Linking Rates of Diffusion and Consumption in Relation to Resources

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ABSTRACT: The functional response is a fundamental model of the relationship between consumer intake rate and resource abundance. The random walk is a fundamental model of animal movement and is well approximated by simple diffusion. Both models are central to our understanding of numerous ecological processes but are rarely linked in ecological theory. To derive a synthetic model, we draw on the common logical premise underlying these models and show how the diffusion and consumption rates of consumers depend on elementary attributes of naturally occurring consumer-resource interactions: the abundance, spatial aggregation, and traveling speed of resources as well as consumer handling time and directional persistence. We show that resource aggregation may lead to increased consumer diffusion and, in the case of mobile resources, reduced consumption rate. Resource-dependent movement patterns have traditionally been attributed to area-restricted search, reflecting adaptive decision making by the consumer. Our synthesis provides a simple alternative hypothesis that such patterns could also arise as a by-product of statistical movement mechanics.

Keywords: functional response, random walk, area-restricted search, consumer resource, diffusion, predator-prey.

Introduction

A major purpose of animal movement is to acquire resources. Indeed, several recent theoretical studies of movement, such as studies of Lévy walks or multiphasic random walks, focus on adaptive movement strategies that increase and perhaps even maximize the rate of resource encounter (Grünbaum 1998; Benhamou 2007; Bartumeus et al. 2008; James et al. 2008; Reynolds and Rhodes 2009). Despite the intimate relationship between the study of animal movement and that of consumer-resource interactions, formal links between the two fields are rare, perhaps due to the enormous complexity inherent in spatially explicit processes. Simple kinetic mechanisms (e.g., klinokinesis and or-

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thokinesis; Gunn 1975; Benhamou and Bovet 1989) are extremely useful in linking consumer movement rates to local resource abundance and thus in predicting the spatial distribution of consumers in a heterogeneous environment (Patlak 1953; Turchin 1991; Wilson and Richards 2000). However, the explicit mechanism underlying the regulation of speed or turn frequency in response to resources is often not postulated, thus hampering our ability to derive the process from first principles. An exception is a study by Kareiva and Odell (1987; followed by a theoretical investigation by Grünbaum 1998), which provided an empirically derived functional relationship between turn frequency and satiety. Here we take an alternative approach, one based on the common logic underlying two fundamental ecological models (Turchin 2001), the functional response and the random walk. Our aim is to provide a fresh perspective on the mechanistic relationship between rates of movement and consumption and to argue that naturally occurring movement patterns might be usefully viewed in light of this relationship.

The functional response relates a consumer's intake rate to the availability of resources (Solomon 1949). This concept is fundamental to our understanding of many ecological and evolutionary processes, such as optimal foraging, population regulation, and food web stability (Oaten and Murdoch 1975; Dunbrack and Giguere 1987; Turchin 2001). An explicit mathematical form of the functional response was formulated independently by Holling (1959) and by Rashevsky (1959). Although many alternative mathematical formulations have been suggested (e.g., Abrams and Ginzburg 2000; Jeschke et al. 2002 and references therein), Holling's type I and II are the most common forms observed in real systems, having been documented dozens of times (Jeschke et al. 2002). Both functional-response equations rely on the implicit assumption that the rate of resource encounter (per unit search time) is constant over space and time. Hence, consumers are assumed to travel through a field of randomly distributed resources at a constant speed, with straight, randomly ori-

ented trajectories between sequential resource encounters (McKenzie et al. 2009). Indeed, paths of straight movement with appreciable distances have been documented in several organisms in a variety of different habitats (Turchin 1998), including army ants in Panama's rain forest (Franks and Fletcher 1983), elk in Canada's boreal forests (Morales et al. 2004), and various marine predators (Sims 2008).

