Funktionelle Reaktionen von Konsumenten:
die SSS Gleichung und ihre Anwendung

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Zusammenfassung

Der Zusammenhang zwischen der pro Kopf Konsumtionsrate und der Nahrungsdichte wird in der Ökologie als funktionelle Reaktion bezeichnet und ist das Thema dieser Dissertation. Jeweils zum ersten Mal seit den 70er Jahren gebe ich hier einen Überblick über sowohl theoretische als auch empirische Arbeiten zur funktionellen Reaktion. Dabei zeige ich eine Lücke in der bisherigen Theorie und fülle diese mit einem neuen Modell, der SSS Gleichung.

Dieses Modell kann man beispielsweise dazu verwenden, die Auswirkungen von Beutetier-Verteidigungen auf Konsumtionsraten von Räubern vorherzusagen. Diese Vorhersagen sind korrekt im Vergleich zu den bisher einzigen existierenden entsprechenden empirischen Daten, welche hier vorgestellt werden.

Eine weitere Anwendungsmöglichkeit der SSS Gleichung ist die Einteilung von Konsumenten in zwei Gruppen, handling-limitierte und verdauungslimitierte, wobei erstere für das Angreifen und die Aufnahme von Nahrung (beides zusammen wird als handling bezeichnet) mindestens so viel Zeit benötigen wie für die Verdauung; deren Konsumtionsrate wird deshalb von deren handling time bestimmt. Die meisten Konsumenten sind in ihrer Konsumtionsrate jedoch verdauungslimitiert. Sie können ‚satt' werden und sollten daher von Zeitdruck befreit sein, wenn die Nahrung häufig genug ist, um schnell gefunden zu werden und auch die übrigen Umweltbedingungen gut sind. Eine von mir durchgeführte Analyse empirischer Daten deutet an, dass zumindest Herbivore in der Natur tatsächlich häufig von Zeitdruck befreit zu sein scheinen. Diese Analyse zeigt damit einen Schwachpunkt bisheriger Verhaltensmodelle, welche ausnahmslos vom Gegenteil, also permanentem Zeitdruck, ausgehen.

In meiner Zusammenfassung empirischer funktioneller Reaktionen zeige ich, dass filtrierende Konsumenten charakteristischerweise einen bestimmten Typ funktioneller Reaktionen zeigen. Nachdem ich die SSS Gleichung dahingehend erweitert habe, dass sie die Besonderheiten von Filtrierern berücksichtigt, kann ich dieses Ergebnis erklären: Die Ursache scheint die Eigenschaft von Filtrierern zu sein, während der Nahrungssuche und -aufnahme in der Lage zu sein, weitere Nahrungspartikel zu fangen oder zu fressen und auch andere Aktivitäten auszuführen, z.B. nach Räubern Ausschau zu halten.

Ich erweitere die SSS Gleichung außerdem um den sog. Konfusionseffekt. Ein solcher Effekt liegt vor, wenn ein Räuber, der mit einem Schwarm seiner Beutetiere konfrontiert ist, nicht in

der Lage ist, die vielen Sinneseindrücke neuronal zu verarbeiten. Ich vergleiche die erweiterte SSS Gleichung mit empirischen Daten zur funktionellen Reaktion von ‚konfusen' Räubern und stelle nicht nur eine qualitative, sondern auch eine quantitative Übereinstimmung fest. In diesem Abschnitt zeige ich auch, dass der Konfusionseffekt ein häufig auftretendes Phänomen ist, besonders bei taktilen Räubern und solchen visuellen Räubern, die agile Beutetiere jagen.

Abschließend zeige ich weitere, bisher nicht verwirklichte Anwendungsmöglichkeiten der SSS Gleichung im speziellen und des Konzepts der funktionellen Reaktion im allgemeinen.

Inhaltsverzeichnis

Jeschke, J.M.; Tollrian, R. 2000. Density-dependent effects of prey defences. *Oecologia* 123, 391-396.

Jeschke, J.M.; Kopp, M.; Tollrian, R. 2002. Predator functional responses: discriminating between handling and digesting prey. *Ecol. Monogr.* 72, 95-112.

Jeschke, J.M.; Tollrian, R. Eingereicht a. Full and lazy herbivores.

Jeschke, J.M.; Kopp, M.; Tollrian, R. Eingereicht. Consumer-food systems: Why type I functional responses are exclusive to filter feeders.

Jeschke, J.M.; Tollrian, R. Eingereicht b. Correlates and consequences of predator confusion.

1. Einführung, Zusammenfassung der Artikel und Ausblick

1.1. Einführung

Der Name „funktionelle Reaktion“ reiht sich ein in die Liste unglücklich gewählter Bezeichnungen, er ist unspezifisch, also nichts sagend, und hat in unterschiedlichen Disziplinen unterschiedliche Bedeutungen. In der Ökologie wurde er besetzt von Solomon (1949), welcher eine funktionelle Reaktion bezeichnete als den Zusammenhang zwischen der Dichte einer Nahrung (Nahrungsdichte) und der Menge, die ein Konsument von dieser Nahrung pro Zeiteinheit aufnimmt (Konsumtionsrate). Funktionelle Reaktionen verbinden also zwei Trophieebenen miteinander, sind deshalb für Populationsbiologen sehr wichtig und werden folgerichtig in den meisten ökologischen Lehrbüchern behandelt (Begon et al. 1996, Ricklefs 1996). Das gilt mit Einschränkung auch für die Evolutionsbiologie (Futuyma 1997). Hier sind funktionelle Reaktionen deshalb von Bedeutung, weil sie zwei fitnessrelevante Parameter beinhalten: die Konsumtionsrate und das Prädationsrisiko (Sebens 1982, Stephens & Krebs 1986, Brown et al. 1993). Als letztes Beispiel für an funktionellen Reaktionen interessierte Biologen seien Verhaltensökologen genannt. Diese versuchen, Verhalten mit Hilfe von evolutionsbiologischen Argumenten zu erklären. Zum Beispiel ist die gesamte optimal foraging-Theorie untrennbar mit funktionellen Reaktionen verbunden (Stephens & Krebs 1986). Auch der Verdünnungseffekt, welcher häufig als Ursache für Aggregationen von Beutetieren genannt wird, lässt sich nur im Zusammenhang mit funktionellen Reaktionen verstehen (Hamilton 1971, Bertram 1978, Jeschke & Tollrian, eingereicht b).

Nach Holling (1959a) lassen sich funktionelle Reaktionen in drei Typen einteilen: Typ I, II und III (Abb. 1)[1]. Diese Einteilung wird bis heute verwendet und deckt in der Tat die meisten empirisch beobachteten funktionellen Reaktionen ab (Jeschke et al., eingereicht). Jedoch kommt es bei rund jeder zehnten funktionellen Reaktion vor, dass die Konsumtionsrate bei hoher Nahrungsdichte wieder abnimmt. Solche Reaktionen werden aufgrund ihrer kuppelähnlichen Form als „dome-shaped“ bezeichnet (Holling 1961).

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[1] Die Namen dieser drei Typen sind erneut unspezifisch.

