How vigilance shapes the functional response of herbivores

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Abstract

1. Herbivores in quest of food have to attend areas where predators also concentrate their attacks. They have to deal with two conflicting demands, the need of feeding and that of avoiding predation. Using a theoretical approach, we study the influence of these antagonistic constraints on the shaping of an herbivore's foraging strategy and their consequences in terms of functional response.
2. In our model, the animal may curtail predation risk by being vigilant while foraging and by limiting its time of presence in the feeding area. Being vigilant means either stopping all feeding activities to scan for predators (exclusive vigilance) or using the time spent handling resources to do so, with reduced detection capacities (routine vigilance). Using an optimization criterium, we thus determine how long the animal will stay in the feeding area and how it will share its time and attention while present there, as a function of resource density and predation risk.
3. All behavioural variables show smooth but sometimes non-monotonic variations in response to changes in these environmental conditions. When these variations are taken into account, the instantaneous intake rate of the herbivore, as well as the total biomass of plant consumed, increase in a decelerating but continuous manner with the patch's richness, in qualitative agreement with a type II functional response. This smooth pattern is explained by the possibility for the herbivore, when food abundance rises, to progressively redirect its attention to routine antipredator vigilance.
4. The relative importance of routine vigilance with respect to exclusive vigilance declines when predation risk increases, as well as the duration of the patch's visit and the total quantity of food eaten. The exact shape of the functional response is thus mediated by subtle adjustments of behavioural and attentional priorities, in response to variations in both food availability and predation risk.

Keywords

Antipredator strategies, foraging strategies, functional response, herbivores, predators, trophic cascades, vigilance.

Introduction

Functional response, that is, the relationship between the quantity of resource available and the quantity actually eaten by each consumer, is a major driver of population dynamics (Gotelli, 2008). Identifying realistic functional responses remains challenging, however, because many activities interfere with feeding and influence individual intake rates in the wild (e.g., Skalski & Gilliam, 2001). Antipredator defense, in particular, can monopolize large portions of foraging time and influence both the time spent in the feeding area and the quantity of food collected by each individual (e.g., Hochman & Kotler, 2007). Its effects on an animal's functional response may thus be high (Fortin et al., 2004a; Baker et al., 2010).

The question of relative investment in feeding and in antipredator defense is particularly acute in wild herbivores, which must devote long periods to foraging every day (e.g., Mysterud, 1998), during which they are often exposed to high levels of threat (e.g., Mónus & Barta, 2016). The activities of a foraging herbivore indeed encompass a set of combined decisions simultaneously related to its metabolic needs, to the characteristics of plant patches, and to the modalities of predator activity (e.g., Pöysä, 1987; Berger-Tal et al., 2010; Blanchard et al., 2018).

Within this context, the way the animal gathers information about its environment is of major importance, for different and conflicting reasons. First, attention dedicated to the food patch allows a forager to locate resources or advantageous feeding places (Underwood, 1982). Second, observation of the surroundings, through vigilance, gives a better chance of detecting and escaping predators (Lind & Cresswell, 2005). Although an animal may sometimes receive concomitant signals of different nature (Lima & Bednekoff, 1999), it cannot respond to each of them with maximal efficiency. All depends on the way its attention is shared, which reflects its priorities (Dukas & Kamil, 2000, Hochman & Kotler, 2007).

The present study deals with this question, by investigating the topic of time- and attention sharing strategies for a foraging herbivore exposed to predation, and its functional consequences. To this end, we use a theoretical approach and take into account different features of herbivore behaviour which, to our knowledge, have both received empirical support and motivated theoretical inquiry, but have not been merged within a common theoretical framework.

First, we consider that an herbivore may respond to predation threat both by limiting the time it spends in the foraging area, where predators often concentrate their attacks (Valeix et al., 2009), and by being more vigilant while present in this area (Lendrem, 1983). Considering these two possibilities does indeed considerably enlarge the panel of possibilities for the animal's responses to predators' presence (Brown, 1999; Sirot, 2019), and field studies confirm simultaneous adjustments of patch time and vigilance in response to variations in predation risk (e.g., Lima, 1985; Toïgo, 1999; Embar et al., 2011).

Second, we consider the different types of antipredator vigilance that exist in the wild. An herbivore may indeed totally stop feeding to scan for predators, but it may also be vigilant while handling seeds, fruits or leaves (Popp, 1988; Cowlishaw et al., 2004) or while chewing (Illius & Fitzgibbon, 1994; Fortin et al., 2004b). This situation is however expected to lower its ability to detect predators, because handling postures may partially prevent scanning (for animals handling discrete food items; Kaby & Lind, 2003) and because chewing hinders sensorial abilities (for grazers; Blanchard and Fritz, 2007). Following a terminology that applies to both kinds of herbivores, we will thus consider two distinct types of vigilance (Baker et al., 2011; Périquet et al., 2012). First, exclusive vigilance implies an interruption of all feeding activities and provides the best detection capacities. Second, routine vigilance allows the individual to scan for predators while handling food, including chewing (see

Spalinger and Hobbs, 1992), with reduced detection capacities. Because they monopolize attention, both exclusive and routine vigilance are incompatible with food search.

In the first part of this work, and for the sake of comparison, we study the simplified situation where the herbivore is not subject to predation. It thus dedicates all its attention to the exploration of the food patch. The possibility to detect resources is however greater when the animal raises its head, be it handling food or not, than when it collects food, because it then dominates the food patch, can turn its head in any direction, and can move (e.g., Hopewell et al., 2005; Baker et al., 2010). Our aim is to measure the influence of these varying levels of exploration capacities on the forager's feeding rate, hence, on the shape of its functional response.

In the second part, we study the influence of predation threat on the herbivore's behavioural choices and functional response. The decisions the animal has to make thus concern the duration of its foraging bout, the sharing of its attention between food patch exploration and predator detection, and its relative investment in exclusive and routine vigilance. This model differs from the first one in the sense that it is not purely mechanistic, but involves the derivation of optimal strategies (MaynardSmith, 1978). Finally, we study the influence of these strategies on the herbivore's functional response.

The model

Influence of food patch observation on functional response.

Here we consider that the herbivore is not subject to predation. Its attention is thus entirely dedicated to food detection. We assume that food detection is only possible when the animal raises its head, even if it is handling food, because it can then both observe the patch and move. By contrast, movements and food detection are hindered when the animal's head clings to the substrate to crop food. In this case, and for the sake of simplicity, we assume that finding new food items is precluded.

The proportions of time respectively devoted to exclusively searching for food, *s*, to searching for food while handling food, *h*, and to cropping food, *c*, verify:

$$s + h + c = 1 \qquad (1).$$

When exclusively searching for food, the individual finds food with rate aR, where R denotes resource density and a the area explored per unit of searching time. Similarly, food is found with rate $a'R$ when the animal is searching for food while handling, with $a' \leq a$, because handling may interfere with searching. The overall rate of food discovery is thus given by:

$$f = saR + ha'R \qquad (2).$$

The amount of time necessary to crop one unit of food is denoted by C, and the amount of time necessary to handle it, once it has been cropped, by H. The functional response is then given by the intake rate of the herbivore, i, expressed as a function of resource density R. Note that we always have $i \leq f$, because the animal can never eat more food than it finds.

Optimal time allocation for an herbivore subject to predation.

We now consider that the individual is foraging under the threat of predation. As a response to the perceived level of threat, it adjusts its levels of routine and exclusive vigilance while foraging, as well as the time it spends on the food patch (Favreau et al., 2015).

The animal can never search for food and scan for predators at the same time. The time spent handling food is thus now shared between 'searching food while handling' (proportion of time h_f) and 'routine vigilance' (proportion of time h_r), with $h_f + h_r = h$. Similarly, the time spent observing without handling food is shared between 'exclusively searching for food' (proportion of time s) and 'exclusive vigilance' (proportion of time v). The fifth activity is 'cropping food' (proportion of time c), which is incompatible with observation.

We finally have: $s + c + h_f + h_r + v = s + c + h + v = 1$ (3).

In addition, the individual may at any moment decide to leave the food patch and join a refuge where it is sheltered from predation, but cannot feed. The sixth behavioural variable is thus the time T spent on the patch, with $T \leq T_{max}$, where T_{max} denotes maximum foraging time, and $T_{max} - T$ the time spent in the refuge.

As in the preceding model, the quantity of food detected per unit of searching time is given by equation (2) and the actual intake rate by i, with $i \leq f$. The quantity of food consumed during the patch visit is given by: $Q = iT$. The final reward for the forager is an increasing but decelerating function of this quantity:

$$F(Q) = 1 - \exp(-\varphi Q) \quad (4),$$ where

φ is a constant (see Houston et al., 1993). This reward must however be weighted by the probability of surviving predatory attacks throughout the foraging period. This probability is called S and predatory attacks are assumed to occur randomly, following a Poisson process.

