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Vincent Calcagno, Frédéric Grognard, Frédéric Marie Hamelin, Eric Wajnberg, Ludovic Mailleret. The functional response predicts the effect of resource distribution on the optimal movement rate of consumers. *Ecology Letters*, 2014, 17 (12), pp.1570-1579. 10.1111/ele.12379 . hal-01084299

HAL Id: hal-01084299

<https://inria.hal.science/hal-01084299v1>

Submitted on 27 May 2020

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LETTER

The functional response predicts the effect of resource distribution on the optimal movement rate of consumers

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Abstract

Understanding how often individuals should move when foraging over patchy habitats is a central question in ecology. By combining optimality and functional response theories, we show analytically how the optimal movement rate varies with the average resource level (enrichment) and resource distribution (patch heterogeneity). We find that the type of functional response predicts the effect of enrichment in homogeneous habitats: enrichment should decrease movement for decelerating functional responses, but increase movement for accelerating responses. An intermediate resource level thus maximises movement for type-III responses. Counterintuitively, greater movement costs favour an increase in movement. In heterogeneous habitats predictions further depend on how enrichment alters the variance of resource distribution. Greater patch variance always increases the optimal rate of movement, except for type-IV functional responses. While the functional response is well established as a fundamental determinant of consumer–resource dynamics, our results indicate its importance extends to the understanding of individual movement strategies.

Keywords

Behaviour, dispersal, enrichment, Marginal Value Theorem, modelling, patchy habitats, spatial heterogeneity.

Ecology Letters (2014) **17**: 1570–1579

INTRODUCTION

Population biologists and community ecologists have long studied consumer–resource interactions, and the function linking the consumption rate to the density of resource, i.e. the functional response, was promptly identified as a key element. The functional response has been shown to determine the type of density-dependence in predator–prey systems (Hassell 2000), or their stability and response to enrichment (Rosenzweig *et al.* 1971). Qualitative features of the functional response are most of the time sufficient for qualitative prediction, and broad categories of functional responses have thus been identified and documented in a variety of taxa. To understand the factors bringing up these different functional responses, functional response theory repeatedly borrows from behavioural ecology, optimal foraging theory and movement ecology, in order to propose realistic functions grounded in behavioural mechanisms (Abrams 1982; Casas *et al.* 1993; McKenzie *et al.* 2009; Leeuwen *et al.* 2013). The reverse is much less true, however. While much research has offered theoretical predictions on optimal behaviours and optimal movement strategies, these very seldom relate to the functional response. “Functional response” is often not found in the index of modern behavioural ecology or movement ecology textbooks (e.g. Danchin *et al.* 2008; Krebs & Davies 2009; Westneat & Fox 2010; Méndez *et al.* 2013).

The marginal value theorem (MVT; Charnov 1976; Stephens & Krebs 1986; Brown 1988), one of the most successful optimal foraging models, is an example of this. The theorem predicts how long a forager should stay within a

resource patch before leaving in search of a new patch, the so-called optimal residence time. Prediction is based on two synthetic habitat characteristics: (1) the curve of resource acquisition within patches, called the gain function, which encapsulates the search and processing of resource items, and (2) the average time it takes to move between patches, called the travel time, which summarises the distance between patches and the difficulty to reach them. Whereas for simplification, the MVT assumes an ideal patchy structure, this abstracts the often observed tendency of animals to engage in area-restricted search in the presence of resource items (within ‘patches’), and to adopt extensive search in resource devoid areas (‘inter-patch’ movements; McIntyre & Wiens 1999; Klaassen *et al.* 2006; Kuefler *et al.* 2013; Benhamou 2014). The tendency to stay within patches thus controls the speed at which individuals progress through the overall habitat: the longer the average residence time, the smaller the average rate of movement. This connection between residence time and movement speed can be made explicit by formulating the theorem in continuous space (Arditi & Dacorogna 1988). As such, the MVT can serve as a general framework to understand how resource distribution should affect the movement of individuals in structured landscapes (Belisle 2005; Holyoak *et al.* 2008; Owen-Smith *et al.* 2010).

Even though routinely applied to consumer taxa including plants (Pleasants 1989; Astrom *et al.* 1990; Cassini *et al.* 1990; Livoreil & Giraldeau 1997; Wajnberg *et al.* 2000; Davidson & Morris 2001; McNickle & Cahill 2009), the MVT has no specific relationship to consumer–resource interactions. Gain functions may stand for any fitness-improving quantity, which confers high generality but also limited analytical progress

(Stephens & Krebs 1986; Westneat & Fox 2010; Calcagno *et al.* 2014). Accordingly, most MVT studies are concerned with the simplest qualitative predictions that could be drawn from the theorem (Stephens & Krebs 1986; McNamara *et al.* 2006): the effect of increasing the travel time between patches, giving-up densities and the relative exploitation of patches within habitats (for reviews see Nonacs 2001; Wajnberg 2006). In contrast, general predictions on how the average level of resources and their distribution in a habitat should affect overall movement have remained elusive, and the MVT is yet to be fully exploited in this regard.

Here, we introduce into the MVT an explicit resource consumption model, based on a general functional response. Using recent mathematical developments (Calcagno *et al.* 2014), we derive analytically the effect of patch resource levels on optimal residence times, and thus optimal movement rates. We show that predicting the effect of enrichment, albeit difficult based on the original MVT gain functions, simplifies greatly in light of the functional response: it depends on the qualitative type (concavity) of the response (decelerating, linear, or accelerating). We further study how predictions are affected by foraging costs and by the heterogeneity of the resource distribution. In particular, we establish that the average movement rate should invariably increase with habitat heterogeneity, except for type-IV functional responses.