The most fundamental model of animal movement is the random (or Brownian) walk (Codling et al. 2008; Nathan et al. 2008), which assumes that animals move through space in a series of straight, randomly oriented steps (Berg 1983; Kareiva and Shigesada 1983; Turchin 1998; Codling et al. 2008). The assumptions underlying the random-walk model are therefore identical to those governing consumer search rate in functional-response models. Diffusion is a continuum approximation of the discrete random-walk process, where the diffusion coefficient is the determining metric describing the rate of population spread (Turchin 1998). In many applications, the diffusion coefficient is assumed to be constant. However, if diffusion rates vary with local environmental conditions, the resultant spatial distribution of the population would reflect the underlying pattern of environmental heterogeneity (Patlak 1953; Cosner 2005). Hence, the diffusion approximation provides a crucial link among the behavior of individual consumers, spatial heterogeneity of resources, and the resulting spatial distribution of the consumer population (Turchin 1991; Cosner 2005). We use the logical linkage between the random-walk model and the functional-response model to derive the diffusion coefficient of a consumer as functions of the abundance, spatial aggregation, and traveling speed of resources as well as of consumer directional persistence.

Models

Using both analytical and simulation methods, we explore several possible scenarios involving consumer-resource interactions that are broadly representative of many real organisms. In the first scenario, which is simple enough to allow a closed-form solution of the model, we consider static resources that are distributed randomly in space. Consumers are assumed to travel along straight paths until they encounter a resource item, at which point a new travel direction is randomly sampled from a uniform distribution. In the second scenario, which also allows a closed-form solution, we assume that both resources and consumers are mobile, moving in randomly oriented but straight paths across a featureless landscape. The third scenario, which requires computer simulation rather than a closed-form solution, relaxes the assumption of a uniform random resource distribution, comparing outcomes for

various levels of spatial aggregation of resources. The fourth scenario relaxes the assumption of straight movement paths by the consumer, assuming instead that consumers travel according to a correlated random walk (CRW) with a varying degree of directional persistence. This scenario reflects the realistic attribute that animal movement paths are often rather convoluted even when foraging is not involved (Turchin 1998; Nathan et al. 2008).

Scenario I: Randomly Distributed, Static Resources

Simple random walks are characterized by a linear increase of an individual's squared displacement over time. The expectation for this squared displacement, $E(R^2)$, after time t, can be expressed as a function of the mean duration of a single step, $E(\Delta t)$, and the mean squared step length, $E(x^2)$:

$$E(R^2) = \frac{t}{E(\Delta t)} E(x^2). \tag{1}$$

We accordingly derive the expected squared displacement of a consumer by expressing $E(\Delta t)$ and $E(x^2)$ as functions of resource density.

As in Holling's (1959) functional-response models, we assume that consumption events occur whenever a resource item falls within the perception range of a consumer moving in straight lines. We further assume that the consumer's trajectory is truncated when it encounters a resource item, and thus it performs an instantaneous random reorientation after each encounter.

The elapsed time between consecutive encounters of such a consumer, moving at a constant speed, with randomly distributed, immobile resources is exponentially distributed with rate parameter $\lambda_{\Delta t}$. This rate parameter is the product of the effective radius (or the perception range) r, the speed of the consumer v, and the resource density ρ:

$$\lambda_{\Delta t} = 2rv\rho. \tag{2}$$

Note that $2rv$ is also known as the attack rate, sensu Holling (1959). This derivation holds even if the speed is variable, as long as it is sampled from a Maxwell-Boltzmann distribution with mean v (Hutchinson and Waser 2007).

The expected time between successive encounters is

$$E(\Delta t) = \frac{1}{2rv\rho}. \tag{3}$$

If the consumer handles each encountered resource item for a time h before renewing its search, then the expected time between successive encounters is

$$E(\Delta t) = \frac{1}{2rv\rho} + h. \tag{4}$$

Note that the inverse of the step duration is the expected consumption rate, so the reciprocals of equations (3) and (4) are in fact type I and type II functional responses (Holling 1959), respectively.

Similarly, the distance traveled between successive encounters (i.e., the step length) is exponentially distributed with rate parameter λ_x:

$$\lambda_x = 2r\rho. \tag{5}$$

The expectation for the step length is thus

$$E(x) = \frac{1}{2r\rho}, \tag{6}$$

and the expectation for the squared step length is

$$E(x^2) = \frac{1}{2r^2\rho^2}. \tag{7}$$

Note that h is not considered time spent traveling, and so $E(x)$ and $E(x^2)$ are identical for type I and type II consumers.

