferes with the future dynamics of gain acquisition, an indirect loss. But dealing with predators may also imply an immediate expenditure of energy, or the loss of previously acquired food items, representing a direct loss. This is illustrated in Fig. 2b.

In this framework we can classify risk along two axes of severity: (i) the scale at which the normal course of events is disrupted, from local to global, and (ii) the amount of direct loss (Fig. 2c). This produces a huge spectrum of possibilities, but for clarity we will highlight six elemental scenarios, representative of familiar broadly-applicable situations. Disturbance scenarios can be of two extreme types: the transient interruption of foraging activities, without no direct loss (see Fig. 2b), will be called a pure "distraction" scenario. In contrast, risk can mostly have a diffuse direct cost (e.g. increased stress level), in what we call a "costly vigilance" scenario (Fig. 2b). In Escape scenarios, a natural contrast exists between escaping with its current patch harvest ("take-away" scenario; Fig. 2b) and escaping empty-handed ("give-up" scenario). Finally, in Death scenarios, an individual killed may retain all gains hitherto acquired, if gains are converted to fitness in a continuous manner, such as in parasitoids: all hosts parasitized are potential offspring regardless of the mother's fate. We call this the "continuous" scenario (Fig. 2b)), as opposed to the "all or nothing" scenario, where gains are valued in a delayed manner and only survivors benefit (see Arehart et al. 2023, for a similar classification)."All or nothing" is appropriate for a bee whose harvest is worthless if it does not make it back to the nest, or for species that must survive to the reproduction season if energy gains are to have any value.

In the following Section we consider how these different risk scenarios can be incorporated into the MVT. In all cases, parameter β_j will stand for the rate at which disruptions by predators occur while foraging in patch j, thus representing the level of risk (or risk intensity) in the patch. Parameter δ will stand for the direct loss of gain, if any, caused by the occurrence of a disruption event (see Figure 2b). Our general approach will be to (i) derive the expected (or realized) gain function, taking into account the effects of risk, (ii) formulate the suitable fitness proxy, (iii) show that risk-MVT equations are appropriate to define optimal strategies. We will then show the connection between the risk-MVT and Brown's GUD framework.

THE RISK-MVT

Disturbance

We use a simple behavioral model, illustrated in Fig. 2a-b, according to which an individual in a patch can be in one of two states: (i) actively foraging, or (ii) engaged in some anti-predator activity (interrupted). The individual switches from state (i) to state (ii) at rate β_j. Following an interruption, the individual reverts to the actively foraging state (i) at rate γ. This model can describe many different particular situations, from individuals scanning their neighbourhoods after detecting predator-related cues, to individuals dodging or deflecting actual attacks. In all cases, β_j^{-1} is the typical time interval between two consecutive interruptions, and γ^{-1} the typical time it takes to resume foraging after an interruption. In addition, each interruption (i.e. sojourn in state (ii)) may entail a direct loss of gain δ, representing for instance the energetic cost of performing a defensive behaviour.

The above model defines a two-state renewal process (Gallager 2013; Mangel 2006). From standard stochastic theory, we can derive the expected gain of an individual willing to stay for time t in a patch of type j, given a level of risk β_j, as:

$$\tilde{F}_j(t) = F_j\left(\frac{\gamma t}{\beta_j+\gamma}\right) + \frac{t}{4\left(\beta_j+\gamma\right)}F_j''\left(\frac{\gamma t}{\beta_j+\gamma}\right) - \frac{\beta_j\gamma\delta}{\beta_j+\gamma}t \tag{2}$$

where F_j is the original gain function (in the absence of risk, fig. 2b; see Supp. Information for derivations).

The above equation describes a transformation of the gain function, with three easy-to-interpret elements. The first term represents the gains expected given the average time the individual is effectively foraging (rather than interrupted). The fraction of time effectively spent foraging is $\gamma/(\beta_j+\gamma)$, and the realized foraging time, that we shall call $\tilde{t}_j$, equals $\gamma t/(\beta_j+\gamma)$. Realized foraging time accumulates slower than actual (Newtonian) time, representing a discounting effect: future gains are less than the theoretical $F_j(t)$ because of the possible occurrence of interruptions. The second term represents a variance effect: as the number of interruptions effectively experienced during a patch visit, and each recovery time, are random variables, so is the effective foraging time. The original gain function is typically concave (law of diminishing returns), and Jensen's inequality implies that variance reduces the average gain even below $F_j(\tilde{t}_j)$. In other words, $F_j'' < 0$, and the second term is negative. This introduces a cost of uncertainty, that further decreases the height of the average gain function, and also tends to reduce its concavity. Finally, the third term in eq. (2) represents the direct cost of interruptions, proportional to the expected number of interruptions experienced and to δ, the direct loss of gain induced by an interruption.

Disturbance scenarios are thus quite readily accommodated for in the MVT: they solely require the gain function to be transformed according to eq. (2). The transformation simplifies to familiar forms in the two special Disturbance scenarios highlighted in Fig. 2c. Under a pure "distraction" scenario, we set $\delta = 0$ and provided β_j is large enough (as must be the case if risk is to have any significance), the second term in eq. (2) quickly falls to zero. This leaves the first term only, and risk thus amounts to a simple linear rescaling of time. Increasing the level of risk β_j is therefore similar to decreasing the attack rate or rate of resource consumption, an effect commonly discussed in the context of the classical MVT (Charnov and Parker 1995). Conversely, under a "costly vigilance" scenario (Fig. 2c), we set γ to a large value: the first term simplifies to the original gain function $F_j(t)$, the second term vanishes, and the third boils down to $-\beta_j\delta t$. Therefore risk in this scenario simply introduces an additional per-unit-of-time cost of foraging, and increasing risk is analogous to increasing the energetic cost of foraging (Stephens and Krebs 1986). These two effects are illustrated

in Fig. 3a & b using, as for all subsequent examples, a standard gain function $F(t) = 10(1 - \exp(-0.5t))$ (Charnov 1976; Calcagno et al. 2013).

Escape

If the foraging individual is scared away from its patch at rate β_j (Fig. 2a), two possibilities exist at time t. First, the individual may not have been troubled thus far, and gain acquisition has proceeded normally: it has acquired $F_j(t)$. Second, an interruption may have occurred at some time $\nu < t$: in this case the individual left the patch with gains $F_j(\nu)$ only, not $F_j(t)$. As we did above for Disturbance scenarios, we can define $\tilde{t}$, the effective foraging time of an individual that is willing to stay for time t in the patch. It takes value:

$$\tilde{t}_j = \frac{1 - \exp(-\beta_j t)}{\beta_j} \tag{3}$$

providing risk is not entirely absent ($\beta_j > 0$; see Supp. Information for derivation).

An individual willing to spend time t thus stays for only $\tilde{t}_j$ in practice. As for Disturbance scenarios, effective foraging time accumulates slower than actual time, but in this case the rescaling of time is highly non-linear (eq. (3)). Effective foraging time approaches a maximum value of β_j^{-1} as t increases, because in the long run, interruption by a predator happens almost surely. The relationship between the two time-scales is illustrated in Fig. 4a & b. There is still a one-to-one mapping between t and $\tilde{t}_j$, i.e. there exists a function $\tilde{t}_j^{-1}$ that for a given $\tilde{t}_j$ gives the corresponding t_j, obtained by inverting equation (3).