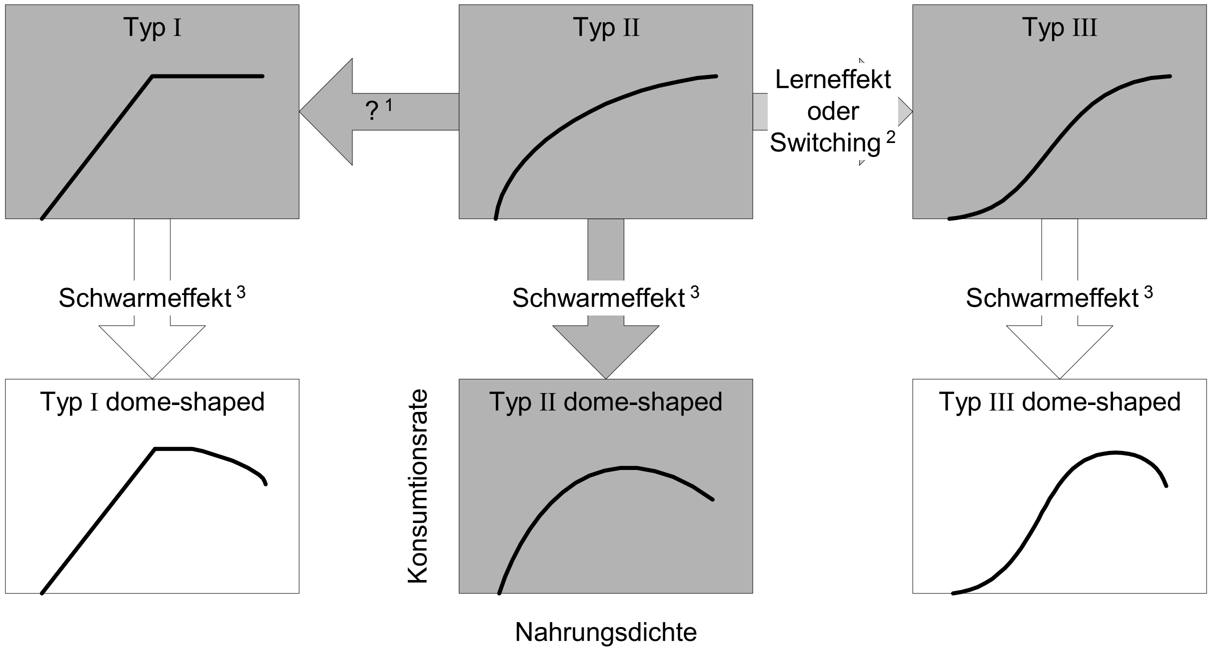

Abbildung 1: Die Typen der funktionellen Reaktion. Typ I, Typ II, Typ III und Typ II dome-shaped sind grau hervorgehoben, da diese am häufigsten sind (Jeschke et al., eingereicht). Von diesen vier Typen wiederum ist der Typ II der mit Abstand häufigste. Da dieser Typ auch der theoretisch einfachste ist (Jeschke et al. 2002 und Jeschke et al., eingereicht), kann er als der ursprüngliche angesehen werden.

[1] Die Bedingungen für eine Typ I funktionelle Reaktion waren vormals unbekannt, werden jedoch in Jeschke et al. (eingereicht) behandelt.

[2] Siehe Holling 1965, Murdoch & Oaten 1975, Hassell et al. 1977, Real 1977, Abrams 1987, Dunbrack & Giguère 1987, Werner & Anholt 1993 und Fryxell & Lundberg 1997.

[3] Siehe Jeschke & Tollrian (eingereicht b).

Nach dem heutigen Stand des Wissens wird die funktionelle Reaktion eines Konsumenten hauptsächlich von drei Faktoren beeinflusst (Jeschke et al. 2002): seiner success rate, handling time und Verdauungszeit. Mathematisch gesehen ist die success rate die Steigung der funktionellen Reaktion im Ursprung. Sie ist das Produkt von, erstens, der Begegnungsrate von Konsument und Nahrung, zweitens, der Wahrscheinlichkeit, dass der Konsument die Nahrung erkennt, die ihm begegnet, drittens, der Hunger-unabhängigen Wahrscheinlichkeit, dass der Konsument die Nahrung angreift, die er als solche erkennt und viertens, der Attackeneffizienz (Attackenerfolgsquote). Die handling time eines Konsumenten ist die Zeit, die er benötigt, um Nahrung anzugreifen und zu sich zu nehmen. Die Verdauungszeit schließlich ist die Darmdurchgangszeit geteilt durch die Darmkapazität (die Menge an Nahrung, die der Darm des Konsumenten gleichzeitig aufnehmen kann).

1.2. Zusammenfassung der Artikel

Im folgenden wird jeder in dieser Dissertation enthaltene Artikel kurz zusammengefasst. Ich erwähne hier auch explizit solche Leistungen, die zu einem Manuskript beigetragen haben, aber nicht von mir oder nicht während meiner Doktorarbeit erbracht wurden. Alle Artikel wurden von mir verfasst.

1.2.1. Jeschke & Tollrian (2000): Density-dependent effects of prey defences

In diesem Artikel beschreiben Ralph Tollrian und ich zum ersten Mal, wie sich Verteidigungen von Beutetieren auf funktionelle Reaktionen auswirken. Als Modellsystem wählten wir *Chaoborus obscuripes - Daphnia pulex*. Da sich Verteidigungen qualitativ unterschiedlich auswirken können, klassifizieren wir sie in zwei Gruppen: success rate-Verteidigungen und handling time-Verteidigungen, wobei erstere die success rate des Räubers verringern und letztere die handling time vergrößern. Unsere experimentellen Daten umfassen beide Verteidigungstypen. Weil dieser Artikel zeitlich vor der Entwicklung der SSS Gleichung (siehe nächster Abschnitt) datiert, klassifizierten wir Verteidigungen aufgrund von Hollings (1959b) Scheibengleichung. Tabelle 1 gibt eine aktualisierte Klassifizierung wider.

Tabelle 1: Eine mögliche Klassifizierung von Verteidigungen.

Verteidigungstyp basierend auf der SSS Gleichung	Verteidigungstyp basierend auf der Scheibengleichung	Beispiel
Success rate-Verteidigung	dito	Tarnung
Handling time-Verteidigung	dito	Hohe Fluchtgeschwindigkeit (dies ist gleichzeitig eine success rate-Verteidigung)
Digestion time-Verteidigung	Handling time-Verteidigung	Einlagerung schwer verdaulicher Substanzen

Die Versuche, die in diesem Artikel beschrieben sind, führte ich während meiner Diplomarbeit durch. Ich habe diesen Artikel trotzdem in die Dissertation mit aufgenommen, weil ich, erstens, die in ihm vorgestellte Klassifizierung von Verteidigungen erst während meiner Doktorarbeit entwickelt habe und ich, zweitens, diesen Artikel komplett während meiner Doktorarbeit geschrieben habe. Ralph Tollrian kommentierte ihn umfangreich.

1.2.2. Jeschke et al. (2002): Predator functional responses: discriminating between handling and digesting prey

Michael Kopp, Ralph Tollrian und ich geben hier den seit 1971 (Royama) ersten Überblick über Modelle zur funktionellen Reaktion und entwickeln außerdem selbst ein Modell, das eine Lücke in der bisherigen Theorie schließt. Wie wir zeigen, gibt es drei Faktoren, die die funktionelle Reaktion eines Konsumenten anerkannterweise stark beeinflussen: seine success rate, seine handling time und seine Verdauungszeit. Die einzigen Modelle, die diese Faktoren auf eine realistische Art und Weise beinhalten, haben 22 oder mehr Parameter. Aufgrund dessen entwickeln wir ein entsprechendes Modell, das weniger Parameter enthält und dadurch besser handhabbar ist: die SSS Gleichung. Wir nehmen dabei an, Konsumenten seien in der Lage, Nahrung gleichzeitig zu handhaben und zu verdauen. Dementsprechend ist eine Konsumtionsrate bei hoher Nahrungsdichte entweder durch die handling time oder die Verdauungszeit des Konsumenten bestimmt und zwar von der längeren dieser beiden Zeiten. Wir teilen Konsumenten aufgrund dessen in handling-limitierte und verdauungslimitierte ein. Ein Blick in die Literatur zeigt, dass die meisten Konsumenten verdauungslimitiert sind. Neben dieser Einteilung von Konsumenten bietet die SSS Gleichung weitere Anwendungsmöglichkeiten, z.B. lassen sich mit ihrer Hilfe die Auswirkungen von Verteidigungen auf funktionelle Reaktionen untersuchen.