Survival probability S depends on the level of risk μ, which denotes the instantaneous probability of a predatory attack. Attacks may occur at any moment, but the probability of

escaping them increases with the part of its attention the animal devotes to vigilance. More precisely, the herbivore is captured when under an attack with a probability P that decreases when its level of exclusive vigilance, v, and, to a lower extent, its level of routine vigilance, h_r, increase, because exclusive vigilance is more efficient than routine vigilance. The link between the probability of capture and vigilance levels is given by:

$P(v,h_r) = \exp(-(Av + Bh_r))$, with $A \geq B$, and the chance of surviving predatory attacks over the entire period spent on the patch by: $S(v,h_r,T) = \exp(-\mu P(v,h_r)T)$ (5).

The final reward for the forager, when the probability of surviving predatory attacks is taken into account, is thus given by: Fitness = $S(v,h_r,T)F(Q)$ (6).

This quantity is used to derive the optimal strategy. Because of the high number of variables, this strategy has to be derived numerically. This means that, for a given set of parameters' values, we systematically explore the space of behavioural variables s, c, h_f, h_r, v and T, and determine, using equation (6), the set of variables that maximizes fitness. This set corresponds to the optimal strategy.

Using this procedure, we allow parameters' values to vary in order to evaluate the influence of each of them, as well as their interactions, on the optimal strategy. The results presented below are representative of the different tendencies emerging during this exploration.

The significance of the different variables and parameters is summarized in Table 1.

Results

Influence of food patch observation on functional response.

Here the herbivore is not subject to predation. The aim of this first model is to explore how a mere mechanistic description of its foraging activity, which incorporates differences in food detection efficiency when head position changes, alters the shape of the functional response.

Foraging time is shared between exclusively searching for food (proportion of time *s*), cropping (proportion of time *c*) and handling food (proportion of time *h*). Food detection only occurs when the animal raises its head, be it handling food or not, and the rate of food discovery is given by equation (2).

The intake rate i corresponds to the quantity of food actually consumed per unit of time, with $i \leq f$. Two situations are possible.

First, the quantity of food discovered per unit of foraging time, *f*, may be fully processed during this unit of foraging time. This means that the animal can eat all the food it finds (i.e., $i = f$) and happens when food density in the environment is not too high. In this situation, harvest rate is limited by encounter rate with resources, and we have: $c + h = Cf + Hf = Ci + Hi \leq 1$

(7).

Re-arrangement of equations (1), (2) and (7) leads to the following expression for the intake rate, as demonstrated in the Appendix: $$i = \frac{aR}{1+\left(C+H\left(1-\frac{a'}{a}\right)\right)aR} \quad (8).$$

Equation (8) is from a mathematical point of view equivalent to a type II functional response. Thus, when the density of resources initially increases, the intake rate rises at a decelerating rate (see figure 1), and the proportion of time spent exclusively searching for food s decreases, while the proportions of time spent cropping and handling increase, because more food is consumed (see figure 2).

We remark that the role played by the handling activity in the functional response's equation is variable. All depends on the ability of the herbivore to discover food while already handling. If this ability is high (i.e., *a'* close to *a*), then the handling activity does not slow the feeding process, because handling fully contributes to searching. Intake rate is only slowed by the cropping rate. If this ability is low (i.e., *a'* close to 0), the effect of handling time adds up to that of cropping.

Second, the quantity of food discovered per unit of foraging time may exceed the processing capacity of the animal. This happens when $Cf + Hf > 1$, which is achieved when : $R > R' = 1/(a'H)$ (9), R' being the resource density above which the animal finds more food than it can eat.

The animal's intake rate is then lower than its discovery rate (i.e., $i < f$) and it does not search for food any more in an exclusive manner (i.e., $s = 0$), as the time spent handling food is sufficient to detect all the resources it will eat (see figure 2). We have then:

$c + h = Ci + Hi = 1$, which gives: $c = C/(C + H)$, $h = H/(C + H)$ and $i = 1/(C + H)$ (10).

The intake rate thus does not increase any more with food density when this density exceeds threshold value R' (see equation (9)). Both cropping and handling thus contribute to limit intake rate and determine its maximum value. This maximum rate is nevertheless reached at a lower density of resource if handling is largely compatible with searching for food (see figure 1).

Optimal time-allocation for an herbivore subject to predation.

Influence of food density.

The situation investigated in the present part is more complex, first, because the herbivore now shares its foraging time between 5 different activities (see figure 3), second, because it also decides how long to stay on the patch (see figure 4). Additionally, the amount of food actually consumed may be measured both by the instantaneous intake rate *i* and by the total quantity *Q* of food consumed when the patch's visit ends (figure 4).

A general conclusion emerging from our results is that an increasing density of food allows the herbivore to consume more resource while investing more in antipredator defense (see figure 4). Both instantaneous intake rate *i* and total quantity of food consumed *Q* do indeed always increase with *R* (figure 4), while increased defense first takes the form of higher vigilance levels, then, of a reduction of the time spent on the patch (see figures 3 and 4).

What initially allows the herbivore to spend more time in vigilance is that, as food becomes easier to find, the time spent searching for it decreases (i.e., *s* decreases, see figure 3). The herbivore can thus feed more while spending less time searching for food, which allows it to be more vigilant. Note that, at low food density, i.e., when feeding is limited by encounter rate with resource, exclusive vigilance is the only type of vigilance present. Routine vigilance begins to be observed precisely when no more time is spent in pure observation of the food patch (i.e., $h_r \neq 0$ when $s = 0$, see figure 3). The reason is that $s = 0$ means that the time spent handling resources is sufficient for the animal to discover all the food it consumes. As a consequence, and as was described in the first part of the study, any further increase in *R* leads the animal to detect more food while handling than it can actually eat. It then begins to devote part of its handling time to vigilance. From this moment on, the intake rate increases with *R* not only because food is found more easily, but also because the overall proportion of

time dedicated to feeding rises, exclusive vigilance being progressively replaced by routine vigilance. In parallel, an increasing feeding rate allows the animal to leave the food patch earlier (figure 4).

We remark that, while the variations in certain variables are non-monotonic (i.e., h_f and v) and if some others may sometimes be equal to 0 (i.e., s and h_r), the combined fluctuations in these variables and in the time dedicated to the patch's visit produce very smooth variations in the feeding rate of the animal while on the patch (i) and in the total quantity of food consumed (Q) (see figure 4). Both quantities regularly increase, with a decelerating rate, with food density.

To evaluate the relative roles of behavioural adjustments on the patch and of patch residence time in this process, we also explore the situation where the possibility to find shelter in a refuge is cancelled, the animal being forced to spend maximum time T_{max} on the patch. Its response to an increasing density of food is then presented in figures 5 and 6. Compared to the preceding situation, we see that all activities involved in feeding are reduced, for the benefit of exclusive vigilance (figure 5). Food intake rate thus decreases, as the animal invests more time in the most efficient type of vigilance. Nevertheless, by staying longer on the patch, it finally consumes a larger quantity of food, provided it survives predators' attacks. The functional response curve is thus slightly lowered if we consider intake rate, and slightly raised if we consider the total quantity eaten. In both cases, its general shape remains unaltered (figure 6).

Influence of predation risk.

Here we investigate the influence of predation risk on the herbivore's behaviour, in conditions of low (figures 7 and 8) and high (figures 9 and 10) food density. As previously, we remark that, when food is scarce, the animal devotes part of its time to searching for food exclusively and none to routine vigilance (i.e., $s \neq 0$ and $h_r = 0$, see figure 7), while, when food is abundant, the opposite pattern is observed (see figure 9).

When food is scarce, the animal initially responds to an increase in predation risk by progressively reducing the proportions of time devoted to searching, cropping, and handling resources, and becomes more vigilant (see figure 7). Attention is thus progressively re-orientated towards predator detection. Then, the animal begins to reduce the time it spends on the patch, without changing anymore the proportions of time dedicated to its different activities (figures 7 and 8). An increasing level of risk thus always leads to a reduction of plant removal, first, because the animal feeds less while on the patch, second, because it spends less time there.

Similar patterns are observed at high food density (see figures 9 and 10), with three important differences. First, the overall level of vigilance is higher; second, routine vigilance is also present; third, the level of risk that leads the animal to curtail the patch's visit is lower. An intriguing fact is that, if the animal globally increases its vigilance when the level of risk rises, this increase must be only attributed to exclusive vigilance, routine vigilance showing an opposite trend. The reason is that, here, all consumed food is found during the handling process, which means that the quantity of food consumed is proportional to h_f. Since this quantity of food is also proportional to the total proportion of time spent handling it (i.e., to $h = h_f + h_r$), h_f and h_r are proportional to one another. Thus, mechanistically, as the quantity eaten declines, the level of routine vigilance also declines. This, in turn, reinforces the need for the animal to increase its level of exclusive vigilance.

