BEHAVIORAL ECOLOGY

When carnivores are "full and lazy"

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Abstract Are animals usually hungry and busily looking for food, or do they often meet their energetic and other needs in the 24 h of a day? Focusing on carnivores, I provide evidence for the latter scenario. I develop a model that predicts the minimum food abundance at which a carnivore reaches satiation and is released from time constraints. Literature data from five invertebrate and vertebrate species suggest that food abundances experienced in the field often exceed this threshold. A comparison of energetic demands to kill rates also suggests that carnivores often reach satiation: for the 16 bird and mammal species analyzed, this frequency is 88% (average across species). Because pressure of time would likely lead to trade-offs in time allocation and thus to a nonsatiating food consumption, these results suggest that carnivores are often released from time constraints.

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Introduction

Animals acquire energy by foraging, i.e. searching for food and handling it, yet they spend surprisingly little time in this activity (Herbers 1981; Bunnell and Harestad 1990). Jeschke et al. (2002) offered a proximate explanation for this pattern. Their review of empirical data indicated that most animals need less time for handling, i.e. capturing and eating, one food item than for digesting it (see also van Gils and Piersma 2004; Karasov and McWilliams 2005). Since digestion is a passive process, it does not prevent animals from foraging. However, digestion influences gut fullness and thus feelings of hunger and satiation. In this way, digestion influences the motivation to forage. Under good environmental conditions, e.g. high food abundance, one can therefore expect that the digestion time of an animal limits its foraging time: a slow digestion leads to a full gut and thus to satiation, so the animal is not motivated or able to spend more time foraging. This is a proximate explanation for the limited foraging times that animals show.

From an evolutionary perspective, one may wonder why animals do not simply digest their meals faster. With his principle of stringency, Wilson (1975) offered an answer to this question (see also Jeschke and Tollrian 2005a): "Time-energy budgets evolve so as to fit to the times of greatest stringency," such as periods of low food abundance (e.g. severe winters), large food requirements (e.g. rearing of offspring), or greatest

alternative demands (e.g. reproductive activities). The principle relies on the assumption that the fittest animals are those whose traits fit to the times of greatest stringency, especially traits that determine their time budgets. One of these traits is digestion time which is, in turn, determined by gut capacity and retention time. If these traits have evolved so as to fit to the times of greatest stringency, they do not necessarily fit to other times. For example, gut capacity should be small during periods of low food abundance because a large gut is energetically demanding and cannot be filled as food is hard to find. During periods of high food abundance, however, food is easy to find and gut capacity should hence be larger. Similarly, gut capacity should be small during periods of low energetic requirements and large during periods of high energetic requirements. It would be optimal for animals to have a phenotypically highly flexible gut, but most guts cannot adjust to environmental conditions and energetic requirements as greatly and as rapidly as these conditions and requirements vary (see next paragraph). If the capacity of such a gut has, for example, evolved so as to fit to periods of low food abundance, it will be "too small" beyond these periods. Accordingly, animals will experience time constraints during but not beyond periods of low food abundance.

Although animal guts are flexible, sometimes extremely as in pythons (Starck and Beese 2001), this flexibility does not usually match the temporal variation in environmental conditions and energetic requirements. According to a review by Karasov and McWilliams (2005), migrating birds are able to double the size of their gut within a week. Red knots (*Calidris canutus*) can increase their gizzard's size by about 0.2–0.5 g/day, so need about 8–20 days for an increase to 8 from 4 g (van Gils et al. 2005b). In spite of this high flexibility, red knots often face digestive constraints (van Gils and Piersma 2004; van Gils et al. 2005a, b). Coming back to the general case, many vertebrates can increase their gut's size by 20–40% within days and by roughly 100% in the long term (Piersma and Drent 2003; Karasov and McWilliams 2005). Food abundances and energetic requirements, however, can show a much higher variation (NERC Centre for Population Biology, Imperial College 1999). As argued above, this imperfect match of dynamics in gut size and dynamics in food abundance and requirements should often lead to "laziness."