Während der Überblick über existierende Modelle zur funktionellen Reaktion auf meiner alleinigen Arbeit beruht, war Michael Kopp an der Entwicklung der SSS Gleichung beteiligt. Er kommentierte das Manuskript außerdem umfangreich. Das trifft auch auf Ralph Tollrian zu.

1.2.3. Jeschke & Tollrian (eingereicht a): Full and lazy herbivores

Basierend auf einer im vorigen Artikel bereits erwähnten Idee (dort im Abschnitt „Digestion-limited predators“ auf S. 106) analysieren Ralph Tollrian und ich Literaturdaten von Herbivoren und zeigen, dass Individuen von 18 der 19 untersuchten Arten genau so viel Zeit mit Fressaktivitäten verbringen, wie sie benötigen, um ihren Darm zu füllen. Obwohl dieses

Ergebnis nicht zwingend zeigt, dass Herbivore oft keinen Zeitdruck haben (‚faul' sind), deutet es zumindest darauf hin. Es widerspricht damit dem Weltbild der meisten Verhaltensökologen, was daran deutlich wird, dass alle (mir bekannten) existierenden optimal foraging-Studien annehmen, Tiere stünden unter permanentem Zeitdruck (für nähere Informationen und Referenzen, siehe Artikel; zur Rolle von Weltbildern in der Wissenschaft, siehe z.B. Gould 1997 oder Brown 2001). Sicherlich, solche Tiere, die unter der permanenten Gefahr leben, gefressen zu werden oder diese Gefahr nicht abschätzen können, müssen versuchen, möglichst viel Zeit in einem Unterschlupf zu verbringen oder sich möglichst wenig zu bewegen, um die Anzahl der Begegnungen mit Räubern zu minimieren. Diese Tiere leben unter permanentem Zeitdruck. Tatsächlich dürften Räuber jedoch nur selten permanent gefährlich sein und Tiere, die in der Lage sind, das zu erkennen, sollten im Falle von guten Umweltbedingungen in der Lage sein, ihren Darm in den risikolosen Tagesabschnitten zu füllen. Unsere Ergebnisse unterstützen diese Überlegung.

Das Manuskript wurde von Ralph Tollrian umfangreich kommentiert und bei *Proc. Natl. Acad. Sci. USA* eingereicht.

1.2.4. Jeschke et al. (eingereicht): Consumer-food systems: Why type I functional responses are exclusive to filter feeders

In diesem Artikel zeigen Michael Kopp, Ralph Tollrian und ich jeweils erstmals, erstens dass und zweitens warum nur Filtrierer Typ I funktionelle Reaktionen zeigen. Die Ansicht, Typ I Reaktionen seien typisch für Filtrierer, ist schon seit langem weit verbreitet, wurde jedoch bisher niemals überprüft. Wir testen und bestätigen diese Ansicht, indem wir einen Überblick über empirische Studien zur funktionellen Reaktion geben. Dieser Überblick ergänzt außerdem Jeschke et al. (2002), wo theoretische Studien zur funktionellen Reaktion zusammengefasst werden; er ist der erste seit 1976 (Hassell et al.) und damit der einzige aktuelle und bei weitem umfangreichste. Das zweite Ergebnis, warum nur Filtrierer Typ I Reaktionen haben, erzielen wir, indem wir Modelle entwickeln und analysieren, die auf der in Jeschke et al. (2002) entwickelten SSS Gleichung basieren.

Während der Überblick über empirische funktionelle Reaktionen auf meiner alleinigen Arbeit beruht, war Michael Kopp an der Entwicklung der in dem Artikel beschriebenen Modelle beteiligt. Er kommentierte das Manuskript außerdem umfangreich, was auch auf Ralph Tollrian zutrifft. Das Manuskript wurde eingereicht bei *Biol. Rev.*

1.2.5. Jeschke & Tollrian (eingereicht b): Correlates and consequences of predator confusion

Ralph Tollrian und ich versuchen in diesem Artikel erstmals, generelle Erkenntnisse über den sog. Konfusionseffekt zu gewinnen. Ein solcher Effekt liegt vor, wenn ein Räuber, der mit einem Schwarm seiner Beutetiere konfrontiert ist, nicht in der Lage ist, die vielen Sinneseindrücke neuronal zu verarbeiten und deshalb eine geringere Attackeneffizienz aufweist. Um herauszufinden, ob der Konfusionseffekt für bestimmte Räubertypen häufiger ist als für andere, führten wir Experimente in vier verschiedenen Räuber-Beute-Systemen durch und durchsuchten die existierende Literatur. Die Mehrheit der in der Literatur vorhandenen Daten stammt von Fischen oder Vögeln als Räuber. Um die Untersuchung des Konfusionseffekts auf eine breitere taxonomische Basis zu stellen, verwendeten wir bei unseren Experimenten die Larven dreier verschiedener Insektenarten (*Aeshna cyanea*, *Libellula depressa* [beide Odonata] und *Chaoborus obscuripes* [Diptera]) und von Alpenmolchen (*Triturus alpestris*). In 14 der 20 bisher untersuchten Räuber-Beute-Systeme (70%) zeigten die Räuber einen Konfusionseffekt, wobei taktile Räuber besonders anfällig zu sein scheinen; visuelle Räuber scheinen von Beuteschwärmen hingegen nur dann beeinträchtigt zu werden, wenn die Beutetiere sehr agil sind. Diese Überlegenheit von visuellen Räubern könnte eine Folge davon sein, dass deren Sinnesorgane eine größere Informationskapazität besitzen (Dusenbery 1992). Um es zu ermöglichen, die ökologischen, evolutionsbiologischen und ethologischen Konsequenzen des Konfusionseffekts zu untersuchen, zeigen wir außerdem dessen Auswirkungen auf die funktionelle Reaktion. Zunächst erweitern wir die in Jeschke et al. (2002) entwickelte SSS Gleichung durch einen Konfusionseffekt und stellen damit das erste funktionelle Reaktionsmodell vor, das einen Konfusionseffekt berücksichtigt. Wie wir in dem Artikel zeigen, ist unser Modell in der Lage, die funktionelle Reaktion von *Chaoborus obscuripes* auf *Daphnia obtusa* vorherzusagen. Die Analyse des Modells widerspricht der weit verbreiteten Ansicht, Räuberkonfusion u.a. durch Schwärme verursachte Beeinträchtigungen des Räubers (Fig. 1 im Artikel) führten unweigerlich zu einer dome-shaped funktionellen Reaktion (vgl. Abb. 1). Tatsächlich können diese Effekt auch einen bisher unbekannten Reaktionstyp hervorrufen (roller-coaster-shaped oder achterbahnähnlich) oder sich gar nicht auf die Form der funktionellen Reaktion auswirken. Diese theoretischen Aussagen können wir durch die experimentellen Daten von den Räuber-Beute-Systemen bestätigen, in denen wir die Präsenz des Konfusionseffekts gezeigt haben: *Aeshna cyanea – Daphnia magna* und *Chaoborus obscuripes* - *Daphnia obtusa.*

Die Experimente im Räuber-Beute-System *Chaoborus obscuripes* - *Daphnia obtusa* führte ich während meiner Diplomarbeit durch, die anderen Experimente wurden unter der Anleitung von Ralph Tollrian und mir von Sonja Hübner, Mechthild Kredler und Eric Röttinger ausgeführt. Michael Kopp leitete die in der Legende zu Abb. 6 angegebene Ungleichung her. Alles andere stammt von mir, also die vergleichende Analyse, das Modell zur funktionellen Reaktion, der qualitative und quantitative Vergleich des Modells mit den empirischen funktionellen Reaktionen sowie der Text selbst. Das Manuskript wurde von Ralph Tollrian umfangreich kommentiert und bei *Am. Nat.* eingereicht.