Discussion

Because alertness and efficient foraging are generally not fully compatible, defining attentional priorities is a permanent obligation for a foraging herbivore (Hochman & Kotler, 2007). The main reason is that, while a feeding individual has to focus its attention towards the interior of its feeding area (Kaby & Lind, 2003; Makowska & Kramer, 2007), a vigilant one gazes, listens or smells outwards (Lima & Bednekoff, 1999). Vigilance is the most extreme form of apprehension, that is, the part of a forager's attention that is redirected from food search to antipredator awareness (Hochman & Kotler, 2004). In the wild, the level of apprehension is indeed variable and notably increases with the perceived level of threat, at the expense of feeding efficiency (Dall et al., 2001; Clark & Dukas, 2003; Kotler et al., 2004). In connection with these findings, we study the strategies determining attentional priorities in an herbivore subject to predation. The level of apprehension is here reflected by the sharing of time between food search and antipredator vigilance, which may differ between the periods when the animal is already handling food and the periods when it is not.

The first model ignores antipredator behaviours and considers that the animal focuses all its observation capacities on food detection. It is used as a reference to later explore the situation where a part of these capacities is devoted to vigilance. The main assumption of this model is that resources may only be detected when the animal is not busy cropping food, because it can then orientate its head freely and move within the patch. The resulting equation linking resource density to the forager's intake rate is equivalent to a type II functional response when resource density is not too high, then, reaches a fixed maximum value (see eqs. (7) and (9)). Food intake rate is initially slowed down by the cropping process, then, at high resource densities, fixed by the combined effects of cropping and handling times. These results coincide with the predictions of Spalinger & Hobbs's (1992) model on herbivore functional responses (see transition between process 1 and process 3 in Spalinger & Hobbs

(1992) and Smart et al., 2008). The positive but decelerating influence of food abundance on intake rate that characterizes the type II functional response is well documented in grazers (Hudson & Frank, 1987; Gross et al., 1993) and in seed-eating animals (Barnard, 1980; Baker et al., 2010), and so is the fact that, when food biomass is high, the intake rate becomes mainly governed by the forager's capacities to process this food (Wilmshurst et al., 1999). We show here that the switching between these two situations occurs when the quantity of food discovered during the handling process matches the quantity of food eaten. At lower food densities, the animal must devote a part of its foraging time to exclusively searching for food (see Fig. 1). At higher food densities, this activity vanishes and the animal begins to find more food than it can eat, which means that part of the information it gathers about its environment is lost. Things change when the herbivore is allowed to re-orientate its attention towards predator detection.

In this respect, feeding and scanning have long been considered as mutually exclusive (Barnard, 1980; Glück, 1987). An increasing feeding rate should then mechanically lead to lower vigilance. Negative correlations between resource density and vigilance are indeed documented in situations where feeding hinders observation of the surroundings (Underwood, 1982; Pöysä, 1987; see also Pays et al., 2012). In many cases however, higher levels of vigilance are observed when food is abundant (see Beauchamp, 2009). A first explanation is that animals living in rich environments are able to sustain high levels of reserves. They can thus invest more in vigilance. This response is observed both on a short time scale after a meal (Pravodusov & Grubb, 1998) and after prolonged periods of intense feeding (Bednekoff & Woolfenden, 2003). A second reason is that feeding enhances vigilance when these activities are compatible with one another, which routine vigilance makes possible (Popp, 1988; Fortin et al., 2004b). Intake rate and overall investment in vigilance can then vary concomitantly, and high biomass of plants be beneficial to predator detection (Fortin et al.,

2004b). The present model accounts for these two possibilities. It shows that animals living in rich environments conciliate high intake rates and high levels of vigilance while on food patches, thanks to routine vigilance, and leave these patches with high levels of reserves. In fact, during our analyses we observed that making routine vigilance more effective does not only increase its use, but also allows the animal to leave the patch sooner, thanks to its higher feeding rate. The advantage of routine vigilance is thus twofold.

The level of routine vigilance is however also strongly influenced by predation risk. More generally, the quantity of plants eaten by the herbivore, as well as its level of exposure to predation, are driven by an important behavioural plasticity, notably concerning the sharing of its attention between food and predator detection. The patterns highlighted here are indeed absent when searching for food cannot take place during handling (Lima, 1988) and when routine vigilance is not allowed to vary in response to predation risk variation (Fortin et al., 2004a).

Identifying routine vigilance in the wild is possible, but requires a part of interpretation (Benhaiem et al., 2008; Favreau et al., 2015). Animals which feed on the ground, then lift their head and gaze outwards while handling or chewing, can be considered as being performing routine vigilance (Baker et al., 2011; Favreau et al., 2013), but the distinction is far from clear for animals that browse plant or tree foliage at head level i.e., when head is up. Moreover, the situation is complexified by a differential use of senses for predator detection and for food search, and by the way handling food interferes with their accuracy (Blanchard & Fritz, 2007).

Nevertheless, empirical studies confirm the combined influence of predation risk and resource abundance on herbivores' behaviour in the wild, and the complex interactions between routine vigilance, food search, and exclusive vigilance (Kotler et al., 2004; Pays et al., 2012). Thus, Fortin et al. (2004b), Benhaiem et al. (2008) and Robinson & Merrill (2013)

show that a high density of palatable plants allows grazing ungulates to increase their level of routine vigilance, while, at low densities of resources, searching for food takes too much time, and they are forced to mostly rely on exclusive vigilance (see Illius & Fitzgibbon (1994)). The influence of resource availability is, however, strongly mediated by variations in predation risk, which is the major driver of vigilance (Favreau et al., 2015). An increasing perception of danger generally triggers higher levels of exclusive vigilance, which competes with feeding (Blanchard & Fritz, 2007; Périquet et al., 2012; van der Meer et al., 2012; Favreau et al., 2013; Bergval et al., 2016), and possibly engenders a reduction of routine vigilance (Hochman et Kotler, 2007; Favreau et al., 2015).

Our model also incorporates the possibility for the herbivore to spend less time in the foraging area. The duration of the patch's visit is then conjointly determined by food availability and predation risk. When food is scarce, the animal uses all available foraging time, even if the risk is present. At higher food densities, it responds to an increasing level of risk by leaving the patch sooner and looking for shelter. Field studies confirm that, when the time available is short, or the density of food low with regards to energetic needs, the herbivores will forage as long as they can (Illius & Gordon, 1987; van der Veen, 2000), even if this makes them more vulnerable to predation (Daly et al., 1992), and provided they do not regularly experience low risk periods during which they can concentrate their feeding activity (Kotler et al., 2010). By contrast, under less critical conditions, animals subject to a high level of risk will leave the area for a refuge sooner (Lendrem, 1983; Kotler et al., 2004) and having eaten less (Hochman & Kotler, 2007). Estimating the real impact of herbivores on plant populations, in particular, their equilibrium densities, thus requires to not only measure the instantaneous intake rate of these animals, but also how long, and how much, they feed every day.

Ultimately, we show that when all types of behavioural adjustments are taken into account, the curves linking resource density to the total quantity of food consumed show the same trends as the type II functional response (see figure 4). In other words, the two-steps mechanism highlighted in the first part of the study vanishes when adaptive antipredator responses are incorporated in the functional response. The situation remains complicated, however, since the quantity of resource actually eaten is also highly dependent on predation risk (see figures 6 and 8). The dynamics of the whole trophic chain is thus affected, the herbivore's behavioural responses to predation risk enhancing the cascading effects that predators create across the three trophic levels (see Schmitz al., 2004 and Preisser et al., 2005).

Antipredator defense is known to influence population dynamics in a deep and complex manner (e.g., Křivan, 1998; Brown et al., 1999; Rinaldi et al., 2004). In addition, natural situations are complexified by numerous effects, such as resource depletion, competition among foragers, and temporal variations in predation risk (e.g., Mitchell & Brown, 1990; Sirot, 2019). Nevertheless, we show here that the derivation of an herbivore's functional response, a prerequisite for the exploration of interactions among populations, not only requires to include vigilance, but also the extent to which it varies across situations. Moreover, the possibility for the consumer to simultaneously consume plants and scan for predators, through variable levels of routine vigilance, will affect vital rates in the three populations. The influence of this process on the dynamics of the community thus certainly deserves to be explored.

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Authors' contributions: ES and OP conceived the ideas. ES built the model and wrote the first draft. OP prepared the figures. PB, AL, and OP have improved the manuscript with significant comments. All authors gave final approval for submission.

Figure 1: Functional response: intake rate as a function of food density *R*.

Parameter values: $a = 1$, $a' = 0.8$ (for intake rate i) or 0.3 (for intake rate i'), $C = 1.5$, $H = 2$.