There are other studies that consider the absence of time constraints, but traditional foraging theory assumes constant pressure of time (reviewed by Stephens and Krebs 1986; Jeschke and Tollrian 2005a; Whelan and Brown 2005; Jeschke et al. 2006), a view that is still

shared by many ecologists today (Gerber et al. 2004; Catania and Remple 2005; Yamamuchi and Yamamura 2005). Overviews of these two opposing schools of thought, physiological ecology versus foraging theory, have been given by Whelan and Brown (2005) and Whelan and Schmidt (2006).

The current study is based on Jeschke and Tollrian (2005a), who analyzed data from 19 herbivorous species and showed that these consumers usually reach satiation in the field, suggesting that they are often released from time constraints. However, an alternative explanation is possible: when herbivores have enough time to reach satiation, they do not necessarily have enough time to choose the most desirable diet. Because herbivores are usually confronted with a high variability in the quality of their food, they seldom have problems finding food of low quality, but they might have trouble finding food of high quality. These circumstances complicate the interpretation of Jeschke and Tollrian's (2005a) results.

By focusing on carnivores, I reduce such problems in the current study, for the quality of their food is less variable (although variation still exists, e.g. van Gils et al. 2005a, b). I develop a model that predicts the food abundance at which a consumer reaches satiation and is released from time constraints. It also predicts how much time a consumer must spend foraging to reach satiation and how much "spare time" it has depending on food abundance. Although the model is not restricted to carnivores, it is most applicable to these consumers, for it considers only one type of food, in particular it does not consider different qualities of food. The model can be extended to different food types but is only used in its basic form here. I parameterize it with carnivore data from the literature and compare published kill rates of free-ranging carnivorous birds and mammals with their energetic demands. The results suggest that carnivores frequently reach satiation and are arguably often released from time constraints.

The model

The model relates time budgets of consumers to the abundance of their food. For simplicity, the model only considers the time a consumer is potentially able to forage, e.g. daylight hours for predators of diurnal prey or for visually foraging consumers. This time is called total time here. It can be divided into foraging time t_f (given as a fraction of total time; hence $0 \leq t_f \leq 1$, dimensionless) and non-foraging time t_{nf} (given as a fraction of total time; hence $0 \leq t_{nf} \leq 1$, dimensionless):

$$t_{\mathrm{f}} = 1 - t_{\mathrm{nf}}. \tag{1}$$

According to Holling (1966), a consumer's consumption rate is reduced by the time the consumer spends nonforaging:

$$y(t_{\mathrm{f}}; x) = (1 - t_{\mathrm{nf}})\, y_{\mathrm{f}}(x) = t_{\mathrm{f}}\, y_{\mathrm{f}}(x), \tag{2}$$

where $y(t_{\mathrm{f}}; x)$ is consumption rate over longer periods of time (dimension in SI units: s^{-1}), x is food abundance (dimension in SI units: m^{-2} for a two-dimensional system, e.g. a terrestrial system, and m^{-3} for a 3D system, e.g. an aquatic system), and $y_{\mathrm{f}}(x)$ is consumption rate when $t_{\mathrm{f}} = 1$. Most previous studies that explicitly stated the relationship between food uptake and foraging time follow Eq. 2, i.e. they assumed a linear relationship (Real 1977; Owen-Smith and Novellie 1982; Abrams 1984, 1990; McNamara and Houston 1994); Schmitz et al. (1998) assumed a hyperbolic relationship. These models have thus assumed a strictly monotonously increasing relationship, i.e. a trade-off between foraging and nonforaging. They thereby neglected consumer satiation: a typical consumer finds food relatively fast when it is abundant, thus having a lot of ''spare time'' where foraging does not make sense due to satiation (see Introduction). It may use this spare time for nonforaging activities without reducing the amount of food assimilated.