MODEL AND METHODS

Patches are characterised by their resource level n_0 . Once an individual enters a patch and starts to exploit it, the resource level drops, and we denote by $n(t)$ its value after t time units. Note that the resource level is usually considered a number or a density, but may also be a percentage for species that respond to the fraction of not-attacked-yet resource (e.g. parasitoids or tree-browsers; Astrom *et al.* 1990; Wajnberg *et al.* 2000). In this context, the gain function of an individual is given by

$$F(t) = \gamma \int_0^t h(n(\tau)) d\tau - vt - \mu T, \quad (1)$$

with initial condition $n(0) = n_0$.

The first term represents resource intake (gross gain), with parameter γ a conversion factor controlling the value of the resource. The instantaneous rate of resource consumption, summed from 0 to t , is given by the functional response h (Holling 1959; Hassell 2000). Foraging costs, if any, are discounted to obtain net gain (Stephens & Krebs 1986; Brown 1988). Parameter v represents the per-unit-of-time cost when in the patch, and parameter μ the cost when moving between patches, given that it takes on average T units of time to find a patch (Stephens & Krebs 1986).

The dynamics of resource depletion are governed by the classical consumption equation

$$\dot{n} = -h(n)/S \quad (2)$$

where the positive constant S accounts for the scale (e.g. surface, volume or total number, depending on what n is) of patches.

Taken together, eqns 1 and 2 can generate very diverse shapes of gain function, depending on the functional response h and on the foraging costs μ and v (Fig. 1). A pattern of diminishing returns is ensured by resource depletion, even though type-IV functional responses may cause gain functions to be initially accelerating, i.e. sigmoid, for high resource levels. Importantly, qualitatively dissimilar functional responses can yield qualitatively similar gain functions (Fig. 1a).

According to the MVT, optimal foragers should stay in patches for some time t^* , as defined by

$$\dot{F}(t^*) = \frac{F(t^*)}{T + t^*} \quad (3)$$

The optimal residence time t^* makes both sides of the equation equal to the long-term average rate of gain (a proxy of fitness), which is then maximised. This equation has a well-known graphical solution, illustrated in Fig. 1b. One prediction is that patches should be depleted down to a certain resource level $n^* = n(t^*)$, called the giving-up density (GUD; Brown 1988). The MVT extends to heterogeneous habitats, where different patches have different resource levels. In this case, there is one similar equation for each type of patch, though no graphical solution exists (see online Supporting Information).

Equations 1, 2 and 3 together define the optimal residence time t^* for some resource level n_0 . Even though the equations cannot be solved explicitly, we can characterise the effect of n_0 on t^* , for any functional response, through sensitivity analysis (Calcagno *et al.* 2014). Only key results will be presented in the main text; all mathematical derivations are collected in the online Supporting Information. Analytical predictions will be confronted with numerical simulations of eqns 1–3, for specific functions classically used for functional responses. We first present results for homogeneous habitats, and then study the consequences of patch heterogeneity.

RESULTS

Effect of enrichment on movement rate

If one considers the gain function only, as is customary in MVT studies, predicting the sign of variation of t^* with n_0 is quite difficult: it requires estimating precisely the second time-derivative of F (Supporting Information). However, when stated in terms of the functional response h , predictions simplify greatly. The optimal residence time increases with enrichment if and only if:

$$\left. \frac{dh}{dn} \right|_{n^*} > \frac{h(n_0) - h(n^*)}{n_0 - n^* + T(v - \mu)/S\gamma} \approx \frac{h(n_0) - h(n^*)}{n_0 - n^*} \quad (4)$$

The rightmost expression is exact if foraging costs are similar ($v = \mu$) or are neglected, as is often done when resource acquisition translates directly into offspring production (e.g. for parasitoids laying eggs in hosts; Hassell 2000; Wajnberg 2006). It is thus a good approximation when costs are small