Following the same approach as before, we can express the gains acquired on average by an individual willing to stay in the patch for t time units (see Supp. Information for derivations), as:

$$\tilde{F}_j(t) = F_j(\tilde{t}_j) + \frac{(\sinh(\beta_j t) - \beta_j t)\exp(-\beta_j t)}{\beta_j^2} F''(\tilde{t}_j) - \beta_j \delta \tilde{t}_j \tag{4}$$

As eq. (2), this describes a transformation of the original gain function, with the same three components. The first term represents a discounting effect: future gains are devalued because of the risk that an interruption occurs before. The second term represents, again, the cost of uncertainty: as function F is typically concave, the gains effectively acquired on average, $\tilde{F}_j(t)$, are less than $F_j(\tilde{t}_j)$, for the stochasticity in the time of the interruption. The third term is the direct cost of being interrupted, if any.

Albeit conceptually similar, the transformation of course differs quantitatively. Setting $\delta = 0$, i.e. dropping the third term, describes the "take-away" scenario in which an escaping individual retains the amount of gain harvested in the patch. If, alternatively, an escaping individual must abandon all gains acquired in the patch ("give-up" scenario; Fig. 2c), we set the direct cost δ to $F_j(\nu)$, and the transformed gain function (4) simplifies to (see Supp. Information) $F_j(t)\exp(-\beta_j t)$. In that case, risk imposes a classical form of exponential discounting on the gain function.

A major difference from Disturbance scenarios, however, is that risk not only transforms the expected gain function, but also changes the actual duration of patch visits. The effective foraging time $\tilde{t}$ is also the effective residence time. As a consequence, the long term average rate of gain, though still an appropriate fitness proxy, is equal to

$$\frac{\left\langle \tilde{F}_j(t_j) \right\rangle}{T + \langle \tilde{t}_j \rangle}$$

with effective residence times at the denominator. In intuitive terms, an individual suffering from interruptions has gains lower than expected (numerator), but also wastes less time than expected (denominator), the latter effect partly counterbalancing the former.

Since the long-term rate of gain differs from that in the classical MVT (eq. (1)), it is not possible to use the transformed gain function $\tilde{F}$ (eq. (4)) directly. To circumvent the issue, we must introduce the gain function G, defined as

$$G_j(.) \equiv \tilde{F}_j\left(\tilde{t}^{-1}(.)\right) \tag{5}$$

that returns the expected gain level, but as a function of the effective time $\tilde{t}$ (remember that $\tilde{t}^{-1}$ is obtained by inverting eq. (3)), rather than of Newtonian time.

From this, it is straightforward to rewrite the long term rate of gain as $\left\langle G_j(\tilde{t}_j)\right\rangle / \left(T + \left\langle \tilde{t}_j \right\rangle\right)$, and it follows that the optimal strategy can be determined from the equation

$$G_i'(\tilde{t}_i^*) = \frac{\left\langle G_j(\tilde{t}_j)\right\rangle}{T + \left\langle \tilde{t}_j \right\rangle} \tag{6}$$

This is a legitimate MVT equation analogous to (1), albeit a generalized one, because it is stated on the transformed timescale $\tilde{t}$ rather than on the Newtonian timescale. Hence, in addition to transforming the gain functions, Escape scenarios require operating a transformed timescale. The MVT cannot be formulated on the regular Newtonian timecale, and one should turn to the risk-generalized MVT equation (6). Once this is done, Escape scenarios are perfectly amenable to all familiar MVT analyses, including graphical solutions and constructs, as illustrated in Fig. 4a & b for the "take away" and "give up" scenarios, respectively.

Death

We finally move from fear to death. We assume mortality occurs at rate β_j when in a patch of type j, and at rate β_T when traveling between patches (this is a background morality rate; Arehart et al. (2023)). The average death rate over the sequence of patch visits is thus the arithmetic mean of the different death rates, weighted by the fraction of time spent in each state:

$$\overline{\beta} = \frac{\beta_T T + \langle \beta_j t_j \rangle}{T + \langle t_j \rangle} \tag{7}$$

From this the average lifespan is $1/\overline{\beta}$, and the probability to survive until the end of an entire sequence (of total duration t_R) is $\exp(-\overline{\beta} t_R)$. Obviously we expect $1/\overline{\beta}$ and t_R to be much larger than $T + \langle t_j \rangle$.

Unlike previous scenarios, risk here has negligible impact on the typical patch visit and gain function, as it occurs by definition only once. However, it affects the duration of the entire sequence of patch visits, so that usual rate maximization does not hold. A suitable fitness proxy is the expected amount of gain harvested in total over the entire sequence of patch visits (Brown 1988). As long as there is no long term trend in habitat characteristics, an individual accumulates gain at a constant average rate of $\langle F_j(t_j) \rangle / (T + \langle t_j \rangle)$, during a foraging sequence of total length t_R, but dies at rate $\overline{\beta}$. At that scale, we can equate the situation with that of just one patch visit in Escape scenarios: the risk level is $\overline{\beta}$, the theoretical duration is t_R, and the gain function is linear. Therefore, we can directly obtain the expected amount of gain from eq. (4), in which the linearity of gain accumulation makes the second term (cost of uncertainty) vanish to zero (see SI for details).

Maximizing the average total gain is still quite far from MVT-like rate-maximization, but things simplify greatly in the two extreme Death scenarios (Fig. 2c). First, in the "continuous" scenario, we set $\delta = 0$ and let t_R go to infinity, so that the expected total gain reduces to

$$\frac{1}{\overline{\beta}} \frac{\langle F_j(t_j) \rangle}{T + \langle t_j \rangle} = \frac{\langle F_j(t_j) \rangle}{\beta_T T + \langle \beta_j t_j \rangle}$$

Again, this is not a MVT long-term rate of gain, because Newtonian time does not appear at the denominator. Rather, what appears is time weighted by the instantaneous level of risk. We can use the same approach as for Escape scenarios, and introduce $\tilde{t_j} \equiv \beta_j t$ and $\tilde{T} \equiv \beta_T T$, and the corresponding transformed gain function $G_j(.) \equiv \tilde{F}_j \left(\tilde{t}_j^{-1}(.) \right) = F_j(./\beta_j)$. From this, we can determine the optimal strategy just as above, using the risk-generalized MVT equation eq. (6).

Differences from the classical MVT are thus of the same kind as in Escape scenarios: the Newtonian timescale is not the appropriate optimization domain, and must be transformed. The transformation of time is simpler in this case: it is a linear rescaling, as illustrated in Fig. 4c. This transformation is quite different from the previous ones, in that $\tilde{t_j}$ is not a realized duration, and not strictly speaking a time (it has no dimension). It still has a very natural interpretation: all patches are not treated on equal footing, as in riskier patches time is over-weighted, and risk effectively accelerates the flow of time as perceived by the individual (Figure 4c). More formally, the transformed time quantifies the infinitesimal probability of dying, when performing a particular activity (foraging in a given patch, or moving between patches). Such "risk-penalized time" is a common concept in the theory of decision analysis, where it is known as the micromort unit, introduced by Howard (Howard 1989, 2007) to evaluate the relative dangerousness, defined as an increase in the likelihood of dying, of human activities. Our $\tilde{t}$ is thus directly equivalent to micromorts, and optimal foragers can be seen as allocating units of micromorts following the MVT.