By substituting equations (3) and (7) into equation (1), we can express the expected mean squared displacement $E(R^2)$ of a type I consumer moving through (and interacting with) a field of randomly distributed resources as a function of the resource density ρ:

$$E(R^2) = \frac{tv}{\rho r}. \tag{8}$$

Similarly, the expected mean squared displacement of a type II consumer is expressed by substituting equations (4) and (7) into equation (1):

$$E(R^2) = \frac{tv}{\rho r(1 + 2\rho rvh)}. \tag{9}$$

Thus, under the assumptions outlined above, resource locations are synonymous with potential turning points of a consumptive random walker.

Einstein (1905) linked the Lagrangian mean squared displacement of randomly moving particles to the corresponding Eulerian diffusion rate (in two dimensions):

$$E(R^2) = 4tD, \tag{10}$$

where D is the diffusion coefficient. It is thus possible to express the diffusion coefficient of ideal consumers as a function of resource density by substituting equation (8) (for type I consumers) or equation (9) (for type II consumers) into equation (10):

$$D = \frac{v}{4\rho r}, \tag{11}$$

$$D = \frac{v}{4\rho r(1 + 2\rho rvh)}. \tag{12}$$

Hence, our model predicts that diffusion rates should be inversely related to resource density, regardless of whether the consumer has a linear (type I; $h = 0$; eq. [11]) or a hyperbolic (type II; $h > 0$; eq. [12]) functional response.

Scenario II: Randomly Distributed, Mobile Resources

If resources travel at exactly the same constant speed as the consumer, the only required modification is the multiplication of the relative speed (the speed of the consumer relative to the resources) by the constant $4/\pi$ (Hutchinson and Waser 2007). Hence, for a type II consumer, the functional response is now expressed as

$$\frac{1}{E(\Delta t)} = \frac{(8/\pi)vr\rho}{1 + (8/\pi)vr\rho h}, \tag{13}$$

whereas the diffusion coefficient becomes

$$D = \frac{\pi v}{16\rho r[1 + (8/\pi)\rho rvh]}. \tag{14}$$

Alternatively, both consumers and resources may have variable movement speeds sampled from independent Maxwell-Boltzmann distributions, with expectations given by $v_{consumer}$ and $v_{resource}$, respectively (Skellam 1958; Hutchinson and Waser 2007). Under these conditions, the mean relative speed $\bar{v}$ is defined as

$$\bar{v} = \sqrt{v_{consumer}^2 + v_{resource}^2}, \tag{15}$$

and the type II functional response is

$$\frac{1}{E(\Delta t)} = \frac{2r\bar{v}\rho}{1 + 2r\bar{v}\rho h}. \tag{16}$$

As long as there is no correlation between speed and step length, the diffusion coefficient can be expressed as

$$D = \frac{v_{consumer}^2}{4r\bar{v}\rho(1 + 2r\bar{v}\rho h)}. \tag{17}$$

Scenario III: Aggregated Resources

We used computer simulations to consider modifications to the ideal-gas-based model presented thus far. The first modification relates to the effect of resource spatial distribution (rather than just mean density) on rates of diffusion and consumption of a type II consumer (see app. B, available in a zip file, for the full Matlab simulation

code). We employed a Neyman-Scott point process (Neyman and Scott 1952; Ripley 1977) to generate nonhomogeneous distributions of resources with different levels of spatial aggregation. Two variables determine the aggregation level in a Neyman-Scott point pattern: the standard deviation of the Gaussian location of resource items within a clump and the mean of the Poisson-distributed clump size (i.e., the number of resource items per clump). In the results presented here, aggregation was varied by changing the latter while keeping the former constant (0.01 spatial units).

Our simulation procedure is designed to estimate the distance traveled by a mobile consumer between consecutive consumption events across nonhomogeneous resource landscapes. Each simulation begins with the generation of a Neyman-Scott point pattern of resources within a two-dimensional domain. Neyman-Scott clusters are added at randomly placed positions in space until the overall point density in the entire domain reaches the desired value (100 resource items per unit area). The focal simulation arena is located in the center of this domain. In accordance with the assumptions of the analytical model, in which steps always begin and end with consumption events (James et al. 2010), a randomly chosen resource within the simulation arena is assigned as the starting point for the consumer. The consumer is then assumed to travel along a vertical corridor of width $2r$. The nearest occurrence at which a resource item falls within this corridor is noted, the distance traveled is recorded, and the simulation is terminated. Should the consumer reach the boundary of the simulation arena before encountering a resource, the corridor is extended into a new focal arena embedded within an extension of the spatial domain. This process is repeated for 10,000 replicated search trajectories.

