PREDATOR FUNCTIONAL RESPONSES: DISCRIMINATING BETWEEN HANDLING AND DIGESTING PREY

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Abstract. We present a handy mechanistic functional response model that realistically incorporates handling (i.e., attacking and eating) and digesting prey. We briefly review current functional response theory and thereby demonstrate that such a model has been lacking so far. In our model, we treat digestion as a background process that does not prevent further foraging activities (i.e., searching and handling). Instead, we let the hunger level determine the probability that the predator searches for new prey. Additionally, our model takes into account time wasted through unsuccessful attacks. Since a main assumption of our model is that the predator's hunger is in a steady state, we term it the steady-state satiation (SSS) equation.

The SSS equation yields a new formula for the asymptotic maximum predation rate (i.e., asymptotic maximum number of prey eaten per unit time, for prey density approaching infinity). According to this formula, maximum predation rate is determined not by the sum of the time spent for handling and digesting prey, but solely by the larger of these two terms. As a consequence, predators can be categorized into two types: handling-limited predators (where maximum predation rate is limited by handling time) and digestion-limited predators (where maximum predation rate is limited by digestion time). We give examples of both predator types. Based on available data, we suggest that most predators are digestion limited.

The SSS equation is a conceptual mechanistic model. Two possible applications of this model are that (1) it can be used to calculate the effects of changing predator or prey characteristics (e.g., defenses) on predation rate and (2) optimal foraging models based on the SSS equation are testable alternatives to other approaches. This may improve optimal foraging theory, since one of its major problems has been the lack of alternative models.

Key words: consumer-resource systems; consumption rate; digestion-limited predators; digestion time; functional response models; handling-limited predators; handling time; hunger level; predation rate; predator–prey systems; steady-state satiation (SSS) equation.

Introduction

The relationship between predation rate (i.e., number of prey eaten per predator per unit time) and prey density is termed the ''functional response'' (Solomon 1949). It is specific for each predator–prey system. The term predator is meant in its broadest sense here, i.e., it includes carnivores, herbivores, parasites, and parasitoids. The functional response is an important characteristic of predator–prey systems and an essential component of predator–prey models: Multiplying the functional response with predator population density and a time factor yields the total number of prey eaten in the period of interest, e.g., one year or one prey generation. Given further information, such as actual predator density and an energy conversion factor, one can assess future population densities of both predator and prey. With a mechanistic functional response model, as presented in this study, one can predict the effects

of changing predator or prey characteristics (e.g., defenses) on predation rate.

Previous Models: A Brief Review

Scientists have been modeling functional responses since the 1920s (reviewed by Holling 1966, Royama 1971), although the term ''functional response'' was only introduced in 1949 by Solomon. Since, to our knowledge, the last review of functional response models dates back to 1971 (Royama), we provide an overview of models published since 1959 together with the most important factors incorporated in each model (Table 1). In addition, Fig. 1 shows a ''family tree'' of these functional response models. Holling (1959*a*) has categorized functional responses into three main types, which he called type I, II, and III. Our discussion will focus on type II functional responses, since these have been most frequently observed (Hassell et al. 1976, Begon et al. 1996). They are characterized by a hyperbolic curve. Starting at low prey densities on the abscissa, predation rate first increases almost linearly until it gradually slows down to reach an upper limit.

TABLE 1.　A selection of functional response models.

	Model											
Features	A (C)	B (C)	C (CP)	D (C)	E (P)	F (C)	G (F)	H (F)	I (F)	J (P)	K (C)	L (C)
Components												
Success rate[1]	+	+	+	+	+	+	+	$\overset{+}{+}$	$\overset{+}{+}$	$\overset{+}{+}$	+	$\overset{+}{+}$
Probability of attack	−	−	−	−	−	−	−	−	+	−	−	−
Handling time[2]	−	−	−	−	−	−	−	−	−	−	+	$\overset{+}{+}$
Searching and handling overlapping[3]	−	−	−	−	−	−	−	−	−	−	−	−
Hunger and satiation[4]	+	$\overset{+}{+}$	+	+	+	$\overset{+}{+}$	$\overset{+}{+}$	+	$\overset{+}{+}$	+	−	$\overset{+}{+}$
Handling prey ≠ digesting prey	−	−	−	−	−	−	−	−	−	−	−	+
Adaptive behavior[5]	−	−	−	−	−	−	−	+	+	−	−	−
Incomplete consumption[6]	−	−	−	−	−	+	−	−	−	−	−	+
Nonforaging activities[7]	−	−	−	−	−	−	−	−	−	−	−	+
Spatial heterogeneity[8]	−	+	−	−	−	−	−	−	−	−	−	−
Temporal heterogeneity[9]	−	−	−	−	−	−	−	−	−	−	−	−
Stochasticity[10]	−	−	−	−	−	−	+	−	−	+	−	−
Environmental conditions[11]	−	−	−	−	−	−	−	−	−	−	−	−
Predator injury by prey	−	−	−	−	−	−	−	−	−	−	−	−
Inducible defenses[12]	−	−	−	−	−	−	−	−	−	−	−	−
Dependent on prey density												
Prey density	+	+	+	+	+	+	+	+	+	+	+	+
Decreasing prey density[13]	−	−	−	+	+	+	−	−	−	+	−	−
Alternative prey[14]	−	−	−	−	−	−	−	−	+	−	−	−
Learning or switching[15]	−	−	−	−	−	−	−	−	−	−	−	−
Swarming effect[16]	−	−	−	−	−	−	−	−	−	−	−	−
Dependent on predator density												
Predator density	−	−	+	+	+	−	−	−	−	−	−	−
Interference between predators[17]	−	−	+	−	−	−	−	−	−	−	−	−
Multiple predator effects[18]	−	−	−	−	−	−	−	−	−	−	−	−
Functional response types												
Type I	−	−	−	−	−	−	+	−	−	−	−	+
Type II	+	+	+	+	+	−	+	−	−	+	+	+
Type III	−	−	−	−	−	−	−	−	+	−	−	−
Dome shaped	−	−	+	−	−	−	−	−	−	−	−	−
Other forms[19]	−	−	−	−	−	+	−	+	+	−	−	+

Notes: Small capital letters in parentheses under models indicate the kind of predator that the model was primarily designed for: c, carnivores; F, filter feeders; H, herbivores, P, parasites or parasitoids. In the body of the table, "+" means the model includes that component, "$\overset{+}{+}$" means the model additionally includes subcomponents, and "−" means the model does not include that component. Sources for models are as follows: (A) Gause (1934), Ivlev (1961), Eq. 1; (B) Rashevsky (1959; no overall model but different equations); (C) Watt (1959); (D) Royama (1971: Eq. 3.12), see also Nakamura (1974: Eq. 15); (E) Royama (1971: Eq. 3.24); (F) Nakamura (1974); (G) Sjöberg (1980); (H) Lam and Frost (1976); (I) Lehman (1976); (J) Casas et al. (1993); (K) Disc equation (Holling 1959b), Eq. 2; (L) Invertebrate model (Holling 1966; see also Metz and van Batenburg 1985a,b); (M) Vertebrate model (Holling 1965); (N) Holling and Buckingham (1976); (O) Rao and Kshiragar (1978); (P) Metz et al. (1988; see also Metz and van Batenburg 1985a, b); (Q) Cushing (1968); (R) Tostowaryk (1972); (S) Random predator equation (Royama 1971, Rogers 1972); (T) Random parasite equation (Royama 1971, Rogers 1972); (U) Beddington (1975); (V) Hassell et al. (1977); (W) Longstaff (1980); (X) Mills (1982); (Y) Crowley (1973); (Z) Oaten and Murdoch (1975); (AA) Real (1977); (BB) McNair (1980); (CC) Abrams (1982); (DD) Dunbrack and Giguere (1987); (EE) Abrams (1990a); (FF) Descriptive equation (Fujii et al. 1986); (GG) Ungar and Noy-Meir (1988); (HH) Random patch model (Lundberg and Åström 1990; see also Lundberg and Danell 1990); (II) Juliano (1989); (JJ) Fryxell (1991; see also Wilmshurst et al. 1995, 1999, 2000); (KK) Spalinger and Hobbs (1992; see also Laca et al. 1994, Shipley et al. 1994); (LL) Farnsworth and Illius (1996; see also Laca et al. 1994, Shipley et al. 1994); (MM) Hirakawa (1997b; see also Laca et al. 1994, Shipley et al. 1994); (NN) Farnsworth and Illius (1998; see also Laca et al. 1994, Shipley et al. 1994); (OO) Ruxton and Gurney (1994); (PP) Cosner et al. (1999) [This model closes a gap between density dependent and ratio dependent functional response models. Purely ratio dependent models are not included in Table 1, but see Arditi and Ginzburg (1989). However, as Berryman et al. (1995) have written: "Note that prey-dependent functional responses can be transformed into ratio-dependent functional responses by substituting the prey/predator ratio for prey density in the equation."]; (QQ) Streams (1994); (RR) Schmitz (1995; see also Abrams [1990c] and review by Schmitz et al. [1997]); (SS) Abrams and Schmitz (1999); (TT) Berec (2000; see also Engen and Stenseth 1984); (UU) SSS equation (Eq. 13).