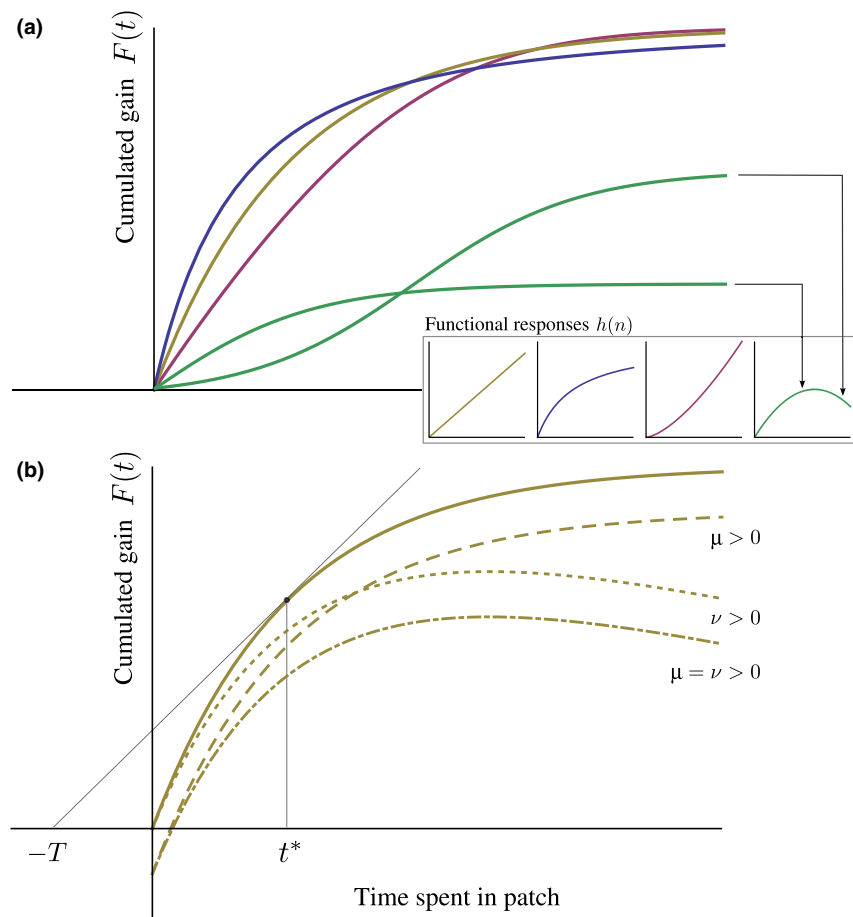


Figure 1 Gain functions for resource consumers. **(a)** Functions resulting from four contrasted functional responses (linear, decelerating, accelerating and dome-shaped/type-IV; *inset*) and no foraging costs. Functions used: Holling's type-II disk equation (decelerating); $n^{3/2}$ (accelerating); quadratic polynomial (type-IV). In the latter case, two resource levels were used (*arrows*). Note that the gain function is sigmoid for the higher resource level, not for the lower. **(b)** Introducing foraging costs. Cost of moving between patches (μ ; *dashed curve*); cost within patches (ν ; *dotted curve*); or both (*dotted-dashed curve*). The starting point was the linear case from panel a (*solid curve*), for which the graphical solution of the MVT eqn 3 is also shown: the line going through $(-T, 0)$ is tangential to the gain function at t^* .

relative to potential patch value (big $S\gamma/T$) and/or are not too different.

Inequality 4 constitutes a simple qualitative criterion on the type of functional response, on the interval of resource levels (n^*, n_0) . Starting with the rightmost expression, we see that a linear functional response $h(n) = bn$ yields the equality $dh(n^*)/dn = (h(n_0) - h(n^*)) / (n_0 - n^*) = b$. From this, we deduce that the inequality is never satisfied when h is accelerating (concave-up), and always satisfied when h is decelerating (concave-down), on (n^*, n_0) . A graphical argument is presented in the Supporting Information (Fig. S1). As a consequence, the optimal movement rate should increase with n_0 for accelerating functional responses (e.g. Holling type-III at low resource levels). Conversely, it should decrease with n_0 for decelerating functional responses (e.g. Holling type-II). A linear functional response is the knife-edge case where the optimal movement strategy does not change with enrichment. These predictions are corroborated by numerical simulations presented in Fig. 2a. We used a flexible power-law function $h(n) = n^\theta$ (Rosenzweig *et al.* 1971) to span the range from decelerating ($0 < \theta < 1$) to accelerating ($\theta > 1$) responses. The variation of t^* switches sign when crossing the linear case

(Fig. 2b). When foraging costs are not negligible and are not the same between and within patches, predictions are simply shifted (Fig. 2b). If costs are greater within patches ($\nu > \mu$), $T(\nu - \mu)/S\gamma$ is positive and the inflated denominator makes inequality 4 easier to satisfy: enrichment is thus more likely to decrease movement. Conversely, if costs of moving between patches are greater ($\mu > \nu$), the inequality is harder to satisfy: enrichment is more likely to increase movement. Costs of moving thus have the indirect effect of favouring an increase in movement with enrichment, even though their direct effect is to lower the optimal movement rate (Stephens & Krebs 1986).

These results can also be applied to more complex functional responses. Type-IV functional responses do not yield particular predictions; they behave just like decelerating (type-II) responses. In contrast, sigmoid functional responses (e.g. Holling type-III) should cause the optimal residence time to decline, and then rise again, under sustained enrichment. This follows from their being accelerating at low resource levels and decelerating at high resource levels. The optimal rate of movement is thus maximum for some intermediate resource level, as confirmed in numerical simulations (Fig. 3). Note