To calculate diffusion rates, we focus on a type II consumer traveling at a constant speed in accordance with the ideal-gas assumptions. For each simulated step-length distribution, we estimated $E(\Delta t)$ and $E(x^2)$, substituted these values into equation (1) to determine $E(R^2)$, and then used equation (10) to calculate the diffusion rate. To verify that the values derived through equations (1) and (10) accurately describe simulated diffusion rates, we independently simulated 10 trajectories of 1,000 consumption events each. The diffusion coefficient of each trajectory was calculated directly by dividing the observed squared displacement by four times the duration of the trajectory, and the resulting values were plotted against the mean field approximations derived through equations (1) and (10) (see app. A in the online edition of the *American Naturalist*).

To address the possibility that mobile resources have a heterogeneous distribution, we assume that resource mobility is sufficient to allow for complete remixing of the

system during the time required to handle a single resource. By the time the consumer renews its search, its location is accordingly independent of the location of all resource clusters. Hence, instead of originating from a resource item, consumers in these simulations originated from a random point in space. Consumer speed was multiplied by $4/\pi$ to account for resource mobility (see "Scenario II: Randomly Distributed, Mobile Resources" above). Otherwise, steps were simulated in the exact same manner as described above. Note that this simulation approach is suitable only when the position of the consumer is assumed independent of all other system components at the beginning of each step (James et al. 2010).

Scenario IV: CRW Consumers

So far we have assumed that animals move along perfectly straight paths until they encounter a resource. Here we use computer simulations to consider a more realistic pattern of consumer movement (see app. C, available in a zip file, for the full Matlab simulation code). Consumer movement between resource encounters was simulated as a correlated random walk with steps of constant length (0.001 spatial units) across an infinite two-dimensional space. The direction of each step was randomly drawn from a Von Mises distribution with concentration parameter k, where the value of k determines the directionality of the movement. This k is inversely proportional to the sinuosity of the movement path (sensu Benhamou 2004), so that $k = \infty$ corresponds to pure straight-line motion between resource encounters (as in all previous scenarios). As before, a consumption event occurs whenever a resource item is within the consumer's detection range (0.0001 spatial units), and each consumption event leads to reorientation. Each consumed resource is immediately replaced by a new, randomly positioned resource item. Diffusion and consumption rates were calculated, using equations (1) and (10), on the basis of a sample of 1,000 consumption events for different resource densities and different k values.

Results

Scenario I: Randomly Distributed, Static Resources

Consumption rates increased with resource density (eqq. [3], [4]). The form of this response was linear, in the case of a type I functional response, or decelerating as the consumption rate approached the asymptote (h^{-1}), in the case of a type II functional response (fig. 1*a*). An increase in the rate of resource acquisition was accompanied by increased tortuosity of the movement path, resulting in an exponentially declining function for consumer diffusion
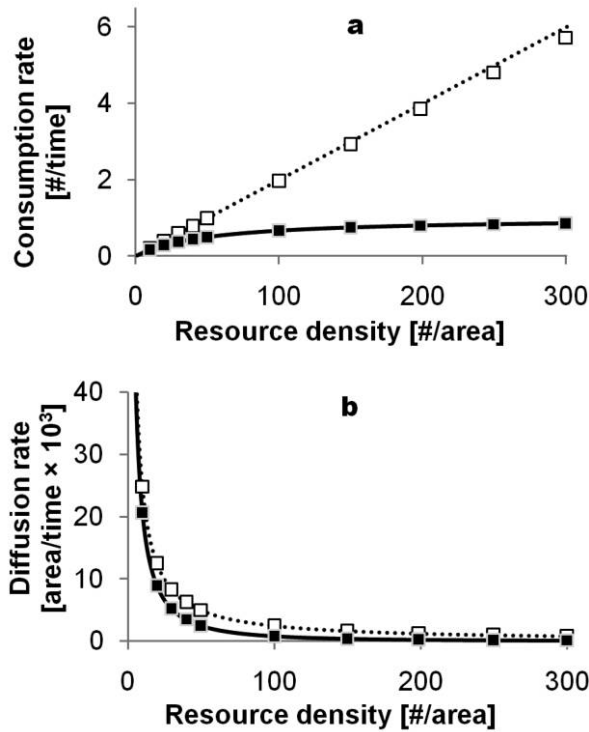
Figure 1: Predictions of the closed-form scenario I model for consumption (*a*) and diffusion (*b*) rates as functions of resource density (dashed and solid lines represent type I and type II consumers, respectively). Open and filled squares represent results of numerical simulations of the diffusion-consumption process for type I and type II consumers, respectively, who are searching for randomly distributed, immobile resources. Parameter values are as follows: $r = 0.0001$, $h = 1$, $v_{\text{consumer}} = 100$, $v_{\text{resource}} = 0$ (see app. B, available in a zip file, for simulation code).