I will show that consumer satiation lets the trade-off between foraging and nonforaging activities disappear if food abundance exceeds a certain threshold. As a basic model, I use the steady-state satiation equation (SSS equation; Jeschke et al. 2002):

$$y_{\mathrm{f}}(x) = \begin{cases} \dfrac{1+ax(b+c)-\sqrt{1+ax\left(2(b+c)+ax(b-c)^2\right)}}{2abcx} & a,b,c,x>0 \\[2ex] \dfrac{ax}{1+abx} & b>0, c=0 \\[2ex] \dfrac{ax}{1+acx} & b=0, c>0 \\[2ex] ax & b=c=0 \\[1ex] 0 & a=0 \text{ or } x=0 \end{cases}$$

with

success rate $a = \beta\gamma\varepsilon$,

handling time $b = \dfrac{t_{\mathrm{att}}}{\varepsilon} + t_{\mathrm{eat}}$,

digestion time $c = t_{\mathrm{g}}/g$,

$$\tag{3}$$

where β is the encounter rate between a searching consumer and a single food item (dimension in SI units: $m^2\,s^{-1}$ for a 2D system, and $m^3\,s^{-1}$ for a 3D system); γ is the probability that the consumer detects encountered food (dimensionless); ε is efficiency of attack (dimensionless), i.e. the proportion of successful

attacks; t_{att} is attacking time per food item (s); t_{eat} is eating time per food item (s); t_{g} is gut retention time (s); and g is gut capacity (dimensionless), i.e. the number of food items the gut of a satiated animal holds. In the SSS equation, the asymptotic maximum consumption rate is

$$\lim_{x \to \infty} y_{\mathrm{f}}(x) = \frac{b+c-\sqrt{(b-c)^2}}{2bc}$$

1) handling – limited consumers:

$$b \geq c \quad \Leftrightarrow \quad \lim_{x \to \infty} y_{\mathrm{f}}(x) = \tfrac{1}{b}$$

2) digestion – limited consumers:

$$c > b \quad \Leftrightarrow \quad \lim_{x \to \infty} y_{\mathrm{f}}(x) = \tfrac{1}{c}$$

$$\Leftrightarrow \lim_{x \to \infty} y_{\mathrm{f}}(x) = \frac{1}{\max(b;c)}. \tag{4}$$

More details are given in Jeschke et al. (2002, 2006). Thus, at a very high (strictly speaking: infinite) food abundance, consumption rate is either determined by the consumer's corrected handling time b (handling-limited consumer) or by its corrected digestion time c (digestion-limited consumer). Handling-limited consumers cannot become satiated and are therefore always time constrained. Most consumers seem to be digestion-limited, however (Jeschke et al. 2002).

I now address the question: At which food abundance is a consumer released from time constraints? The question can also be formulated as: At which food abundance does nonforaging not reduce food uptake? Imagine a consumer that has to invest a given amount of time avoiding predators, lying in the shade, and reproducing. If this time spent nonforaging reduces food uptake, the consumer is time-constrained, otherwise not. Digestive pauses can alternatively be used for nonforaging activities without reducing food uptake (see Introduction). I therefore call these pauses spare time t_{sp} (given as a fraction of total time; hence $0 \leq t_{\mathrm{sp}} \leq 1$, dimensionless). Total spare time can be calculated as

$$\begin{aligned} t_{\mathrm{sp}}(x) &= (c - \text{mean time between two} \\ &\qquad \text{ingestions in case of } t_{\mathrm{nf}} = 0)\, y_{\mathrm{f}}(x) \\ &= (c - 1/(ax) - b)\, y_{\mathrm{f}}(x). \end{aligned} \tag{5}$$

