

## MULTI-TASKING BY MAMMALIAN HERBIVORES: OVERLAPPING PROCESSES DURING FORAGING

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**Abstract.** Mammalian herbivores can carry out multiple tasks without interrupting food processing, but this possibility is not considered in existing foraging models. We develop a mechanistic functional response to account for herbivores' ability to search for their next food bite and walk away from competitors while chewing vegetation. We demonstrate how the possibility of multi-tasking can buffer intake rate from competition and vigilance. The functional response of herbivores can be density independent until a threshold of competitors is reached in the food patch, and only then does it become density dependent. Herbivores also should be capable of maintaining food intake rate, despite important resource depletion in the foraging patch. The possibility of animal movements during food processing offers herbivores opportunities for cost-free vigilance. When individuals find their next bite before they have finished chewing the current bite, the remaining chewing time becomes "spare time" that could be spent in vigilance without reducing food intake rate. Modeling of optimal vigilance demonstrates that such cost-free vigilance might importantly alter expected patterns of scanning by mammalian herbivores. Assuming that interference increases with competitor density, spare time available for scanning should decrease as the number of herbivores in a food patch increases. Foraging constraints on food intake thus can provide a mechanistic explanation for the commonly observed decline in herbivore vigilance with increasing group size.

**Key words:** competition; food intake rate; foraging constraints; foraging models; functional response of herbivores; group size; mammalian herbivores; multi-tasking; optimal vigilance; overlap between foraging processes; spare time.

### INTRODUCTION

The functional relationship between food characteristics and the rate of food intake by consumers, their functional response, plays a central role in many ecological theories. For example, predictions of consumer–resource dynamics (Fryxell and Lundberg 1997), optimal vigilance (Brown 1999), and optimal diet (Fryxell 1991, Farnsworth and Illius 1998, Fortin et al. 2002) critically rely on this relationship. Functional responses that faithfully characterize organisms are important to better understand and interpret multiple aspects of their ecology, as well as of the ecology of the species with which they interact.

Mammalian carnivores and herbivores are faced with distinct foraging challenges, which can lead to fundamental differences in the mechanisms controlling their rate of resource intake. Carnivores often spend substantial amounts of time searching for and pursuing their prey (Fanshawe and Fitzgibbon 1993, Krause and Godin 1995, Hebblewhite and Pletscher 2002), and after prey are killed, may require several minutes to several days to consume the prey. In contrast, herbivores spend relatively little time finding and capturing food

items because plants are stationary, often widely distributed in the environment, and highly concentrated in space (Stephens and Krebs 1986, Gross et al. 1993*b*). Mammalian herbivores spend significant foraging time chewing plant material (Laca et al. 1994, Pastor et al. 1999, Fortin et al. 2002) to release the digestible intracellular contents and ensure adequate mixing of plant material with saliva to form a bolus that can be swallowed. While chewing this vegetation, herbivores have an opportunity to start looking for additional food items (Spalinger and Hobbs 1992, Farnsworth and Illius 1996). In other words, searching and handling food are not mutually exclusive processes for mammalian herbivores. This overlap between foraging processes, together with the potential for rapid encounter with food items, sets mammalian herbivores apart from carnivores.

Pioneering work on functional responses (Holling 1959) and optimal foraging theory (Stephens and Krebs 1986) did not account for the possibility of overlap between foraging processes, making such models more appropriate for foraging carnivores than mammalian herbivores. More recently, however, some of the distinctiveness of foraging by herbivores has been recognized by Spalinger and Hobbs (1992), who presented mechanistic functional responses that included overlap between chewing and searching. Their modeling approach implies that the time spent chewing vegetation

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in the mouth might be longer than the time required to encounter the next bite, in which case the instantaneous rate of food intake would be independent of travel time and intake rate would be limited by the food processing rate instead of the encounter rate (Spalinger and Hobbs 1992, Farnsworth and Illius 1996, Fortin 2001, Fortin et al. 2002). Empirical evidence indicates that processing-limited foraging should be common among large mammalian herbivores (Bradbury et al. 1996, Illius et al. 2002).

Although foraging observations of mammalian herbivores are now commonly evaluated by accounting for the overlap between chewing and searching (e.g., Gross et al. 1993b, Pastor et al. 1999, Fortin et al. 2002, Illius et al. 2002, Hobbs et al. 2003), the ecological implications of overlaps between foraging processes are still underappreciated. Herbivores should be able not only to search for additional food items while chewing vegetation, but also to walk away from competitors. Such an opportunity of movement while chewing should buffer intake rate from interference competition, but models of interference have yet to account for such a possibility (e.g., Beddington 1975, Free et al. 1977, Sutherland 1996, Ward et al. 2000). Also, herbivores should finish chewing vegetation in the mouth before they can crop additional plants (Spalinger and Hobbs 1992, Gross et al. 1993a, b, Illius et al. 2002). On this basis, Illius and Fitzgibbon (1994) were first to point out that whenever herbivores encounter their next bite before they finish chewing the vegetation already in the mouth, the remaining chewing time becomes "spare time." Spare time can be spent doing various activities, such as being vigilant, without reducing vegetation intake rate. Given the importance of distinguishing mechanisms regulating functional response (Hobbs et al. 2003), spare time is a valuable ecological variable because it exposes the leeway that herbivores have before intake rate becomes controlled by food encounter rate instead of processing rate.

Here, we develop a mechanistic functional response that allows mammalian herbivores not only to search for food, but also to interact with conspecifics while chewing vegetation. Using model simulations of elk (*Cervus canadensis*), we then illustrate how multi-tasking by foraging herbivores can buffer the food intake rate from the effect of exploitation and interference competition. We also provide an algebraic formulation of spare time, making possible its calculation for mammalian herbivores foraging among conspecifics. Illius and Fitzgibbon's (1994) considered that foragers use spare time to scan their surroundings; here we apply this idea in the context of group foraging. Vigilance during spare time should reduce predation risks without influencing herbivores' rate of food intake. Still, the trade-off between food intake rate and predation risks might be such that optimal foragers must accept a certain reduction of food intake due to vigilance (Lima and Dill 1990, McNamara and Houston 1992, Brown

1999, Brown et al. 1999, Kotler et al. 2002). We explore how the possibility of multi-tasking by herbivores foraging among conspecifics might alter predictions of optimal vigilance.

#### DEVELOPMENT OF FUNCTIONAL RESPONSE

We developed our mechanistic functional response based on the model of Spalinger and Hobbs (1992). Like these authors, we modeled intake rate over brief time intervals. Our foraging model thus describes instantaneous intake rates during foraging, and does not account for digestive processes. Digestive processes are especially important to estimate intake rate over longer temporal scales (e.g., daily rate of food intake, Fryxell 1991, Fortin et al. 2002). Spalinger and Hobbs (1992) recognized that the instantaneous rate of food intake at a given point in time could be limited by one of three processes, which they simply define as processes 1–3. Foragers can locate food items only at short distances during process 1, whereas they navigate directly from plant to plant during process 2. Consequently, the functional response includes one more parameter (describing the detection range of food items) when based on process 1 than on process 2. These two functional responses are nonetheless structurally equivalent, as they both model a rate of food intake limited by the encounter rate with food items (Spalinger and Hobbs 1992). Unlike processes 1 and 2, chewing time during process 3 is equal to or exceeds the time required to encounter food items, limiting intake rate by the rate of vegetation processing in the mouth. Given the similarity between processes 1 and 2, we restricted our modeling efforts to processes 2 and 3. However, equations related to process 2 can be modified to reflect process 1 by substituting  $2\sqrt{D}$  by  $wD$ , where  $D$  is plant density (or bite density, because we assume one bite per plant), and  $w$  is width of search path.