[1] Success rate consists of four subcomponents: (1) encounter rate, (2) probability of detection, (3) hunger-independent probability of attack, and (4) efficiency of attack; empirical values for the attack efficiencies of predators have been reviewed by Curio (1976), Vermeij (1982), and Packer and Ruttan (1988).

[2] Handling time (per prey item) includes attacking time (including evaluating, pursuing, and catching time) and eating time. See also Anholt et al. (1987), Demment and Greenwood (1988), Laca et al. (1994), Parsons et al. (1994), and Shipley et al. (1994).

[3] Important for queueing predators (Juliano 1989; see also Visser and Reinders 1981, Lucas 1985, Lucas and Grafen 1985) and vertebrate herbivores (Spalinger and Hobbs 1992, Parsons et al. 1994, Farnsworth and Illius 1996, 1998, Hirakawa 1997b; see also Laca et al. 1994, Shipley et al. 1994).

TABLE 1. Extended.

Model																		
M (C)	N (C)	O (C)	P (C)	Q (F)	R (C)	S (C)	T (P)	U (CP)	V (CP)	W (C)	X (C)	Y (F)	Z (C)	AA (C)	BB (C)	CC (C)	DD (CF)	EE (C)
±	±	+	+	±	+	+	+	+	+	+	+	+	+	+	±	+	+	+
−	−	+	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	+
±	±	±	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
±	±	+	±	−	−	−	−	−	−	−	±	+	±	−	−	−	−	−
+	+	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	+
−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	+	+
+	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	+	−	+
+	+	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	+
−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
−	−	+	+	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−
−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
−	−	−	−	−	+	+	+	+	+	+	+	−	−	−	−	−	−	−
−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	+	−	−	+
+	+	−	−	−	−	−	−	+	−	−	−	−	+	+	+	+	+	−
−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−
−	+	−	−	+	−	−	−	+	−	−	−	−	−	−	−	−	−	−
−	+	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−
−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
+	+	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
+	+	+	−	−	−	−	−	+	−	−	−	+	+	+	+	+	+	−
+	+	−	+	−	+	−	−	−	−	−	−	−	−	−	−	+	−	−
+	+	−	+	−	−	−	−	−	−	−	−	+	−	−	−	+	−	−

[4] Some models include predator satiation via a maximum predation rate determined by the characteristics of the digestive system ("+"). Other models include the fact that the predator's gut content is increased by ingestion and decreased by digestion ("‡"). See also Campling et al. (1961), Curio (1976), Belovsky (1978, 1984a, b, c, 1986a, b, 1987), Mayzaud and Poulet (1978), Bernays and Simpson (1982), Murtaugh (1984), Crisp et al. (1985), Demment and Greenwood (1988), Verlinden and Wiley (1989), Illius and Gordon (1991), Doucet and Fryxell (1993), Forchhammer and Boomsma (1995), Henson and Hallam (1995), Hirakawa (1997a), and Wilmshurst et al. (2000).

[5] See also Belovsky (1978, 1984a, b, c, 1986a, b, 1987), Cook and Cockrell (1978), Sih (1980, 1984), Owen-Smith and Novellie (1982), McNair (1983), Abrams (1984, 1987, 1989, 1990b, c, 1991, 1992, 1993), Engen and Stenseth (1984), Formanowicz (1984), Lucas (1985), Wanink and Zwarts (1985), Stephens and Krebs (1986), Anholt et al. (1987), Demment and Greenwood (1988), Belovsky et al. (1989), Verlinden and Wiley (1989), Åström et al. (1990), Lundberg and Danell (1990), Mitchell and Brown (1990), Abrams and Matsuda (1993), Doucet and Fryxell (1993), Werner and Anholt (1993), McNamara and Houston (1994), Forchhammer and Boomsma (1995), Hirakawa (1995, 1997a), Fryxell and Lundberg (1997), Leonardsson and Johansson (1997), Rothley et al. (1997), Schmitz et al. (1997), and Wilmshurst et al. (2000).

[6] See also Buckner (1964), Johnson et al. (1975), Curio (1976), Cook and Cockrell (1978), Sih (1980), Owen-Smith and Novellie (1982), McNair (1983), Formanowicz (1984), Lucas (1985), Lucas and Grafen (1985), Metz and van Batenburg (1985a, b), Åström et al. (1990), Lundberg and Danell (1990), and Fryxell and Lundberg (1997).

[7] For example, avoidance of top predators, migration, molting, reproductive activities, resting, sleeping, territorial behavior, thermoregulation, and times of slow rates of metabolism like winter dormancy; see also Belovsky (1978, 1984a, b, c, 1986a, b, 1987), Caraco (1979), Herbers (1981), Bernays and Simpson (1982), Owen-Smith and Novellie (1982), Abrams (1984, 1991, 1993), Stephens and Krebs (1986), Belovsky et al. (1989), Verlinden and Wiley (1989), Bunnell and Harestad (1990), Mitchell and Brown (1990), McNamara and Houston (1994), Forchhammer and Boomsma (1995), Hirakawa (1997a), Leonardsson and Johansson (1997), and Rothley et al. (1997).

[8] See also Griffiths and Holling (1969), Paloheimo (1971a, b), Oaten (1977), May (1978), Real (1979), McNair (1983), Belovsky et al. (1989), Blaine and DeAngelis (1997), Fryxell and Lundberg (1997), and Wilmshurst et al. (2000), among others.

[9] For example, diel or annual periodicity (Curio 1976, Bernays and Simpson 1982, Belovsky et al. 1989, Forchhammer and Boomsma 1995).

[10] See also Paloheimo (1971a, b), Curry and DeMichele (1977), Curry and Feldman (1979), McNair (1983), Lucas (1985), and Metz and van Batenburg (1985a, b).

[11] For example, precipitation, temperature (Fedorenko 1975, Thompson 1978, Bernays and Simpson 1982), and wind.

[12] Behavioral and morphological defenses, that are not permanently present but are induced by the predator (e.g., Fryxell and Lundberg 1997, Karban and Baldwin 1997, Tollrian and Harvell 1999, Jeschke and Tollrian (2000).

[13] See also Curry and DeMichele (1977).

TABLE 1. Extended.

Features	Model															
	FF (CP)	GG (H)	HH (H)	II (C)	JJ (H)	KK (H)	LL (H)	MM (H)	NN (H)	OO (C)	PP (C)	QQ (C)	RR (CH)	SS (H)	TT (C)	UU (C)
Components																
Success rate[1]	+	±	+	+	+	+	+	±	+	+	+	±	+	+	+	±
Probability of attack	−	+	−	+	+	−	−	+	+	−	−	+	+	+	+	−
Handling time[2]	+	±	+	+	+	±	±	±	±	+	+	+	+	−	+	±
Searching and handling overlapping[3]	−	−	−	+	−	+	+	+	+	−	−	−	−	−	−	−
Hunger and satiation[4]	−	−	−	−	+	−	−	+	+	−	−	−	+	+	−	±
Handling prey ≠ digesting prey	−	−	−	−	+	−	−	+	+	−	−	−	+	−	−	+
Adaptive behavior[5]	−	+	+	+	+	−	−	+	+	−	−	−	+	+	+	−
Incomplete consumption[6]	−	−	+	+	−	−	−	−	−	−	+	−	−	−	−	−
Nonforaging activities[7]	−	−	−	−	+	−	−	+	+	−	−	−	+	+	−	−
Spatial heterogeneity[8]	−	−	−	−	+	−	−	+	−	+	+	−	+	+	−	−
Temporal heterogeneity[9]	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−
Stochasticity[10]	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−
Environmental conditions[11]	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Predator injury by prey	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Inducible defenses[12]	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Dependent on prey density																
Prey density	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Decreasing prey density[13]	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−
Alternative prey[14]	−	+	+	+	−	−	−	+	+	−	−	−	+	+	+	−
Learning or switching[15]	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−
Swarming effect[16]	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Dependent on predator density																
Predator density	−	−	−	−	+	−	−	−	−	−	+	−	−	−	−	−
Interference between predators[17]	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−
Multiple predator effects[18]	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Functional response types																
Type I	−	−	−	+	−	−	+	+	+	−	−	−	+	+	−	−
Type II	+	+	−	+	+	+	+	+	+	+	+	+	+	−	+	+
Type III	+	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−
Dome shaped	+	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−
Other forms[19]	+	−	+	+	+	−	+	+	+	−	−	−	+	+	+	−

[14] See also Belovsky (1978, 1984a, b, c, 1986a, b, 1987), Owen-Smith and Novellie (1982), Engen and Stenseth (1984), Metz and van Batenburg (1985a), Wanink and Zwarts (1985), Abrams (1987, 1989, 1990b, c), Belovsky et al. (1989), Abrams and Matsuda (1993), Doucet and Fryxell (1993), Parsons et al. (1994), Forchhammer and Boomsma (1995), Fryxell and Lundberg (1997), Rothley et al. (1997), Schmitz et al. (1997), and Wilmshurst et al. (2000).