Asymptotical maximum spare time for a digestion-limited consumer is

$$\lim_{x \to \infty} t_{\mathrm{sp}}(x) = 1 - b/c. \tag{6}$$

Spare time is graphically represented in Fig. 1; it is negative at low food abundances (i.e. nonforaging
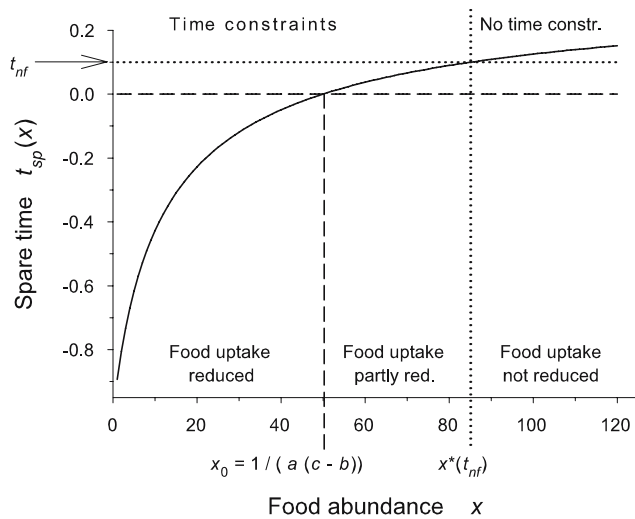
Fig. 1 Consumer spare time $t_{sp}(x)$ as a function of food abundance x; t_{sp} becomes positive at $x_0 = 1/[a\,(c-b)]$. In the example, the consumer invests 10% ($t_{nf} = 0.10$) of its time nonforaging. For $x \leq x_0$, this nonforaging fully reduces food uptake; for $x_0 < x < x^*(t_{nf})$, food uptake is partly reduced; and for $x \geq x^*(t_{nf})$, there is no reduction in food uptake at all. Model inputs: $a = 2$, $b = 0.02$, $c = 0.03$

reduces food uptake here) and positive at high food abundances. The threshold food abundance x_0, where spare time t_{sp} becomes positive, is

$$t_{sp}(x_0) = 0 \Leftrightarrow x_0 = 1/(a\,(c-b)). \qquad (7)$$

In Fig. 1, the consumer needs to spend 10% of its time nonforaging. Food abundance x determines whether this nonforaging reduces food uptake: below the threshold food abundance x_0, nonforaging fully reduces food uptake according to Eq. 2; between x_0 and $x^*(t_{nf})$, the consumer has some spare time to invest in nonforaging, so food uptake is only partly reduced; finally, if food abundance exceeds $x^*(t_{nf})$, spare time exceeds necessary nonforaging time and food uptake is consequently not reduced at all.

Let us now ask: When does additional foraging increase food uptake? We can address this question on the basis of our previous considerations. If $x \leq x_0$, food uptake increases in proportion to foraging time t_f according to Eq. 2; if $x > x_0$, food uptake increases in proportion to t_f until it reaches its maximum where nonforaging time equals spare time, i.e. $t_{nf} = t_{sp} \Leftrightarrow t_f = 1 - t_{sp}$. These considerations can mathematically be summarized as

$$y(t_f; x) = \begin{cases} t_f\,y_f(x) & x \leq x_0 \\ \dfrac{t_f\,y_f(x)}{1 - t_{sp}(x)} & x > x_0 \ \wedge \ t_f < 1 - t_{sp}(x) \\ y_f(x) & x > x_0 \ \wedge \ t_f \geq 1 - t_{sp}(x), \end{cases} \quad (2a)$$

for $t_{sp}(x)$ see Eq. 5. Equation 2a is a corrected version of Eq. 2 and is depicted in Fig. 2 (cf. Weiner 2000). The consumption rate at the threshold food abundance $y(t_f; x_0)$ can now also be easily calculated. After inserting x_0 into Eq. 2a and simplifying, we get

$$y(t_f; x_0) = \frac{t_f}{b}\left(1 - \sqrt{1 - \frac{b}{c}}\right). \qquad (8)$$