#### Process 2

Rate of food intake ( $I$ , in grams per minute) corresponds to the total amount of food ingested ( $K$ , in grams) divided by the total amount of time spent foraging ( $T_f$ , in minutes), where  $T_f$  could represent, for example, the length of a foraging bout. We consider that gregarious foragers have to spend time searching ( $T_s$ , in minutes), cropping ( $T_{crop}$ , in minutes) and chewing ( $T_{chew}$ , in minutes) vegetation, as well as interacting with competitors ( $T_w$ , in minutes). We refer to cropping as the removal of plant tissue with the mouth (tongue or teeth), whereas we define chewing as up-and-down cycles of the jaw, each terminating when the molars occlude (Hobbs et al. 2003). Because of the possibility of multi-tasking,  $T_{chew}$  overlaps with  $T_s$  and  $T_w$ . Given that  $T_{chew} < T_s + T_w$  during process 2, the total time spent foraging is  $T_f = T_s + T_w + T_{crop}$ , and food intake rate during process 2 is as follows:

TABLE 1. Description of the variables used in the mechanistic functional response (Eqs. 1–14).

Variable	Description	Units
$A$	food patch area	$m^2$
$b$	average encounter rate with each competitor during a foraging bout	encounters·min <sup>-1</sup> ·competitor <sup>-1</sup>
$D$	plant density, which also corresponds to bite density because each plant provide a single bite	bites/m <sup>2</sup> or plants/m <sup>2</sup>
$\bar{h}$	average time required for cropping a bite in absence of chewing	min/bite
$I$	per capita rate of food intake, with $I_t$ being the intake rate at time $t$	g/min
$K$	total amount of food ingested, which is equal to $\lambda ST_s$	g
$N$	total number of herbivores in a food patch	no. herbivores
$R_{\max}$	rate of food processing in absence of cropping	g/min
$S$	bite size	g/bite
$T_f$	total time spent foraging	min
$T_{\text{chew}}$	total chewing time, which is equal to $\lambda T_s S / R_{\max}$	min
$T_{\text{crop}}$	total cropping time, which is equal to $\lambda T_s \bar{h}$	min
$T_s$	search time	min
$t_w$	foraging time “lost” due to the interference of conspecifics	min/encounter
$T_w$	foraging time lost upon encounters with conspecifics	min
$V_{\max}$	searching velocity	m/min
$Z$	proportion of foraging time made up of spare time	unitless
$\lambda$	encounter rate with bites of food	bites/min

$$I = \frac{K}{T_s + T_w + T_{\text{crop}}}. \quad (1)$$

$K$  and  $T_{\text{crop}}$  can be expressed as linear functions of  $T_s$ , given that food encounters are linearly related to  $T_s$  (Stephens and Krebs 1986: 14). If  $\lambda$  (in bites per minute) is the rate of encounter with bites of food and  $S$  (grams per bite) represents the mass of these bites, then the amount of food encountered and eaten ( $K$ ) during the total time spent foraging equals  $\lambda ST_s$ . Consequently, the total time spent cropping vegetation ( $T_{\text{crop}}$ ) is the product of the total number of bites encountered,  $\lambda T_s$ , and the time require to crop each bite ( $\bar{h}$ , in minutes per bite; Spalinger and Hobbs 1992), i.e.,  $\lambda T_s \bar{h}$ .

We assume that interference occurs when an individual cannot forage at given locations due the behavior of competitors. For example, a forager might have to leave its current location due to the approach of a competitor. Such disturbances are generally brief, but common for elk and bison (*D. Fortin, personal observations*). The forager would then have to start searching for food, while avoiding the competitors.  $T_w$  thus represent the foraging time lost by not having access to certain locations. Interference would increase foraging time overall by increasing search time. We also consider that a bite can be cropped successfully only when the animal is undisturbed during the period  $T_{\text{crop}}$ . We assume that interference during cropping is negligible because a plant generally can be cropped within a few seconds (0.5–2.5 seconds for mammalian herbivores eating forbs; Gross et al. 1993b). Under these assumptions,  $T_w$  can then be expressed as a linear function of  $T_s$ , as well as of the encounter rate with each competitor while foraging ( $b$ , encounters per minute per competitor), the foraging time “lost” following each conspecific encounter ( $t_w$ , in minutes per encounter), and the number of competitors ( $N - 1$ ), as follows:

$$T_w = bt_w(N - 1)T_s. \quad (2)$$

Substituting for  $K$ ,  $T_s$ ,  $T_w$ , and  $T_{\text{crop}}$  into Eq. 1 yields

$$I = \frac{\lambda S}{1 + bt_w(N - 1) + \lambda \bar{h}}. \quad (3)$$

The rate of encounters with food items ( $\lambda$ ) depends on the animal’s search efficiency and the spatial distribution of food. For simplicity, we followed Hobbs et al. (2003) by assuming that plants are randomly distributed and that animals can navigate directly from plant to plant using vision or smell (i.e., process 2 instead of process 1). The distance (in meters) between individual plants that are randomly distributed averages  $(2\sqrt{D})^{-1}$  (Clark and Evans 1954), where  $D$  is plant density (number of plants per square meter). We further assume that animals take a single bite per plant (Hobbs et al. 2003, Gross et al. 1993b); hence  $D$  corresponds to both plant or bite density (number of plants or bites per square meter; see Table 1). Under these assumptions, the encounter rate with bites (number of bites per minute) is found by

$$\lambda = V_{\max} 2\sqrt{D} \quad (4)$$

where  $V_{\max}$  (in meters per minute) is the herbivore’s search velocity. Intake rate during process 2 now can be described using simple mechanistic processes by expanding Eq. 3 with Eq. 4:

$$I = \frac{V_{\max} 2\sqrt{D} S}{1 + bt_w(N - 1) + V_{\max} 2\sqrt{D} \bar{h}}. \quad (5)$$

Notice that, in absence of interference competition, Eq. 5 becomes equivalent to Eq. 3 of Hobbs et al. (2003) for random food distribution.