[15] Learning includes training effects; switching means either switching between prey types (in this case, there is a "+" at "alternative prey") or behavioral switching, e.g., from sitting and waiting to cruising. Only those models that explicitly consider learning or switching have "+" here. Optimal foraging models where switching is a simulation result have "−" here. For an experimental example of the interaction between learning and spatial distribution see Real (1979); see also Fryxell and Lundberg (1997) and Kaiser (1998).

[16] A swarming effect decreases predation rate with increasing prey density. It can be the result of (1) a better or earlier detection of the predator by prey, (2) a worse detection of prey by the predator, (3) a better active prey defense, (4) predator confusion which usually decreases probability or efficiency of attack, (5) clogging of filters (in case of filter feeders), or (6) accumulation of toxic prey substances. The form of the functional response can be dome shaped in this case. See Miller (1922), Brock and Riffenburgh (1960), Mori and Chant (1966), Tostowaryk (1972), Halbach and Halbach-Keup (1974), Neill and Cullen (1974), Nelmes (1974), Milinski and Curio (1975), Bertram (1978), Lazarus (1979), Williamson (1984), Morgan and Godin (1985), Landeau and Terborgh (1986), and Inman and Krebs (1987).

[17] Interference also includes prey exploitation by other predators. Only those models that consider interference inclusively and prey exploitation explicitly have "+" here. Models that account for a decreasing prey density through predation and the number of predators present and include prey exploitation in an implicit way have "−" here. See also models by Griffiths and Holling (1969), Hassell and Varley (1969), Royama (1971, model in §4i), DeAngelis et al. (1975), Curry and DeMichele (1977), Parker and Sutherland (1986), Korona (1989), Ruxton et al. (1992), Holmgren (1995), Fryxell and Lundberg (1997), and Doncaster (1999); for empirical studies, see Norris and Johnstone (1998), Triplet et al. (1999), or references in Holmgren (1995).

[18] Soluk (1993), Sih et al. (1998).

[19] Crowley (1973) and Farnsworth and Illius (1996), intermediate type I/II; Nakamura (1974), type II similar; Lam and Frost (1976), Fujii et al. (1986), type I similar; Lehman (1976), partly type I similar; Metz et al. (1988) and random patch model (Lundberg and Åström 1990), hyperbolic (type II similar) functional response without an asymptote; Abrams (1982), Juliano (1989), Fryxell (1991), Schmitz (1995), Hirakawa (1997b), Farnsworth and Illius (1998), Abrams and Schmitz (1999), and Berec (2000), various forms; see also Parsons et al. (1967, type II with a threshold prey density, corresponding empirical curves in the same study and in Parsons et al. (1969), Cook and Cockrell (1978; double plateau functional responses), Abrams (1987, 1989; decreasing functional responses), and Fryxell and Lundberg (1997; various forms).
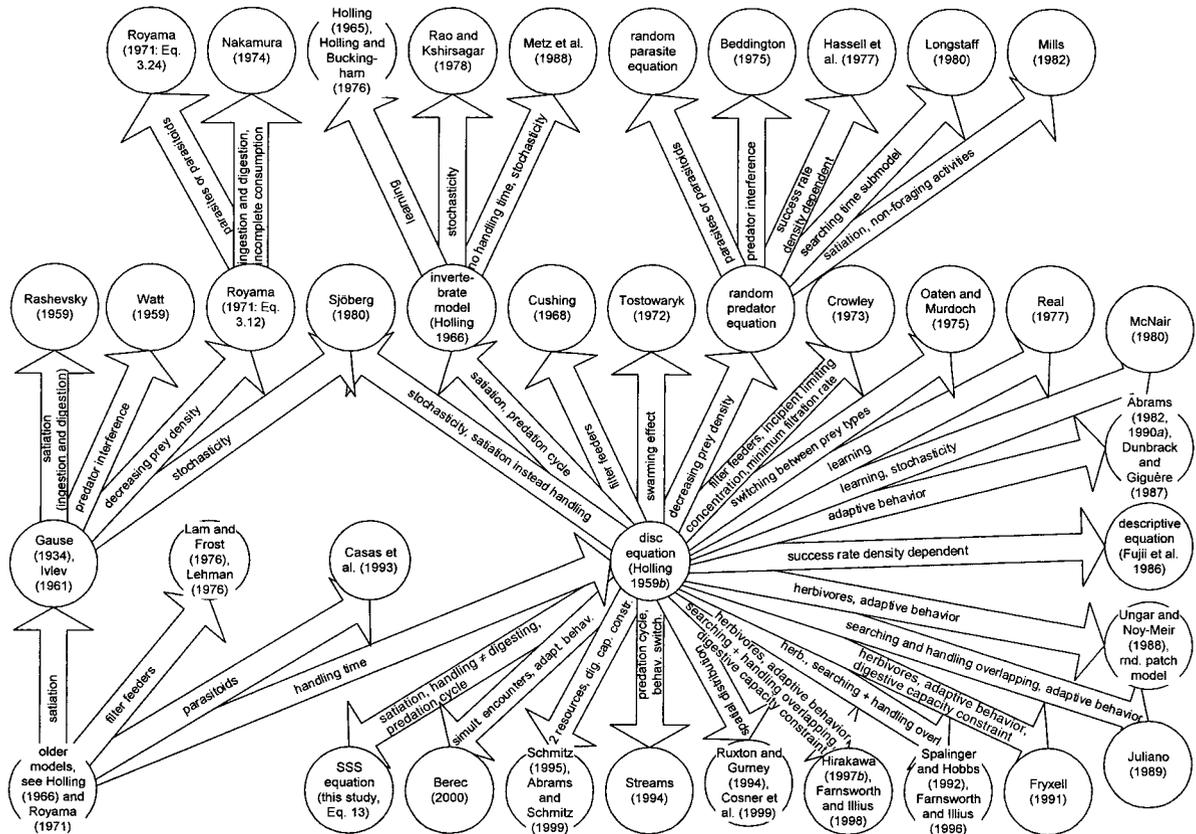
Fig. 1. A "family tree" of functional response models.

All functional response models include a factor that determines the curve's gradient at the origin ("success rate" which is a measure of the predator's hunting efficiency; it has been termed the "rate of successful search" by Holling [1959a, b, 1965, 1966]).

Handling and digestion

Limitation of predation rate at high prey densities has usually been attributed to either handling time or satiation. However, the exact nature of these two factors and their relationship has been modeled in a variety of different ways and this has led to considerable confusion. The point is that handling prey is an active process whereas digestion is a background process. As a consequence, in contrast to handling prey, digestion does not directly prevent the predator from further searching or handling. Rather, digestion influences the predator's hunger level, which in turn influences the probability that the predator searches for new prey. It is thus necessary to discriminate digestion from handling in a functional response model. In the following, we briefly review existing models with respect to their treatment of these two factors. In our opinion, no completely satisfying solution to the problem exists to date.

Models including satiation but not handling time.—

Although purely phenomenological, the Gause-Ivlev equation (Gause 1934, Ivlev 1961) has usually been viewed as the classical satiation model

$$y(x) = y_{max} (1 - \exp [-a' \, x]) \qquad (1)$$

where a' is hunting success (dimension in SI units: m^2 for a two-dimensional system, e.g., a terrestrial system, and m^3 for a three-dimensional system, e.g., an aquatic system), x is prey density (individuals/m^2 or individuals/m^3, respectively), y is predation rate (s^{-1}), and y_{max} is asymptotic maximum predation rate as x approaches infinity (s^{-1}). In the common interpretation, the digestive system determines y_{max}, and the functional response curve gradually rises to this value. Rashevsky (1959) has extended the Gause-Ivlev equation by modeling satiation more mechanistically: the predator's gut content is increased by ingestion and decreased by digestion. Other models including satiation but not handling time have been developed by Watt (1959), Parsons et al. (1967), Royama (1971), Nakamura (1974), Lam and Frost (1976), Lehman (1976), Sjöberg (1980), Crisp et al. (1985), Metz and van Batenburg (1985b), Metz et al. (1988), Abrams (1990c), Casas et al. (1993; parasitoid egg load as analogous to hunger level), Henson and Hallam (1995), and Abrams and Schmitz (1999).