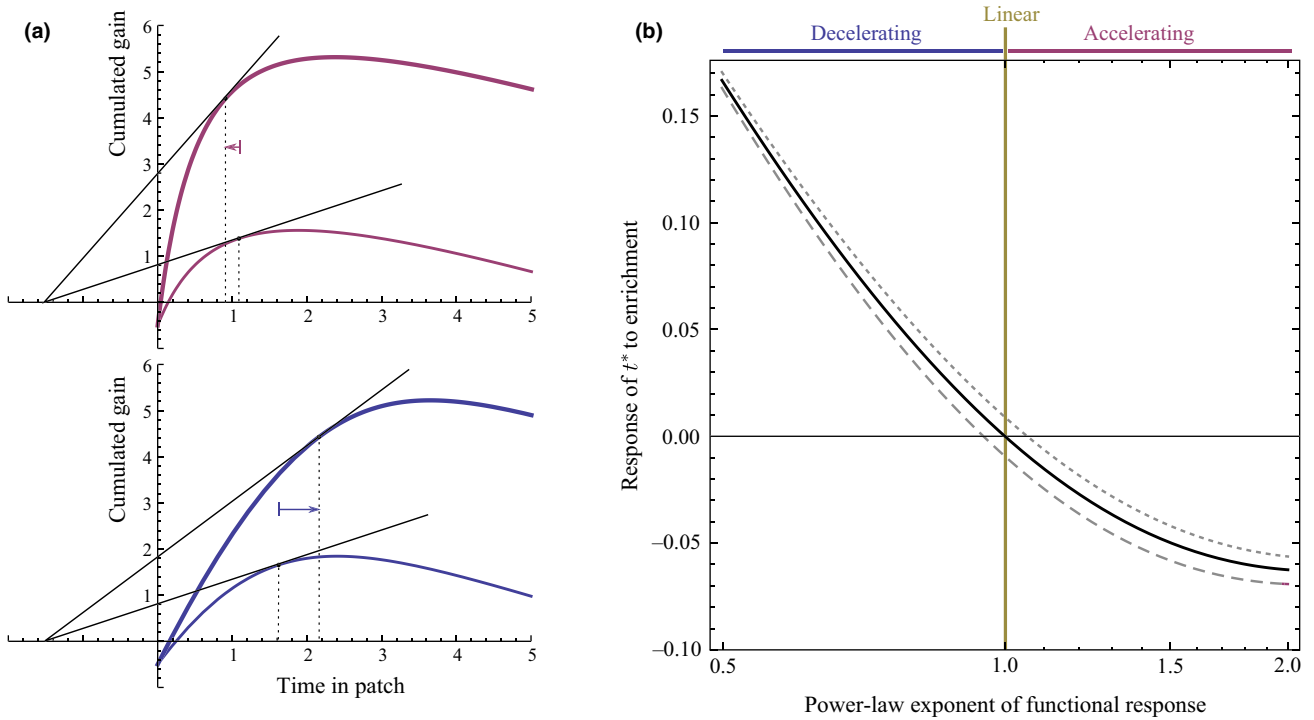


Figure 2 Enrichment in homogeneous habitats. (a) The optimal residence time t^* increases with enrichment in the case of a decelerating functional response (Holling’s type-II disk equation; *bottom*); but decreases in the case of an accelerating functional response ($n^{3/2}$; *top*). (b) Numerically computed proportional variation of t^* with n_0 (*y-axis*), as a function of the power-law exponent θ in the functional response n^θ (*x-axis*; log-scale). *Solid curve*: no foraging costs, and equal costs; *Dashed curve*: cost of moving between patches only; *Dotted curve*: cost within patches only. Remember that the movement rate decreases with t^* .

that the movement-maximising resource level does not coincide with the inflection point of the functional response (Fig. 3). In the absence of foraging costs, it is always greater, and foraging costs may shift its position up or down, depending on whether μ or ν is greater (eqn 4; Fig. 3).

Enrichment in heterogeneous habitats

So far all patches were assumed to have the same resource level n_0 . In nature, it is arguably more common for the distribution of resources to depart from homogeneity, different

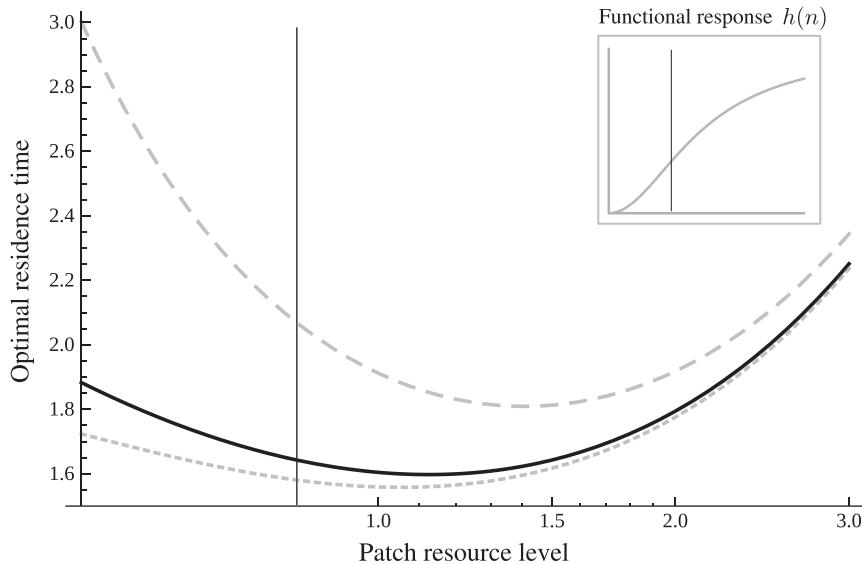


Figure 3 Sigmoid (type-III) functional responses. The numerically computed optimal residence time t^* (*y-axis*) is plotted as a function of resource level (*x-axis*; log scale). The disk equation $n^2/(2+n^2)$ was used for the functional response (*inset*). Its inflection point is materialised by a vertical solid line. *Solid curve*: no foraging costs, or equal costs; *Dashed curve*: cost of moving between patches only; *Dotted curve*: cost within patches only. Remember that the movement rate decreases with t^* .

patches having different resource levels. An important question is how the average rate of movement should respond to overall enrichment. Does it behave just like in an average homogeneous habitat, or does the resource distribution matter? To answer this question, we study how the average residence time $\langle t_j^* \rangle$ varies with the average resource level $\langle n_{0j} \rangle$. The bracket notation stands for the average over the habitat: if a fraction p_j of patches has some characteristic y_j , $\langle y_j \rangle = \sum_j p_j y_j$.

There are many different ways to enrich a heterogeneous habitat. All can be described by an impact vector $\mathbf{x} = (x_1, x_2, \dots)$, containing the distribution of the enrichment effort over the different patch-types. Graphically, this defines a direction in the space of patch resource levels, along which enrichment proceeds (Fig. 4a). Using the same methods as before (Supporting Information), it can be shown that the average residence time increases with enrichment if and only if

$$\left. \frac{dh}{dn} \right|_{n^*} > \frac{\langle h(n_{0j}) \rangle_H - h(n^*)}{\langle n_{0j} \rangle - n^* + T(v - \mu)/S\gamma} \approx \frac{\langle h(n_{0j}) \rangle_H - h(n^*)}{\langle n_{0j} \rangle - n^*}, \quad (5)$$

where $\langle h(n_{0j}) \rangle_H$ is a harmonic mean, weighted by the impacts x_j :

$$\langle h(n_{0j}) \rangle_H = \langle x_j \rangle / \left\langle \frac{x_j}{h(n_{0j})} \right\rangle. \quad (6)$$

Inequality 5 is very similar to ineqn 4, n_0 at the denominator being replaced with its average value. However, $h(n_0)$ at the numerator is replaced with the weighted harmonic mean in eqn 6, not by $h(\langle n_{0j} \rangle)$. Compared to a homogeneous habitat of average richness, predictions thus further depend on how enrichment is distributed over patches. The main result is that predictions are shifted in a direction controlled by the relative quality of enriched patches. Again, the type of functional response is key: in general, enriching rich patches, by increasing the harmonic mean $\langle h(n_{0j}) \rangle_H$, favours an increase in movement rate, and enriching poor patches favours a decrease, but the opposite can be true for type-IV responses.