1.3. Ausblick

Funktionelle Reaktionen wurden bisher v.a. in populationsbiologischen Modellen eingesetzt. Hier genügen phänomenologische Reaktionsmodelle, weil es i.d.R. nur auf die Form oder Qualität der Reaktion ankommt. Auch gibt es nach Jeschke et al. (eingereicht) keinen Hinweis darauf, dass man im Labor qualitativ falsche funktionelle Reaktionen erhalten würde. So lässt sich wohl erklären, warum die meisten Wissenschaftler üblicherweise sehr einfache Reaktionsmodelle verwenden (Abschnitt „Phenomenological vs. mechanistic models“ auf S. 101 in Jeschke et al. 2002) und sich nur selten die Mühe machen, empirische funktionelle Reaktionen im Freiland zu messen (Jeschke et al., eingereicht). Inwiefern sich die drei Reaktionstypen I, II und III in ihrem Einfluss auf Populationsdynamiken unterscheiden, ist schon seit längerem bekannt (Begon et al. 1996), genauso, welche Konsumenten Typ II und III Reaktionen haben und warum (Begon et al. 1996, Jeschke et al., eingereicht). Seitdem Jeschke et al. (eingereicht) letzteres auch für Typ I Reaktionen gezeigt haben, sind die dringendsten Fragen bzgl. der unterschiedlichen Reaktionstypen wohl geklärt.

Es sollte jetzt versucht werden, funktionelle Reaktionen quantitativ zu verstehen. Dieses Verständnis ist z.B. die Voraussetzung dafür, Populationsdynamiken quantitativ vorherzusagen, zu erfassen, warum manche Tierarten größere Populationsdichten oder –schwankungen aufweisen als andere. Außerdem könnte dann auch das Potenzial des Konzepts der funktionellen Reaktion für die Evolutionsbiologie und Ethologie ausgeschöpft werden. Für die Vorhersage des Verhaltens von Konsumenten werden i.d.R. klassische und mittlerweile von vielen, z.B. von Brown (1999) und Jeschke & Tollrian (eingereicht a), als veraltet eingestufte optimal foraging-Modelle verwendet. Diese beruhen auf der phänomenologischen Scheibengleichung von Holling (1959b; Stephens & Krebs 1986). Zeitgemäßere optimal foraging-Modelle könnten z.B. basierend auf der in Jeschke et al. (2002) entwickelten SSS Gleichung entwickelt werden. Eine weitere und für mich viel versprechende Anwendungsmöglichkeit funktioneller Reaktionen bietet sich im Rahmen einer der größten Fragen der Biologie überhaupt: Was ist Fitness? Obwohl jeder Biologe eine Idee von diesem so wichtigen Begriff hat, gibt es keine konkrete allgemein gültige Definition (Benton & Grant 2000, Brommer 2000). Außerdem sind übliche Fitnessmaße wie die Reproduktionsrate zwar intraspezifisch interpretierbar, nicht jedoch interspezifisch. Makroevolutionäre und –ökologische Fragen lassen sich mit ihnen nicht beantworten, z.B. warum es momentan kein größeres Landlebewesen gibt als den Afrikanischen Elefanten

(*Loxodonta africana*). Um solche Fragen beantworten zu können, muss man für Fitness ein allgemein gültiges oder zumindest makroevolutionär gültiges Maß finden, wobei energetische Fitnessmaße in diesem Zusammenhang besonders viel versprechend erscheinen (Sebens 1982, Stephens & Krebs 1986, Brown et al. 1993). Da Tiere Energie zu sich nehmen, indem sie Nahrung konsumieren, könnte die funktionelle Reaktion als Fitness-definierender Faktor auch in der Evolutionsbiologie und Makroökologie die Wichtigkeit erlangen, die sie in der Populationsbiologie innehat.

1.4. Danksagungen

Ralph Tollrian und Wilfried Gabriel möchte ich zunächst dafür danken, dass sie mich auf dem Weg zu dieser Dissertation das haben untersuchen lassen, was mich am meisten interessierte. Sie haben erkannt, dass v.a. interessierte Forscher Wissen schaffen. Ralph Tollrian hatte für mich außerdem immer ein offenes Ohr und diskutierte meine Manuskripte mit mir häufig und umfangreich. Auch Wilfried Gabriel war stets für mich da, wenn ich ihn brauchte. Michael Kopp danke ich für seine Mitwirkung an zwei Artikeln (Jeschke et al. 2002 und Jeschke et al., eingereicht). Diejenigen Leute, die zu einzelnen Manuskripten in Form von Kommentaren u.ä. beigetragen haben, sind dort namentlich erwähnt. Auch bei Ihnen bedanke ich mich genauso wie bei allen übrigen in der Karlstraße arbeitenden Ökologen und Limnologen, die einen Anteil an der sehr guten Arbeitsatmosphäre hatten und / oder haben.

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Density-dependent effects of prey defences

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Abstract In this study, we show that the protective advantage of a defence depends on prey density. For our investigations, we used the predator-prey model system *Chaoborus*-*Daphnia pulex*. The prey, *D. pulex*, forms neckteeth as an inducible defence against chaoborid predators. This morphological response effectively reduces predator attack efficiency, i.e. number of successful attacks divided by total number of attacks. We found that neckteeth-defended prey suffered a distinctly lower predation rate (prey uptake per unit time) at low prey densities. The advantage of this defence decreased with increasing prey density. We expect this pattern to be general when a defence reduces predator success rate, i.e. when a defence reduces encounter rate, probability of detection, probability of attack, or efficiency of attack. In addition, we experimentally simulated the effects of defences which increase predator digestion time by using different sizes of *Daphnia* with equal vulnerabilities. This type of defence had opposite density-dependent effects: here, the relative advantage of defended prey increased with prey density. We expect this pattern to be general for defences which increase predator handling time, i.e. defences which increase attacking time, eating time, or digestion time. Many defences will have effects on both predator success rate and handling time. For these defences, the predator's functional response should be decreased over the whole range of prey densities.

Key words *Chaoborus obscuripes* · *Daphnia pulex* · Density dependence · Functional response · Inducible defences

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Introduction

Most organisms form defences against predators (we define the term predator in a broad sense, i.e. including carnivores, herbivores, parasites, and parasitoids). Such defences reduce the predator's prey uptake, or from the prey's point of view: they reduce predation risk (number of prey eaten divided by prey density). This protective advantage of a defence probably varies with prey density, and since prey density in natural environments will rarely be constant, information about density dependence is essential to understand the function and the evolution of defence systems (see Baldwin 1996).

For our study, we took advantage of special properties of inducible defence systems. They allow the precise calculation of defence effects, because otherwise identical (even at the genetic level in our system) animals, with and without defences, can be compared. Inducible defences have been reported from diverse organisms [recently reviewed in Karban and Baldwin (1997) and Tollrian and Harvell (1999)].

We studied density-dependent effects in the predator-prey model system *Chaoborus obscuripes*-*Daphnia pulex*. *Chaoborus* larvae (Diptera) live in freshwater ponds and are mainly nocturnal and tactile ambush predators (Duhr 1955; Teraguchi and Northcote 1966; Giguère and Dill 1979; Smyly 1979; Riessen et al. 1984). When exposed to chemicals released by *Chaoborus* larvae, juveniles of the water-fleas *Daphnia pulex* (Crustacea) build pedestals on the dorsal carapace with associated spines called neckteeth (Krueger and Dodson 1981; Tollrian 1993). In combination with other protective features (Spitze and Sadler 1996), this inducible defence effectively reduces the predation rate (Krueger and Dodson 1981; Tollrian 1995; reviewed in Tollrian and Dodson 1999). Studying the underlying mechanism of this defence, Havel and Dodson (1984) found higher escape probabilities after body contact with *Chaoborus* for daphnids with neckteeth. To examine density-dependent effects, we compared predation rates of *Chaoborus obscuripes* for neckteeth-defended *Daphnia* with predation rates for undefended *Daphnia* over a range of prey densities in separate feeding experiments.