Model parameterizations

Methods

I parameterized the model with data from the literature in order to estimate values for the threshold prey density x_0, i.e. the density at which a predator is beginning to become satiated and released from time constraints. I then compared the estimates for x_0 with prey densities measured in the field. To calculate x_0, values are needed for the parameters success rate a, handling time b, and digestion time c (see Eq. 7). If available, I used measurements of subparameters that could be directly transferred to values of a, b, and c. If the values for a and/or c could not be calculated in this way, I estimated them by fitting a functional response equation with a nonlinear regression model to the functional response of the focal predator. (The functional response of a predator is the number of prey items it consumes per time period as a function of prey density). This is only possible if the functional response is of type II (Holling 1959; Jeschke et al. 2004). For
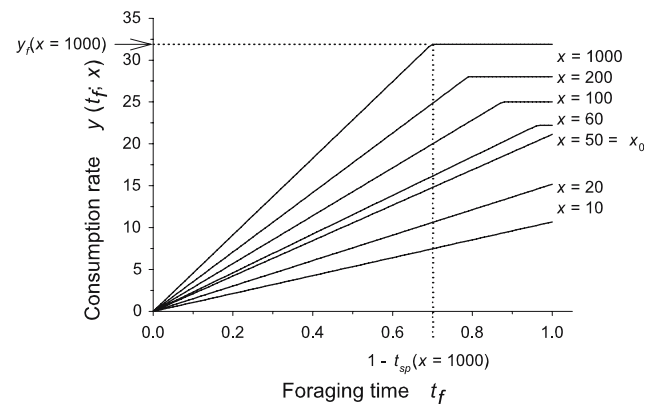
Fig. 2 Consumption rate $y(t_f; x)$ as a function of foraging time t_f, given for different food abundances x (Eq. 2a). Up to the threshold density x_0 [$= 1/(a(c-b))$, Eq. 7; here: $x_0 = 50$], y is proportional to t_f, and Eq. 2a equals Eq. 2. Above x_0, y is still proportional to t_f if $t_f < 1 - t_{sp}(x)$ [for spare time $t_{sp}(x)$, see Eq. 5]. In case of $x > x_0$ and $t_f \geq 1 - t_{sp}(x)$, y cannot be further increased by investing more time in foraging, so it remains constant. Model inputs: $a = 2$, $b = 0.02$, $c = 0.03$

estimating c, I only used long-term responses because only these include predator satiation effects. Handling times b were only estimated on the basis of direct measurements of subparameters, not by using functional responses, for it is usually impossible to extract reliable estimates of b from functional response curves (Fox and Murdoch 1978; Abrams 1990; Caldow and Furness 2001; Jeschke et al. 2002; Jeschke and Tollrian 2005b). I analyzed all species for which I had the necessary data available except for wading birds where data for several species were available. To prevent a taxonomic bias, I included only one arbitrarily chosen wader in my analysis.

Results

The results of the model parameterizations suggest that natural prey densities can be sufficiently high to allow predator satiation and release from time constraints (Table 1). The frequency of such densities experienced by predators is currently unclear, however, due to lacking data.

Kill rates

Methods

Another approach to estimate how often carnivores are satiated or released from time constraints is to compare their field kill rates with their energetic demands. For this approach, the following data are needed: FR, a functional response of the carnivore measured in the field; DIET, the relationship between the relative frequency of the prey species in the diet of the predator (related to biomass) and prey density; M, the average body mass of a prey individual; and FMR, the average field metabolic rate of a carnivore individual. I used these data as follows:

1. Each data point of the field functional response (FR) gave the number of prey individuals killed per carnivore in a certain time period. I used this number together with DIET and M in order to calculate the kill rate (KR) in grams of prey per carnivore per day.

2. To calculate the demand in grams of prey per carnivore per day, I first estimated energetic demand E_{demand} (cf. Willmer et al. 2000) as

$$E_{demand} = (FMR + E_p)/AE = FMR\,(1 + PE)/AE$$
$$= 1.18\,FMR\,(1 + PE), \qquad (9)$$

where E_p is energy invested in production (growth or reproduction), PE ($= E_p/FMR$) is production efficiency (dimensionless; see Humphreys 1979 for quantitative values), and AE is assimilation efficiency, which is about 0.85 for carnivores on average (Willmer et al. 2000). I then divided E_{demand} (kJ/day) by 7 in order to calculate