To understand this, we first assume that all enrichment is concentrated on one single patch-type i . The corresponding impact vector is parallel to one axis in the space of patch resource levels ($x_i = 1$ and $x_{j \neq i} = 0$; Fig. 4a). From eqn 6, it follows $\langle h(n_{0j}) \rangle_H = h(n_{0i})$. Compared to inequality 4, ineqn 5 is thus easier to satisfy (which favours a decrease in movement) if $h(n_{0i}) < h(\langle n_{0j} \rangle)$, but more difficult to satisfy (which favours an increase in movement) if $h(n_{0i}) > h(\langle n_{0j} \rangle)$. For all increasing functional responses (including type-III), this implies, respectively, $n_{0i} < \langle n_{0j} \rangle$, i.e. a poorer-than-average patch, and $n_{0i} > \langle n_{0j} \rangle$, i.e. a richer-than-average patch.

As an example, with a linear functional response and no foraging costs, enrichment had no effect in a homogeneous habitat (Fig. 2). In a heterogeneous habitat, enriching the poorer patches should thus decrease the average movement rate, and enriching the richer patches should increase movement. This can be verified in the numerical simulations of Fig. 4a. We can further see that for type-II functional responses (Fig. 4b), enriching the richer patches can increase the average movement rate, whereas enrichment always decreased movement in homogeneous habitats. Conversely, for accelerating

responses (Fig. 4c), enriching the poorer patches can decrease the average movement rate, which enrichment can never do in a homogeneous habitat. Of course, if the enriched patches have average richness, $h(n_{0i}) = h(\langle n_{0j} \rangle)$ and we recover in all cases exactly the same predictions as for a homogeneous habitat (see Fig. S2 in Supporting Information). Interestingly, the effect of enrichment on the average movement rate does not depend, qualitatively, on the number of patches impacted (p_i), only on their relative quality.

Type-IV functional responses may yield different predictions because they can be decreasing functions of resource level. In such cases, $h(n_{0i}) < h(\langle n_{0j} \rangle)$ if n_{0i} is greater, not smaller, than average. Predictions are thus reversed: enriching the poorest patches favours an increase in the optimal movement rate, and vice versa. This occurs at high enough resource levels, for which the gain functions have sigmoid shape (Fig. 1a). At lower resource levels, predictions are as for other functional responses.

These results help understand what happens if several patch-types are enriched simultaneously: the outcome will depend on whether poor or rich patches are most impacted. For instance, one natural way to enrich a heterogeneous habitat is to spread the enrichment effort evenly over all patches. Formally, this means $x_i = x_j$ for all i and j , corresponding to an impact vector parallel to the first diagonal (Fig. 4a). Poor and rich patches are all enriched with equal intensity, which we have seen has opposite effects on $\langle t_j^* \rangle$. However, since the poor patches are proportionally more impacted, the effects do not balance out: the poor patches dominate (see Supporting Information). The net result is thus to favour a decrease in the movement rate, compared to the prediction for a homogeneous habitat, as is visible in Fig. 4a, except for type-IV functional responses at high resource levels. Another interesting enrichment scenario is to have all patches impacted in equal proportion, so that the impact vector has elements x_j proportional to n_{0j} (Fig. 4a). In these conditions, the contributions of the different patch-types do balance out perfectly, and the response of movement always has the same sign (though possibly different magnitude) as in a homogeneous habitat (see Supporting Information). This can be verified in all panels of Fig. 4.

Overall, a heterogeneous habitat responds to enrichment just like a homogeneous habitat if only average patches are enriched, or if all patches are enriched by proportionally the same amount. These scenarios increase the mean of the resource distribution without otherwise changing its heterogeneity, as measured by the coefficient of variation (CV). The difference in predictions between homogeneous and heterogeneous habitats is thus determined by how enrichment affects the CV of the resource distribution (Fig. 4a). This prompts us to study the intrinsic effect of habitat heterogeneity on the optimal movement rate.

Effect of resource heterogeneity on movement rate

Whereas it is well established that in heterogeneous habitats individuals should spend more time on better patches (Stephens & Krebs 1986; Valone & Brown 1989; Wajnberg *et al.* 2000), it is not clear how the overall rate of movement