Models including handling time but not satiation.—In contrast, there are a number of models that include handling time but no predator satiation effects (Holling 1959*b,* Cushing 1968, Royama 1971, Rogers 1972, Tostowaryk 1972, Beddington 1975, Hassell et al. 1977, Real 1977, Cook and Cockrell 1978, Curry and Feldman 1979, Longstaff 1980, McNair 1980, Visser and Reinders 1981, Abrams 1982, 1987, 1990*a,* Fujii et al. 1986, Dunbrack and Giguère 1987, Ungar and Noy-Meir 1988, Juliano 1989, Lundberg and Åström 1990, Spalinger and Hobbs 1992, Parsons et al. 1994, Ruxton and Gurney 1994, Streams 1994, Farnsworth and Illius 1996, Fryxell and Lundberg 1997, Cosner et al. 1999, Berec 2000). The most popular functional response model today, Holling's (1959*b*) disc equation, belongs to this class:

$$y(x) = \frac{ax}{1 + abx} \tag{2}$$

where *a* is success rate (dimension in SI units: m^2/s or m^3/s, respectively; note that the dimensions of *a* and *a'* [Gause-Ivlev equation] differ), *b* is predator handling time per prey item (s), *x* is prey density (individuals/m^2 or individuals/m^3, respectively), and *y* is predation rate (s^{-1}). The curve's gradient at the origin is equal to *a,* and the asymptotic maximum for *x* as *x* approaches infinity is $1/b$. The disc equation is mathematically equivalent to the Michaelis-Menten model of enzyme kinetics and the Monod formula for bacterial growth. The Royama-Rogers random predator equation (Royama 1971, Rogers 1972) is a modification of the disc equation that accounts for a decreasing prey density in the course of an experiment or between discrete prey generations. In the original paper (Holling 1959*b*), the parameter *b* of the disc equation denoted the general meaning of ''handling time'' at that time, i.e., the sum of attacking time t_{att} (per prey item; including evaluating, pursuing, and catching time) and eating time t_{eat} (per prey item):

$$b = t_{att} + t_{eat}$$

$$\Leftrightarrow \text{asymptotic maximum predation rate}$$

$$= (t_{att} + t_{eat})^{-1} \tag{3}$$

with handling time *b* as it was originally defined by Holling (1959*b*).

Holling originally developed the disc equation as a mechanistic model for an artificial predator–prey system: humans ''preying'' on paper discs (Holling 1959*b*). Compared to natural predator–prey systems, however, it is now clear that the underlying assumptions are unrealistic (Hassell et al. 1976). Two points have met the most severe criticism: First, the predator does not become satiated, and second, the disc equation assumes that every attack by the predator is successful, i.e., attack efficiency ε = 100%. Attack efficiencies <100% can be incorporated into the disc equation by defining *b* as

$$b = t_{att}/\varepsilon + t_{eat}$$

$$\Leftrightarrow \text{asymptotic maximum predation rate}$$

$$= (t_{att}/\varepsilon + t_{eat})^{-1}. \tag{4}$$

In using this definition, handling time includes time wasted through unsuccessful attacks (see also Mills 1982, Abrams 1990*a,* Streams 1994).

Models including both handling time and satiation.—One approach to include both handling time and digestion time is to sum them up or to increase handling time by a ''digestive pause'' (Crowley 1973, Rao and Kshirsagar 1978, Mills 1982, Henson and Hallam 1995), i.e., an inactive time period related to digestion (Holling 1965, 1966). When modeled this way, digestion is not distinguished from handling. Mills (1982) used this concept to extend the disc equation by interpreting its parameter *b* as

$$b = t_{att} + t_{eat} + s t_{dig}$$

$$\Leftrightarrow \text{asymptotic maximum predation rate}$$

$$= (t_{att} + t_{eat} + s t_{dig})^{-1} \tag{5}$$

where *s* is satiation per prey item (dimensionless) and t_{dig} is digestion time per prey item (s; see Table 2).

A second way to consider both handling and digestion time is to combine the disc equation (which already includes handling time) with a digestive capacity constraint (Fryxell 1991, Schmitz 1995, Hirakawa 1997*b,* Farnsworth and Illius 1998). This constraint limits maximum predation rate but does not otherwise affect the functional response. These models therefore discriminate between handling and digesting prey. However, neither the process of digestion, nor the predator satiation level are considered. The approach to combine handling time with a digestive capacity constraint has its origins in linear programming models (e.g., Belovsky 1978, 1984*a, b, c,* 1986*a, b,* 1987, Doucet and Fryxell 1993, Forchhammer and Boomsma 1995).

The only family of models that treats digestion as a background process, which influences foraging activities but does not prevent them, is Holling's (1966) invertebrate model and its extensions (Holling 1965, Holling and Buckingham 1976, Curry and DeMichele 1977, Metz and van Batenburg 1985*a*). In the invertebrate model, the predation cycle is subdivided into several stages, and each stage depends on predator hunger level. After a meal, the predator is assumed to undergo a digestive pause and then continues searching when it is hungry again. While searching, the predator simultaneously continues digestion of its last meal. The invertebrate model therefore discriminates between handling and digesting prey. Here, the length of the digestive pause depends on hunger level. Since hunger level in turn depends on prey density, the length of the digestive pause depends on prey density. This is in contrast to the models mentioned above (Eq. 5), where the length of the digestive pause is unrealistically as-

TABLE 2. The SSS equation parameters.

Parameter	Description	Dimension†	Defined for
β	Encounter rate = number of encounters between a searching predator and a single prey item; an encounter is defined as an arrival of a prey item in the predator's encounter volume	m^3/s	$[0; \infty]$
γ	Probability that the predator detects encountered prey	−	$[0; 1]$
ε	Efficiency of attack = proportion of successful attacks	−	$[0; 1]$
s	Satiation per prey item = reciprocal capacity of the hunger-determining part of the gut (mostly stomach or crop); example: if the stomach capacity of a human is equal to 10 potatoes, then $s = 0.1$	−	$[0; \infty]$
t_{att}	Attacking time per prey item = time between prey detection and end of attack	s	$[0; \infty]$
t_{dig}	Digestion time per prey item = food transit time (= 50% emptying time) for the hunger-determining part of the gut, e.g., stomach transit time for humans	s	$[0; \infty]$
t_{eat}	Eating time per prey item = time between capture and finished ingestion	s	$[0; \infty]$

Note: The parameters can be summarized by a (success rate [m^3/s]), b (corrected handling time [s]), and c (corrected digestion time [s]), see Eq. 13.

† In SI units and given for a three-dimensional system, e.g., an aquatic system; in the case of a two-dimensional system, e.g., a terrestrial system, m^3 must be replaced by m^2.

sumed to be constant. The term ''digestive *pause*'' relates to foraging activities only: predators may well use the digestive pause for nonforaging activities, for example, for looking out for top predators or for sleeping. However, because of its 22 parameters, the invertebrate model is extremely unwieldy, and its extensions are even more elaborate.

Phenomenological vs. mechanistic models

Probably because of their mathematical simplicity, the Holling (1959*b*) disc equation (Eq. 2), the Royama-Rogers random predator equation (Royama 1971, Rogers 1972), and the Gause-Ivlev equation (Gause 1934, Ivlev 1961; Eq. 1) have been the most popular functional response models. However, they must be considered phenomenological. That is, although they correctly reproduce the shape of natural (type II) functional responses, they are not able to explain the underlying mechanism; or, in other words, its parameters cannot all be mechanistically explained. In the cases of the disc equation and the random predator equation, the parameter a (success rate) can be mechanistically explained (Holling 1966, Ungar and Noy-Meir 1988, Streams 1994, Hirakawa 1997*b*; see also Eq. 7 below), but not the parameter b (handling time). When fitting the disc equation or the random predator equation to an empirical curve, the resulting value for b is a mixture of different biological processes (Table 1) including handling (attacking and eating) and digestion. As we have pointed out above, handling is an active process, whereas digestion is a background process. They cannot be adequately condensed into only one parameter. In the case of the Gause-Ivlev equation, neither parameter can be mechanistically explained. Its parameter a' (hunting success) differs in its dimension from the parameter a of the disc equation and the random predator equation; a' lacks a mechanistic explanation. The other parameter, y_{max}, is just the asymptote of the curve; there

is no mechanistic linkage to the processes of ingestion and digestion.

Their mathematical simplicity renders the disc, the random predator, and the Gause-Ivlev equation as functional response submodels in predator–prey population models. However, for a deeper understanding of the functional response, mechanistic models are necessary. The parameters of mechanistic models can all be mechanistically explained. These models can thus, for example, be used to calculate the effects of changing predator or prey characteristics (e.g., defenses) on predation rate.