If gains are converted to fitness only if the individual survives to the end of the foraging period t_R ("all-or-nothing" scenario; Fig. 2c), the total expected gain reduces to:

$$\frac{\langle F_j(t_j) \rangle \, t_R \exp(-\overline{\beta} t_R)}{T + \langle t_j \rangle}$$

This very much resembles a regular MVT long term rate of gain, stated on the Newtonian timescale, with all gain functions multiplied by the duration of the foraging session t_R and the survival probability $\exp(-\overline{\beta} t_R)$. This seems a simple multiplicative transformation, simpler than the ones derived above, but there is a fundamental difference: since $\overline{\beta}$ is a function of all residence times (eq. (7)), the gain function in one patch depends not only on the residence time in that patch and on travel time, but also on the residence times in all other patches. This makes the gain functions entangled, a major deviation from MVT theory. Therefore, in the "all-or-nothing" scenario, we can formulate the problem as a MVT in homogeneous habitats only, i.e. when all patches have similar characteristics. In such conditions, the MVT can be stated on the Newtonian time-scale, just as for Disturbance scenarios, using the transformed gain function:

$$\widetilde{F}(t) = F(t) \exp\left(-\frac{\beta_T T + \beta t}{T + t} t_R \right)$$

The effect of this transformation is illustrated in Fig. 3c. Again, this is possible in homogeneous habitats only.

Connection to Brown's GUD framework

Brown's theory states that when leaving a patch, an individual should balance four different marginal rates, so that the following equation holds

$$H = C + P + MOC \tag{8}$$

Here H is the marginal of resource harvesting and C the marginal metabolic cost of foraging, two quantities also found in the MVT. The marginal rate of gain $F_i'(t_i^*)$ in eq. (1) is indeed a net gain, equal to the gross rate of energy gain minus the per-time unit energetic cost of foraging (Stephens and Krebs 1986), i.e. $H - C$. Finally, P is the marginal cost of predation and MOC the "missed opportunity cost", both terms lacking from the MVT. As Brown's equation focuses on a particular point in time with no particular global context, the MOC is needed to justify that the individual is not doing something else at that time, and to ensure that the sum of marginal rates cancels out.

It is straightforward to rewrite the classical MVT equation (1) as

$$H = C + \frac{\langle F_j(t_j^*)\rangle}{T + \langle t_j^*\rangle}$$

to exhibit its analogy with Brown's equation. Here the predation cost P is, obviously, zero, and the long-term average rate of gain (Charnov's E_n^*) plays the role of the MOC. Indeed, since the MVT provides a specific global context, MOC can be defined explicitly in terms of the gain functions, travel time, and optimal residence times.

Now the question is whether generalizing the MVT to predation risk introduces, as in eq. (8), a fourth additive term: the predation cost P. Obviously, under the costly vigilance scenario, we saw that risk introduced an additional cost term in the gain function, and it is indeed straightforward to state the MVT under "Brownian" form as

$$H = C + \beta_i \delta + E_n^*$$

In the Death scenarios, the fitness proxy was the product of E_n^*, the long-term rate of gain, and a second term representing survival (either the average life-span or the probability of survival, depending on the scenario). If, as before, we split the net gain F into a gross harvest rate (H) and a foraging cost (C), we can obtain the following expression (see SI for derivation):

$$H = C + \frac{\langle F_j(t_j^*)\rangle}{p_i} D \frac{\partial \overline{\beta}}{\partial t_i} + E_n^*$$

with p_i the relative frequency of i patches and D the average duration of the entire foraging sequence, i.e. $1/\overline{\beta}$ and t_R in the continuous and all-or-nothing scenarios, respectively.

This again exhibits a full analogy with the "Brownian" form (eq. (8)), the P term involving the marginal change in the average death rate. Incidentally, the all-or-nothing scenario was the one assumed by Brown (1988), and we recover exactly the same equation in that case.

Unfortunately, in the other cases (distraction, and Escape scenarios; Fig. 2c), the impacts of risk are more intricate and a neat four-fold additive partitioning cannot be achieved. These forms of risk are thus "Charnovian" but cannot be put in "Brownian" form. All the above results are summarized in Table 1.

EXAMPLE PREDICTIONS

Having introduced the risk-MVT, we now present some applications. By gradually increasing the level of risk in a habitat, for a given gain function and travel time, we can investigate how the optimal strategy deviates from the original risk-free MVT ($\beta = \beta_T = 0$).

Greater risk in patches can be expected to shorten optimal residence times, in a form of protection against risk (risk avoidance). Less intuitively, greater risk lowers the overall quality of the habitat, which from classical MVT theory increases residence time (Stephens and Krebs 1986; Calcagno et al. 2013). It is therefore not straightforward to predict what the net effect should be (McNamara and Houston 1987).

Predictions for the different risk scenarios, as they can be deduced from the graphical constructs in Figures 3 and 4, are presented in Figure 5. Two types of optimal times are shown for each scenario: the optimal residence time on the Newtonian timescale t^*, and the effective foraging timescale $\tilde{t}^*$.

Optimal residence times on the Newtonian timescale (t^*) generally decreased with risk level, as could be expected from risk avoidance considerations, but could also increase with risk under two scenarios ("distraction" and "take-away"; Fig. 5). In a distraction scenario, since repeated interruptions by predators mostly reduce the amount of time effectively spent foraging, an optimal forager should compensate by staying longer. In contrast, in a costly vigilance scenario, the optimal strategy commands to leave earlier, in order to avoid the direct loss of gain imposed by predators. The two types of "Disturbance" scenarios thus yield opposite predictions, underlining the need to distinguish among different modes of predator-induced risk.

Interestingly, in the distraction scenario, optimal residence time increases with risk on the Newtonian timescale, but the effective foraging time $\tilde{t}^*$ decreases nonetheless (Fig. 5). This indicates that albeit in the distraction scenario an optimal forager compensates for more frequent interruptions by delaying its departure, the compensation is less than perfect and does not suffice to maintain the effective foraging time at a constant value. Therefore, patch exploitation decreases, and thus GUD increases, with risk, in all Disturbance scenarios.

In Escape scenarios, optimal residence time increases with risk in the take-away scenario (Figure 5). Hence, an optimal forager should compensate for the early interruption of patch visits by extending its persistence (theoretical residence time), taking maximum advantage of those lucky visits where no interruption occurs. However, the opposite is true if predator interruptions imply losing the gains acquired in the patch (give-up scenario; 5). In that case, the optimal strategy is to leave earlier, in a effort to reduce the chances of being interrupted.

In the take-away scenario, optimal residence time increases with risk on the Newtonian timescale, but decreases on the transformed timescale, i.e. the effective residence time decreases (Figure 5). The observed duration of patch visits would thus on average be shorter in riskier habitats, even though individuals are willing to stay longer. In the give-up scenario, optimal residence time decreases on both time-scales.

In Death scenarios, optimal residence time invariably decreases with risk (Fig. 5). Even if an individual retains all its gains when killed, it is never good to increase residence time when patches are riskier: the optimal strategy is to leave earlier, avoiding the risk of death. The decline in residence time is of course more pronounced if gains are converted into fitness in a delayed manner (all or nothing scenario; Fig. 5).