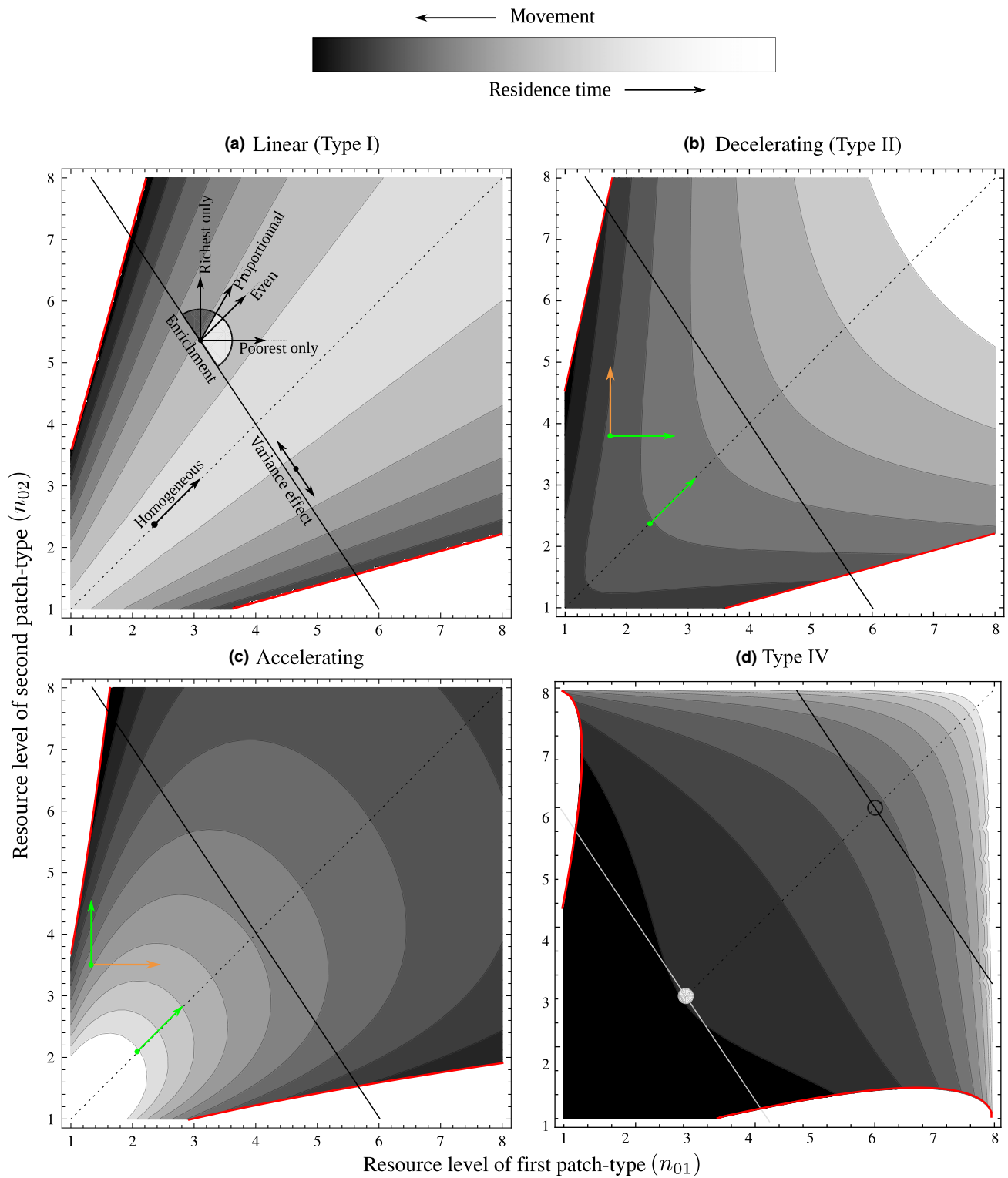


Figure 4 Heterogeneous habitats. Contour plots of the numerically computed average optimal residence time, for two patch-types of resource levels n_{01} (x -axis) and n_{02} (y -axis), and frequencies $p_1 = 0.6$ and $p_2 = 0.4$. Movement increases from white to black (legend). Functional responses as in Fig. 1a, with no foraging costs. Along the diagonal the habitat is effectively homogeneous. Possible enrichment scenarios (impact vectors) are illustrated in (a). Vectors in the white section decrease the coefficient of variation of resource levels, those in the shaded section increase it. The variance effect corresponds to moving along isolines of average richness (solid lines). In (b) and (c), enrichment scenarios that yield reversed predictions compared to a homogeneous habitat are highlighted (orange vectors; as opposed to green vectors). In (d), movement can increase (filled circle) or decrease (open circle) with heterogeneity. Red boundaries delineate pairs of patch-types that are both effectively exploited.

should vary with patch variance. To understand the intrinsic effect of heterogeneity, we can analyse the effect of making patches more or less similar, keeping the average resource level constant, i.e. a variance effect. This corresponds to having impact vectors parallel to an isoline of average richness (Fig. 4a). As this is not enrichment, some x_j values in the impact vector are negative, and ineqn 5 does not apply. However, predictions are even clearer (Supporting Information): the variation of $\langle t_j^* \rangle$ has the same sign as $\langle x_j/h(n_{0j}) \rangle$. Considering only two patches, the conclusion is that making them more dissimilar, i.e. increase patch variance, should always increase (decrease) the average movement rate, for increasing (decreasing) functional responses (see Supporting Information). This is consistent with our previous results, as enriching the richest patches and impoverishing the poorest were individually shown to favour an increase in the movement rate, with the exception of type-IV responses. The prediction is stronger though, since the sign of variation is predicted regardless of the concavity of the functional response. Here, what matters is the slope of the functional response.

Applying the argument to all pairs of patches in a habitat, we conclude that for a given average resource level, the optimal rate of movement is minimal when resources are distributed homogeneously, and increases with patch variance, except for type-IV functional responses at high resource levels. The prediction applies at the level of entire habitats: for the same average resource level, more heterogeneous habitats should generally cause individuals to move more. This is visi-

ble in the numerical results of Figure 4 (note that the pattern is inverted at sufficiently high resource levels in Fig. 4d). It also applies if only a few individual patches are manipulated in an otherwise constant habitat. In this case, the movement-promoting effect of patch variance is preserved, though slightly less pronounced than for whole habitats (Fig. 5).

DISCUSSION

The MVT offers a general theoretical connection between the attributes of patchy habitats and optimal movement strategies (Stephens & Krebs 1986). Residence times are an important aspect of individual life histories, amenable to observation and with definite connections to behaviour and decision-making (McNamara *et al.* 2006; Wajnberg 2006). Moreover, they determine the rate of movement, and thus the realised connectivity between the different parts of a landscape (Belisle 2005), ultimately affecting patterns at larger scales, such as the spatial spread of introduced populations or the magnitude of gene flow (Bowler & Benton 2005). In consequence, it is of great interest to understand how optimal residence times should respond to enrichment and vary with the distribution of resources. By coupling the MVT to an explicit resource consumption model, we obtained general predictions regarding how the optimal residence times, and thus the average movement rate, should vary with the level of resource and its distribution over patches. Two main results emerged: (1) the effect of enrichment can be predicted quite simply in terms of