Table 1 Parameterizations of the model for digestion-limited carnivores

Carnivore species	Prey species	Success rate a	Handling time b	Digestion time c	Threshold prey density x_0[a]	Actual field prey density
Calliopius laeviusculus (Crustacea: Amphipoda)	*Mallotus villosus* (capelin eggs)	>0.028 cm³/h[b]	0.043 h[c]	2.2 h[c]	<17 cm⁻³	≤76 cm⁻³ [d]
Hierodula crassa (Insecta: Mantodea)	Flies	0.021 m²/h[e]	0.02 h[e]	0.49 h[e]	101 m⁻²	Highly variable
Chaoborus obscuripes (Insecta: Diptera)	*Daphnia* spp.	0.11 L/h[f]	0.00038 h[f]	0.7 h[f]	13 L⁻¹	≤10.000 L⁻¹ [g]
Macrobiotus richtersi (Tardigrada)	*Acrobeloides nanus*	0.0004 cm³/min[h]	0.9 min[h]	10 min[h]	275 cm⁻³	≤3000 cm⁻³ [i]
Calidris canutus (red knot) (Aves)	*Mytilus edulis* (blue mussel)	0.16 m²/min[j]	0.010 min[j]	0.5 min[j]	13 m⁻²	10–5000 m⁻² [j]

[a] Threshold prey density x_0 is calculated according to Eq. 7 as $x_0 = 1/(a(c - b))$

[b] DeBlois and Leggett (1991) fitted the Gause-Ivlev equation to their functional response data: $y = 11.29/day\,[1 - exp(-0.06\ cm^3\ x)]$. This equation does not account for the depletion of prey that occurred during the experiments. Its gradient at the origin is thus a minimum estimate of the success rate a; it is 11.29/day 0.06 cm³ = 0.028 cm³/h

[c] DeBlois and Leggett (1991)

[d] Reviewed by DeBlois and Leggett (1991)

[e] Holling (1966): encounter rate $\beta = 0.042\ m^2/h$ (pp. 32, 34, 56), detection probability $\gamma = 0.80$ (p. 56), attack efficiency $\varepsilon = 0.63$ (p. 56) → success rate $a = 0.021\ m^2/h$

[f] J. M. Jeschke (pers. obs.)

[g] Malone and McQueen (1983), Davies (1985), and Kvam and Kleiven (1995)

[h] J. M. Jeschke and K. Hohberg, unpublished data

[i] K. Hohberg, unpublished data

[j] van Gils and Piersma (2004)

DEMAND (g/day) (the energy content of animals is according to Peters 1983 on average about 7 kJ/g-wet mass). The complete formula for DEMAND is thus

$$\text{DEMAND in g/day} = 0.169\,\text{FMR in kJ/day}\,(1 + \text{PE}). \tag{10}$$

In order to account for estimation errors, values for DEMAND are reported as ranges, calculated as estimated mean values $\pm10\%$.

3. Finally, I compared KR with DEMAND.

In applying this method, one has to be aware of tautology. For example, studies on birds of prey often report field functional responses that were not actually measured but calculated from the birds' diets by assuming that the kill rates equaled the birds' demands (Korpimäki and Norrdahl 1991; Nielsen 1999; Salamolard et al. 2000). Similarly, some studies used doubly labeled water to estimate an animal's demand and used this value, in turn, to estimate its kill rate (e.g. Feltham and Davies 1996). Kill rates obtained in either of these ways were not used here.

Results

I found the needed data for this analysis only for birds and mammals. For these two groups, I analyzed a representative sample of 16 species (electronic supplementary material; Fig. 3). Kill rates usually met or exceeded energetic demands in these species. For example, in only 1 (3%) out of the 38 reported cases did environmental conditions not allow wolves (Canis lupus) to meet their demands. This was, however, not always the case; in two out of two cases, conditions did not allow Arctic skuas (Stercorarius parasiticus) to meet their demands. Taking all species together, environmental conditions did not allow demands to be met in $12 \pm 6.3\%$ of the cases (mean $\pm$ SE, $N = 16$). Of the 88% where demands were met, kill rates were within the range of estimated demands ($\pm10\%$) in $27 \pm 9.5\%$ of the cases and exceeded demands by more than 10% in $61 \pm 11.0\%$ of the cases.