Overall, increasing the risk level β can decrease or increase the average residence time, depending on the risk scenario considered. The theoretical residence time can increase with risk level in Disturbance and Escape scenarios, In those cases, residence times observed in the field and measured in experimental risk-free assays can respond to risk level in opposite directions. This occurs, whatever the type of risk, if predator interruptions do not cause any direct loss of gain (distraction and take-away scenarios; Fig. 2c).

OPTIMAL BOLDNESS

The risk-MVT, beyond optimal residence times, can be used to study the level of risk-taking of optimal foragers. We can indeed extend the micromort notion (Howard 1989), encountered as the risk-MVT domain in the Death scenario above, to all other scenarios, even those for which it does not naturally appear in MVT calculations. Micromorts quantify the amount of risk effectively taken by individuals. In Death scenarios, more micromorts allocated directly imply greater chances of being killed during a patch visit, and a shorter average lifespan. In Escape scenarios, micromorts quantify the probability of being chased away by a predator, and in Disturbance scenarios, the average number of interruptions an individual endures before leaving a patch. In all cases, they are a quantitative measure of the amount of risk an individual is willing to take per patch visit, i.e. of its boldness Wilson et al. (1994). This provides complementary insights into the optimal behavior, and we thus introduce the "optimal boldness", b^*, defined as $b^* = \beta t^*$.

Results for optimal boldness are shown in Figure 6. Unsurprisingly, boldness is lower when the type of risk is more severe: it is maximal in Disturbance scenarios and minimal in Death scenarios, consistent with our classification of risk severity (Fig. 2). This conforms well to the intuition that individuals can afford to be more daring when risk is less punishing. But results are less straightforward regarding an increase in risk intensity (risk level β) for a given severity. Quite generally, optimal boldness increases with risk level, similar to what was observed in the continuous scenario Figure 6. When the habitat gets more risky, individuals tend to become bolder, taking more risks. Therefore the MVT optimal strategy can be described as risk-prone. Only in the costly vigilance and all-or-nothing scenarios, provided risk gets sufficiently important, do we observe the opposite: a decline in boldness with risk. In such cases, the MVT optimal strategy switches from risk proneness to risk aversion in very risky habitats. Remark that in the give-up scenario, the trend in boldness does not reverse but does considerably slow down, compared to the take-away scenario (Fig. 6). We can presume that increasing the direct loss caused by interruptions δ (for instance adding a direct energetic cost on top of the loss of gains) could generate the same hump-shaped pattern as in the costly vigilance and all or nothing scenarios. Therefore, even though different risk scenarios produced contrasted predictions in terms of optimal residence times, predictions are much more consistent in terms of boldness: optimal foragers generally tend to become bolder as risk increases, unless risk is high enough and causes important direct loss of gain (Fig. 2).

DISCUSSION

Optimal foraging theory has produced two very successful frameworks to apprehend patch-leaving decisions. First, Charnov's Marginal Value Theorem (MVT) elegantly captured the effect of patch quality and resource acquisition, but failed to consider predation risk. Subsequently, Brown's GUD-theory introduced the notion of predation risk and risk avoidance, but did not retain all MVT ingredients. The end result is that the two theories have remained surprisingly

disconnected, each used to address one or the other facet of the problem. As we have shown here, although there is a formal equivalence between the two theories, an important difference is that Brown's theory is more abstract and does not specify a particular life-cycle or habitat context. In contrast, the MVT is derived from a specific model of sequential patch visits, rendering the different components defined explicitly and computable from global habitat properties. For instance, the MOC (missed-opportunity cost), an abstract quantity, is replaced with the long-term average rate of gain, a measurable fitness proxy. Therefore Brown's equation includes the MVT as a special case, with the tremendous advantage of including predation risk, but this comes at the price of reduced concreteness and predictive possibilities. Even though more sophisticated and flexible frameworks exist that can describe optimal strategies with greater realism (Tenhumberg et al. 2001; Davidson and El Hady 2019; Arehart et al. 2023), the conceptual simplicity of the MVT and of Brown's deterministic theories remains unmatched. But since both have strengths and weaknesses, it would be desirable to combine them into a single framework.

In this article we have demonstrated that the MVT can readily be extended to make predictions under predation risk, and propose that the risk-MVT (rMVT) serve as a single framework unifying the two previous ones. Compared to the classical MVT, the main difference introduced by fear or death is conceptually very simple: one may have to switch from considering the standard ("Newtonian") timescale in favor of a transformed timescale. The MVT is ultimately a matter of time budget (time travelling versus time exploiting) and rate-maximization, but it turns out that the timescale on which one apply these concepts should match the timescale effectively perceived by individuals. In the presence of risks, the latter does not always equate the usual Newtonian time, but can rather be a transformed timescale. For instance, it can correspond in practical terms to the expected time effectively spent in patches, as realized when taking potential interruptions into account, rather than the "ideal" time an individual would stay if uninterrupted. Rate-maximization thus applies in the face of risk, albeit the relevant time needs not flow at the same pace in habitat portions that have difference levels of risk. It is quite universally true in biology that organisms do not perceive time uniformly, but rather in a relative way, depending on internal state and external factors. One famous example is the degree-day timescale in ectotherm physiology (Charnov and Gillooly 2003). The transformed timescale of the rMVT makes similar biological sense, and the Newtonian optimal residence times t^* can be easily recovered from the transformed residence times $\tilde{t}_j^*$ through a plot of t_j^{-1}, as shown in Fig. 4a & b.

Less surprisingly, the presence of risk also implies alterations of the gain functions, as most other habitat alterations do (Stephens and Krebs 1986; Calcagno et al. 2013; Davis et al. 2022). The transformation of the gain function imposed by risk can be understood as the combination of three simple effects. First, risk introduces a discounting of future gains, since an interruption might occur before having the chance to acquire those future gains. Second, risk induces a cost of uncertainty: randomness in the occurrence of predator encounters combined with the concavity of gain acquisition in patches creates an emerging cost of risk. Last, risk may have a direct cost through energy expenditure and/or the loss of previously-acquired resource items. Once the gain function has been appropriately transformed to reflect to the type of risk considered and, possibly, switching to the effective timescale, the rationale of the MVT is unchanged, and the rMVT can address all types of risk scenarios. The rMVT otherwise rests on the same assumptions as the MVT. In particular, it assumes individuals behave as though they have knowledge of the (expected) characteristics of a patch upon entering it, rather than estimating these progressively based on experience. These assumptions and their behavioral implications are well understood and have been extensively investigated (Green 1980; McNamara 1982; Stephens and Krebs 1986; Nonacs 2001; Wajnberg 2006).

Compared to Brown's (1988) GUD-theory framework, the risk-MVT presents several advantages. One is that the different marginal terms involved in Brown's eq. (8) are explicitly defined. Hence, as for the classical MVT, we can relate them to global habitat characteristics and, in principle at least, estimate them independently. More importantly, it highlights that the different marginal terms are intertwined and cannot vary freely: their dependence on common underlying habitat characteristics necessarily introduces correlations between some of them. For instance, the MOC term is dependent on both P and C. The predation cost P, in Death scenarios, is a function of average patch yield and thus on the foraging cost C. Worse, if the cost of foraging is not assumed to be constant through time, then all four terms become entangled through the optimal residence time. When varying one habitat characteristic (such as the travel time, patch quality, foraging cost or predation risk level) all four terms thus necessary covary. The risk-MVT mechanistically describes the pattern of covariation and thus allows to predict the consequences of sustained changes in habitat parameters, such as the risk level β. In contrast, increasing the predation cost P in eq. (8), all else equal, cannot yield the kind of predictions here obtained.