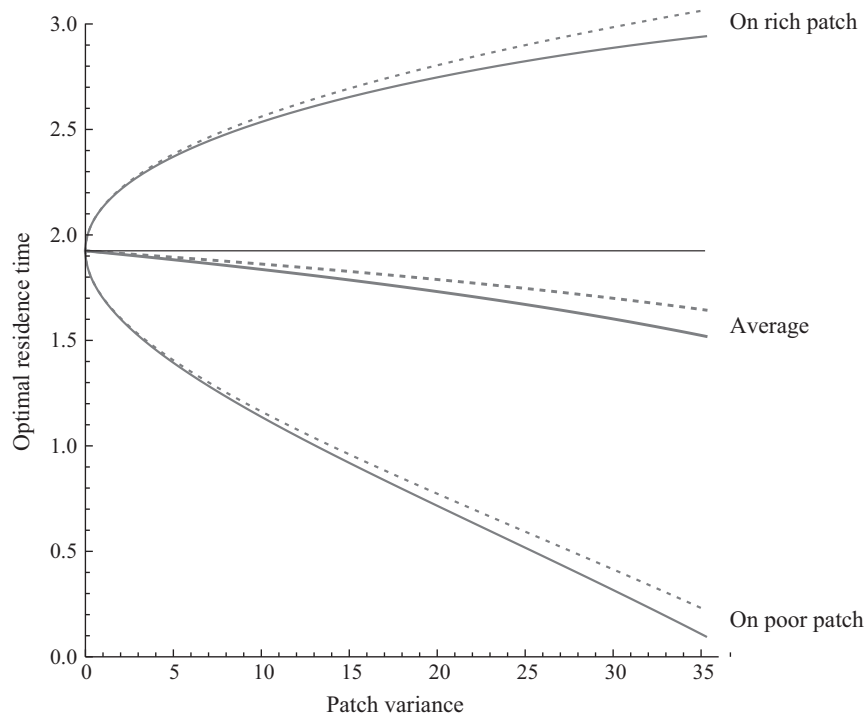


Figure 5 Variance effect. For increasingly dissimilar patch-types (x -axis), the optimal residence time on the richer patches, on the poorer patches and the average residence time $\langle t_j^* \rangle$ are shown. The average resource level is constant at $\langle n_{0j} \rangle = 6$. *Solid lines:* the two patch-types compose the entire habitat, in equal frequencies. *Dotted lines:* the two patch-types are just two individual patches, in an otherwise unchanged habitat. In both cases, the average residence time drops below its value in the homogeneous case (*horizontal dashed line*). Holling's type-II functional response; foraging costs within patches $v = 0.1$; travel time $T = 1.5$. Remember that the movement rate decreases with t^* .

the type of functional response, and (2) increasing habitat heterogeneity should in general cause an increased rate of movement.

Increasing the average resource level of habitat patches does not have a universal effect on the optimal rate of movement: the latter may vary in any direction. Though this was suspected from graphical intuition (Danchin *et al.* 2008), no general picture has emerged for lack of analytical tractability. Theoretical investigations had to stick with simple gain functions, for which it was reported that the optimal strategy was invariant to enrichment (e.g. Charnov & Parker 1995; Calcagno *et al.* 2014). Indeed, the most often used gain function $n_0(1 - \exp(-bt))$ amounts, in the context of resource consumers, to assuming a linear (type-I) functional response and no foraging costs, in which case enrichment has no effect on the optimal movement rate. However, this invariance here proved to be a knife-edge case. In general, an optimal forager should adjust its movement rate following enrichment, in one direction or the other, and this depends directly on the type of functional response: it should move less between patches if the functional response is decelerating (e.g. type-II), but move more if it is accelerating. One consequence of this is that sigmoid functional responses (e.g. type-III) cause the optimal movement rate to be maximised for some intermediate resource level (Fig. 3). This big picture can be shifted in one direction or the other when foraging costs are taken into account. Costs of foraging within patches (v) and costs of moving between patches (μ) make the optimal movement rate more likely to decrease or to increase with enrichment, respectively. Predictions remain unchanged if the two costs are similar, however ($\mu = v$).

It seems paradoxical at first that a forager should spend less time on patches that have been enriched, and thus waste proportionally more time moving between patches. What is even more paradoxical is that this outcome is most likely when costs of moving are high ($\mu > v$). This seemingly contradicts the more intuitive results that, in a given habitat, a forager should always stay longer on the better patches (Brown 1988; Wajnberg *et al.* 2000), and that greater costs of moving (higher μ) should make individuals more sedentary (Stephens & Krebs 1986). To understand this behavioural 'paradox of enrichment' (Rosenzweig *et al.* 1971), one must first realise that increasing the quality of patches does increase the rewards of staying longer in a patch, but simultaneously increases the rewards of moving to another patch. The net variation of the optimal strategy depends on the balance between these two forces (Calcagno *et al.* 2014). This metaphor helps understand the role of the functional response. An accelerating functional response is such that enrichment mostly boosts the rate of resource consumption in the early stages of patch exploitation, but not so much in later stages. This is because the shape of the function works against resource depletion, so that the rate of consumption varies less and less as time passes. On the contrary, with a decelerating functional response, the boost in consumption rate is modest in freshly entered patches, but more pronounced towards the end of patch exploitation. Hence, the rewards of moving to a new patch increase more in the first case, and that of staying longer in the local patch increase more in the second. Our

results indicate that the two forces cancel out only for linear functional responses and identical foraging costs; otherwise they may swing the balance either way. This balance of forces also explains the counterintuitive interaction between the cost of moving and enrichment. Indeed, with greater costs of moving, individuals move less frequently between patches, and thus relatively overexploit patches compared to the optimum in the absence of costs. Upon enriching patches, the increased rewards of moving to a fresh patch thus surpass the increased rewards of staying in an already overexploited patch, making the optimal rate of movement more likely to increase overall.