rates that asymptotically approaches zero at high resource densities (fig. 1*b*). Increased resource density dampened movement rates more severely in type II than in type I functional responses (fig. 1*b*), simply because of the additional time spent handling resources (eqq. [11], [12]). Hence, high resource density enhanced consumption, whereas it suppressed diffusion rates due to the mechanical truncation of the movement trajectory.

Scenario II: Randomly Distributed, Mobile Resources

The incorporation of resource mobility (eqq. [13]–[17]) did not fundamentally change these predictions. While the consumption rate of type I consumers was extremely sensitive to changes in resource speed, this was rarely the case for type II consumers because consumption rates were usually limited by handling time (fig. 2*a*). Diffusion rates of both consumer types decreased with resource speed due

to increased resource encounter rates (fig. 2*b*). In any case, resource mobility per se reinforced but otherwise had no qualitative effect on the trends predicted by our model and presented in figure 1.

Scenario III: Aggregated Resources

When resources were not aggregated (i.e., a Neyman-Scott point pattern with a constant clump size of 1; fig. 3*a*, 3*b*, *left-hand sides*), our simulation results were in full agreement with the results of the analytical models (scenarios I and II; fig. 1). However, once resources became aggregated, consumer diffusion rates increased with the level of resource aggregation (fig. 3*b*). This increase is the result of the modified distribution of step lengths with increased frequency of very short steps (within resource clusters) and very long steps (between resource clusters). This in-
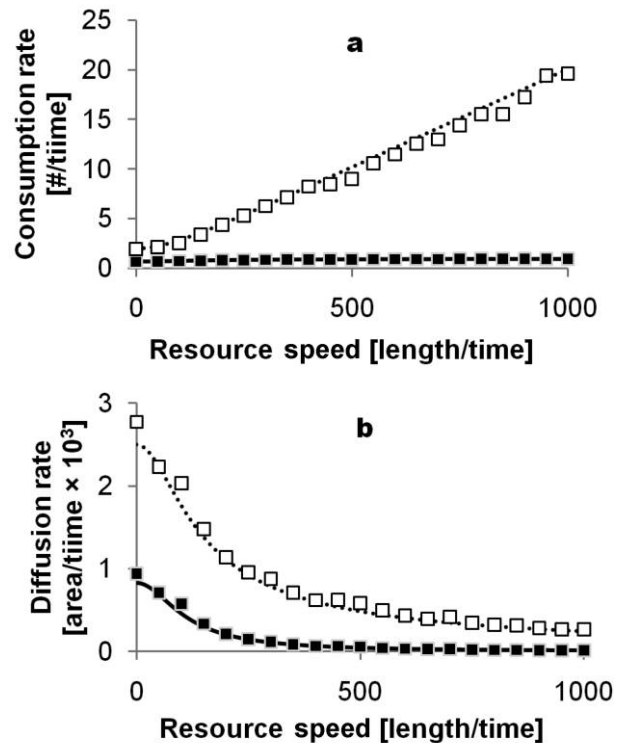