A second advantage of the risk-generalized MVT is its ability to address most types of risk scenarios one can imagine (Moll et al. 2017; Arehart et al. 2023). Indeed, predators (or dominant competitors) can have a range of impacts on foraging individuals, beyond the obvious consumptive (mortality) effects. Non-consumptive effects are pervasive and multifarious, ranging from distraction to increased metabolic level to spatial relocation. Even though consumptive effects have historically received the greatest attention in ecology, non-consumptive effects are increasingly recognized are equally important, if not dominant (Peckarsky et al. 2008). This is especially true if one does not restrict its attention to predators, but also to competitors (from the same or other dominant species), as these seldom cause death but can still profoundly affect a forager's behavior. According to the classification of risk severity we proposed in Fig. 2b, six elemental risk scenarios can be recognized, all of which can be studied with the risk-generalized MVT. The only limitation is the ability to describe heterogeneous habitats in the all-or-nothing scenario. In contrast, Brown's result was derived in the context of consumptive effects (all-or-nothing scenario), but three out of the five remaining scenarios cannot be fit into the framework: a simple P term does not emerge and the equation does not apply (see Table 1).

Encompassing different risk scenarios (Arehart et al. 2023) is important, because as our results showed, predation risk can have contrasted effects on optimal patch leaving strategies depending on how exactly it disrupts the foraging process. The most familiar prediction that greater risk in patches should select for shorter residence times is often true, but not always: the opposite can also be optimal, as we found in Disturbance and Escape scenarios when risk does not cause any direct loss of gain (Fig. 5). It follows that in general situations, with intermediate direct costs, we might observe more complex, non-monotonous, trends in optimal residence time along gradients of risk, with an initial increase followed by an eventual decrease. Only in Death scenarios can a decrease of optimal residence time with risk always be expected, irrespective of the details. Predation risk should therefore not be treated as one monolithic component impacting foraging decisions, but the diversity of ways through which predation risk can disrupt foragers should be recognized. In particular, the lethal effects of predators do not necessarily have the same consequences as non-lethal (non-consumptive) effects.

An additional advantage of the risk-generalized MVT is that the associated transformed timescales, beyond their technical utility, bear intrinsic behavioral significance. Transformed timescales are closer to what is actually experienced by individuals and also to what can be quantified from observational data. For instance, in Disturbance scenarios, the

transformed timescale is the effective (realized) foraging time, taking into account interruptions. The latter can be measured directly from *in natura* observations, potentially taking advantage of video recording and computer-vision to classify the individual as actively foraging or not at any moment. In addition, this quantity controls the amount of resource harvested, and thus the observed GUD. In Escape scenarios, the transformed timescale is the average duration of patch visits as actually observed in the field, while the optimal residence time is a theoretical maximum one would observe in experimental predator-free patches. The two timescales are thus complementary, even though the MVT holds in general only if formulated on the latter. For instance, an interesting result is that in several cases the two types of optimal times respond to risk in opposite directions. This occurred in the distraction and take-away scenarios (Fig. 5. We can thus predict a negative correlation between optimal residence time and effective foraging time along a gradient of risk. In other words, an experimenter might observe, counter intuitively, a positive correlation between GUD and residence time along a gradient of risk, or opposite responses of residence time depending on the type of measurement conducted (predator-free experimental patches or *in natura* observations).

In Death scenarios, the transformed timescale is a risk-penalized time equivalent to the micromort scale from decision analysis (Howard 1989, 2007). It therefore directly translates into the probability of observing death in a given patch visit, or to the average lifespan of the forager, as one would measure in the field. An interesting prediction is that, if the forager only converts its gains into fitness at the end of some prescribed period (all-or-nothing scenario), there can exist a non-monotonous trend of the probability of death (or equivalently of average lifespan) as risk increases. Initially, an increase in risk would reduce lifespan, but eventually, the individual should shorten residence time to such an extent that the rend reverses, and survival actually increases with risk (Fig. 5 and 6).

Finally, the risk-generalized MVT allows to interpret optimal strategies in terms of risk-proneness or risk-aversion (Dammhahn and Almeling 2012). Indeed, by extending the micromort timescale to all scenarios, we can get a consistent metric of individual boldness Wilson et al. (1994), defined as the quantity of risk an individual is willing to endure before leaving a patch. While optimal giving-up times are useful to confront with observed patch visit durations and inform us on the individual's willingness (motivation) to stay in a patch, their value on the rMVT timescale gives greater insight into the individual's behavior in terms of risk taking, as they define what may be called "optimal boldness". An interesting result is that optimal patch-leaving strategies can overall be described as risk-prone, in the sense that optimal boldness generally increases with risk (Fig. 6), switching to risk-aversion only in some scenarios and when the risk level becomes very high. Maximizing resource intake thus promotes boldness, consistent with a prediction of McNamara and Houston (1987).

A general pattern that emerges is that, under the two-axis classification of risk scenarios, we proposed (Fig. 2b), the most salient distinction is between risk scenarios that cause a direct loss of gains versus scenarios that only compromise the dynamics of resource acquisition (5 and 6). The two sorts of scenarios, be they of the Disturbance, Escape or Death type, produced qualitatively different predictions (in terms of the correlation between effective and Newtonian residence times, or in terms of optimal boldness) from which they can be discriminated. Another salient conclusion is that risk severity (Fig. 2b) and risk intensity (the risk level β) have very different implications and cannot be used interchangeably. Increasing risk severity across scenarios invariably shortens optimal residence times and reduces optimal boldness, as one would expect intuitively (Fig. 5 and 6). On the contrary, increasing risk intensity within any given risk scenario can perfectly extend optimal residence, and generally selects for greater boldness.

In conclusion, we proposed in this article the risk-MVT as a unified framework combining the strengths of Charnov's classical MVT and Brown's GUD theory. Since the risk-MVT retains most of the MVT structure, it is amenable to all existing MVT methods, such as graphical constructs (Stephens and Krebs 1986), dimensional analysis (Stephens and Dunbar 1993; Charnov and Parker 1995) or sensitivity analysis (Calcagno et al. 2013), allowing to investigate the impact of risk on optimal strategies, interactions with e.g. the distribution of resources or collective decision-making (Calcagno et al. 2014; Davis et al. 2022). Possibilities are plentiful, well beyond the simple predictions presented in the present article. We suggest the risk-MVT can be a platform to better integrate resource acquisition and risk avoidance, two cornerstones of foraging theory.

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Data accessibility. No new data was generated during this work. The R script and citation data used to generate the bibliometric Figure 1 are available at Zenodo (https://doi.org/10.5281/zenodo.10058431).

Conflict of interest disclosure. The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article.

Author contributions. V.C. conducted the research and wrote the manuscript. All coauthors were involved in discussing the ideas and in preparing the main manuscript. F.H. reviewed the Supporting Information. Authors are listed in alphabetical order.