Density-dependent effects of predation can be characterized by the functional response of a predator, which can most easily be described by the two variables *a* and *b* (Holling 1959):

$$y(x) = \frac{atx}{1+abx}, \quad \text{Holling's disc equation} \qquad (1)$$

where a=success rate, b=handling time per prey item, t=experimental time, x=prey density, and y=no. of prey eaten. The disc equation simulates a type II functional response which is a hyperbolic curve. The curve's gradient in the origin is equal to at, and the asymptotic maximum for $x \rightarrow \infty$ is t/b. In other words: according to the disc equation, the functional response of a predator at low prey densities is mainly defined by the predator's success rate, whereas at high prey densities it is mainly defined by the predator's handling time. Success rate *a* is the product of four components: (1) encounter rate, (2) probability of detection, (3) probability of attack, and (4) efficiency of attack. A synonym for the predator-oriented term "success rate" is the prey-oriented term "vulnerability". Handling time *b* describes the effect of prey density on predation rate. It includes time spent for attacking, eating, and digesting prey (Holling 1966).

We used our system to study effects of two different types of defences: (1) defences which decrease success rate, and (2) defences which increase handling time.

1. The neckteeth defence decreases the efficiency of attack (Havel and Dodson 1984) and thus decreases success rate *a*. This results in a decreased prey uptake at low prey densities. Since success rate does not limit maximum prey uptake (when prey density is high enough), at very high densities there should be no difference between predation rates on neckteeth-defended and undefended prey. As a consequence, the relative advantage of defended prey over undefended prey should be greatest at low prey densities and should gradually decline as density increases.
2. Defences which increase handling time do not prevent ingestion. They are therefore not adaptive in typical predator-prey systems where predator attacks are lethal for the prey. However, they *are* adaptive in systems where an initial attack is not lethal and the individual prey itself can benefit (e.g. in herbivore-plant systems). We experimentally simulated the density-dependent effects of this type of defence by comparing the functional responses of *Chaoborus* to two size classes of *D. pulex* which had similar vulnerabilities, but which differed in body mass. The difference in body mass led to a difference in digestion time and thus in handling time. Normally, bigger prey not only increase handling time but also affect other components of the predation cycle. However, in the *Chaoborus*-*Daphnia* system differently sized prey can have similar vulnerabilities, because encounter rate increases with prey size whereas efficiency of attack decreases with prey size, leading to a dome-shaped vulnerability-size function (Pastorok 1981). According to the disc equation, an increased handling time should result in an increasing relative advantage with increasing prey density. The advantage should rise to an asymptotic value, defined by the maximum prey uptake of both defended and undefended prey. In other words: the relative advantage should increase with prey density and should remain constant at prey densities on the plateaus of the two functional response curves.

Materials and methods

Organisms

As predators we used fourth instar larvae of *Chaoborus obscuripes*, which is a large species of the genus *Chaoborus* [length 11.59±0.057 mm (mean±SE), *n*=180]. The larvae were caught in a fishless pond in Langenbach near Munich and kept in a dark climate-controlled room (4°C). As prey we used the clone *Daphnia pulex* R9, which has also been used in previous studies (Tollrian 1993, 1995). We cultured this clone at 20°C in an artificial medium: 1.11 l medium consisted of 700 ml tap water, 400 ml ultrapure water, and 10 ml SMB medium [for SMB medium see Miyake (1981)]. We used the same medium for the experiments. The water-fleas were fed daily, ad libitum, with *Scenedesmus obliquus*.

We used three different types of prey: (1) second juvenile instar *D. pulex* of the typical morph (2 TM); (2) second juvenile instar *D. pulex* of the neckteeth morph (2 NM); and (3) third juvenile instar *D. pulex* of the typical morph (3 TM). Since second instar juveniles carry the biggest neckteeth (Tollrian 1993) and suffer the highest predation (Tollrian 1995), we chose this instar to study the effects of neckteeth. Typical and neckteeth morph daphnids did not differ in size (means±SE): 823±11.5 µm (*n*=26) for 2 TM, 825±7.1 µm (*n*=25) for 2 NM. There is no indication that the neckteeth defence per se influences *Chaoborus* digestion time. We therefore assume that *Chaoborus* digestion time mainly depends on *Daphnia* body size and, thus, should be equal for neckteeth-defended and undefended *Daphnia*. For *Chaoborus* larvae, digestion time is the most important component of handling time, as both attacking and eating times are relatively short: digestion time=several hours (Giguère 1986), attacking time ≤0.003 s, eating time≈15 s (Pastorok 1981). Consequently, *Chaoborus* handling time can be assumed to be equal for neckteeth-defended and undefended *Daphnia*.

To experimentally simulate the effects of a defence which increases digestion time, we compared typical second and third instars (1071±16.0 µm, *n*=25) of *D. pulex*. Third instars have a larger body size but very similar vulnerabilities to second instars (see Results).

To obtain the experimental animals we isolated cohorts of 30 to 40 juvenile *D. pulex* which were born on the same day and reared them in 5-l beakers. Since the first two clutches of daphnids consist of smaller and more size-variable neonates (Ebert 1993), we only used juveniles from third and subsequent clutches. To obtain water-fleas with neckteeth, we additionally placed net cages into half of the beakers. We placed 20 *C. obscuripes* into each net cage and fed them daily with 60±10 *D. pulex*. This *Chaoborus* density ensured maximal neckteeth induction (Tollrian 1993).

Two days before starting an experiment, we transferred predators from the cold storage room to the experimental room for acclimatization. We fed the larvae prior to each experiment because using pre-starved chaoborids would have resulted in an overestimation of feeding rates (Spitze 1985). We isolated the predators 11 h before starting an experiment, to avoid over-stimulation of their mechanoreceptors and to simulate a diel feeding pause. We performed experiments with single predators in 2-l beakers filled with 500 ml medium with algae and a defined number of daphnids. Predation experiments at each density were replicated 5 or 10 times. The feeding trials lasted 12 h and were performed in the dark, at night. Temperature was recorded with a thermograph [20.25±0.06°C (mean±SE), n=245]. At the end of an experiment, we removed the predator and counted all remaining live and dead daphnids.

We used a total of 9225 *D. pulex*, and found 132 (1.43%) dead but not eaten after the experiments. The type of prey had no influence on the number of uneaten dead daphnids (two-way ANOVA: "prey", P=0.69, $F_{2,\,217}$=0.37, interaction "prey×density", P=0.85, $F_{16,\,217}$=0.64; SPSS for Windows 8.0, SPSS). To avoid overestimation of prey consumption, we counted uneaten dead water-fleas as surviving prey.

Analysis

We analysed the functional response data with logistic regression (Trexler et al. 1988; Hosmer and Lemeshow 1989; Juliano 1993; Trexler and Travis 1993; Sokal and Rohlf 1995; Hardy and Field 1998). We performed three blocks of logistic regression analyses. First, we calculated estimated functional response curves. Here, the independent variable was "prey density" and the dependent variable was the variable "eaten" (1=individual was eaten, 0=individual survived). We started with estimating the appropriate scale (normal, squared, or cubed) for the variable "prey density" (Hosmer and Lemeshow 1989). For all three types of prey, it was not necessary to use squared or even cubed prey densities. After performing logistic regression for each type of prey, we calculated estimated functional responses as estimated predation risks multiplied with prey density. Second, we calculated *estimated* relative advantages of the two types of defence. Here, we used four independent variables: "prey density", "type of prey", and the two interaction variables "density×2 NM" and "density×3 TM". The dependent variable was the variable "survived" (1=individual survived, 0=individual was eaten). Finally, we calculated 95% confidence intervals and P-values for the *observed* relative advantages separately for each prey density with the independent variable "type of prey" and the dependent variable "survived". We defined the relative advantage of defended prey as the odds ratio of survival for defended against undefended prey=(number of defended prey survived/number of defended prey eaten)/(number of undefended prey survived/number of undefended prey eaten). An odds ratio >1 means an advantage, an odds ratio equal to 1 means no advantage, and an odds ratio <1 means a disadvantage (Sokal and Rohlf 1995).