THE STEADY-STATE SATIATION (SSS) EQUATION

We have shown that a handy mechanistic functional response model that realistically incorporates handling and digesting prey has been lacking so far. In this section, we therefore develop such a model: the steady-state satiation (SSS) equation. It is based on the disc equation and divides the predation cycle into five stages: search, encounter, detection, attack, and eating (Fig. 2). We assume that these stages are mutually exclusive. Each stage is characterized by two components: The amount of time needed for its completion and the conditional probability that the predator reaches this stage given that it has reached the previous one (exception: encounter; here, it is not a probability but a rate; note that the encounter rate can have a value larger than unity). Digestion is modeled as a background process influencing the predator's hunger level, which in turn determines the probability that the predator searches for prey.

The SSS equation components, parameters, and assumptions

The SSS equation components are given in Table 1 and its parameters in Table 2. Like nearly every model, the SSS equation is a compromise between realism and
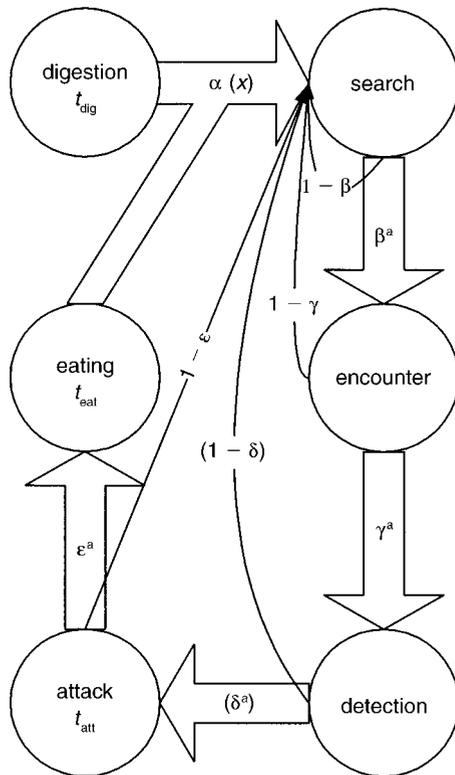
FIG. 2. The predation cycle. We divide the predation cycle into five stages: search, encounter, detection, attack, and eating. A predator enters a predation cycle under the probability to search, $\alpha(x)$; this is determined by the predator's hunger level, which in turn is influenced by digestion time. Then the predator successively reaches the following stages. The probability that the predator reaches a stage under the condition that it has reached the previous stage is given in the corresponding arrow, e.g., the probability that the predator detects a prey under the condition that it has encountered that prey is γ (exception: β is not a probability but a rate [encounter rate]; note that it can be larger than unity). Since δ is set as unity in the SSS equation (assumption 8), it is given in parentheses here. Terms in circles indicate time demands of corresponding stages per prey item. We assume that the stages are mutually exclusive (assumption 4). Terms with a superscript "a" determine predator success rate (a).

applicability. It is more realistic than the disc equation, but it is reductive compared to nature. The SSS equation is a conceptual model that can, for example, be used to assess how changing predator or prey characteristics (e.g., defenses) qualitatively affect the functional response. The point of the SSS equation is not to quantitatively predict real functional response curves. It is therefore not necessary to incorporate too many features into the model, which would render it unwieldy. However, extensions for specific predator–prey systems are possible; these will allow us to make quantitative predictions with the model as well. For this purpose, references given in Table 1 may be helpful.

The assumptions of the model are as follows:

1) There is only a single predator and a single type of prey.

2) The prey density is constant.

3) Prey are independently and randomly distributed.

4) Stages of the predation cycle exclude each other (Fig. 2).

5) The probability that the predator searches (under the condition that it is not handling prey), $\alpha(x)$, is directly proportional to the predator's hunger level $h(x)$.

6) The hunger level $h(x)$ depends on the fullness of a certain part of the gut (e.g., stomach, crop).

7) The hunger level $h(x)$ at a given prey density x is in a steady state, which is determined by an equilibrium of ingestion and digestion.

8) The probability of attack, δ, is unity, i.e., whenever a searching predator encounters and detects a prey, it will attack.

9) The probability that the predator detects encountered prey, γ, the efficiency of attack ε (i.e., the proportion of successful attacks), the attacking time t_{att} (per prey item), the eating time t_{eat} (per prey item), and the digestion time t_{dig} (per prey item) are constant.

The SSS equation

To develop the SSS equation, we start with the disc equation and modify it sequentially. In step 1, each stage of the predation cycle is included explicitly; in step 2, predator satiation is included by influencing the probability of searching.

The stages of the predation cycle are (1) search, (2) encounter, (3) detection, (4) attack, and (5) eating (Fig. 2). The probabilities that a predator reaches these stages are (1) the probability α that a predator not occupied with handling searches for prey, (2) the encounter rate β between a searching predator and an individual prey, (3) the probability γ that the predator detects an encountered prey individual, (4) the probability δ that the predator attacks a detected prey individual, and (5) the probability ε that an attack is successful, i.e., the efficiency of attack. We now incorporate these probabilities into the disc equation.

The searching probability $\alpha(x)$.—In the disc equation, the predator shows only two kinds of behavior: searching for and handling prey. Therefore, the probability that the predator searches for prey under the condition that it is not handling prey, $\alpha(x)$, is unity. To allow values below unity, $\alpha(x)$ has to be incorporated explicitly into the disc equation:

$$y(x) = \frac{\alpha(x)ax}{1 + \alpha(x)abx}. \tag{6}$$

Note that α depends on prey density x because it is affected by the predator's hunger level (see the next paragraph and assumption 5), which in turn depends on prey density (see the next paragraph and assumption 7): $\alpha(h) = \alpha(h(x)) = \alpha(x)$.

The encounter rate β, the probability of detection γ, the probability of attack δ, and the efficiency of attack

ε.—The product of all these terms is predator success rate a. However, for simplicity, we set $\delta = 1$ (assumption 8). Thus,

$$a = \beta\gamma\varepsilon. \qquad (7)$$

The encounter rate β can be calculated by various formulae from different authors. For a three-dimensional model, e.g., in aquatic systems, one may use the equation given by Gerritsen and Strickler (1977). For an analogous two-dimensional model, e.g., in terrestrial systems, see Koopman (1956), and for a three-dimensional model with a cylindrical instead of a spherical encounter volume, see Giguère et al. (1982). For further models, see Royama (1971: Eq. 4e.6), Getty and Pulliam (1991), Parsons et al. (1994), Hirakawa (1997b), and reviews from Schoener (1971) and Curio (1976). Here, for simplicity, β is not calculated by one of these formulae but is a model input; probability of detection γ and efficiency of attack ε are also model inputs.

Explicitly incorporating efficiency of attack ε allows us to account for time wasted through unsuccessful attacks. Thus, handling time b can be calculated according to Eq. 4.

The second and final step in deriving the SSS equation is to incorporate digestion. We do this by assuming that

$$\alpha(x) = h(x). \qquad (8)$$

This is assumption 5 and is also assumed by Rashevsky (1959). The hunger level $h(x)$ is the proportion of empty volume of that part of the gut that is responsible for feelings of hunger and satiation in the predator under consideration (mostly stomach or crop); $h(x)$ is defined for [0; 1], where $h = 0$ means no hunger, i.e., full gut, and $h = 1$ means 100% hunger, i.e., empty gut. Empirical studies usually find a hyperbolic relationship between starvation time and hunger level, e.g., Holling (1966) for mantids (*Hierodula crassa* and *Mantis religiosa*), Antezana et al. (1982) for krill (*Euphausia superba*), Hansen et al. (1990) for copepods (*Calanus finmarchicus*), and several works on fish (reviewed by Elliott and Persson 1978). This hyperbolic relationship can be described by the following differential equation:

$$\frac{dh(x)}{dt} = \frac{1 - h(x)}{t_{dig}} - sy(x). \qquad (9)$$

Since we assume a constant prey density (assumption 2), the equilibrium hunger level can be obtained by setting $dh(x)/dt = 0$, giving

$$h(x) = 1 - s{\cdot}t_{dig}{\cdot}y(x). \qquad (10)$$

We define $c = s{\cdot}t_{dig}$ as "corrected digestion time", i.e., digestion time corrected for gut capacity. Therefore,

$$h(x) = 1 - c{\cdot}y(x). \qquad (11)$$

Inserting Eq. 11 into Eqs. 8 and 6 yields

$$y(x) = \frac{(1 - c{\cdot}y(x))ax}{1 + (1 - c{\cdot}y(x))abx}. \qquad (12)$$

Solving for $y(x)$ finally gives the following SSS equation:

$$y(x) = \begin{cases} \dfrac{1 + ax(b + c) - \sqrt{1 + ax(2(b + c) + ax(b - c)^2)}}{2abcx} \\ \qquad\qquad a, b, c, x > 0 \\[6pt] \dfrac{ax}{1 + abx} \qquad b > 0 \qquad c = 0 \\[6pt] \dfrac{ax}{1 + acx} \qquad b = 0 \qquad c > 0 \\[6pt] ax \qquad\quad\; b = c = 0 \\[6pt] 0 \qquad\qquad a = 0 \quad \text{or} \quad x = 0 \end{cases} \qquad (13)$$

with success rate $a = \beta\gamma\varepsilon$, corrected handling time $b = t_{att}/\varepsilon + t_{eat}$, and corrected digestion time $c = st_{dig}$.