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TABLES

Risk scenario	Charnovian?	rMVT domain	Brownian?
None (original MVT)	YES	Newtonian time	YES
Disturbance (distraction)	YES	Newtonian time	NO
Disturbance (costly vigilance)	YES	Newtonian time	YES
Escape (take-away)	YES	realized time	NO
Escape (give-up)	YES	realized time	NO
Death (continuous)	YES	micromorts	YES
Death (all or nothing)	YES†	Newtonian time	YES

†in homogeneous habitats.

Table 1

A summary of results. For the different forms of risk (rows), we indicated whether the problem is amenable to a risk-MVT formulation ("Charnovian"); the domain (timescale) on which the r-MVT is to be formulated, and whether the effect of risk conforms to a predation cost as in Brown's GUD framework ("Brownian").

FIGURE LEGENDS

Figure 1

Charnov (1976) and Brown (1988): some bibliometric facts. *Left*: Total number of citing articles as a function of time, from 1976. Note the logarithmic scale and the approximately linear (i.e. exponential) growth of citation counts in recent decades. Regression lines over the past 20 years are also shown. *Right*: Overlap (Sorensen index) in citing articles (black) and in citing authors (including all co-authors of citing articles; blue) from 1990. Indices were computed over sliding windows of five years. Dotted lines represent the index values expected under chance, i.e. assuming independent citations.

Figure 2

Introducing risk into the MVT. (a) Risk is modeled as stochastic events that disrupt the normal unfolding of a patch visit as time passes (x-axis). Three types of disruptions are possible. In Disturbance scenarios (green), each event (broken arrows) switches the individual from the actively foraging state to the interrupted state (y-axis). It takes some time for the individual to switch back to foraging. In Escape scenarios (blue), each event prematurely interrupts the patch visit and forces the individual to move to the next patch. Last, in Death scenarios (red), the event event kills the individual and interrupts both the current patch visit and the entire foraging sequence. (b) A typology of risk in the MVT. Risk can be classified according to two axes of severity: the scale at which risk operates (y-axis) and whether it entails a direct loss of gain (x-axis). This produces six elementary combinations.

Figure 3

The risk-MVT: scenarios in which we can operate on the Newtonian time-scale, as in the original theories. In these cases, the usual MVT graphical construction can be applied to find the optimal strategy, provided a straightforward modifications of the gain function F. From left to right: "Distraction" scenario, or when the individual spends a fraction of its residence time being vigilant or hiding, rather than accumulating gains; "Costly vigilance scenario", or when risk-induced stress or behaviors cause additional energetic expenses by the individual; "All or nothing" death scenario, or when the individual dies with no gains if successfully attacked by a predator.

Figure 4

The risk-MVT: scenarios in which we must operate on a transformed time-scale, not on the traditional Newtonian timescale. The same graphical resolution as in the original MVT can still be applied (bottom panels), but the optimal strategy is defined on the transformed timescale. The residence transformed residence times can then be translated back onto the natural timescale, using the map between the two (top panels). From left to right: "Take away" scenario, or when the individual can flee from a predator whiel retaining its current gains in the patch; "Give-up" scenario, or when escaping entails a loss of the current gains in the patch; "Continuous" death scenario, or when death suppresses any future gains, but does not remove those already accumulated.

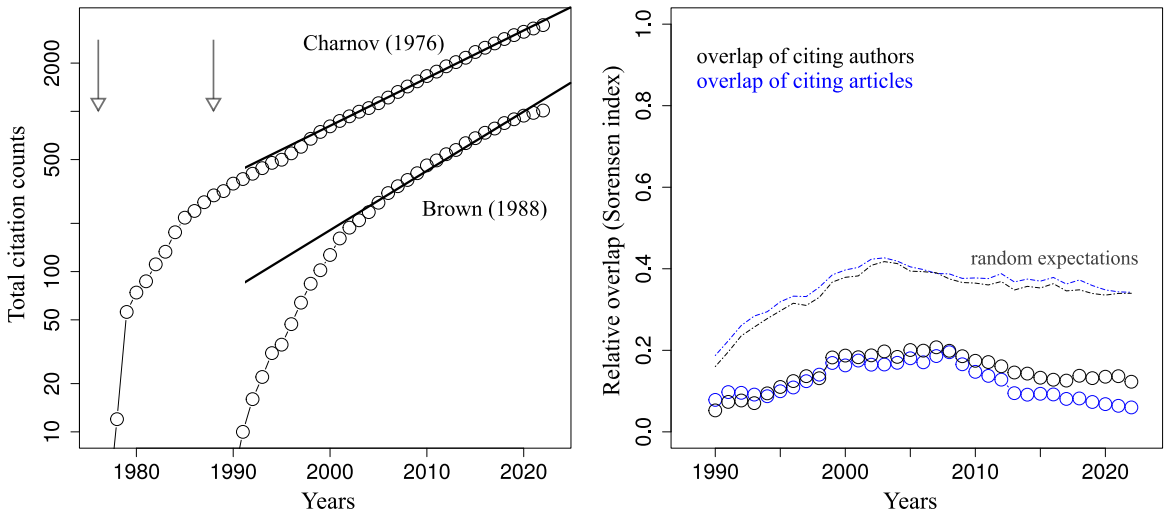
Figure 5

Example rMVT predictions: the effect of increasing risk on optimal residence time. Four different risk scenarios are considered. I each case, the level of risk when foraging in a patch (β; x-axis) is increased. The rMVT operates on a transformed timescale in the first three scenarios, in which case the optimal strategy is shown both on the transformed (orange) and Newtonian (blue) timescale. In all cases, the travel time was $T = 1$. Background morality rates were $\beta_T = 0.03$ ("continuous" scenario) or $\beta_T = 0.01$ ("all or nothing" scenario). There was no background mortality in the other scenarios.

Figure 6

Example rMVT predictions: "optimal boldness". The optimal boldness, here quantified as the total amount of risk taken at the optimal strategy (βt^*; y-axis) is shown as the level risk β is increased. All six risk scenarios (see Fig. 2) are considered. Note as in most cases, optimal boldness is an increasing function of risk intensity. Same parameters as in Fig. 5.