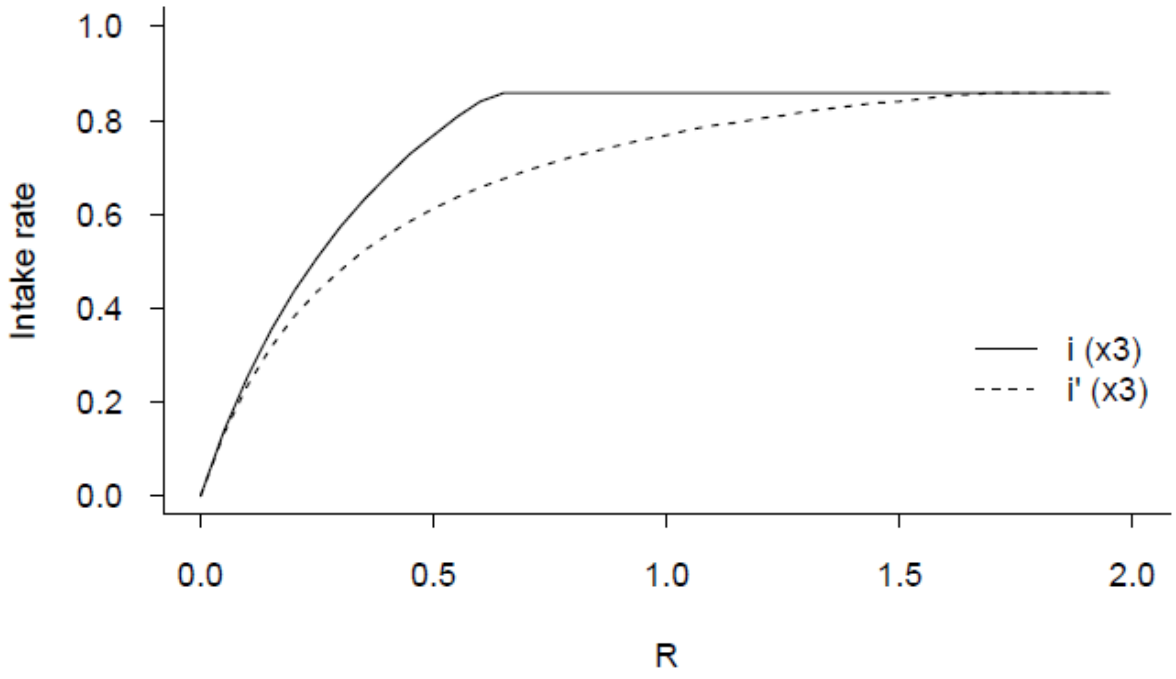

Figure 2: Proportions of time dedicated to exclusively searching for food, *s*, cropping, *c*, and handling food, *h*, as a function of resource density *R*.
Parameter values: : $a = 1$, $a' = 0.8$, $C = 1.5$, $H = 2$.

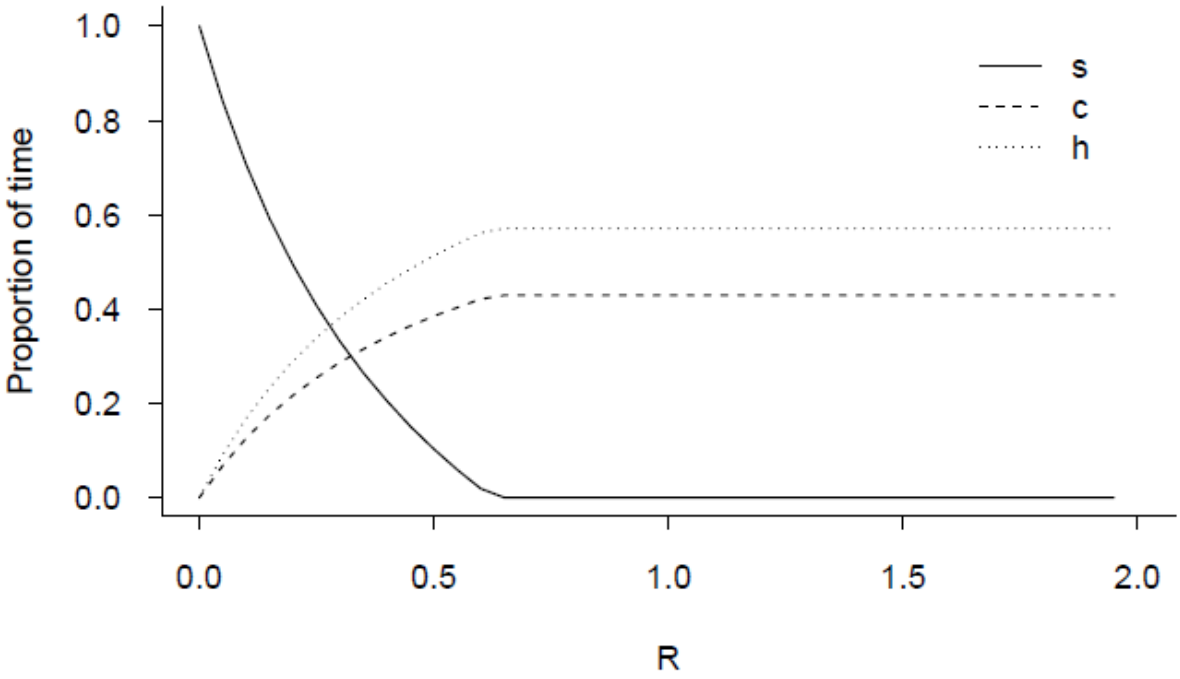

Figure 3: Proportions of time dedicated to exclusively searching for food, *s*, cropping, *c*, searching for food while handling, h_f, routine vigilance, h_r, and exclusive vigilance, *v*, as a function of resource density *R*.
Parameter values: $a = 1$, $a' = 0.8$, $C = 1.5$, $H = 2$, $A = 2$, $B = 1$, $\varphi = 2$, $\mu = 0.15$, $T_{max} = 8$.

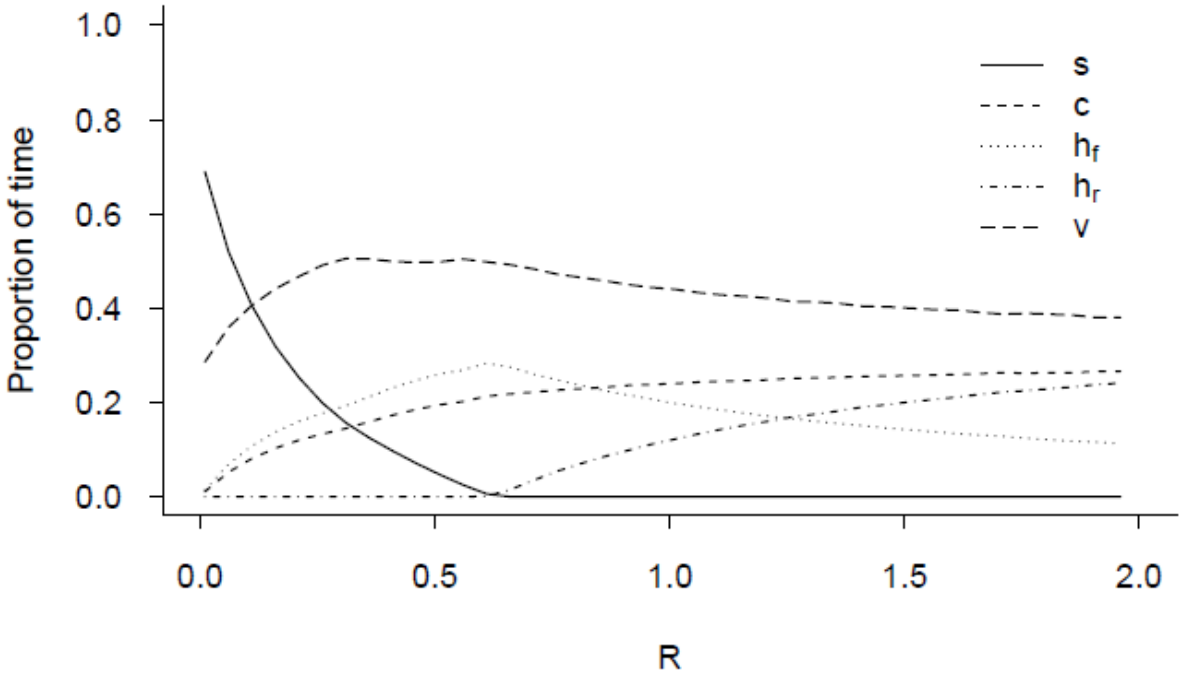

Figure 4: Intake rate, *i*, total quantity of food consumed, *Q*, and duration of patch visit, *T*, as a function of resource density *R*. These quantities are linked by relationship: $Q = iT$.
Parameter values: same as figure 3.