For details on deriving Eq. 13 from Eq. 12, see Appendix A. For $c = 0$ (i.e., no satiation), the SSS equation simplifies to the disc equation but with the definitions of Eq. 13 for a and b. For $b = 0$ (i.e., zero handling time), the SSS equation simplifies to the disc equation but with c instead of b, i.e., digestion time replaces handling time in this case. Finally, without any handling time or satiation ($b = c = 0$), there are no density dependent effects and so, predation rate is directly proportional to prey density.

Properties of the SSS equation

The SSS equation produces type II functional responses (Fig. 3). As in the disc equation, the gradient at the origin is equal to the predator's success rate a:

$$\lim_{x \to 0} \frac{dy(x)}{dx} = a. \qquad (14)$$

The asymptotic maximum predation rate for prey density as x approaches infinity is

$$\lim_{x \to \infty} y(x) = \frac{b + c - \sqrt{(b - c)^2}}{2bc} = \frac{1}{\max(b; c)}.$$

where, for handling-limited predators,

$$b \geq c \Leftrightarrow \lim_{x \to \infty} y(x) = \frac{1}{b}$$

and, for digestion-limited predators,

$$c > b \Leftrightarrow \lim_{x \to \infty} y(x) = \frac{1}{c}. \qquad (15)$$

Thus, the larger one of the two terms b and c determines the asymptotic maximum predation rate. This is, because digestion is a "background process", i.e., handling and digestion can be carried out simultaneously. The slower one of these two processes is then limiting.

A) Handling-limited predators

B) Digestion-limited predators

C) Attack efficiency, ε

Predation rate (individuals per unit time)

Prey density (individuals per unit area or volume)
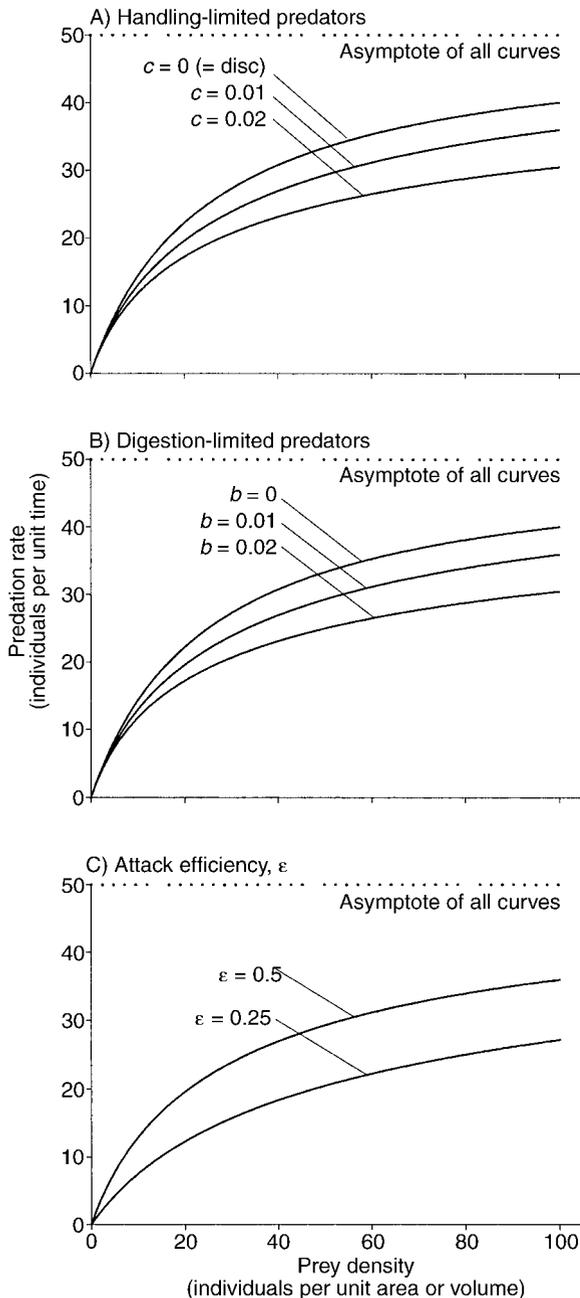
FIG. 3. Graphs of the SSS equation (Eq. 13). (A) Handling-limited predators. Model inputs were success rate $a = 2$, corrected handling time $b = 0.02$, and corrected digestion time $c = 0, 0.01,$ or 0.02, respectively; thus, $b \geq c$. All curves are type II functional responses, and for all curves, asymptotic maximum predation rate $= 1/b = 50$ (Eq. 15). However, this asymptotic maximum is approached more slowly as digestion time becomes more important. For $c = 0$, the SSS equation is equal to the disc equation (Eq. 2). (B) Digestion-limited predators. Model inputs were $a = 2$, $b = 0, 0.01,$ or 0.02, respectively, and $c = 0.02$; thus, $c \geq b$. All curves are type II functional responses, and for all curves, asymptotic maximum predation rate $= 1/c = 50$ (Eq. 15). However, this asymptotic maximum is approached more slowly as handling time becomes more important. For $b = 0$, the SSS equation is equal to the disc equation, when b is replaced by c there.

When corrected handling time exceeds corrected digestion time ($b \geq c$, condition 1), the asymptotic maximum predation rate is $1/b$. This is the same situation as in a disc equation when attack efficiencies <100% are considered (see Eq. 4). We call predators under this condition "handling-limited predators." Fig. 3a shows graphs of the SSS equation for handling-limited predators. Although the asymptote is independent of c, it is approached more slowly as digestion time becomes more important, i.e., large digestion times result in a slower rise of the curve. As c approaches 0, the SSS curve approaches a disc equation curve (with a correction for attack efficiencies <100%).

When corrected digestion time exceeds corrected handling time ($c > b$, condition 2), the asymptotic maximum predation rate equals $1/c$. We call predators under this condition "digestion-limited predators." Fig. 3b shows graphs of the SSS equation for digestion-limited predators. With larger handling times, the asymptote is approached more slowly, yet the asymptote itself is independent of b. As b approaches 0, the SSS curve approaches a disc equation curve with digestion in place of handling (c instead of b) as the limiting factor.

SSS equation curves are more flexible than disc equation curves. Thus, it is impossible to satisfyingly fit the disc equation to a SSS equation curve (with the exceptions $b = 0$ or $c = 0$). This is, because, in the disc equation, one parameter (b) determines the curve's asymptote, and two parameters (a and b) determine how the curve reaches this asymptote, i.e., the curve's slope. In contrast, in the SSS equation, one parameter (the larger one of the parameters b and c) determines the curve's asymptote, and three parameters (a, b, and c) determine how the curve reaches this asymptote.

Fig. 3c illustrates how time wasted through unsuccessful attacks (attack efficiency $\varepsilon < 100\%$) reduces the slope of the functional response curve (and, in case of handling-limited predators, the asymptotic maximum predation rate).

DISCUSSION

We have developed a handy mechanistic functional response model (the SSS equation) that realistically

←

(C) Effect of attack efficiency ε. Model inputs were $a = 2$ (corresponding $\varepsilon = 0.5$) or 1 ($\varepsilon = 0.25$), $b = 0.01$ ($\varepsilon = 0.5$, $t_{att} = 0.0025$, $t_{eat} = 0.005$; b [Eq. 13] $= 0.0025 / 0.5 + 0.005 = 0.01$) or 0.015 ($\varepsilon = 0.25$, $t_{att} = 0.0025$, $t_{eat} = 0.005$; b [Eq. 13] $= 0.0025 / 0.25 + 0.005 = 0.015$), and $c = 0.02$. When attack efficiency is halved (from 0.5 to 0.25), the gradient at the origin is halved ($a = 2$ or 1, Eq. 14) and the predation rate is decreased at almost all prey densities. However, in case of a digestion-limited predator (as in our example), asymptotic maximum predation rate remains constant ($1/c = 50$, Eq. 15). In the case of a handling-limited predator (graph not shown), b is increased, and thus asymptotic maximum predation rate is decreased.

incorporates success rate, handling time, and satiation. The satiation level is assumed to linearly decrease hunting activities. The SSS equation thereby fills a gap in functional response theory, because previous models either do not treat satiation in a realistic way (since they do not discriminate between handling and digesting prey or simply include satiation by a maximum predation rate, i.e., a digestive capacity constraint) or are extremely unwieldy.