Figure 2: Predictions of the closed-form scenario II model for consumption (*a*) and diffusion (*b*) rates as functions of resource speed. Dashed and solid lines represent type I and type II consumers, respectively. Open and filled squares represent results of numerical simulations of the diffusion-consumption process for type I and type II consumers, respectively, who are searching for randomly distributed, mobile resources with Maxwell-Boltzmann distributed speeds. Parameter values are as follows: $r = 0.0001$, $h = 1$, $v_{\text{consumer}} = 100$, $\rho = 100$ (see app. C, available in a zip file, for simulation code).
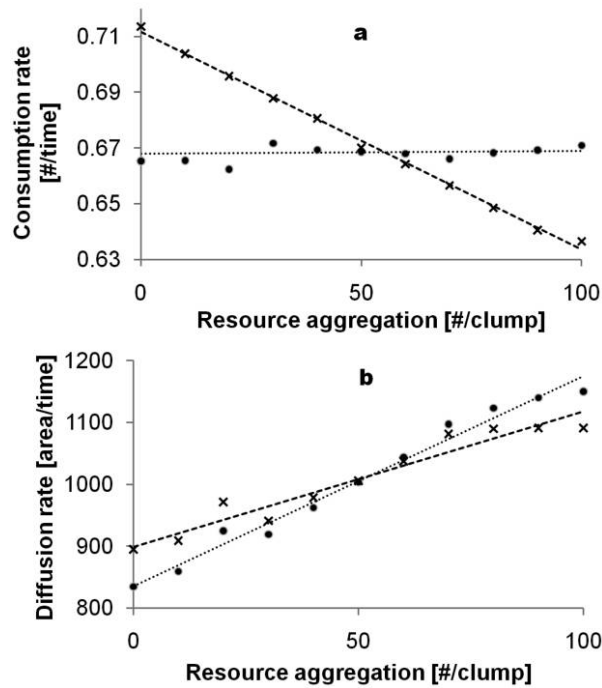
Figure 3: Simulated consumption (*a*) and diffusion (*b*) rates for type II consumers as functions of resource aggregation. Variable levels of resource aggregation were generated by varying the mean clump size of the Neyman-Scott process while holding constant the standard deviation of the within-clump dispersal and the mean resource density over the entire landscape ($\sigma = 0.01$ and $\rho = 100$, respectively). A null clump size (*left-hand side*) corresponds to a random distribution of resources as assumed in the ideal gas–based model (see also figs. 1, 2). Each circle and each X represents a result for immobile ($v_{resource} = 0$) and mobile ($v_{resource} = 100$) resources, respectively. Dotted and dashed trend lines represent linear regressions based on results for immobile and mobile resources, respectively. Other parameter values are as follows: $r = 0.0001$, $h = 1$, $v_{consumer} = 100$ (see app. B, available in a zip file, for simulation code).

creased the variance of the step-length distribution, resulting in increased $E(x^2)$ and thus increased D.

Despite strong effects of resource aggregation on consumer diffusion rates, consumption rates were insensitive to resource aggregation as long as resources were immobile (fig. 3*a*). While the consumption rate of nonaggregated, mobile resources (fig. 3*a*, *left-hand side*) was well predicted by the analytical model (eq. [13]), consumption rates of mobile resources decreased as the level of resource aggregation increased (fig. 3*a*).

Scenario IV: CRW Consumers

Results from our numerical simulations indicated that consumption rates were relatively insensitive to consumer directionality, as reported in some previous studies (e.g.,

Hutchinson and Waser 2007; McKenzie et al. 2009; James et al. 2010; but see Scharf et al. 2006; Bartumeus et al. 2008 for different model variants). Only for highly tortuous paths (i.e., low *k* value) were there appreciable reductions in consumption rates compared with those predicted by the analytical model (fig. 4*a*, 4*b*). For a type I consumer, the suppressive effect of tortuous movement on consumption rates was proportionate to resource density (fig. 4*a*). However, this was not the case for a type II consumer, because the asymptotic limit imposed by handling time buffered the effects of movement directionality (fig. 4*b*).

On the other hand, consumer diffusion rates were extremely sensitive to movement directionality. For consumers traveling along highly directional paths, diffusion rates declined exponentially with resource abundance in a manner that was well predicted by our scenario I analytical model (fig. 4*c*, 4*d*). However, even mild deviation from straight-line movement resulted in depressed diffusion rates that were much less sensitive to resource density (fig. 4*c*, 4*d*). Regardless of the functional-response type, at low resource densities or for consumers with highly tortuous movement paths, the diffusion rate was determined solely by directionality. It was only when either directionality or resource density were very high that consumer diffusion became sensitive to resource density (fig. 4*c*, 4*d*).