### Process 3

The rate of food intake during process 3 is limited by the food processing rate, i.e.,  $I = K/(T_{\text{crop}} + T_{\text{chew}})$ , be-

cause  $T_{\text{chew}} \geq T_s + T_w$ . The total time spent chewing vegetation ( $T_{\text{chew}}$ ) is the product of the total number of bites encountered and consumed,  $\lambda T_s$ , and the time require to chew each bite,  $S/R_{\text{max}}$ , where  $R_{\text{max}}$  is the maximum rate of processing of food in the mouth (i.e., chewing rate, in grams per minute; Spalinger and Hobbs 1992).  $R_{\text{max}}$  typically ranges from 0.2 to 74.6 g/min (Gross et al. 1993b). Given that  $K = \lambda S T_s$ ,  $T_{\text{crop}} = \lambda T_s \bar{h}$ , and  $T_{\text{chew}} = \lambda T_s S/R_{\text{max}}$ , as previously defined, intake rate simply corresponds to the size of plant bites divided by the time required to crop and chew these bites (see Farnsworth and Illius 1996: Eqs. 16 and 17):

$$I = \frac{S}{\bar{h} + \frac{S}{R_{\text{max}}}} = \frac{R_{\text{max}} S}{R_{\text{max}} \bar{h} + S}. \quad (6)$$

This corresponds to Spalinger and Hobbs's (1992: Eq. 30) functional response for herbivores foraging in food-concentrated patches.

*Boundary conditions between processes and general composite functional response*

The fundamental difference between processes 2 and 3 lies in the activities that can be entirely accomplished while the animal is chewing. During process 2, it takes longer to find the next bite and to interact with conspecifics than to chew the vegetation in the mouth:

$$T_{\text{chew}} = \lambda T_s \frac{S}{R_{\text{max}}} < T_s + T_w. \quad (7)$$

Eq. 7 can be rearranged and expanded using Eqs. 2 and 4 to characterize, with simple foraging mechanisms, the conditions under which process 2 applies:

$$\frac{V_{\text{max}} 2\sqrt{DS}}{R_{\text{max}}} - [1 + bt_w(N - 1)] < 0. \quad (8)$$

Consequently, the rate of food intake becomes limited by the rate of food processing (cropping and chewing), i.e., process 3, when chewing time equals or exceeds search time and time lost to interference competition (i.e.,  $V_{\text{max}} 2\sqrt{DS}/R_{\text{max}} - (1 + bt_w[N - 1]) \geq 0$ ). By considering processes 2 and 3, as well as their boundary conditions, we obtain a composite functional response:

$$I = \begin{cases} \frac{V_{\text{max}} 2\sqrt{DS}}{1 + bt_w(N - 1) + V_{\text{max}} 2\sqrt{Dh}} \\ \text{if } \frac{V_{\text{max}} 2\sqrt{D} S}{R_{\text{max}}} - [1 + bt_w(N - 1)] < 0 \\ \frac{R_{\text{max}} S}{R_{\text{max}} \bar{h} + S} \text{ otherwise.} \end{cases} \quad (9)$$

*Proportion of foraging time made up of spare time*

By definition, spare time is the amount of chewing time that exceeds the time required to encounter bites

and the foraging time "lost" to interference competition, i.e.,  $V_{\text{max}} 2\sqrt{DS}/R_{\text{max}} - (1 + bt_w[N - 1]) > 0$ . Hence, spare time does not exist during process 2 (see inequality 8), and can be present only during process 3 (Illius and Fitzgibbon 1994). The proportion of foraging time made up of spare time ( $Z$ ) can be found from the difference between the total time spent chewing and the total time spent searching and interacting with competitors, divided by the total time spent foraging during process 3:

$$Z = \frac{\lambda T_s \frac{S}{R_{\text{max}}} - (T_s + T_w)}{\lambda T_s \left( \bar{h} + \frac{S}{R_{\text{max}}} \right)} \quad (10)$$

which can be expanded and rearranged to

$$Z = \frac{V_{\text{max}} 2\sqrt{DS} - R_{\text{max}} [1 + bt_w(N - 1)]}{V_{\text{max}} 2\sqrt{D} (R_{\text{max}} \bar{h} + S)}. \quad (11)$$

During process 3, a mammalian herbivore foraging among conspecifics thus could spend a maximum proportion  $Z$  of foraging time in vigilance without reducing its rate of food intake.

ILLUSTRATIONS OF PROPERTIES OF THE FUNCTIONAL RESPONSE

*Interference competition*

To illustrate the effect of increasing herbivore density (number of individual per food path) on intake rate by foragers capable of multi-tasking (Eq. 9), we considered the hypothetical situation in which an elk ( $R_{\text{max}} = 52.95$  g/min,  $\bar{h} = 0.012$  min/bite,  $V_{\text{max}} = 60$  m/min,  $S = 1$  g/bite; cf. Gross et al. [1993b], Shipley et al. [1996]) forages in a meadow where  $D = 0.5$  bite/m<sup>2</sup>, and where conspecifics interact with each other according to  $b = 0.05$  encounter·min<sup>-1</sup>·competitor<sup>-1</sup> and  $t_w = 0.15$  min/encounter (Fig. 1). Although our model assumes that the foraging time lost due to interference competition increases linearly with the number of competitors in the food patch (implied by  $bt_w[N - 1]$  in Eq. 2), the rate of food intake remains insensitive to the increase in the number of conspecifics as long as animals can find their next bite before they finish chewing the current one (process 3; Fig. 1). The rate of food intake is maintained, however, at the expense of spare time. A certain amount of spare time otherwise available at low competitor density must instead be used to walk away from conspecifics at high density. In other words, the amount of time during which the animal is still chewing vegetation after having encountered the next plant decreases with the number of herbivores in the food patch.

The decrease in  $Z$  with increasing group size is a general feature of our foraging model that holds beyond our elk example, as indicated by the partial derivative of Eq. 11 with respect to  $N$ :

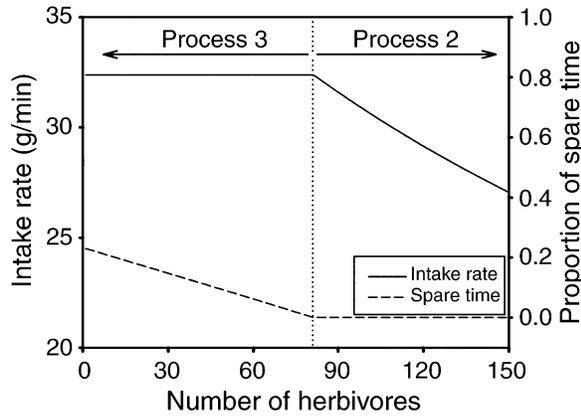


FIG. 1. Effect of number of conspecifics in a food patch on individual rate of food intake and on the proportion of foraging time consisting of spare time. The vertical dotted line represents the number of herbivores where the instantaneous rate of vegetation intake changes from being limited by food processing rate (process 3) to being limited by food encounter rate (process 2). Intake rate was determined with Eq. 9, whereas proportion of spare time during process 3 was calculated using Eq. 11. Parameters used in this example were  $V_{\max} = 60$  m/min,  $R_{\max} = 52.95$  g/min,  $\bar{h} = 0.012$  min/bite,  $t_w = 0.15$  min/encounter,  $b = 0.05$  encounters $\cdot$ min $^{-1}$  $\cdot$ competitor $^{-1}$ ,  $D = 0.5$  bite/m $^2$ , and  $S = 1$  g/bite, which could be representative of foraging elk. See Table 1 for definition of terms.

$$\frac{\partial Z}{\partial N} = \frac{-R_{\max} b t_w}{V_{\max} 2\sqrt{D}(R_{\max} \bar{h} + S)}. \quad (12)$$

Given that each parameter of Eq. 12 is necessarily positive, interference competition leads to  $\partial Z/\partial N < 0$ , indicating that density-dependent effects reduce the amount of spare time during process 3 of foraging.