Results

D. pulex with neckteeth had a distinctly lower predation risk compared to typical *D. pulex* (Fig. 1). The estimated relative advantage for neckteeth morphs at a density equal to 0 was 3.58 (99.9% confidence interval, 2.40–5.34; Table 1), so the neckteeth significantly reduced *Chaoborus* success rate. This relative advantage was significantly decreasing with increasing prey density (Table 1, interaction term "2 NM×density", P<0.001). Nevertheless, the relative advantage remained significant, even at very high prey densities (all P<0.001, except for 20 *Daphnia*/500 ml, P<0.05; Fig. 2a).

Both age classes of typical morphs of *D. pulex* had similar vulnerabilities (Figs. 1, 2b; Table 1). The relative advantage for the third instar increased with prey density (interaction term "3 TM×density" in Table 1, P<0.05). The difference in predation rates was significant only for

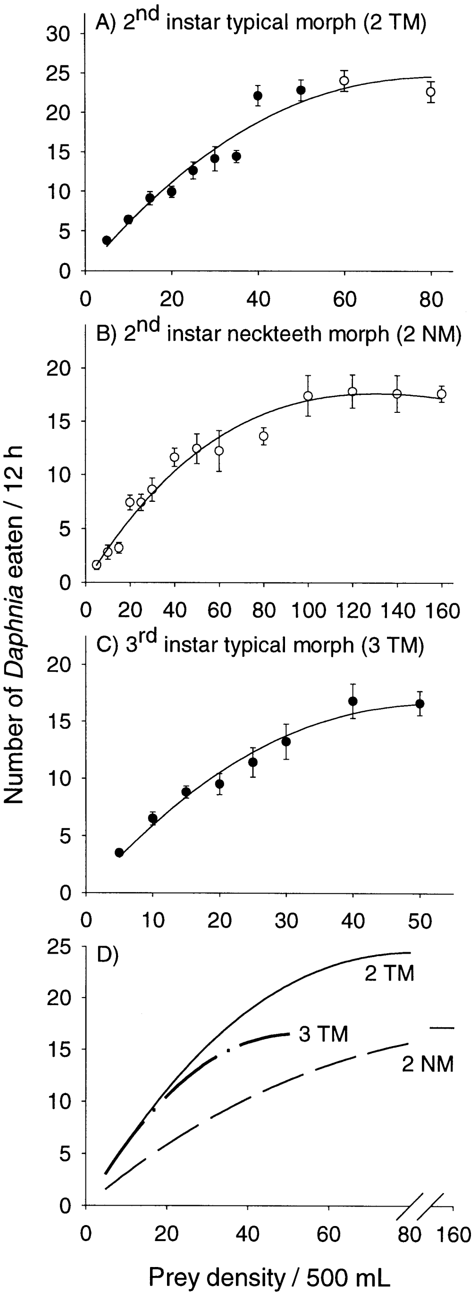

Fig. 1 The functional responses of *Chaoborus obscuripes* to *Daphnia pulex*. *Circles* represent means (±SE), *filled circles* indicate ten replicates, *open circles* indicate five replicates. *Lines* are fitted functional response curves using logistic regression analyses. For the second juvenile instar of *D. pulex* of the typical morph (*2 TM*), y=[exp(0.5690–0.0174x)×x]/[1+exp(0.5690–0.0174x)]; for the second juvenile instar of *D. pulex* of the neckteeth morph (*2 NM*), y=[exp(–0.7059–0.0088x)×x]/[1+exp(–0.7059–0.0088x)]; for the third juvenile instar of *D. pulex* of the typical morph (*3 TM*), y=[exp(0.6419–0.0270x)×x]/[1+exp(0.6419–0.0270x)]; where x= prey density and y=number of prey eaten. Note that abscissas as well as ordinates have different scales

Table 1 Results of overall logistic regression analysis, dependent variable "survived". Model fit: Hosmer-Lemeshow test C=11.63, 8 *df*, P=0.17]. Note, b is a statistical term of the logistic regression analysis; it is different from the handling time b in the disc equation (Eq. 1). *2 TM* Second juvenile instar of *Daphnia pulex* of the typical morph, *2 NM* second juvenile instar of *D. pulex* of the neckteeth morph, *3 TM* third juvenile instar of *D. pulex* of the typical morph

Variable	b	SE(b)	exp(b)	P-value[a]
Constant (=2 TM)	–0.5690	0.0866		
2 NM	1.2755	0.1216	3.5806	***
3 TM	–0.0729	0.1486	0.9297	n.s.
Density	0.0174	0.0019		
2 NM×density	–0.0085	0.0021	0.9915	***
3 TM×density	0.0096	0.0039	1.0097	*

*P<0.05, ***P<0.001, *n.s.* P≥0.05

[a] P-values for exp(b) indicate significant deviation from 1

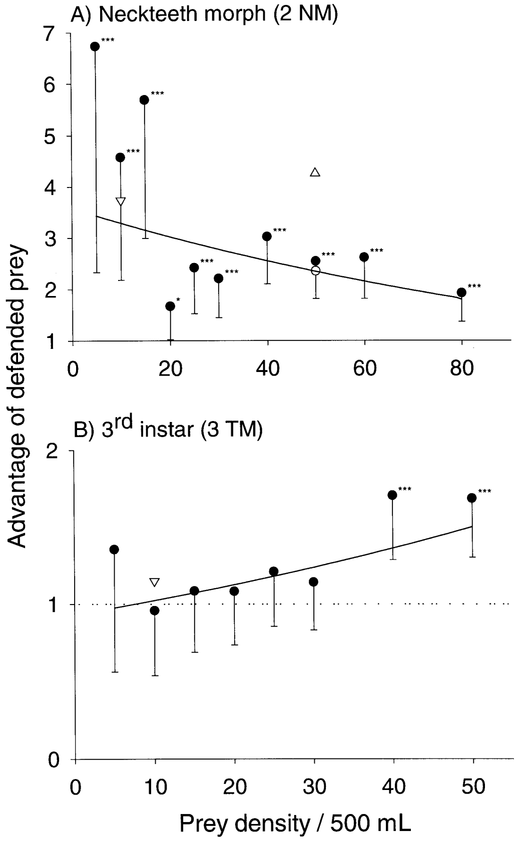

Fig. 2A,B Density-dependent relative advantages of defended prey. The relative advantage is the odds ratio of survival for defended against undefended prey. * indicate significant advantages, i.e. significant deviation from a value of 1 (*P<0.05, ***P<0.001). *Filled circles* represent means (–95% confidence interval), *solid lines* are logistic regression lines: **A** 2 NM, y=exp(1.2755–0.0085x); **B** 3 TM, y=exp(–0.0729+0.0096x); where x=prey density and y=advantage of defended prey. *Open triangles pointing down* indicate data from Tollrian (1995) {predator: *Chaoborus crystallinus*; difference in length (Dl)=[(length of neckteeth morph–length of typical morph)/length of typical morph]× 100%=0%}. *Open triangles pointing up* indicate data from Parejko (1991) (*Mochlonyx* sp.; Dl=4.45%). *Open circles* indicate data from Krueger and Dodson (1981) (*Chaoborus americanus*; Dl=9.38%). Note that abscissas as well as ordinates have different scales. For abbreviations, see Fig. 1

the two highest prey densities tested: 40 and 50 *Daphnia*/500 ml (both P<0.001; Fig. 2b).