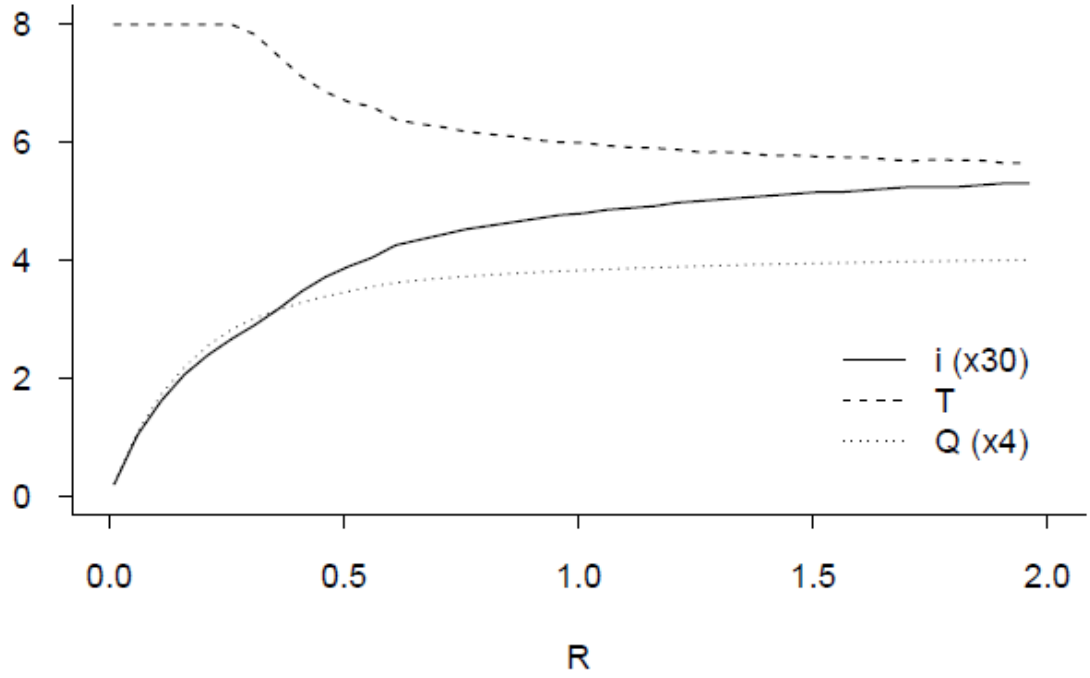

Figure 5: Proportions of time dedicated to exclusively searching for food, *s*, cropping, *c*, searching for food while handling, h_f, routine vigilance, h_r, and exclusive vigilance, *v*, as a function of resource density *R*, when time spent on the patch is fixed.
Parameter values: $a = 1$, $a' = 0.8$, $C = 1.5$, $H = 2$, $A = 2$, $B = 1$, $\varphi = 2$, $\mu = 0.15$, $T = T_{max} = 8$.

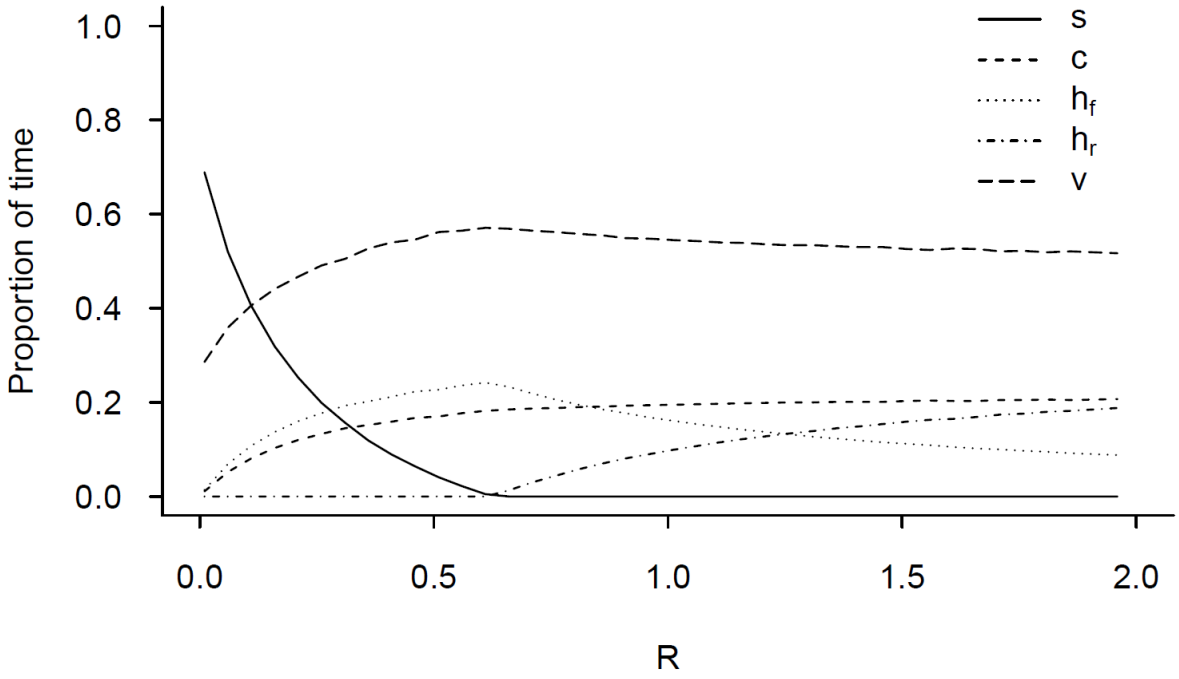

Figure 6: Intake rate, *i*, total quantity of food consumed, *Q*, and duration of patch visit, *T*, as a function of resource density *R*, when time spent on the patch is fixed. These quantities are linked by relationship: $Q = iT$. Parameter values: same as figure 5.

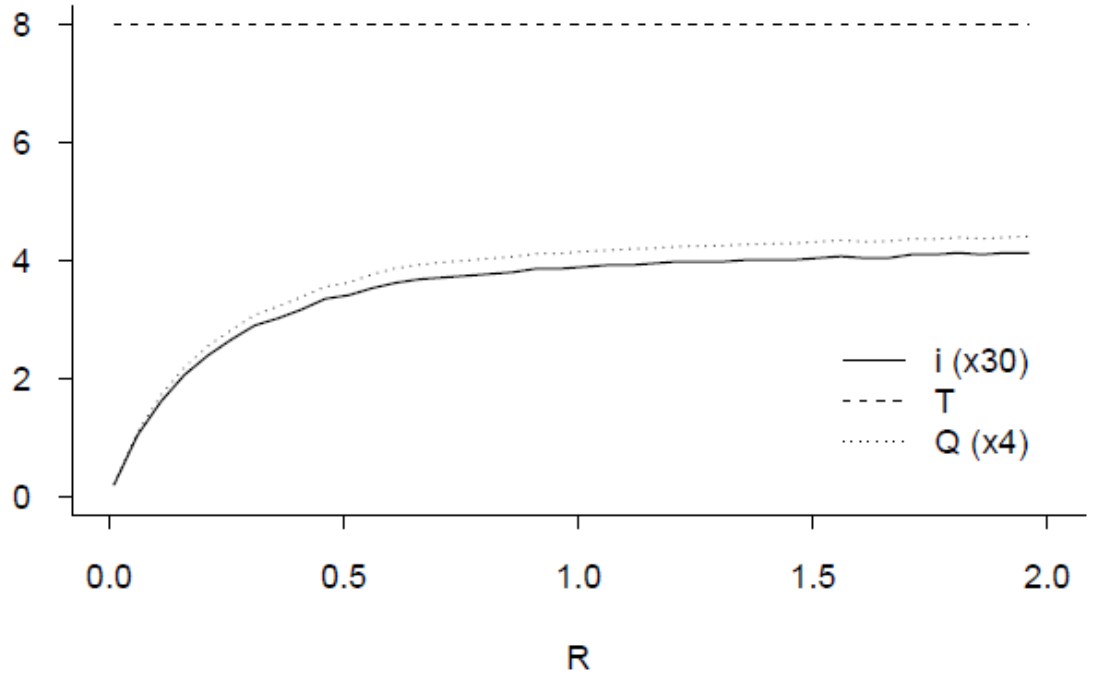

Figure 7: Proportions of time dedicated to exclusively searching for food, *s*, cropping, *c*, searching for food while handling, h_f, routine vigilance, h_r, and exclusive vigilance, *v*, as a function of predation risk μ, when food density is low.
Parameter values: $a = 1$, $a' = 0.8$, $C = 1.5$, $H = 2$, $A = 2$, $B = 1$, $\varphi = 2$, $R = 0.2$, $T_{max} = 8$.