As the number of conspecifics increases in the food patch, interference competition eventually can become so constraining that animals do not have the time to encounter the next bite before they have finished chewing the vegetation already in the mouth (i.e., Eq. 8 becomes true), and foraging switches from a process 3 to a process 2 of foraging (Fig. 1). This critical herbivore threshold ( $N'$ ) is lower for herbivores that chew their food rapidly and interact intensively with conspecifics:

$$N' = \frac{V_{\max} 2\sqrt{D}S - R_{\max}}{R_{\max} b t_w} + 1. \quad (13)$$

When  $N \geq N'$ , no more spare time is available, the functional response becomes density dependent, and intake rate declines with increasing group size (Fig. 1). Hence, whereas the rate of vegetation intake is density independent during process 3, intake rate becomes density dependent during process 2.

#### Exploitative competition

We further evaluated the effect of competition on rate of food intake and spare time by accounting for

the gradual decrease in plant density (which also corresponds to bite density; Table 1) that occurs as foraging time in a patch progresses. Considering our functional response that predicts per capita rate of food intake (grams per minute per herbivore), and assuming that foraging occurs randomly across a food patch of area  $A$  (in square meters), bite density declines over time:

$$D_t = D_{t-1} - \frac{I_{t-1}N}{SA} \quad (14)$$

where  $D_t$  is the density of bites of vegetation left in the patch (at time  $t$ ) following one minute of foraging by all  $N$  herbivores, and  $I_{t-1}N$  is the intake rate (at time  $t-1$ ) in the patch by all consumers combined. Given this dynamical change in plant density, the per capita rate of food intake at time  $t$  ( $I_t$ ) can be found at each time step for an herbivore exposed to both interference and exploitative competition, by using  $D_t$  (Eq. 14) in our composite functional response (Eq. 9). The proportion of foraging time made up of spare time at time  $t$  ( $Z_t$ ) can be estimated similarly with Eq. 11.

We illustrate the effect of exploitative competition on  $I_t$  and  $Z_t$  by assuming that a group of 15 elk ( $R_{\max} = 52.95$  g/min,  $\bar{h} = 0.012$  min/bite,  $V_{\max} = 60$  m/min,  $S = 1$  g/bite,  $b = 0.1$  encounter $\cdot$ min $^{-1}$  $\cdot$ competitor $^{-1}$ , and  $t_w = 0.3$  min/encounter) forage in a 0.5-ha meadow that offers vegetation of initial density  $D_{\text{initial}} = 15$  bites/m $^2$ . As long as process 3 prevails, foragers maintain their maximum rate of vegetation intake; hence, food gets depleted at a constant rate. This steady temporal decrease in food availability translates into a nonlinear increase in the distances between the randomly distributed plants because the interplant distance corresponds to  $(2\sqrt{D_t})^{-1}$ . As a consequence, the increase in travel time between plants (thus between bites) accelerates with foraging time, causing a decrease in spare time that accelerates over time (Fig. 2). In absence of interference competition ( $b t_w [N - 1] = 0$ ), animals benefit from more spare time for a longer period of time than when competitors interact with each other. The absence of interference intensifies the rate of resource depletion and the food patch reaches complete depletion slightly faster, but spare time still decreases nonlinearly over time (Fig. 2).

Our simulations reveal that, due to the rapid search velocity observed among mammalian herbivores (Shiely et al. 1996), process 3 of foraging should prevail until vegetation drops to very low food densities. Indeed, the instantaneous rate of food intake of our simulated elk was controlled by the rate of food processing instead of food encounter until  $D$  decreased to 0.39 bite/m $^2$  (i.e., 1963 individual plants left in the 0.5-ha patch) in the presence of interference competition, and to 0.19 bite/m $^2$  (i.e., 974 plants in the patch) in the absence of interference. The entire patch that originally offered 75 000 bites became entirely depleted after 2.62

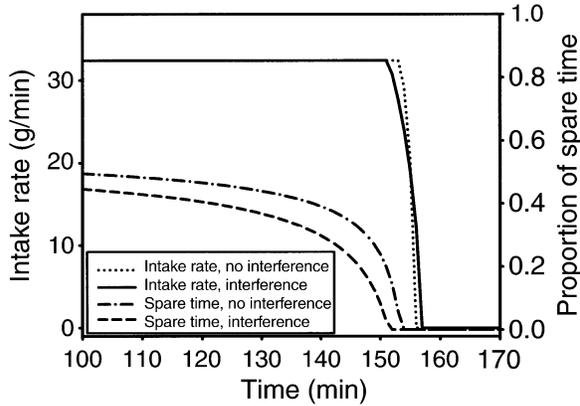


FIG. 2. Temporal variation in per capita rate of food intake and proportion of spare time for a group of 15 simulated elk consuming the vegetation found in a 0.5-ha patch where interference competition was present or absent. Parameters used in this example were  $V_{\max} = 60$  m/min,  $R_{\max} = 52.95$  g/min,  $\bar{h} = 0.012$  min/bite,  $t_w = 0.30$  min/encounter,  $b = 0.10$  encounters $\cdot$ min $^{-1}$  $\cdot$ competitor $^{-1}$ ,  $D_{\text{initial}} = 15$  bite/m $^2$ , and  $S = 1$  g/bite. Intake rate equals 0 when the vegetation patch becomes entirely depleted.

and 2.58 hours of foraging in the presence and absence of interference, respectively (Fig. 2). Of this time, only the last 5 minutes in the presence of interference and the last 2 minutes in the absence of interference of foraging were controlled by vegetation encounter rate (process 2) instead of processing rate (process 3). The number of herbivores in the food patch was constant in these simulations. Increasing herbivore density would reduce the per capita number of bites obtained from the food patch, would make process 3 start sooner, and also would cause the complete depletion of the food patch to occur earlier. However, increasing the number of herbivores in the food patch would not affect the rate of food intake during process 3. In this manner, herbivores can compete with each other in a density-dependent manner beyond that indicated by the functional response alone.

#### Optimal vigilance

We now explore the proportion of foraging time that a mammalian herbivore should devote to vigilance while foraging within a food path, given its possibility of multi-tasking. Optimal vigilance was determined following Brown (1999), an approach based on the survivor's fitness in the absence of predation ( $F$ ) and the probability of surviving predators in order to realize the gain in fitness ( $p$ ), as well as the effect of vigilance on the fitness of the surviving forager ( $\partial F/\partial u$ ) and on the probability of surviving ( $\partial p/\partial u$ ). Whereas Brown (1999) provides a detailed description of his model, here we point out a few differences with our approach.