A second important result is the prediction that, all else equal, making resource levels more variable among patches (i.e. increasing patch variance) increases the optimal movement rate, under quite general conditions (Fig. 4). Previous theoretical MVT studies did not detect this variance effect of the resource distribution (Olsson & Holmgren 1999). When a heterogeneous habitat is enriched, the variance effect adds onto the enrichment effect discussed above, possibly confusing it. As an example, simulation studies often use Poisson or negative binomial distributions for resource levels, whose mean parameter is used to vary habitat richness (e.g. Olsson & Holmgren 1999; Wajnberg *et al.* 2013). Our results explain why in these simulations, despite assuming linear functional responses and no foraging costs, a decline in movement with enrichment is observed, contradicting analytical investigations (Charnov & Parker 1995). This is really not an enrichment effect, but rather a variance effect: a by-product of increasing the mean of such distributions is to decrease their coefficient of variation, and it is this reduced heterogeneity that causes the optimal movement rate to decline (see Fig. 4a). This indicates that the scaling of variance to mean is a critical property of the resource distribution in heterogeneous habitats.

Though correlational and experimental studies have often reported that individuals move faster through resource-depleted areas and spend more time in resource-rich areas (e.g. Avgar *et al.* 2013; Kuefler *et al.* 2013), it is not clear how these two effects should play out. Our results indicate that individuals would under-consider, i.e. quit faster, poor patches to a greater extent than they over-consider rich patches (Fig. 5). This effect is reminiscent, although in a different context, of the risk allocation hypothesis for foragers that alternate between low-risk and high-risk environments (Lima & Bednekoff 1999; Westneat & Fox 2010). It states that upon increasing the contrast between the two environments, individuals should decrease their feeding time (increase vigilance) in the disfavourable (high-risk) environment at a faster rate than increase their feeding time in the favourable (low-risk) environment, if a greater fraction of time is spent in the latter. In our model, there is added complexity as individuals adaptively control the time they spend in the different patch-types, but the end result is that they allocate more time to favourable (rich) patches. Hence, there is a striking similarity: individuals disregard the disfavourable condition (poor patches/high-risk environments) at a faster rate than they specialise onto the favourable (rich patches/low-risk environments). In our movement context, the net effect is to make individuals move more (sample more patches) when there is greater spatial heterogeneity in the distribution of resources. This is not

an expected result, considering that spatial heterogeneity in diffusion rate is in itself known to decrease the overall rate of spread (Shigesada & Kawasaki 1997). But heterogeneity in movement rate cannot be a substitute for heterogeneity in resource level, which underlines the importance of using explicit ecological models to connect resources and movement (Schick *et al.* 2008).

Interestingly, simulation studies of Bayesian foragers have observed that average patch residence time decreased with patch heterogeneity (Green 1980; Olsson & Holmgren 1999), in agreement with our general finding. Bayesian foraging models incorporate some realistic behavioural constraints and stochasticity in resource capture (McNamara *et al.* 2006). This causes some deviations from the ideal MVT predictions. In particular, Bayesian foragers do not respond as strongly to patch variance, and there remains a positive association between patch richness and GUD (Olsson & Holmgren 1999; McNamara *et al.* 2006). Such conservative strategies are frequently observed in animals (Valone & Brown 1989; Nonacs 2001). That the effect of habitat variance on average movement rate is nevertheless as expected from the MVT suggests it is a robust prediction.

Some experimental evidence indicates that habitat heterogeneity promotes overall movement. Food-deprived darkling beetles tended to have greater net movement when resources were disposed in a clumped manner rather than more uniformly in experimental fields (McKenzie *et al.* 2009). *Achillea millefolium* roots grew over greater total distance when soil was enriched as patches rather than homogeneous (McNickle & Cahill 2009). In artificial patchy mesocosms, Godbold *et al.* (2011) reported that net movement of various macroarthropods was greater when resource distribution was more heterogeneous. Though this is in general agreement with our prediction, data that explicitly connect resources and individual movements are still too rare to draw any conclusion, especially at the level of whole habitats (Avgar *et al.* 2013). It is thus important to stress that the prediction applies not only at the habitat level but also for any pair of patches within a given habitat (Fig. 5). Hence, standard experimental methods involving artificial patches with controlled resource content can be readily used to test the prediction, provided focus is on average residence time rather than giving-up densities (Valone & Brown 1989; Morris & Davidson 2000; Price & Correll 2001).

In summary, we showed that the distribution of resources has two distinct effects on the optimal movement rate: (1) an average effect, and (2) a variance effect. Both are strongly conditioned by the shape of the functional response, though in different ways. The average effect can be positive or negative, depending on the concavity of the functional response (i.e. decelerating, linear or accelerating). The variance effect can also be positive or negative, but this depends on the slope of the functional response (i.e. decreasing or not). Both effects operate simultaneously when enriching heterogeneous habitats, so that enrichment can have contrasted effects depending on the variance-to-mean scaling.

Since type-II functional responses are considered to be by far the most common (Jeschke *et al.* 2002), increasing the

average level of resource and its variance are both expected to decrease movement quite generally. However, there is ample variation among taxa (Jeschke *et al.* 2004). Type-III functional responses are not so uncommon, especially in invertebrates, and for such organisms a non-monotonous effect of enrichment on movement rate can be expected. The effect of enrichment should be weakest and most variable for organisms that harbour type-I functional responses, such as filter-feeders, while organisms with type-IV responses could respond differently to the level of habitat heterogeneity depending on the average resource level. Our results show that the functional response is central in determining the response of optimal foragers to the resource level in their habitat, as it is central in determining the temporal dynamics of consumer–resource interactions in population and community ecology. We suggest that further coupling of optimal foraging studies and explicit consideration of the functional response (e.g. Price & Correll 2001; Nolet & Klaassen 2009; Avgar *et al.* 2011) would be beneficial, and may help explain some of the observed variability. By linking MVT and consumer–resource theories, we hope to stimulate investigations of how changes in resource distributions impact movement strategies in fragmented habitats.

ACKNOWLEDGEMENTS

We thank Jacques Brodeur for discussions. VC was funded by INRA, project AAP-SPE-2012-04-05-20.

AUTHORSHIP

LM, FG & EW initiated the work. VC conducted the research with LM & FG. VC wrote the manuscript with input from all authors.

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Editor, David Hosken

Manuscript received 28 July 2014

First decision made 18 August 2014

Manuscript accepted 11 September 2014