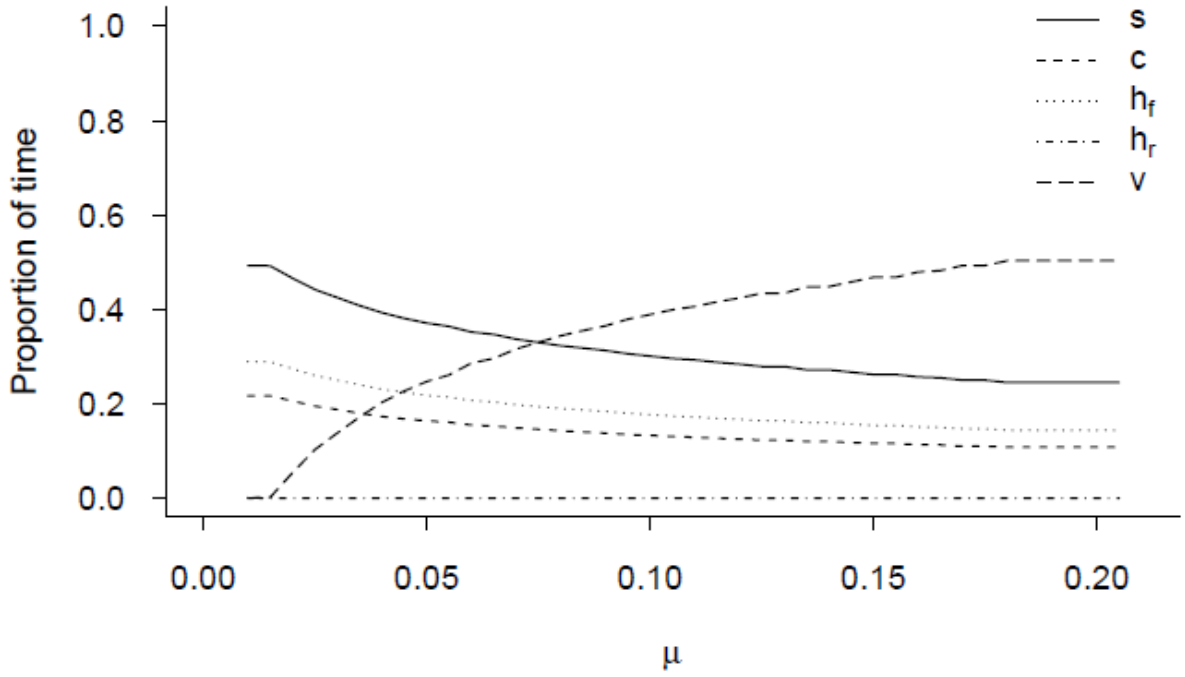

Figure 8: Intake rate, i, total quantity of food consumed, *Q*, and duration of patch visit, *T*, as a function of predation risk μ, when food density is low. These quantities are linked by relationship: $Q = iT$.
Parameter values: same as figure 7.

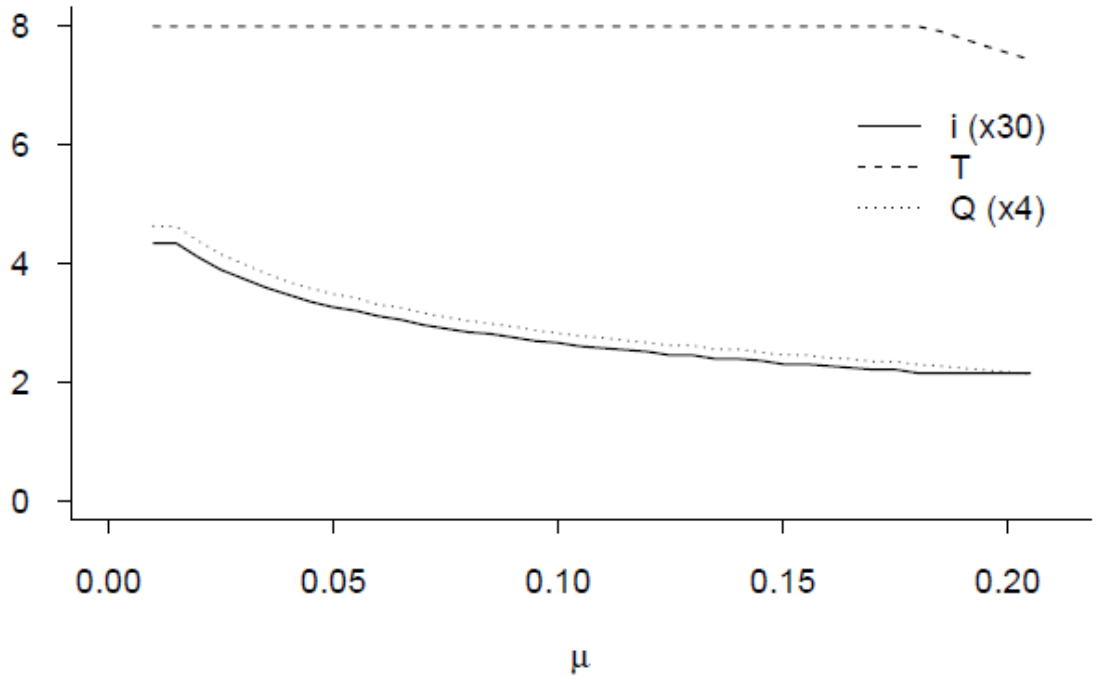

Figure 9: Proportions of time dedicated to exclusively searching for food, *s*, cropping, *c*, searching for food while handling, h_f, routine vigilance, h_r, and exclusive vigilance, *v*, as a function of predation risk μ, when food density is high.
Parameter values: $a = 1$, $a' = 0.8$, $C = 1.5$, $H = 2$, $A = 2$, $B = 1$, $\varphi = 2$, $R = 1$, $T_{max} = 8$.

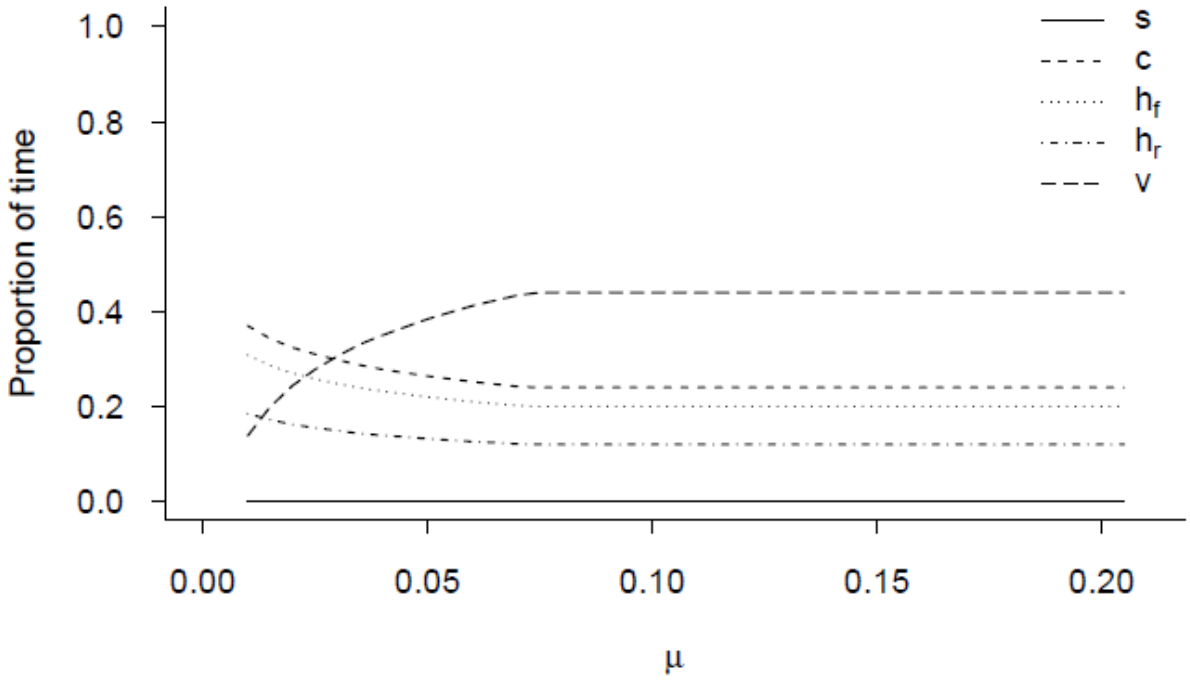

Figure 10: Intake rate, *i*, total quantity of food consumed, *Q*, and duration of patch visit, *T*, as a function of predation risk μ, when food density is high. These quantities are linked by relationship: $Q = iT$.
Parameter values: same as figure 9.