Discussion

The results of the model parameterizations and the analysis of kill rates suggest that carnivores, especially birds and mammals, frequently reach satiation in the field. The results are in line with Huey et al. (2001) and Arrington et al. (2002) who showed that the average percentage of lizards and fish with empty stomachs is
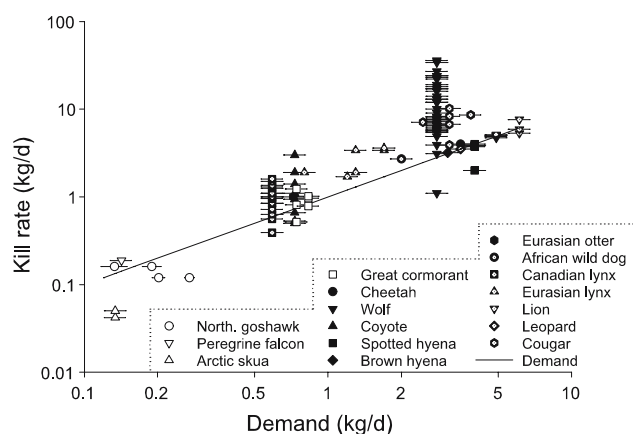
Fig. 3 Kill rates of free-ranging carnivorous birds and mammals compared to their demands. The latter are given as ranges, calculated as estimated mean values $\pm10\%$, in order to account for estimation errors. Underlying data are given in the electronic supplementary material

rather low (13 and 16%, respectively). According to Jeschke and Tollrian (2005a), herbivores also frequently reach satiation in the field. From this perspective, it is understandable why so many data points of field functional responses lie on the satiation plateau, and why field consumption rates are usually less strongly related to food abundance than lab-consumption rates (reviewed by Jeschke et al. 2004; Goss-Custard et al. 2006). In the words of Van Orsdol (1986): "The amount of food consumed by lions does not appear to correlate with prey density. The Southern Circuit in Ishasha occupied an area of high prey density, yet had a level of food intake only slightly higher than the Mweya pride. This is because prey in Ishasha are 'superabundant'; an increase in prey density would have little or no effect on food intake." (p. 387)

The results also arguably suggest that carnivores, at least birds and mammals, are released from time constraints on many days of their life because such constraints would likely lead to trade-offs in time allocation and thus to a nonsatiating food consumption. These results can be evolutionarily explained by Wilson's (1975) principle of stringency, as outlined in the Introduction. A shortcoming of this principle is that it ignores energy-conserving mechanisms such as fat reserves: it ignores the fact that during periods of low stringency (high food abundance or low requirements), animals can accumulate fat reserves or store food that can be used during periods of high stringency (low food abundance or high requirements). It would be valuable to extend the theory in this direction, e.g. by way of dynamic programming models.

A possible objection to the "laziness" hypothesis is that animals reaching satiation on a given day might not be able to satisfy all of their other needs: perhaps they have enough time to fill their gut, but not to find a mate. This objection could be valid sometimes in those cases where satiation is just reached, but not when kill rate exceeds demand. Another argument against "laziness" is that animals always have to avoid their predators, so they can never be released from time constraints. This claim is valid under the condition that foraging always comes with the risk of predation. Specifically, predators must be permanently present (i.e. so close that an encounter is possible) or the animal cannot assess predator presence. Not all animals have predators, however, and those that do are not permanently in their proximity. As Sih et al. (2000) pointed out: "In spite of its near ubiquity in nature, until recently no theory has focused explicitly on the effects of temporal variation in risk on prey behavior" (but see Brown et al. 1999; Lima and Bednekoff 1999; Brown and Kotler 2004). Many, if not most, animals can also assess the presence of their predators (Caro 2005), but the accuracy of these assessments certainly varies among species. Animal behavior is often affected by predators even in their absence (Brown et al. 1999; Brown and Kotler 2004), although such "fear" does not necessarily lead to time constraints. Living in a group increases the probability of detecting predators, for many eyes see more, and reduces the amount of time that is spent being vigilant (Pulliam 1973; Bertram 1978; Elgar 1989; Beauchamp 2003; Fortin et al. 2004). Finally, looking out for predators does not necessarily distract from foraging, as, for example, chewing and being vigilant are not mutually exclusive (Fortin et al. 2004). Although more research is needed before we know how often predator avoidance leads to time constraints, it is clear that time constraints are not inevitable. Many carnivores seem to be released from them on numerous days of their life.

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