Estimation of  $\partial F/\partial u$  requires information on the relationship between scanning and intake rate (Brown 1999). Consistent with the derivation of our foraging model, we assume that the proportion of foraging time

spent vigilant while not chewing vegetation ( $u$ , which excludes vigilance during  $Z$ ) increases the total foraging time by a factor  $(1 + u)$ . The net foraging gain during  $T_f$  is given by  $e$ , which then corresponds  $e = K/(1 + u) = IT_f/(1 + u)$ , and the effect of vigilance on the fitness of the surviving forager is found by

$$\frac{\partial F}{\partial u} = \left( \frac{\partial F}{\partial e} \right) \left( \frac{\partial e}{\partial u} \right) = \left( \frac{\partial F}{\partial e} \right) \left[ \frac{-IT_f}{(1 + u)^2} \right]$$

where  $I$  corresponds to Eq. 5 or Eq. 6, depending on whether the mammalian herbivore experiences foraging process 2 or 3, respectively.

Estimation of  $\partial p/\partial u$  requires information on predation risk, which relates to the probability of predators being present in the foraging area ( $P_p$ ), as well as to the functional relationships among predator detection, dilution, and herbivore group size. Based on Dehn (1990), we set the probability of an individual dying from predation to  $\mu = P_p \exp(-u_{\text{tot}}YN)/N$ , where the total amount of vigilance is  $u_{\text{tot}} = u + Z$  during process 3, and  $u_{\text{tot}} = u$  during process 2 (recall that  $Z = 0$  during process 2), and where  $Y$  covaries with the chance of escaping predators despite an attack.  $Y$  could scale, for example, with the time of detection by the herbivore once the predator leaves cover to attack (Dehn 1990). Vigilance during spare time decreases predation risks without reducing food intake rate (Illius and Fitzgibbon 1994); hence, herbivores should always spend at least  $Z$  proportion of their time scanning. Setting the probability of surviving predators during  $T_f$  to  $p = \exp(-\mu T_f)$  following Brown (1999), the effect of vigilance on safety becomes

$$\frac{\partial p}{\partial u} = P_p Y \exp(-YNu_{\text{tot}}) p T_f.$$

Expressions for  $\partial F/\partial u$  and  $\partial p/\partial u$  can be substituted into Eq. 11 of Brown (1999) to determine the optimal level of vigilance for mammalian herbivores:

$$(u^* + Z) \ln(1 + u^*) = -\ln \left[ \frac{I(\partial F/\partial e)}{FP_p Y} \right] \frac{1}{2YN}. \quad (15)$$

Using this equation, we can determine the proportion of foraging time that herbivores experiencing process 2 optimally should spend scanning while not chewing vegetation ( $u^*$ ) by setting  $Z = 0$  and replacing  $I$  with Eq. 5. For individuals experiencing process 3,  $u^*$  can also be found for a given set of parameters by calculating  $Z$  with Eq. 11 and  $I$  with Eq. 6. The optimal level of total vigilance is then found by  $u_{\text{tot}}^* = u^* + Z$ .

Simulations based on Eq. 15 indicate that foragers should be more vigilant as the probability of encountering predators increases, and as the marginal value of net foraging gain ( $\partial F/\partial e$ ) decreases (Fig. 3). These trends in vigilance that are expected when foraging processes can overlap (i.e., based on our functional response) are similar to trends anticipated in the case of non-overlapping foraging processes (cf. Brown

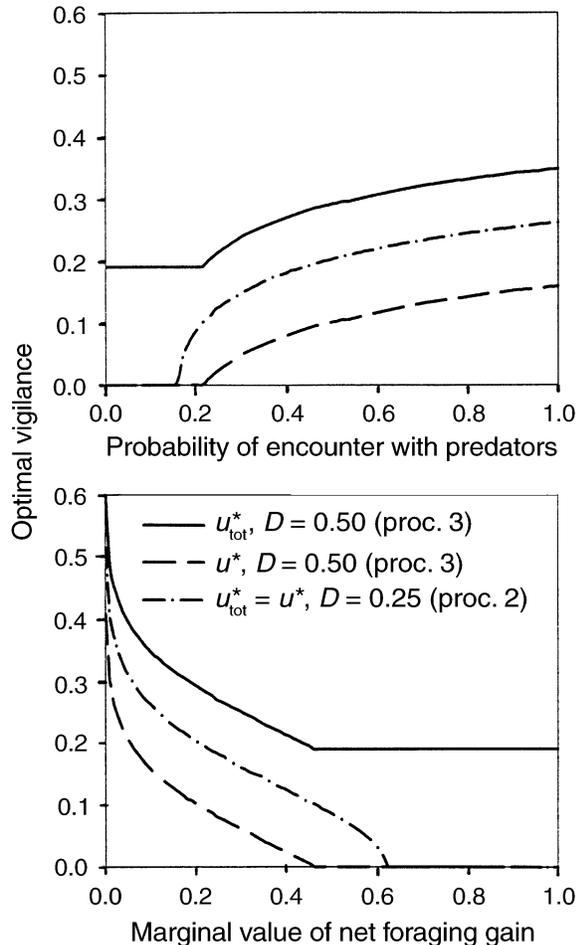


FIG. 3. The effect of probability of encounter with predators and marginal value of net foraging gain on the optimal level of vigilance while not chewing food ( $u^*$ ) and total vigilance ( $u_{\text{tot}}^* = u^* + Z$ ) for two densities of plants. Foraging processes 2 and 3 are experienced under  $D = 0.25$  and  $0.50$ , respectively. Parameters used in this example were  $V_{\text{max}} = 60$ ,  $R_{\text{max}} = 52.95$ ,  $\bar{h} = 0.012$ ,  $t_w = 0.15$ ,  $b = 0.05$ ,  $S = 1$ ,  $N = 15$ ,  $F = 30$ ,  $Y = 1$ ,  $\partial F/\partial e = 0.2$ , and  $P_p = 0.5$ , where  $F$  is the survivor's fitness in the absence of predation,  $Y$  reflects the chance of escaping predators despite an attack,  $\partial F/\partial e$  corresponds to the marginal value of net foraging gain, and  $P_p$  is the probability of predators being present in the foraging area.

1999). Also as in Brown (1999), we observed that vigilance while the animal is not chewing vegetation ( $u^*$ ) should decrease with increasing rate of food intake (or food abundance), which implies that  $u^*$  should be lower during process 3 than process 2 (Fig. 3). When we also consider vigilance during spare time, however, mammalian herbivores can be expected to spend an overall greater proportion of their foraging time being vigilant ( $u_{\text{tot}}^*$ ) during process 3 than process 2 (Fig. 3). Also, unlike foragers that cannot benefit from spare time (cf. Brown 1999), mammalian herbivores are expected to devote at least a proportion  $Z$  of time scanning, even under low probability of encounter with predators or

high marginal value of net foraging gain. This is because scanning during  $Z$  decreases predation risks without reducing food intake rate (Illius and Fitzgibbon 1994).