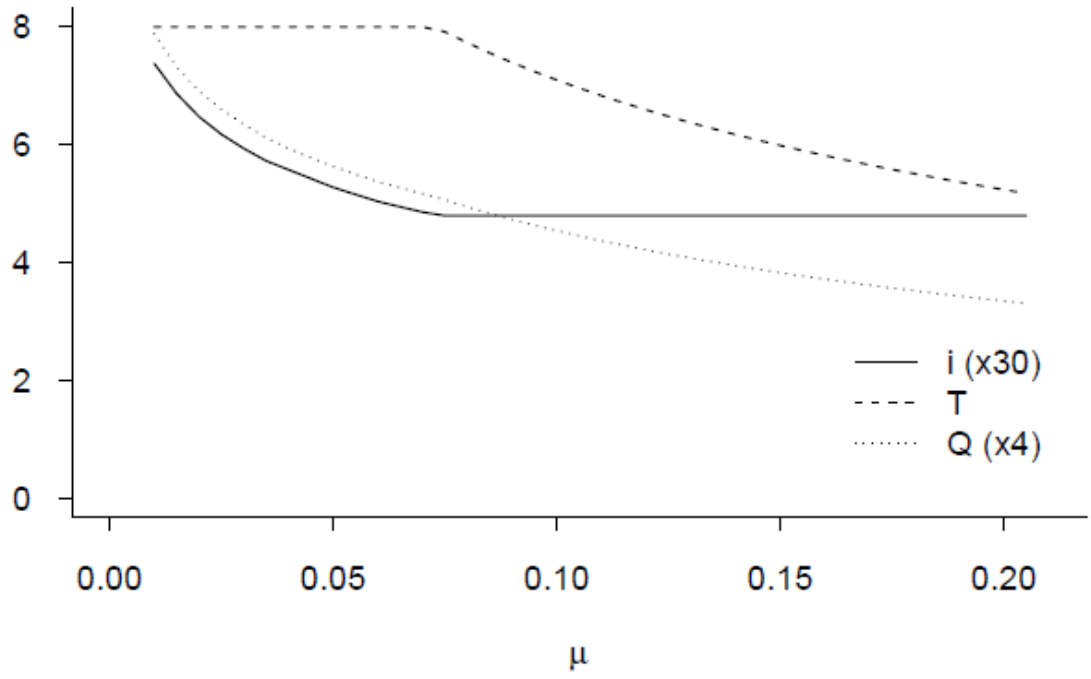

Table 1: Variable and parameters:

Behavioural variables	
s	Proportion of time spent exclusively searching for food
c	Proportion of time spent cropping food
h $(=h_f + h_r)$	Proportion of time spent handling food
h_f	Proportion of time spent searching food while handling food
h_r	Proportion of time spent in routine vigilance
v	Proportion of time spent in exclusive vigilance
T	Patch residence time
Parameters	
a	Area of food discovery when the animal is exclusively searching for food
a' $(< a)$	Area of food discovery when the animal is searching while already handling food
A	Effect of exclusive vigilance on the probability of escaping predation
B $(< A)$	Effect of routine vigilance on the probability of escaping predation
μ	Rate of predatory attacks
R	Resource density
T_{max}	Maximum residence time on the food patch
φ	Speed with which terminal fitness saturates with the quantity of food eaten

References

Baker, D. J., Stillman, R. A., Smith, B. M., Bullock, J. M., & Norris, K. J. (2010). Vigilance and the functional response of granivorous foragers. *Functional Ecology*, 24(6), 1281-1290. https://doi.org/10.1111/j.1365-2435.2010.01735.x

Baker, D. J., Stillman, R. A., Smart, S. L., Bullock, J. M., & Norris, K. (2011). Are the costs of routine vigilance avoided by granivorous foragers? *Functional Ecology*, 25(3), 617-627. https://doi.org/10.1111/j.1365-2435.2010.01829.x

Barnard, C. J. (1980). Flock feeding and time budgets in the house sparrow (*Passer domesticus* L.). *Animal Behaviour*, 28, 295-309. https://doi.org/10.1016/S0003-3472(80)80032-7

Beauchamp, G. (2009). How does food density influence vigilance in birds and mammals? *Animal Behaviour*, 78(2), 223-231. https://doi.org/10.1016/j.anbehav.2009.04.029

Bednekoff, P. A., & Woolfenden, G. E. (2003). Florida scrub-jays (*Aphelocoma coerulescens*) are sentinels more when well-fed (even with no kin nearby). *Ethology*, 109(11), 895-903. https://doi.org/10.1046/j.0179-1613.2003.00926.x

Benhaiem, S., Delon, M., Lourtet, B., Cargnelutti, B., Aulagnier, S., Hewison, A. J. M., Morellet, N., & Verheyden, H. (2008). Hunting increases vigilance levels in roe deer and modifies feeding site selection. *Animal Behaviour*, 76(3), 611-618. https://doi.org/10.1016/j.anbehav.2008.03.012

Berger-Tal, 0., Mukherjee, S., Kotler, B. P., & Brown, J. S. (2010). Complex state-dependent games between owls and gerbils. *Ecology Letters*, 13, 302-310. doi: 10.1111/j.1461-0248.2010.01447.x

Bergvall, U. A., Svensson, L., & Kjellander, P. (2016). Vigilance adjustments in relation to long- and short term risk in wild fallow deer (*Dama dama*). *Behavioural Processes*, 128, 58-63. https://doi.org/10.1016/j.beproc.2016.04.005

Blanchard, P., & Fritz, H., (2007) Induced or routine vigilance while foraging. *Oikos*, 116(10), 1603-1608.

Blanchard, P., Lauzeral, C., Chamaillé-Jammes, S., Brunet, C., Lec'hvien, A., Péron, G., & Pontier, D. (2018). Coping with change of predation risk across space and time through complementary behavioral responses. *BMC Ecology*, 18, 60. https://doi.org/10.1186/s12898-018-0215-7

Brown, J. S. (1999). Vigilance, patch use and habitat selection: foraging under predation risk. *Evolutionary Ecology Research*, 1, 49-71.

Clark, C. W., & Dukas, R. (2003). The behavioral ecology of a cognitive constraint: limited attention. *Behavioral Ecology*, 14(2), 151-156. https://doi.org/10.1093/beheco/14.2.151

Cowlishaw, G., Lawes, M. J., Lightbody, M., Martin, A., Pettifor, R., & Rowcliffe, J. M. (2004). A simple rule for the cost of vigilance: empirical evidence from a social forager. *Proceedings of the Royal Society B*, 271(1534), 27-33. https://doi.org/10.1098/rspb.2003.2522

Dall, S. R. X., Kotler, B. P., & Bouskila, A. (2001). Attention, 'apprehension' and gerbils searching in patches. *Annales Zoologici Fennici*, 38(1), 15-23.

Daly, M., Behrends, P. R., Wilson, M. I., & Jacobs, L. F. (1992). Behavioural modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert

rodent, *Dipodomys merriami*. *Animal Behaviour*, 44, 1-9. https://doi.org/10.1016/S0003-3472(05)80748-1

van der Meer, E., Pays, O., & Fritz, H. (2012). The effect of simulated African wild dog presence on anti-predator behavior of kudu and impala. *Ethology*, 118(10), 1018-1027. https://doi.org/10.1111/eth.12003

van der Veen, I. T. (2000). Daily routines and predator encounters in yellowhammers *Emberiza citrinella* in the field during winter. *Ibis*, 142(3), 413-420. https://doi.org/10.1111/j.1474-919X.2000.tb04437.x

Dukas, R., & Kamil, A. (2000). The cost of limited attention in blue jays. *Behavioral Ecology*, 11(5), 502-506. https://doi.org/10.1093/beheco/11.5.502

Embar, K., Kotler, B. P., & Mukherjee, S. (2011). Risk management in optimal foragers: the effects of sightlines and predator type on patch use, time allocation and vigilance in gerbils. *Oikos*, 120, 1657-1666. doi: 10.1111/j.1600-0706.2011.19278.x

Favreau, F-R., Pays, O., Goldizen, A. & Fritz, H. (2013). Short-term behavioural responses of impalas in simulated antipredator and social contexts. *PloS One*, 8(12), e84970. doi: 10.1371/journal.pone.0084970

Favreau, F-R., Pays, O., Fritz, H., Goulard, M., Best, E. C., & Goldizen, A. (2015). Predators, food and social context shape the types of vigilance exhibited by kangaroos. *Animal Behaviour*, 99, 109-121.

Fortin, D., Boyce, M., & Merrill, E. H. (2004a). Multi-tasking by mammalian herbivores: overlapping processes during foraging. *Ecology*, 8(8), 2312-2322.