Like the widely used disc equation, the SSS equation produces type II functional response curves. However, there are several differences. First, because of its third parameter, the SSS equation is more flexible than the disc equation. The differences are largest when handling time and digestion time are of the same order of magnitude (Fig. 3). On the contrary, if one of these two factors is negligibly small, the curve becomes virtually identical to that of the disc equation. Second, the disc equation assumes an attack efficiency equal to 100%. When this is not the case, the maximum predation rate is decreased because of time spent for unsuccessful attacks. Although mentioned by Mills (1982), Abrams (1990a), and Streams (1994), this effect has not been incorporated into most models. It is contrary to the basic idea of the disc equation that the parameters a and b are independent (Holling 1965, 1966). In nature, predator attack efficiencies seldom reach 100% (see Curio 1976, Vermeij 1982, and Packer and Ruttan 1988). Taking unsuccessful attacks into account is especially important for predators with nonnegligible attacking times. Third and most important, the disc equation (with b interpreted as in Eq. 5) does not discriminate between handling and digesting prey. The SSS equation, on the other hand, takes into account their different nature, and as a result, the maximum predation rate (prey density approaches infinity) is not determined by the sum of time spent for handling and digesting prey (as in Eq. 5), but by the maximum of these two terms. Accordingly, we have classified predators into handling-limited and digestion-limited predators. Note that this classification only refers to high prey densities. At intermediate prey densities, our model shows that also handling-limited (digestion-limited) predators experience diminished feeding rates because of time spent for digesting (handling) prey (Figs. 3a, b).

Handling-limited predators

Handling-limited predators handle (corrected for attack efficiencies <100%) prey slower than they digest them. For parasites and parasitoids, this means that they handle hosts slower than they produce eggs. In handling-limited predators, therefore, prey uptake increases with the amount of time spent for searching and handling prey. We consequently expect that, independent of prey density, handling-limited predators forage almost all of their available time (i.e., the time not needed for nonforaging activities, such as avoidance of top predators, migration, molting, reproductive activities, resting, sleeping, territorial behavior, thermoregulation, or times of slow rates of metabolism like winter dormancy).

The easiest method to detect a handling-limited predator is to directly measure corrected handling time (according to Eq. 4) as well as corrected digestion time (according to Eq. 13) and to compare them. However, all predators, from whom both measurements are available in the literature, are digestion-limited (see next section).

Another method to detect a handling-limited predator is:

1A) Through observation, directly measure predator handling time b according to Eq. 4.

1B) (Alternative to 1A) Perform short-term feeding experiments to get a short-term functional response without satiation effects. Fit the disc equation (if eaten prey was replaced) or the random predator equation (if eaten prey was not replaced) to the data to get b (handling time according to Eq. 4).

2A) Measure long-term maximum feeding rate y_{max} (with satiation) at an extremely high prey density.

2B) (Alternatively to 2A) Perform long-term feeding experiments, ideally starting with predators in a steady hunger state, or do a field study. Fit the disc equation or the random predator equation to the data to get y_{max}.

3) If $b \approx 1/y_{max}$, it is likely that the predator is handling limited.

We have applied this method to available literature data and have found three candidates for handling-limited predators. First, in the host–parasitoid system *Silo pallipes* (Trichoptera: Goeridae)–*Agriotypus armatus* (Hymenoptera: Agriotypidae), Elliott (1983) directly measured the handling time of *A. armatus* and found $b = 20.0$ min. In addition, he fitted the random predator equation to field data: $1/y_{max} = 19.4–20.1$ min, thus $b \approx 1/y_{max}$. Second, in the predator–prey system *Ochromonas* sp. (a heterotrophic flagellate)–*Pseudomonas* sp. (a bacterium), Fenchel (1982a) directly measured the handling time of *Ochromonas* as $b = 20$ s. In addition, he performed long-term experiments (Fenchel 1982b): $1/y_{max} = 19$ s, thus $b \approx 1/y_{max}$. Third, in the predator–prey system *Polinices duplicatus* (a naticid gastropod that drills through the shells of its prey)–*Mya arenaria* (Bivalvia), the handling time of *P. duplicatus* in the long-term enclosure experiments of Edwards and Huebner (1977) can be estimated by data from Edwards and Huebner (1977) and Kitchell et al. (1981; Appendix B): $b = 1.4$ d; $1/y_{max} = 1.6$ d, thus $b \approx 1/y_{max}$. Similarly, Boggs et al.'s (1984) results have indicated that *P. duplicatus* is also handling limited when feeding on another bivalve, *Mercenaria mercenaria*. In their study, *P. duplicatus* spends ~75% of its time in handling (i.e., drilling and eating) *M. mercenaria*; total foraging time (i.e., searching time plus handling time) was therefore at least 75%. This exceeds by far corresponding values for digestion-limited pred-

ators (see *Discussion: Digestion-limited predators*), corroborating our expectation that handling-limited predators should spend more time in foraging than digestion-limited predators.

Further examples for handling-limited predators can likely be found in other parasitoids, protozoans, and drilling gastropods. In general, however, handling-limited predators seem to be rare.

Digestion-limited predators

Digestion-limited predators digest prey items slower than they handle them. For parasites and parasitoids, this means they produce eggs slower than they handle hosts. At high prey densities, therefore, predation uptake does not further increase with the amount of time spent for searching and handling prey. This releases trade-off situations at high prey densities and closes the gap between optimal foraging and satisficing theory (J. Jeschke, *personal observation*; for satisficing, see Herbers [1981] and Ward [1992, 1993]).

The vast majority of predators seems to be digestion limited (see also Weiner 1992). Examples have been reported from mollusks (veliger larvae: Crisp et al. [1985]; common or blue mussel [*Mytilus edulis*], Bayne et al. [1989]), crustaceans (*Branchipus schaefferi, Streptocephalus torvicornis,* Dierckens et al. [1997]; *Calliopius laeviusculus,* DeBlois and Leggett [1991]; *Daphnia* spp., Rigler [1961], McMahon and Rigler [1963], Geller [1975]; *Calanus pacificus,* Frost [1972]; other copepods: Paffenhöfer et al. [1982], Christoffersen and Jespersen [1986], Head [1986], Jonsson and Tiselius [1990]), insects (*Chaoborus* spp. larvae, reviewed by Jeschke and Tollrian [2000]; the grasshoppers *Circotettix undulatus, Dissosteira carolina, Melanoplus femur-rubrum,* and *Melanoplus sanguinipes,* Belovsky [1986*b*]; dusty wing larvae [*Conwentzia hageni*], green lacewing larvae [*Chrysopa californica*], red mite destroyer larvae [*Stethorus picipes*], Fleschner [1950]), birds (Woodpigeons [*Columba palumbus*], Kenward and Sibly [1977]; Oystercatchers [*Haematopus ostralegus*], Kersten and Visser [1996]; hummingbirds [*Selasphorus rufus*], Hixon et al. [1983], Diamond et al. [1986]), and mammals (moose [*Alces alces*], Belovsky [1978]; pronghorn antelopes [*Antilocapra americana*], bison [*Bison bison*], elk [*Cervus elaphus*], yellow-bellied marmots [*Marmota flaviventris*], mule deer [*Odocoileus hemionus*], white-tailed deer [*Odocoileus virginianus*], bighorn sheep [*Ovis canadensis*], Columbian ground squirrels [*Spermophilus columbianus*], Rocky Mountain cotton tails [*Sylvilagus nuttali*], Belovsky [1986*b*]; cattle [*Bos taurus*], Campling et al. [1961]; beavers [*Castor canadensis*], Belovsky [1984*b*], Doucet and Fryxell [1993], Fryxell et al. [1994]; Thomson's gazelles [*Gazella thomsoni*], Wilmshurst et al. [1999]; human beings [*Homo sapiens*], Belovsky [1987]; snowshoe hares [*Lepus americanus*], Belovsky [1984*c*]; meadow voles [*Microtus pennsylvanicus*], Belovsky [1984*a*]; muskoxen [*Ovibus moschatus*], Forchhammer and Boomsma [1995]; sheep [*Ovis aries*], Blaxter et al. [1961]; shrews [*Sorex araneus, S. caecutiens, S. isodon*], Saariko and Hanski [1990]).