The optimal level of total vigilance ( $u_{\text{tot}}^*$ ) should decrease with increasing bite density during process 2, but  $u_{\text{tot}}^*$  and  $D$  should covary positively during process 3 because of the increase of  $Z$  with  $D$  (Fig. 4A). Despite the possibility of maintaining a certain level of vigilance without reducing intake rate (i.e., scanning during  $Z$ ), it might be optimal for mammalian herbivores to accept a reduction in food intake by further increasing their vigilance (i.e.,  $u^* > 0$ ), especially when the marginal value of net foraging gain ( $\partial F/\partial e$ ) is low (Fig. 4). Also, the optimal level of total vigilance ( $u_{\text{tot}}^*$ ) generally should decline with increasing group size (Fig. 4B). As for the vigilance model of McNamara and Houston (1992) based on non-overlapping processes, we observed that  $u_{\text{tot}}^*$  should decline (or remain 0) with increasing group size for foragers experiencing process 2 (i.e., when  $Z = 0$ ). During process 3, however, vigilance while not chewing food ( $u^*$ ) may display various relationships with  $N$ . For example,  $u^*$  might decrease sharply before increasing slightly (Fig. 4B, process 3:  $\partial F/\partial e = 0.2$ ). This positive covariation between  $u^*$  and  $N$  is a consequence of density-dependent effects on spare time:  $Z$  decreases with  $N$ , leading to a decline in the vigilance associated with  $Z$  that affects an individual's safety. Whenever the decrease in individual safety associated with the decline in vigilance during spare time is faster than the increase in safety inherent to belonging to a larger group, maintaining fitness would require herbivores to compensate by increasing  $u^*$  despite the increase in  $N$  (Fig. 4B). Finally,  $u^*$  might remain 0 despite changes in group size, especially when  $\partial F/\partial e$  is high (Fig. 4B, process 3:  $\partial F/\partial e = 0.8$ ). In this case, a decrease in  $u_{\text{tot}}^*$  with increasing group size would still be expected due to changes in  $Z$ . This result confirms that, as indicated previously (Fig. 1), a decrease in vigilance with  $N$  may be expected due to foraging constraints alone.

## DISCUSSION

We provide a mechanistic functional response developed to determine the rate of food intake by gregarious herbivores capable of carrying out brief activities while chewing food. Our study demonstrates how multi-tasking by mammalian herbivores can buffer food intake rate from time spent in competitive interactions and vigilance. This demonstration is significant because it reveals that, by not accounting for the possibility of multi-tasking, current foraging models should overestimate the effect of interference and exploitative competition on the food intake rate of mammalian herbivores. Likewise, classical foraging models might incorrectly predict the effect of scanning on community dynamics by assuming that antipredator vigi-

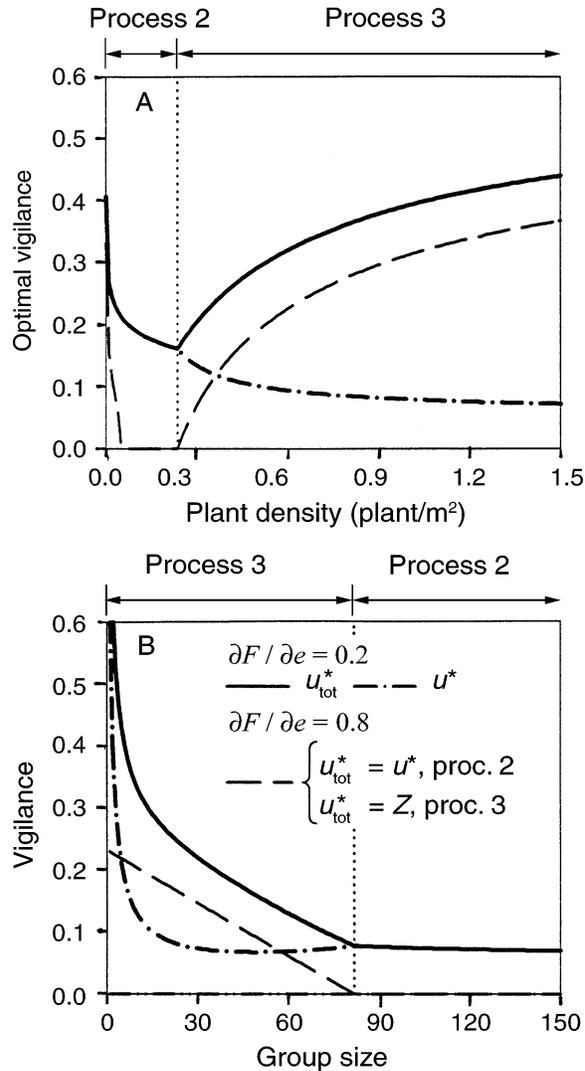


FIG. 4. The effect of plant density and group size on the optimal level of vigilance while not chewing food ( $u^*$ ) and total vigilance ( $u_{tot}^* = u^* + Z$ ) for two levels of  $\partial F / \partial e$ . The vertical dotted line delimits processes 2 and 3 of foraging. Notice that for  $\partial F / \partial e = 0.8$ ,  $Z = 0$  and  $u_{tot}^* = u^*$  during process 2, whereas  $u^* = 0$  and  $u_{tot}^* = Z$  during process 3. Parameters were  $V_{max} = 60$ ,  $R_{max} = 52.95$ ,  $\bar{h} = 0.012$ ,  $t_w = 0.15$ ,  $b = 0.05$ ,  $S = 1$ ,  $F = 30$ ,  $Y = 1$ , and  $P_p = 0.5$ .

lance reduces the vegetation intake rate of foragers capable of multi-tasking.

*Competitive interactions*

Our theoretical framework recognized that short-term food intake can be limited by the time required either to process or to encounter food (Spalinger and Hobbs 1992, Farnsworth and Illius 1996, Fortin et al. 2002). The intake rate of a gregarious herbivore is controlled by the food processing rate (process 3) only when it takes longer to chew the current bite than to walk away from competitors and to find the next food

bite. Such multi-tasking by foraging herbivores can produce a functional response that exhibits both density-independent and density-dependent characteristics, depending on food abundance and the extent of competitive interactions (Fig. 1). The possibility of a functional response that can be density independent despite the presence of competitors constitutes an important addition to the theory of interference competition. Current models consider that the presence of competitors is necessarily costly (e.g., Hassell and Varley 1969, Beddington 1975, Free et al. 1977, Ward et al. 2000), and that the functional response is simply density dependent (Fryxell and Lundberg 1997). Our model indicates that the overlap between foraging processes can buffer the effect of interference competition on food intake rate, which may remain at a maximum despite the presence of competitors. Given the key role of functional responses in linking consumer-prey populations, the consideration of multi-tasking by foraging herbivores can be a crucial component of plant-herbivore models.