Discussion

Consumers ranging from bacteria (Berg 2000) to wildebeest (Holdo et al. 2009) tend to linger in areas of high resource abundance. Movement rates have been accordingly suggested as a proxy for delineating profitable areas within the landscape (Barraquand and Benhamou 2008). Numerous empirical studies have demonstrated slower, more tortuous movements in habitats with abundant resources (Klaassen et al. 2006; Kuefler and Haddad 2006; de Knegt et al. 2007; Weimerskirch et al. 2007; Fryxell et al. 2008; Westerberg et al. 2008; Dias et al. 2009; Kuefler et al. 2010). It is often assumed that such nonrandom movement patterns are the result of an adaptive behavioral response to local resource abundance, commonly termed area-restricted search (Tinbergen et al. 1967), in which the consumer decides to decrease speed (orthokinesis) or increase turning angle (klinokinesis) after encountering a resource patch (Jander 1975; Pyke et al. 1977; Kareiva and Odell 1987; Benhamou and Bovet 1989; Biesinger and Haefner 2005 and references therein). Our model offers an alternative mechanistic explanation.

We have demonstrated that under a wide range of conditions, the rate of diffusion should be strongly influenced by resource density even without any decisive behavioral response to resource abundance or spatial heterogeneity.
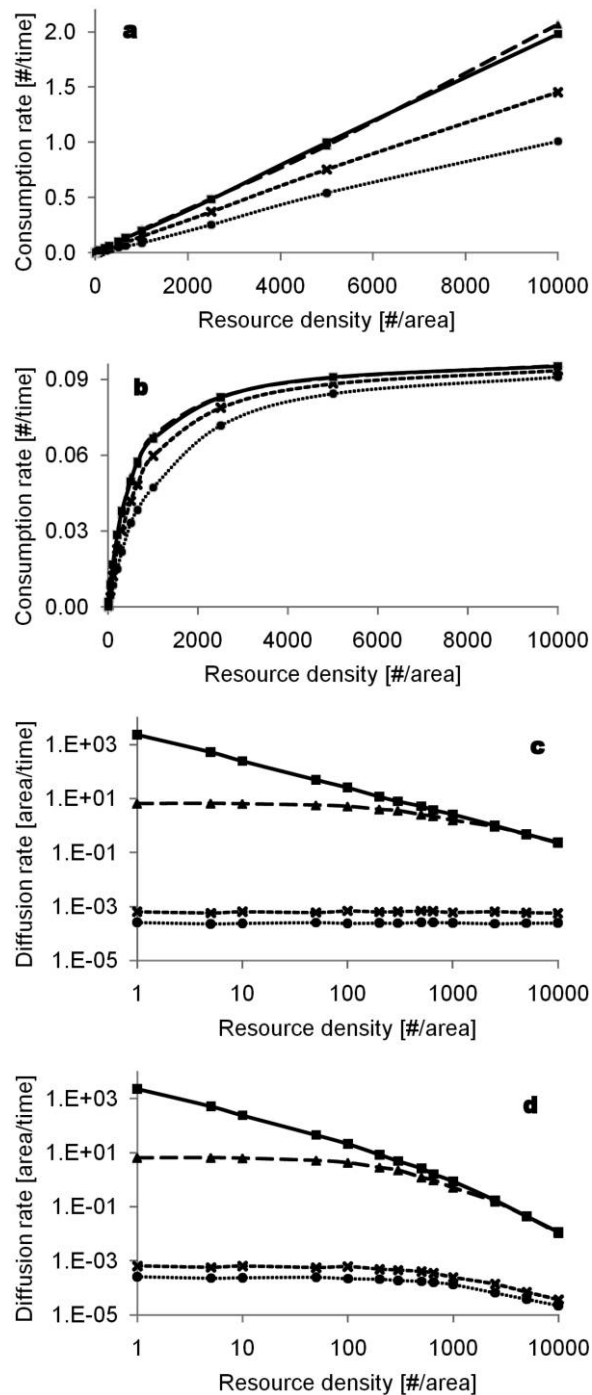
Figure 4: Simulated consumption (*a, b*) and diffusion (*c, d*) rates as functions of resource density for type I (*a, c*) and type II (*b, d*) consumers with four levels of directionality: $k = \infty$ (straight-line movement; *squares*), $k = 5{,}000$ (high directional autocorrelation; *triangles*), $k = 1$ (low directional autocorrelation; *Xs*), and $k = 0$ (pure random walk; *circles*). Note that all axes are log scaled. Other parameter values are as follows: $h = 10$, $r = 0.0001$, $v_{consumer} = 100$, $v_{resource} = 0$ (see app. D, available in a zip file, for simulation code).

