

## *Time and energy constraints: reply to Nolet and Klaassen (2005)*

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The energy intake of a consumer can theoretically be limited either by the time it has available to forage or by its capacity to process energy. Nolet and Klaassen (2005; termed “NK” henceforth) recently provided evidence that Bewick’s swans (*Cygnus columbianus bewickii*) are time limited during migration when food abundance is low. Based on this finding, they suggested that animals are not always energy-processing limited but can be time limited during demanding phases of the year. We agree with them. However, NK claimed that their finding was surprising because “the common notion is that also in the field animals are generally energy-processing limited (Jeschke et al. 2002).” (p. 302 in NK) NK misquoted us at this and similar passages of their text (Abstract, pp. 303, 309), thereby telling an invalid story. We here correct this misquotation in order to avoid future confusion.

Based on a functional response model that includes both the handling time  $b$  a consumer needs to attack and ingest a food item and the digestion time  $c$  a consumer needs to internally process a food item, we classified consumers in Jeschke et al. (2002) as either handling limited (if  $b \geq c$ ) or digestion limited (if  $b < c$ ). It is important to note, but has been overlooked by NK, that this classification only refers to situations with maximal food abundance: handling-limited consumers are those that are limited by their handling time at very high food abundances, whereas digestion-limited consumers are those that are limited by their digestion time at very high food abundances. Empirical data reviewed in Jeschke et al. (2002) suggest that most consumers are digestion limited according to this classification. Because the classification applies to optimal environmental conditions, especially very high food abundances, and

does not consider non-foraging activities, it does not apply to typical field conditions. This is the basis of the misquotation in NK. In a more recent study not cited by NK, we addressed the limitation in the field (Jeschke and Tollrian 2005): handling-limited consumers are time limited under field conditions because they are already time limited under optimal conditions. Digestion-limited consumers, on the other hand, should be time limited during demanding environmental conditions, e.g. severe winters, and energy-processing limited under average or good environmental conditions. This reasoning is based on Wilson’s (1975) principle of stringency that “time-energy budgets evolve so as to fit to the times of greatest stringency” (see Jeschke and Tollrian 2005 for more details). The categories of consumer limitation according to Jeschke et al. (2002) and Jeschke and Tollrian (2005) are summarized in Table 1. Thus, we never wrote (and do not believe) that consumers are energy-processing limited under all conditions. In Jeschke et al. (2002), we did not address limitation in the field. In Jeschke and Tollrian (2005), we addressed this limitation and concluded that consumers should be time limited during demanding periods. By exploring such a demanding period (migration in a poor year), NK found evidence for time limitation, a result that perfectly matches the predictions of Jeschke and Tollrian (2005).

We also do not agree that “[a]nimals are generally considered not to be time-limited but rather to be energy-processing-limited” (Abstract in NK). NK are not quoting studies other than Jeschke et al. (2002) in support of this statement. As outlined above, Jeschke et al. (2002) does not support this statement. In fact, we are not aware of any foraging study that has assumed animals to be permanently energy-processing

Table 1. Categories of consumer limitation.

Category according to Jeschke et al. (2002) <sup>1</sup>	Criterion	Examples (reviewed by Jeschke et al. 2002)	Limitation in the field
Handling limitation	$b \geq c$	Few animals, e.g. <i>Agriotypus armatus</i> , <i>Polinices duplicatus</i>	Always time limitation
Digestion limitation	$b < c$	Most animals, e.g. copepods, grasshoppers, hummingbirds, oystercatchers, cattle, deer, hare, humans, marmots, shrews, squirrels	Time limitation if environmental conditions are demanding <sup>2</sup> , otherwise digestion limitation or no limitation <sup>3</sup>

Notes: <sup>1</sup>The categorization according to Jeschke et al. (2002) corresponds to optimal environmental conditions, especially very high food abundances. <sup>2</sup>This probably was the situation of the swans explored by NK in the poor year 1995. <sup>3</sup>See Wilson (1975), Jeschke and Tollrian (2005).

limited. Many studies have assumed the opposite, i.e. permanent time limitation, a view underlying all classical foraging models which do not consider satiation effects (Stephens and Krebs 1986). These models are still in use today (Gerber et al. 2004, Catania and Remple 2005, Yamauchi and Yamamura 2005). Many more modern foraging models that consider satiation also assume permanent time limitation (Belovsky 1978, Owen-Smith and Novellie 1982, Verlinden and Wiley 1989, Fryxell 1991), but there are exceptions (Newman et al. 1995, Fortin et al. 2002). Foraging ecologists have traditionally assumed permanent time limitation, whereas physiological ecologists have assumed the predominance of digestion limitation (Whelan and Brown 2005). Recent publications by van Gils et al. (2003, 2005), Karasov and McWilliams (2005), Whelan and Brown (2005), and others indicate that the two schools of thought are finally coming together.

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