The overlap between foraging processes also buffers intake rate from food patch depletion. As illustrated with our simulated elk, mammalian herbivores have the potential to maintain their rate of food intake despite food depletion, until the vegetation in the patch reaches a very low density of food resources. This food density threshold depends on factors such as herbivore density, intensity of competitive interactions, chewing time, and foraging velocity. The buffering effects of multi-tasking would make it challenging to detect an influence of competition on intake rate under natural conditions. Mammalian herbivores can reach successive bites of vegetation rapidly due to their high foraging velocity (Shiple et al. 1996). For example, a 266-kg elk could travel as much as 9.9 m while chewing a bite of vegetation (Hobbs et al. 2003). At greater distances, intake rate becomes limited by the encounter rate with bites (process 2), instead of by the rate of food processing (process 3). We conducted simulations that were based on parameter values realistic for foraging elk (Gross et al. 1993b, Shiple et al. 1996). During these simulations, the rate of food intake remained constant (i.e., process 3 prevailed), unaffected by depletion, during approximately the first 96% of foraging time that preceded complete resource depletion. Consistent with this result, Illius et al. (2002) observed that the gain function of browsing roe deer (*Capreolus capreolus*) generally remains independent of food depletion. The review by Illius et al. (2002) of foraging studies on browsers led them to conclude that gain functions should be virtually linear among most herbivore species, because process 3 would predominate. Likewise, field studies on grazing herbivores generally report a decline in bite rate with food abundance that is most consistent with process 3 of foraging (cf. Bradbury et al. 1996).

Although we restricted our examples to foraging elk, multi-tasking should also apply to large browsers (cf. Illius et al. 2002), as well as to smaller mammalian herbivores. For example, Hobbs et al. (2003) indicate that herbivores such as lemming (*Dicrostonyx groenlandicus*), black-tailed prairie dog (*Cynomys ludovicianus*), and domestic rabbit (*Oryctolagus cuniculus*) can travel extensive distances (see threshold  $d^*$  in Hobbs et al. [2003]) while chewing bites of vegetation, which constitutes direct evidence of overlapping processes in mammalian herbivores. Our foraging model thus is relevant for a wide array of mammalian herbivores.

#### Spare time and vigilance

We calculated spare time based on common assumptions of foraging models for mammalian herbivores (Spalinger and Hobbs 1992, Gross et al. 1993b, Illius and Fitzgibbon 1994, Illius et al. 2002, Hobbs et al. 2003). Certain of these assumptions may, however, not be suitable for all systems of mammalian herbivores. For example, we calculated spare time assuming that a forager would crop, chew, and swallow one food bite at a time, as also assumed by Illius and Fitzgibbon (1994) and Hobbs et al. (2003). But when food is highly concentrated in space, herbivores can crop several bites successively, and then chew these bites for a given period of time (Pastor et al. 1999). Under certain assumptions, this behavior should increase the amount of spare time available to the forager. First, let us assume that  $S$  does not change much during a foraging bout (Pastor et al. 1999), and that  $\bar{h}$  and  $R_{\max}$  do not decrease with the number of bites accumulated in the mouth during cropping (notice that Pastor et al. [1999] provide a foraging model that applies when the assumption of a constant  $\bar{h}$  is violated). Under these assumptions, the proportion of spare time associated with each cropping–chewing sequence should increase with the number of bites ( $i$ ) accumulated before initiation of the chewing bout:

$$Z = \frac{V_{\max} 2\sqrt{D} \sum_i S - R_{\max} [1 + bt_w(N - 1)]}{V_{\max} 2\sqrt{D} \left( R_{\max} \sum_i \bar{h} + \sum_i S \right)}. \quad (16)$$

Assuming that the number of bites accumulated before initiation of chewing bouts has a normal distribution,  $N(i, \sigma^2)$ , during a foraging bout, Eq. 16 can also be used to calculate the average proportion of foraging time consisting of spare time.

Our model further assumes that herbivores cannot crop while chewing (also assumed by Spalinger and Hobbs 1992, Farnsworth and Illius 1996, Illius et al. 2002, Gross et al. 1993a, b). Although this assumption appears to be justified for most herbivores (Spalinger and Hobbs 1992, Bradbury et al. 1996), there is some evidence indicating that chewing and cropping could overlap (Laca et al. 1994, Pastor et al. 1999). Our model

does not allow for this possibility, and such overlap should reduce the amount of spare time that herbivores can devote to vigilance because a certain amount of chewing time could then be used to crop new bites. Despite such a possibility, Spalinger and Hobbs's (1992) foraging model has been shown to reflect faithfully the foraging behavior of several species of mammalian herbivores (Gross et al. 1993b, Hobbs et al. 2003), and to be easily modifiable to better represent other systems of mammalian herbivores (e.g., see Pastor et al. 1999). Given the close link between our modeling approach and that of Spalinger and Hobbs (1992), our mechanistic functional response should also be flexible to variations in assumptions.

Spare time should allow animals to carry out various brief activities, such as getting relief from insect harassment or scanning for conspecifics or predators, without interrupting food intake. Our investigation of optimal antipredator vigilance demonstrates that the possibility of multi-tasking can importantly alter expectations of vigilance. Depending on the relative importance of foraging constraints (Eq. 15), these differences can be as striking as predicting that a given change in the environment should induce an increase instead of a decrease in vigilance. Hence, the interpretation of observed variations in vigilance maintained by mammalian herbivores, as well as speculations on the ecological consequences of maintaining these levels of vigilance (e.g., the effect of vigilance on herbivore recruitment; Laundré et al. [2001]) requires the consideration of multi-tasking by these foragers.

A decline in scanning rate with increasing group size is one of the most consistent observations among herbivore vigilance studies (Elgar 1989, Dehn 1990, Lima and Dill 1990, Quenette 1990). This decrease in vigilance usually is attributed to a reduction of predation risks (Lima 1995). Members of large groups benefit from predator dilution risks and scanning duties are "shared" among group members, allowing for a decrease in individual vigilance while maintaining, or even decreasing, predation risks (Dehn 1990, Lima 1995, Roberts 1996). This explanation of variation in vigilance is based on the premise that scanning necessarily carries the cost of reduced food intake, and that as predation pressure decreases, vigilance is reduced to minimize these costs (Lima 1995, Treves 2000). Our analyses demonstrate that the trade-off between food and safety might be insufficient to explain this general trend in vigilance for mammalian herbivores. The propensity of foragers to reduce their intake rate for greater safety depends largely on factors such as the marginal value of net foraging gain ( $\partial F/\partial e$ ). When  $\partial F/\partial e$  is high, for example, foragers may not accept any decrease in intake rate. Under these conditions, the observed decrease in scanning rate for groups ranging would be entirely due to density-dependent effects on spare time. In other words, this change in vigilance with increasing herbivore density

can be expected in the complete absence of predators or even of any predation history, and might be due to foraging constraints alone. The effect of foraging constraints has been (reviewed by Elgar 1989) and remains (e.g., Bøving and Post 1997, Laundré et al. 2001, Wolff and Van Horn 2003) largely overlooked in vigilance studies, and we suggest that these constraints might play a key role in controlling vigilance of herbivores in natural systems.