FIGURES



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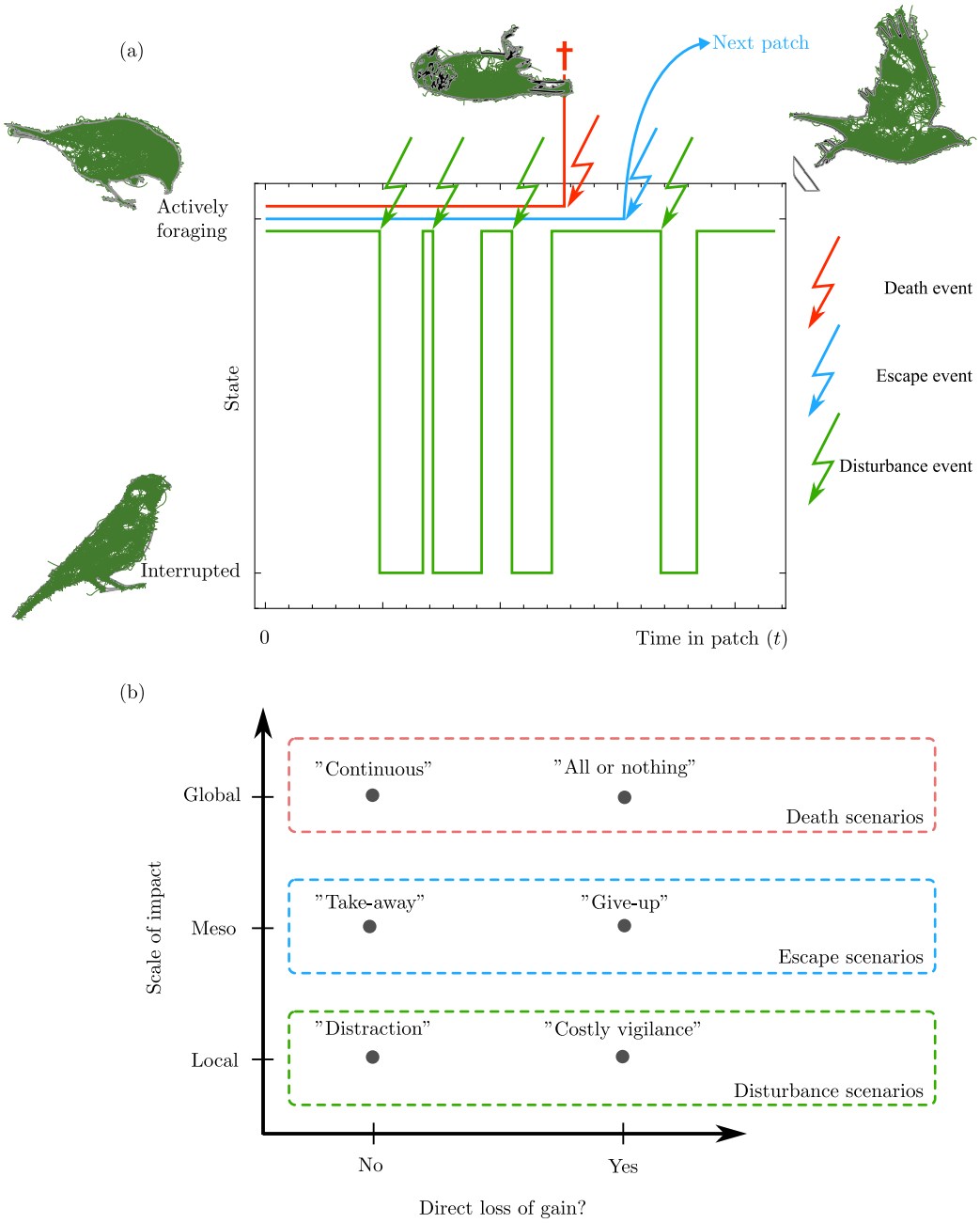

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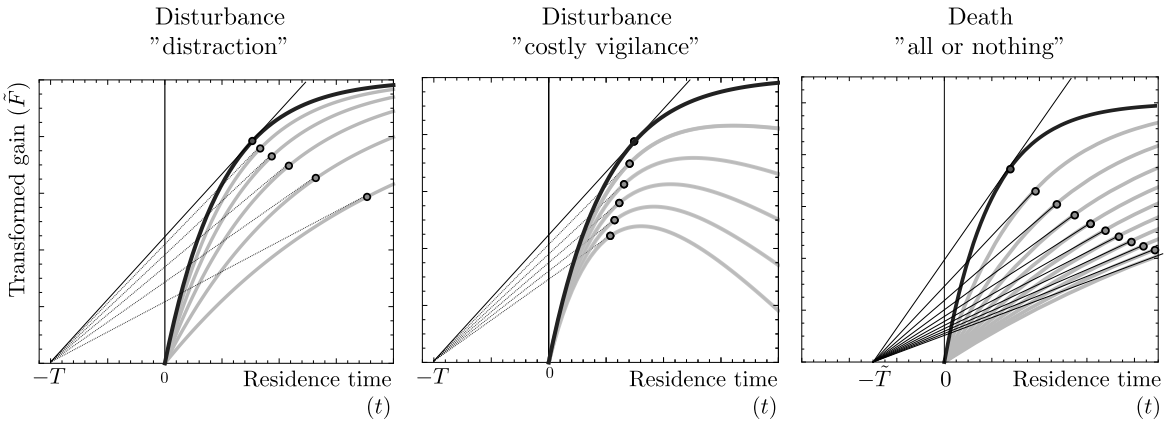

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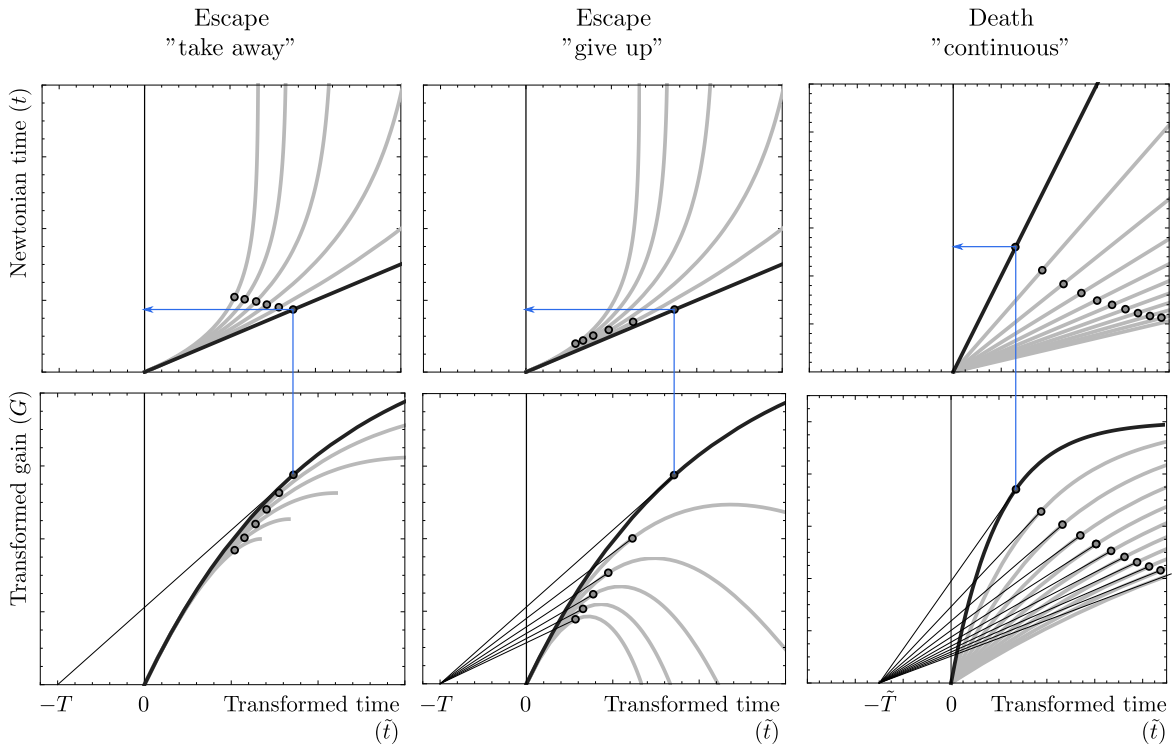

Figure 4

The risk-MVT: scenarios in which we must operate on a transformed time-scale, not on the traditional Newtonian timescale. The same graphical resolution as in the original MVT can still be applied (bottom panels), but the optimal strategy is defined on the transformed timescale. The residence transformed residence times can then be translated back onto the natural timescale, using the map between the two (top panels). From left to right: "Take away" scenario, or when the individual can flee from a predator whiel retaining its current gains in the patch; "Give-up" scenario, or when escaping entails a loss of the current gains in the patch; "Continuous" death scenario, or when death suppresses any future gains, but does not remove those already accumulated.