All three types of prey gave rise to type 2 functional response curves (see Fig. 1) (Holling 1959, 1966). However, the functional response curve of typical morph daphnids reached its plateau at lower prey densities than the functional response curve of neckteeth morph daphnids. The observed mean maximum numbers of prey eaten were: 24 (prey density 60/500 ml) for 2 TM; 17.8 (prey density 120/500 ml) for 2 NM; and 16.8 (prey density 40/500 ml) for 3 TM.

Discussion

Neckteeth – defences which decrease success rate

Neckteeth morph daphnids suffered clearly lower predation rates than typical morphs. So far, all comparable studies have established an advantage for neckteeth-morph water-fleas (Fig. 2a). The quantitative differences between the data obtained in these studies may have been due to the different sizes of the predator species used.

Natural densities of daphnids mostly lie in those regions that we call "low prey densities" (e.g. Dodson 1972). At these densities, our results were in accordance with the hypothesis: Defended prey had a clearly lower vulnerability. However, in contrast to our expectations, we observed a relative advantage of defended *Daphnia* at high prey densities where the plateau of the functional response curve was already reached. To offer an explanation, it might be tempting to assume that, beside the decrease in success rate, handling time was also increased by the neckteeth. E.g. Abrams (1990) pointed out that the parameter b is increased by the average time spent on unsuccessful attacks. However, this effect should be negligibly small for *Chaoborus*. The attack of a *Chaoborus* larva only lasts up to 0.003 s (Pastorok 1981). Thus, an increase in attacking time would be negligible in comparison to the digestion time which lasts several hours (Giguère 1986). This argument also holds for eating time. For *Daphnia* of the size we used in our experiments, *Chaoborus* eating time is only about 15 s

(Pastorok 1981). As a consequence, a possible increase in eating time would not have a significant effect on handling time. The third and last component of handling time is digestion time. There is no reason to assume that a *Chaoborus* larva needs more time to digest a defended compared to an undefended *Daphnia*. To sum up, there was no indication that neckteeth defence notably affected *Chaoborus* handling time. But why did the relative advantage of defended *Daphnia* remain at high prey densities? There are two possible explanations:

1. High prey densities could have caused predator confusion. In other experiments, we have shown that a confusion effect is present in the *Chaoborus-Daphnia* system (unpublished data). For example, at a prey density of 5 *Daphnia*/500 ml, the average attack efficiency of a predator was 43%, and for 160 *Daphnia*/500 ml it was only 33%. At high densities where the functional response for the defended morph should reach the same plateau as the functional response for the typical morph, a confusion effect and the defence could act synergistically. To illustrate this, we computed hypothetical functional response curves that would arise without a confusion effect, i.e. if success rate remained constant at all prey densities. For this, we used the Gause-Ivlev equation (Gause 1934; Ivlev 1961):

   $$y=k\times[1-\exp\,(-ax)], \tag{2}$$

   where a=success rate, k=maximum number of prey eaten, x=prey density, and y=number of prey eaten; $k\approx30$, $x=5$, $y_{\mathrm{TM}}=3.45$, $y_{\mathrm{NM}}=1.44$ (experimental data) $\Rightarrow a_{\mathrm{TM}}\approx0.03$, $a_{\mathrm{NM}}\approx0.012$. Without confusion, the relative advantage of neckteeth morphs would decrease with prey density and would become negligible at very high densities (Fig. 3). This simulation suggests that a confusion effect is a potential explanation.
2. A special feeding characteristic of *Chaoborus* could also be responsible for the remaining advantage. *Chaoborus* larvae do not feed continually but in discrete feeding intervals. A larva can pack several prey items into its pharynx before it makes a digestive pause, which can last several hours (Smyly 1979). The lower success rate may lead to a time delay in crop filling. This is a possible explanation for the step-like form of the functional response curves (Fig. 1). A consequence may have been that with typical prey the larvae were already in the next feeding interval, while with defended prey they were still in the digestive pause. The duration of the predation experiments would then decide whether or not the same plateau will be reached.

Third instar prey-defences which increase handling time

The comparison of the two typical morph instars of *D. pulex* had two main results. First, functional responses were similar for both instars at low prey densities, proving that, although both instars had different sizes, they had similar vulnerabilities. Second, the larger third instar had an increasing relative advantage with increasing prey density. This was in accordance with results from Krylov (1992), Spitze (1985), and Vinyard and Menger (1980), who found similar relationships in other *Chaoborus-Daphnia* systems. This is also known from other predator-prey systems, e.g. *Ischnura-Daphnia* (Thompson 1975), *Notonecta-Culex* (Fox and Murdoch 1978), and *Didinium-Paramecium* (Hewett 1980). The reason is obvious: a predator needs more time to digest larger prey. This results in a lower predation rate for larger prey at high densities. It should be noted that a decreased prey uptake is only disadvantageous for a predator when total energy gain is lower. In our study, the decreased prey uptake was presumably not a disadvantage for the predators since a third instar *Daphnia* provides more energy than a second instar one. In summary, this defence did not affect success rate, only digestion time, giving rise to a relative advantage which increased with prey density.

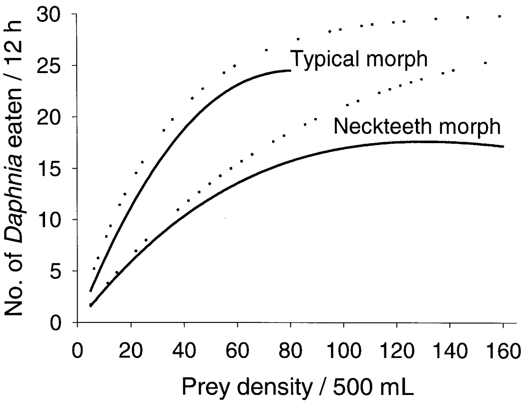

Fig. 3 In this study, the relative advantage of neckteeth-morph *Daphnia* remained significant at very high prey densities. A possible explanation is predator confusion. The observed functional response curves (*solid lines,* fitted with logistic regression analyses; see Fig. 1) are compared with hypothetical curves which would result if there was no confusion effect [*dotted lines*; equations: Gause (1934), Ivlev (1961)]: $y=30\times[1-\exp(-0.03x)]$ for *typical morph*, $y=30\times[1-\exp(-0.012x)]$ for *neckteeth morph*. Without a confusion effect, the difference between the functional responses for typical and neckteeth morph would lose significance at high densities

Conclusions

A lower functional response curve for defended prey is common. This reduction can be based on different types of defence:

Defences which reduce success rate

The success rate can be reduced by: (1) a reduced encounter rate, e.g. predator avoidance; (2) a reduced probability of detection, e.g. camouflage; (3) a reduced probability of attack, e.g. aposematic coloration; or (4) a reduced efficiency of attack (as in this study). Our results show that for these defences the relative advantage of defended prey is highest at low prey densities and decreases with prey density.

Defences which increase handling time

Such defences can, for example, be achieved in plants by incorporation of unpalatable or non-digestible substances. We expect that defences which increase handling time usually evolve in predator-prey systems where attacks are not lethal, e.g. in many herbivore-plant systems. In these systems, the individual prey itself benefits from its defence. Our experimental simulation indicates that the relative advantage of such defences increases with prey density.

However, defences which reduce success rate will frequently additionally increase handling time, e.g. escape reactions decrease attack efficiency and increase attacking time, and armoured structures decrease attack efficiency and often increase eating time. How the predator's functional response is influenced by these combined effects depends on the specific properties of the defence system itself.