For digestion-limited predators, the SSS equation, contrary to Holling's (1959*b*) disc equation (Eq. 2), predicts that foraging time decreases with increasing prey density. This is in accordance with empirical data, for example from birds (Spotted Sandpipers [*Actitis macularia*], Maxson and Oring [1980]; Verdins [*Auriparus flaviceps*], Austin [1978]; Oystercatchers [*Haematopus ostralegus*], Drinnan [1957]; Yellow-eyed Juncos [*Junco phaeonotus*], Caraco [1979]; hummingbirds [*Selasphorus rufus*], Hixon et al. [1983]) and mammals (horses [*Equus caballus*], Duncan [1980]; white-tailed jackrabbits [*Lepus townsendii*], Rogowitz [1997]; sheep [*Ovis aries*], Alden and Whittaker [1970]; mouflon [*Ovis musimon*], Moncorps et al. [1997]; reindeer [*Rangifer tarandus tarandus*], Trudell and White [1981]; greater kudus [*Tragelaphus strepsiceros*], Owen-Smith [1994]).

Finally, natural predators generally spend a major part of their time in resting. For example, *Amoeba proteus, Woodruffia metabolica,* African Fish Eagles (*Haliaetus vocifer*), lions (*Panthera leo*), and wild dogs (*Lyaon pictus*) spend only ~17% of their time in hunting and eating (reviewed by Curio 1976). For further examples, see Herbers (1981) or Bunnell and Harestad (1990). Since resting may be caused by satiation, this may suggest that such predators are digestion limited. It is, however, more reliable, to compare predator foraging and nonforaging times with actual measurements of handling and digestion time. This approach reveals that the time various herbivores spend for feeding can usually be predicted solely from their handling and digestion times (J. Jeschke, *personal observation*). In other words, resting often seems to be motivated by satiation.

Applications of the SSS equation

The SSS equation was designed as a conceptual model for developing general and qualitative predictions about functional responses. It can be used to predict the effects of changing predator or prey characteristics by analyzing changes of the corresponding parameters. For example, the effects of different kinds of prey defenses can be predicted. A defense that reduces the predator's success rate (e.g., camouflage) will have its largest effects at low prey densities. In contrast, an increase in handling time due to a defense (e.g., an escape reaction [decreases success rate and increases handling time]) will lower maximum predation rate in handling-limited predators. In digestion-limited predators, either predation rates will decrease or total foraging time will increase. Finally, an increase in digestion time (e.g., due to barely digestible substances) will lower predation rates at high prey densities in digestion-limited predators (see also Jeschke and Tollrian

2000). The same considerations can be used to formulate hypotheses about optimal investment of predators in raising success rate, handling efficiency, or digestive capacity. More generally, the SSS equation can be linked with cost–benefit models to investigate predator and prey evolution using predation rate as an indirect measure of fitness.

Since the basic SSS equation contains many simplifying assumptions, it should not primarily be viewed as a model for quantitatively predicting functional responses. However, the model is open to modifications to better match the properties of specific predator–prey systems (using numerical analyses when necessary). For example, making attack efficiency ε a decreasing function of prey density allows the modeling of a swarming effect due to predator confusion. After incorporating this confusion effect and accounting for a decreasing prey density, the model adequately predicts the functional response of *Chaoborus obscuripes* larvae (Diptera) feeding on *Daphnia pulex* (Crustacea; J. Jeschke, *personal observation*).

Finally, the concept underlying the SSS equation may be used to improve predator–prey theory in general, e.g., optimal foraging theory. Classical optimal foraging theory is based on the disc equation, considering handling time but not digestion time (reviewed by Stephens and Krebs 1986). In models developed primarily for herbivores, handling time is often combined with a digestive capacity constraint: "linear programming models" (e.g., Belovsky 1978, 1984*a, b, c,* 1986*a, b,* 1987, Doucet and Fryxell 1993, Forchhammer and Boomsma 1995), "digestive rate models" (Verlinden and Wiley 1989, Hirakawa 1997*a, b,* Farnsworth and Illius 1998), and patch selection models (Fryxell 1991, Wilmshurst et al. 1995, 2000). The SSS equation offers an alternative approach for combining handling time with digestion time. Comparing an optimal foraging model based on the SSS equation with existing approaches may improve optimal foraging theory, since one of its major problems has been the lack of alternative models (e.g., Ward 1992, 1993). This may reveal new insights into predator foraging behavior.

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APPENDIX A: FROM EQ. 12 TO EQ. 13

Solving Eq. 12 for $y(x)$ gives the two solutions $y_1(x)$ and $y_2(x)$:

$$y_1(x) = \frac{1 + ax(b + c) + \sqrt{1 + ax[2(b + c) + ax(b - c)^2]}}{2abcx},$$

$$\lim_{x \to 0} y_1(x) \to \infty,$$

$$y_2(x) = \frac{1 + ax(b + c) - \sqrt{1 + ax[2(b + c) + ax(b - c)^2]}}{2abcx},$$

$$\lim_{x \to 0} y_2(x) = 0, \tag{A1}$$

As the limits indicate, only the second solution, $y_2(x)$, makes sense biologically. However, $y_2(x)$ is not defined for $a = 0$, $b = 0$, $c = 0$, or $x = 0$. Eq. 12 helps to find the corresponding equations: For $a = 0$ or $x = 0$, Eq. 12 gives $y(x) = 0$; for $b = 0$, Eq. 12 gives $y(x) = (ac)/(1 + acx)$; for $c = 0$, Eq. 12 gives $y(x) = (ab)/(1 + abx)$; and for $b = c = 0$, Eq. 12 gives $y(x) = ax$.

APPENDIX B

An estimation of *Polinices duplicatus* (Gastropoda: Naticacea) handling time feeding on *Mya arenaria* (Bivalvia) in the year-round experiments of Edwards and Huebner (1977).

Mya size class i	*Mya* length$_i$ [$\pm$ 5 mm]†	*Mya* shell thickness$_i$ [mm]‡	*Polinices* drilling time$_i$ [d]§	$\hat{\varepsilon}_i$‖	$\hat{b}_i$[d]¶	No. preyed n_i (Σ = 385)†
1	15	0.121	0.226	0.95	0.458	73
2	25	0.277	0.517	0.95	1.048	160
3	35	0.433	0.809	0.95	1.639	108
4	45	0.589	1.100	0.95	2.229	26
5	55	0.745	1.392	0.25	4.871	16
6	65	0.901	1.683	0.05	19.355	2

Resulting mean estimated handling time $\hat{b} = \dfrac{1}{385} \sum\limits_{i=1}^{6} \hat{b}_i n_i = 1.4$ d.

† Table 1 in Edwards and Huebner (1977).
‡ Table 3 in Kitchell et al. (1981): *M. arenaria* shell thickness$_i$ (mm) $= -0.113 + 0.0156 \times$ length$_i$ (mm).
§ Kitchell et al. (1981): *P. duplicatus* drilling time $= 1.868$ d/mm.
‖ According to Kitchell et al. (1981), attack efficiency ε of *P. duplicatus* mainly depends on predator and prey size. Given a certain predator size, ε is almost unity for prey below a critical size and almost zero for prey beyond that critical size. The critical size for *M. arenaria* is given in Fig. 7 in Kitchell et al. (1981). The predator sizes are given in Table 3 in Edwards and Huebner (1977). Edwards and Huebner used four individual predators with mean sizes in the relevant period (14 June–29 August, where maximum predation rate $y_{max} = 0.63$ *M. arenaria*/d have been reported for *P. duplicatus*) of 37.9 mm, 41 mm, 42.15 mm, and 50.45 mm, respectively. The corresponding critical *M. arenaria* lengths are roughly 53 mm for the three small predator individuals and 60 mm for the largest one. Therefore, *M. arenaria* of size classes 1, 2, 3, and 4 could be easily attacked by all four predator individuals ($\hat{\varepsilon}_1 = \hat{\varepsilon}_2 = \hat{\varepsilon}_3 = \hat{\varepsilon}_4 = 0.95$), *M. arenaria* of size class 5 could basically only be attacked by one of the four predators ($\hat{\varepsilon}_5 = 0.25$), and *M. arenaria* of size class 6 could only hardly be attacked by all four predators ($\hat{\varepsilon}_6 = 0.05$).
¶ Estimated *P. duplicatus* handling time (for *M. arenaria* size class i):

$$\hat{b}_i \text{ [d]} = [1.5 + (2\varepsilon_i)^{-1}] \times \text{drilling time}_i. \tag{B1}$$

Derivation: From Eq. 4, $\hat{b}_i$ [d] $=$ (drilling time$_i$ / ε_i) + eating time$_i$ = (drilling time$_i$ ε_i) + drilling time$_i$ (Kitchell et al. 1981). However, this calculation overestimates handling time, because it is based on the assumption that unsuccessful drills last as long as successful ones. Assuming that unsuccessful drills last, on average, half the time of successful ones, leads to Eq. B1.