#### CONCLUSION

The possibility of carrying out multiple tasks without reducing food intake sets herbivores apart from carnivores. Overlap between foraging processes can buffer instantaneous food intake rate from competitive interactions. Given sufficient food abundance, an herbivore can maintain its rate of food intake despite time spent walking away from competitors and looking out for predators. The consequences of multi-tasking by foraging herbivores thus could be felt across multiple trophic levels. By being vigilant during their spare time, herbivores can reduce predation risks (Fitzgibbon 1989) while maintaining grazing pressure on plant communities. Thus the impact of herbivory on plant populations could remain at high levels despite competitive interactions. Our results demonstrate that multi-tasking by foraging herbivores can be a substantial consideration in understanding the role of herbivores in ecosystems.

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#### LITERATURE CITED

- Beddington, J. R. 1975. Mutual interference between parasites or predators and its effect on searching efficiency. *Journal of Animal Ecology* **44**:331–340.
- Bøving, P. S., and E. Post. 1997. Vigilance and foraging behaviour of female caribou in relation to predation risk. *Rangifer* **17**:55–63.
- Bradbury, J. W., S. L. Vehrencamp, K. E. Clifton, and L. M. Clifton. 1996. The relationship between bite rate and local forage abundance in wild Thomson's gazelles. *Ecology* **77**:2237–2255.
- Brown, J. S. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. *Evolutionary Ecology Research* **1**:49–71.
- Brown, J. S., J. W. Laundré, and M. Gurung. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* **80**:385–399.
- Clark, P. J., and F. C. Evans. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* **35**:443–453.
- Dehn, M. M. 1990. Vigilance for predators: detection and dilution effects. *Behavioral Ecology and Sociobiology* **26**:337–342.
- Elgar, M. A. 1989. Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biological Reviews* **64**:13–33.
- Fanshawe, J. H., and C. D. Fitzgibbon. 1993. Factors influencing the hunting success of an African wild dog pack. *Animal Behaviour* **45**:479–490.
- Farnsworth, K. D., and A. W. Illius. 1996. Large grazers back in the fold: generalizing the prey model to incorporate mammalian herbivores. *Functional Ecology* **10**:678–680.
- Farnsworth, K. D., and A. W. Illius. 1998. Optimal diet choice for large herbivores: an extended contingency model. *Functional Ecology* **12**:74–81.
- Fitzgibbon, C. D. 1989. A cost to individuals with reduced vigilance in groups of Thomson's gazelles hunted by cheetahs. *Animal Behaviour* **37**:508–510.
- Fortin, D. 2001. An adjustment of the extended contingency model of Farnsworth and Illius (1998). *Functional Ecology* **15**:138–139.
- Fortin, D., J. M. Fryxell, and R. Pilote. 2002. The temporal scale of foraging decisions in bison. *Ecology* **83**:970–982.
- Free, C. A., J. R. Beddington, and J. H. Lawton. 1977. On the inadequacy of simple models of mutual interference for parasitism and predation. *Journal of Animal Ecology* **46**:543–554.
- Fryxell, J. M. 1991. Forage quality and aggregation by large herbivores. *American Naturalist* **138**:478–498.
- Fryxell, J. M., and P. Lundberg. 1997. Individual behavior and community dynamics. Chapman and Hall, New York, New York, USA.
- Gross, J. E., N. T. Hobbs, and B. A. Wunder. 1993a. Independent variables for predicting intake rate of mammalian herbivores: biomass density, plant density, or bite size? *Oikos* **68**:75–81.
- Gross, J. E., L. A. Shipley, N. T. Hobbs, D. E. Spalinger, and B. A. Wunder. 1993b. Functional response of herbivores in food-concentrated patches: tests of a mechanistic model. *Ecology* **74**:778–791.
- Hassell, M. P., and G. C. Varley. 1969. New inductive population model for insect parasites and its bearing on biological control. *Nature* **223**:1133–1136.
- Hebblewhite, M., and D. H. Pletscher. 2002. Effects of elk group size on predation by wolves. *Canadian Journal of Zoology* **80**:800–809.
- Hobbs, N. T., J. E. Gross, L. A. Shipley, D. E. Spalinger, and D. A. Wunder. 2003. Herbivore functional response in heterogeneous environments: a contest among models. *Ecology* **84**:666–681.
- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* **91**:385–398.
- Illius, A. W., P. Duncan, C. Richard, and P. Mesochina. 2002. Mechanisms of functional response and resource exploitation in browsing roe deer. *Journal of Animal Ecology* **71**:723–734.
- Illius, A. W., and C. Fitzgibbon. 1994. Costs of vigilance in foraging ungulates. *Animal Behaviour* **47**:481–484.
- Kotler, B. P., J. S. Brown, S. R. X. Dall, S. Gresser, D. Ganey, and A. Bouskila. 2002. Foraging games between gerbils and their predators: temporal dynamics of resource depletion and apprehension in gerbils. *Evolutionary Ecology Research* **4**:495–518.
- Krause, J., and J.-G. Godin. 1995. Predator preferences for attacking particular group sizes: consequences for hunting success and prey predation risk. *Animal Behaviour* **50**:465–473.
- Laca, E. A., E. D. Ungar, and M. W. Demment. 1994. Mechanisms of handling time and intake rate of a large mammalian grazer. *Applied Animal Behaviour Science* **39**:3–19.
- Laundré, J. W., L. Hernández, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology* **79**:1401–1409.

- Lima, S. L. 1995. Back to the basics of anti-predatory vigilance: the group size effect. *Animal Behaviour* **49**:11–20.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**:619–640.
- McNamara, J. M., and A. I. Houston. 1992. Evolutionarily stable levels of vigilance as a function of group size. *Animal Behaviour* **43**:641–658.
- Pastor, J., K. Standke, K. Farnsworth, R. Moen, and Y. Cohen. 1999. Further development of the Spalinger-Hobbs mechanistic foraging model for free-ranging moose. *Canadian Journal of Zoology* **77**:1505–1512.
- Quenette, P.-Y. 1990. Functions of vigilance behaviour in mammals: a review. *Acta Oecologica* **11**:801–818.
- Roberts, G. 1996. Why individual vigilance declines as group size increases. *Animal Behaviour* **51**:1077–1086.
- Shipley, L. A., D. E. Spalinger, J. E. Gross, N. T. Hobbs, and B. A. Wunder. 1996. The dynamics and scaling of foraging velocity and encounter rate in mammalian herbivores. *Functional Ecology* **10**:234–244.
- Spalinger, D. E., and N. T. Hobbs. 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. *American Naturalist* **140**:325–348.
- Stephens, D. W., and J. R. Krebs. 1986. *Foraging theory*. Princeton University Press, Princeton, New Jersey, USA.
- Sutherland, W. J. 1996. *From individual behaviour to population ecology*. Oxford University Press, Oxford, UK.
- Treves, A. 2000. Theory and method in studies of vigilance and aggregation. *Animal Behaviour* **60**:711–722.
- Ward, J. F., R. Austin, and D. W. Macdonald. 2000. A simulation model of foraging behaviour and the effect of predation risk. *Journal of Animal Ecology* **69**:16–30.
- Wolff, J. O., and T. Van Horn. 2003. Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. *Canadian Journal of Zoology* **81**:266–271.