It is an inevitable by-product of statistical movement mechanics, provided that new directions are sampled at each resource encounter. Movement trajectories generated by our model result in resource-dependent shifts in step-length and turn-angle distributions that are similar to those commonly interpreted as adaptive decision-based foraging strategies. Therefore, our model might be regarded as a null model against which behavioral decision-making hypotheses might be evaluated.

Increased sinuosity following resource encounters is an efficient adaptive strategy for the utilization of patchy resources (Benhamou 2007). In terms of maximizing intake rate, such a strategy is expected to outperform orthokinesis (due to the correlation between speed and encounter rate) and is certainly superior to the simple mechanistic effect demonstrated here. We are not rejecting the notion of area-restricted search via klinokinesis as an adaptive behavioral strategy. Rather, we suggest that inferring such a process on the basis of empirical data requires more substantial evidence than a simple demonstration that turn-angle or step-length distributions vary with local resource abundance. It is by coupling movement data with secondary information, such as the actual locations of resources or foraging activity (e.g., Heinrich 1979; White et al. 1984; Ward and Saltz 1994; Fortin 2003; Fryxell et al. 2008) or the giving-up density (e.g., Brown 1999; Kotler et al. 2004), that the behavioral or cognitive processes underlying emerging movement properties should be investigated.

Our examination of the effects of resource aggregation suggests that consumption rates should be substantially reduced when resources are both aggregated and mobile (e.g., fish schools or ungulate herds). Interestingly, this result appears to disagree with previous theoretical findings by James et al. (2010), who concluded that the functional response should be insensitive to resource spatial aggregation (note that for immobile resources, our results support this conclusion). This apparent discrepancy stems from our explicit inclusion of a handling time, during which the consumer is immobile (a component that was not included in James et al. 2010). As resource groups continue to move during this period of consumer immobility, the consumer effectively initiates each new search from a random position in space relative to other resource groups, including the one that was encountered last. Consequently, the consumer experiences a de facto resource density that is lower than the overall mean density (clusters are by definition less abundant than isolated individuals). This pattern, intuitive as it may be, may play an important role in stabilizing consumer-resource interactions. For example, group formation reduces the overall predation pressure experienced by Serengeti wildebeest, potentially stabilizing their interaction with lions (Fryxell et al. 2007).

Our work provides simple mechanistic understanding of such group-dependent functional responses.

While the analytical null model presented here relies on a highly simplified view of animal movement, it is consistent with the implicit assumptions underlying Holling's functional-response models and the ideal-gas law. In nature, many animals do not travel along straight trajectories but instead alter their courses for reasons other than resource encounter. Our simulations incorporating more realistic movement models on the basis of correlated random walks suggest that the degrees to which diffusion and consumption rates vary with consumer directionality should depend on resource density. When resources are abundant, movement patterns are largely governed by resource encounters. On the other hand, when resources are sparse, movement patterns are determined by the internal capacity to maintain directionality.

To conclude, our models incorporate fundamental attributes of naturally occurring consumer-resource interactions such as resource aggregation and mobility and consumer directionality. We provide simple null mechanisms that explain several empirically observed phenomena, including decreased movement rates in preferred habitats (e.g., Kuefler and Haddad 2006), selective use of resource-rich patches (e.g., Cameron and Spencer 2008), and reduced consumption rates of mobile, aggregated resources (Fryxell et al. 2007). We show that diffusion rates and consumption rates are inextricably linked through common effects superimposed by resource density, heterogeneity, and mobility. Hence, all three interacting factors are consequently important determinants of ecosystem dynamics.

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