Fortin, D., Boyce, M., Merrill, E. H., & Fryxell, J. M. (2004b). Foraging costs of vigilance in large mammalian herbivores. *Oikos*, 107(1), 172-180. https://doi.org/10.1111/j.0030-1299.2004.12976.x

Glück, E. (1987). An experimental study of feeding, vigilance and predator avoidance in a single bird. *Oecologia*, 71, 268-272.

Gotelli, N. J. (2008). A primer of Ecology, 4th ed. Oxford University Press.

Gross, J. E., Shipley, L. A., Hobbs, N. T., Spalinger, D. E., & Wunder, B. A. (1993). Functional response of herbivores in food-concentrated patches: tests of a mechanistic model. *Ecology*, 74(3), 778-791. https://doi.org/10.2307/1940805

Hochman, V. & Kotler, B. P. (2007). Patch use, apprehension, and vigilance behavior of Nubian Ibex under perceived risk of predation. *Behavioral Ecology*, 18(2), 368-374. https://doi.org/10.1093/beheco/arl087

Hopewell, L., Rossiter, R., Blower, E., Leaver, L., & Goto K. (2005). Grazing and vigilance by Soay sheep on Lundy island: influence of group size, terrain and the distribution of vegetation. *Behavioural Processes*, 70(2), 186-193. https://doi.org/10.1016/j.beproc.2005.04.009

Houston, A. I., McNamara, J. M., & Hutchinson, J. M. C. (1993). General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical transactions: Biological Sciences*, 341 (1298), 375-397.

Hudson, R. J., & Frank S. (1987). Foraging ecology of bison in aspen boreal habitats. *Journal of range management*, 40(1), 71-75.

Illius, A. W., & Fitzgibbon, C. (1994). Costs of vigilance in foraging ungulates. *Animal Behaviour*, 47(2), 481-484. https://doi.org/10.1006/anbe.1994.1067

Kaby, U., & Lind, J. (2003). What limits predator detection in blue tits (*Parus caeruleus*): posture, task or orientation? *Behavioral Ecology and Sociobiology*, 54, 534-538.

Kotler, B. P, Brown, J. S, & Bouskila, A. (2004). Apprehension and time allocation in gerbils: the effects of predatory risk and energetic state. *Behavioral Ecology*, 85(4), 917-922. https://doi.org/10.1890/03-3002

Kotler, B. P, Brown, J. S, Mukherjee, S., Berger-Tal, O., & Bouskila, A. (2010). Moonlight avoidance in gerbils reveals a sophisticated interplay among time allocation, vigilance and state-dependent foraging. *Proceedings of the Royal Society, Series B*, 277, 1469-1477. doi:10.1098/rspb.2009.2036

Křivan, V. (1998). Effects of optimal antipredator behavior of prey on predator-prey dynamics : the role of refuges. Theoretical Population Biology, 53, 131-142.

Lendrem, D. W. (1983). Predation risk and vigilance in the blue tit (*Parus caeruleus*). *Behavioral Ecology and Sociobiology*, 14, 9-13.

Lima, S. L. (1985). Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. *Oecologia*, 66, 60-67.

Lima, S. L. (1988). Vigilance and diet selection: the classical diet model reconsidered. *Journal of Theoretical Biology*, 132, 127-43.

Lima, S. L., & Bednekoff, P. A. (1999). Back to the basics of antipredatory vigilance: can nonvigilant animals detect attacks? *Animal Behaviour*, 58(3), 537-543. https://doi.org/10.1006/anbe.1999.1182

Lind, J. & Cresswell, W. (2005). Determining the fitness consequences of antipredation behavior. *Behavioral Ecology*, 16(5), 945-956. https://doi.org/10.1093/beheco/ari075

Makowska, I. J., & Kramer, D. L. (2007). Vigilance during food handling in grey squirrels, *Sciurus carolinensis*. *Animal Behaviour*, 74(1), 153-158.

MaynardSmith, J. (1978). Optimization theory in evolution. *Annual Review of Ecology and Systematics*, 9, 31-56.

Mitchell, W. A., & Brown, J. S. (1990). Density-dependent harvest rates by optimal foragers. *Oikos*, 57, 180-190.

Mónus, F. & Barta, Z. (2016). Is foraging time limited during winter ? – A feeding experiment with tree sparrows under different predation risk. *Ethology*, 122, 20-29.

Mysterud, A. (1998). The relative roles of body size and feeding type on activity time of temperate ruminants. *Oecologia*, 113, 442-446.

Pays, O., Blanchard, P., Valeix, M., Chamaillé-Jammes, S., Duncan, P., Périquet, S., Lombard, M., Ncube, G., Tarakini, T., Makuwe, E., & Fritz, H. (2012). Detecting predators and locating competitors while foraging: an experimental study of a medium-sized herbivore in an African savanna. *Oecologia*, 169, 419-430.

Périquet, S., Todd-Jones, L., Valeix, M., Stapelkamp, B., Elliot, N., Wijers, M., … Loveridge, A. J. (2012). Influence of immediate predation risk by lions on the vigilance of prey of different body size. *Behavioral Ecology*, 23(5), 970-976. https://doi.org/10.1093/beheco/ars060

Popp, J. W. (1988). Effects of food handling time on scanning rates among American goldfinches. *Auk*, 105(2), 384-385. https://doi.org/10.2307/408751

Pöysä, H. (1987). Feeding-vigilance trade-off in the teal (*Anas crecca*): effects of feeding method and predation risk. *Behaviour*, 103(1-3), 108-122. https://doi.org/10.1163/156853987X00297

Pravodusov, V. V., & Grubb, T. C. (1998). Body mass, ambient temperature, time of day, and vigilance in tufted titmice. *Auk*, 115(1), 221-223.

Preisser, E. L., Bolnick, D. B., & Benard, M. F. (2005). Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology*, 86(2), 501-509.

Rinaldi, S., Gragnani, A., & de Monte, S. (2004). Remarks on antipredator behavior and food chain dynamics. *Theoretical Population Biology*, 66, 277-286. https:// doi:10.1016/j.tpb.2004.07.002

Robinson, B. G. & Merrill, E. H. (2013). Foraging-vigilance trade-offs in a partially migratory population: comparing migrants and residents on a sympatric range. *Animal Behaviour*, 85(4), 849-856. https://doi.org/10.1016/j.anbehav.2013.02.004

Schmitz, O., Křivan, V., & Ovadia, O. (2004). Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters*, 7(2), 153-163. https://doi.org/10.1111/j.1461-0248.2003.00560.x

Sirot, E. (2019). Adjustments in compound defensive strategies in response to variation in predation risk. *Animal Behaviour*, 147, 53-60. https://doi.org/10.1016/j.anbehav.2018.10.023

Skalski, G. T. & Gilliam, J. F. (2001). Functional responses with predator interference: viable alternatives to the Holling type II model. *Ecology*, 82(11), 3083-3092.

Smart, S. S., Stillman, R. A., & Norris, K. (2008). Measuring the functional responses of farmland birds: an example for a declining seed-feeding bunting. *Journal of Animal Ecology*, 77(4), 687-695. https://doi.org/10.1111/j.1365-2656.2008.01375.x

Spalinger, D. E., & Hobbs, N. T. (1992). Mechanism of foraging in mammalian herbivores: new models of functional response. *The American Naturalist*, 140(2), 325-348.

Toïgo, C. (1999). Vigilance behavior in lactating female Alpine ibex. *Canadian Journal of Zoology*, 77, 1060-1063.

Underwood, R. (1982). Vigilance behavior in grazing African antelopes. *Behaviour*, 79(2-4), 81-107. https://doi.org/10.1163/156853982X00193

Valeix, M., Fritz, H., Loveridge, A. J., Davidson, Z., Hunt, J. E., Murindagomo, F., & MacDonald D. W. (2009). Does the risk of encountering lions influence African herbivore behavior at waterholes? *Behavioral Ecology and Sociobiology*, 63, 1483-1494.

Appendix: Derivation of the functional response.

The relationships between the herbivore's foraging behaviour and its feeding efficiency connect behavioural variables *s*, *c* and *h* to intake rate *i*. Here we consider the situation where the animal can eat all the food it finds. As demonstrated in the text (see equation (2)), we have: $i = saR + ha'R$.

(A1).

In addition, $s + c + h = 1$ (A2),

because there are only three possible activities (see equation (1)).

Finally, the proportions of time respectively devoted to cropping and to handling food are given by: $c = Ci$ (A3)

and $h = Hi$ (A4),

because the quantity of food consumed per unit of time is *i*.

Since there are 4 variables, simultaneous resolution of equations (A1), (A2), (A3) and (A4) allows to compute each of them as a function of resource density *R*. In particular, we get:

$$i = \frac{aR}{1+(Ca+H(a-a'))R} = \frac{aR}{1+\left(C+H\left(1-\frac{a'}{a}\right)\right)aR} \quad \text{(A5).}$$