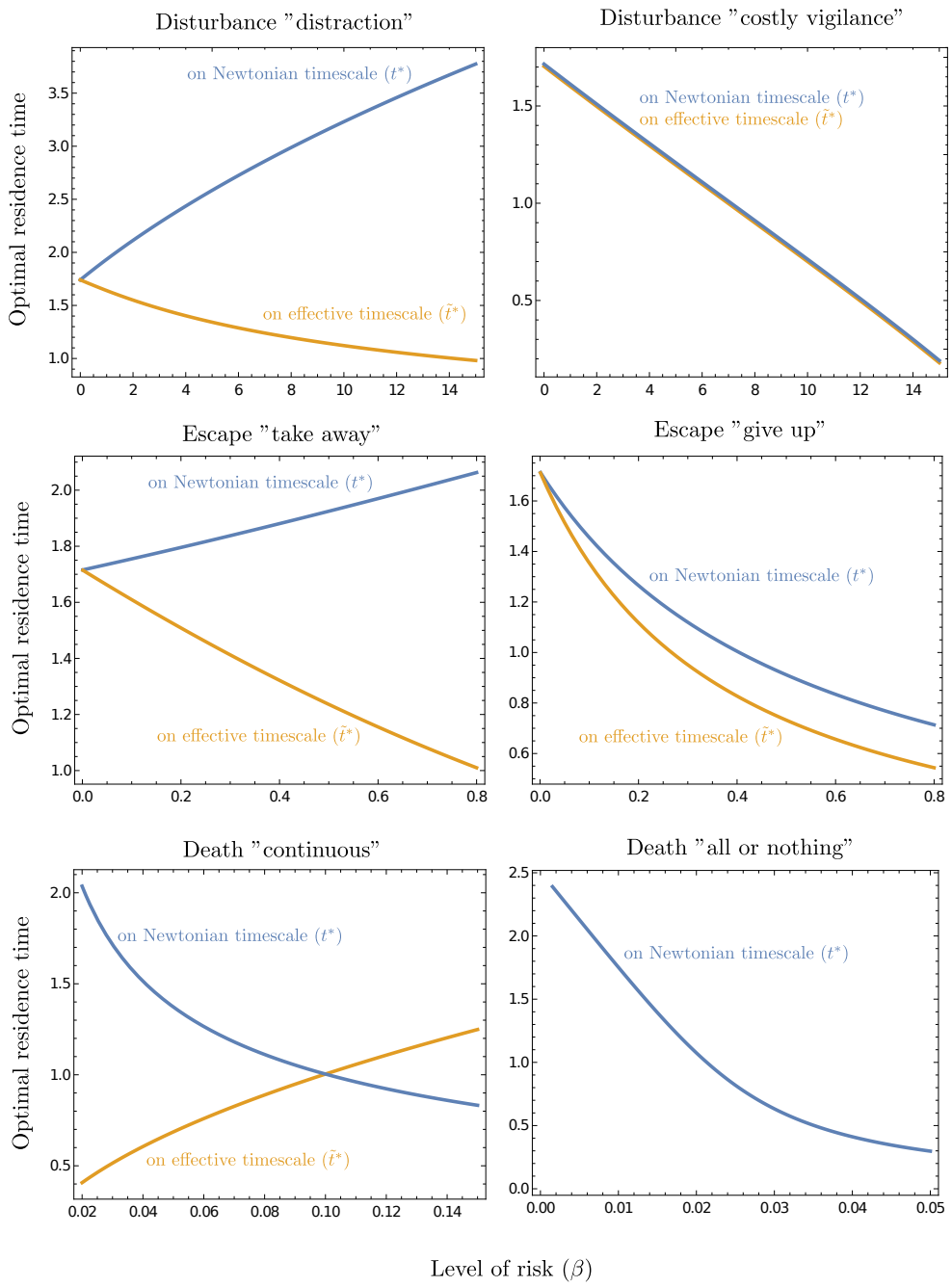

Figure 5

Example rMVT predictions: the effect of increasing risk on optimal residence time. Four different risk scenarios are considered. I each case, the level of risk when foraging in a patch (β; x-axis) is increased. The rMVT operates on a transformed timescale in the first three scenarios, in which case the optimal strategy is shown both on the transformed (orange) and Newtonian (blue) timescale. In all cases, the travel time was $T = 1$. Background morality rates were $\beta_T = 0.03$ ("continuous" scenario) or $\beta_T = 0.01$ ("all or nothing" scenario). There was no background mortality in the other scenarios.

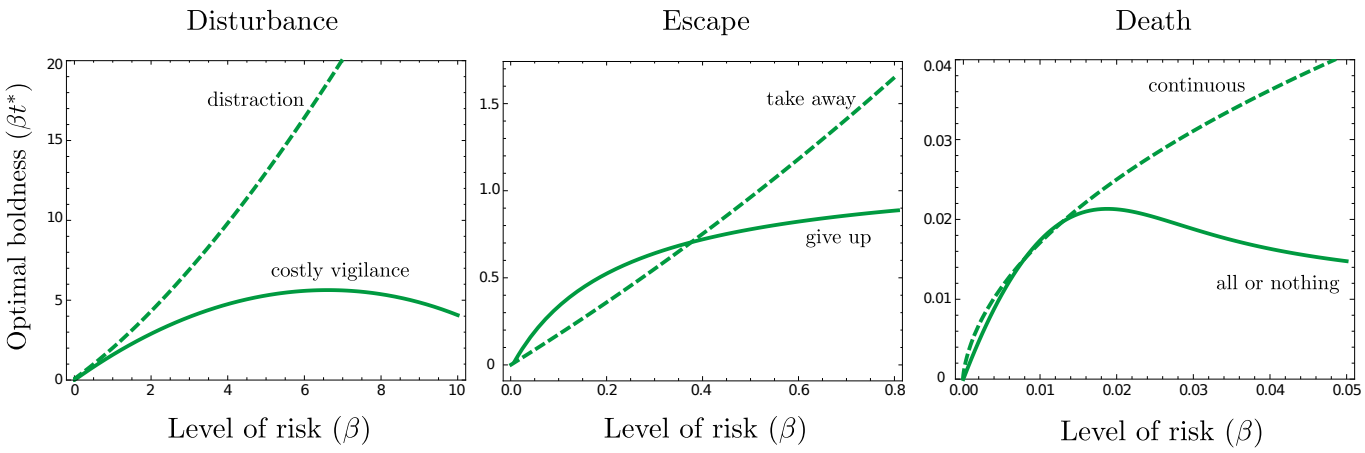

Figure 6

Example rMVT predictions: "optimal boldness". The optimal boldness, here quantified as the total amount of risk taken at the optimal strategy (βt^*; y-axis) is shown as the level risk β is increased. All six risk scenarios (see Fig. 2) are considered. Note as in most cases, optimal boldness is an increasing function of risk intensity. Same parameters as in Fig. 5.