With this study we want to emphasize that all defences which are not 100% protective are density-dependent in their effects on predators and prey. It is therefore essential to integrate these effects in predator-prey models, for example, cost-benefit models of defences.

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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.

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TABLE 1. A selection of functional response models.

Features	Model											
	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]	+	+	+	+	+	+	+	$^{+}_{+}$	$^{+}_{+}$	$^{+}_{+}$	+	$^{+}_{+}$
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]	−	−	−	−	−	+	−	+	+	−	−	+

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, ‘‘$^{+}_{+}$’’ 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 1959*b*), Eq. 2; (L) Invertebrate model (Holling 1966; see also Metz and van Batenburg 1985*a*,*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 1985*a, 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 (1990*a*); (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 (1997*b*; 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 [1990*c*] 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 1997*b*; see also Laca et al. 1994, Shipley et al. 1994).

TABLE 1. Extended.

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

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[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, 1984*a, b, c*, 1986*a, 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 (1997*a*), and Wilmshurst et al. (2000).

[5] See also Belovsky (1978, 1984*a, b, c*, 1986*a, b*, 1987), Cook and Cockrell (1978), Sih (1980, 1984), Owen-Smith and Novellie (1982), McNair (1983), Abrams (1984, 1987, 1989, 1990*b, 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, 1997*a*), 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 (1985*a, 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, 1984*a, b, c*, 1986*a, 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 (1997*a*), Leonardsson and Johansson (1997), and Rothley et al. (1997).

[8] See also Griffiths and Holling (1969), Paloheimo (1971*a, 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 (1971*a, b*), Curry and DeMichele (1977), Curry and Feldman (1979), McNair (1983), Lucas (1985), and Metz and van Batenburg (1985*a, 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, 1984*a, b, c*, 1986*a, b*, 1987), Owen-Smith and Novellie (1982), Engen and Stenseth (1984), Metz and van Batenburg (1985*a*), Wanink and Zwarts (1985), Abrams (1987, 1989, 1990*b, 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).

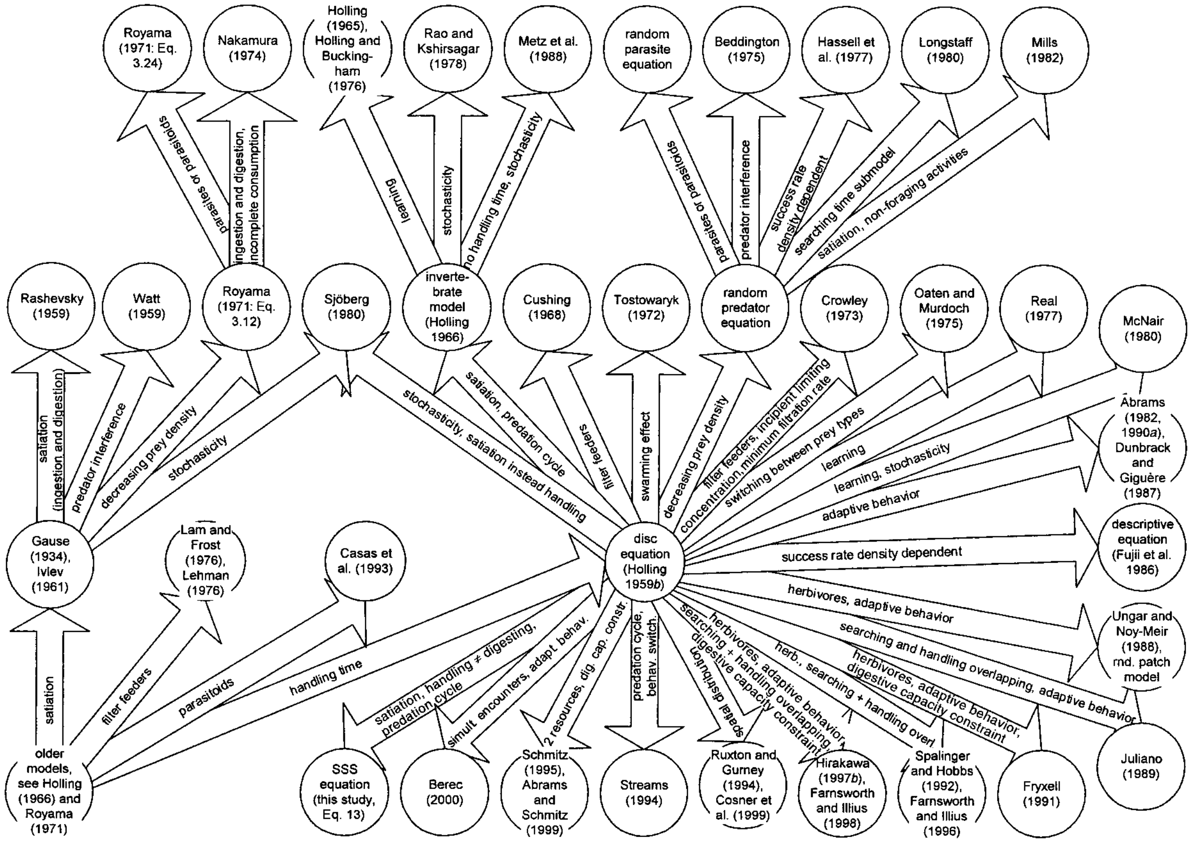

FIG. 1. A "family tree" of functional response models.

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 [1959*a*, *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

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

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 (1985*b*), Metz et al. (1988), Abrams (1990*c*), 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):

$$\begin{aligned} b &= t_{\mathrm{att}} + t_{\mathrm{eat}} \\ &\Leftrightarrow \text{asymptotic maximum predation rate} \\ &= (t_{\mathrm{att}} + t_{\mathrm{eat}})^{-1} \end{aligned} \tag{3}$$

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 $\varepsilon = 100\%$. Attack efficiencies $<100\%$ can be incorporated into the disc equation by defining b as

$$\begin{aligned} b &= t_{\mathrm{att}}/\varepsilon + t_{\mathrm{eat}} \\ &\Leftrightarrow \text{asymptotic maximum predation rate} \\ &= (t_{\mathrm{att}}/\varepsilon + t_{\mathrm{eat}})^{-1}. \end{aligned} \tag{4}$$

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

$$\begin{aligned} b &= t_{\mathrm{att}} + t_{\mathrm{eat}} + st_{\mathrm{dig}} \\ &\Leftrightarrow \text{asymptotic maximum predation rate} \\ &= (t_{\mathrm{att}} + t_{\mathrm{eat}} + st_{\mathrm{dig}})^{-1} \end{aligned} \tag{5}$$

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

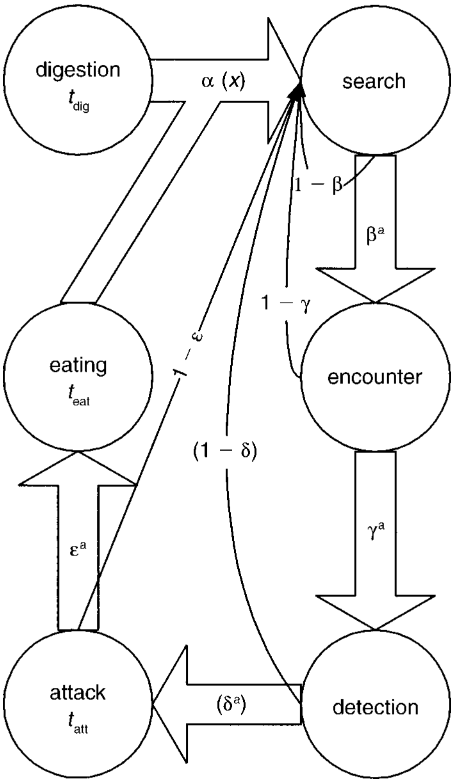

FIG. 2. The predation cycle. We divide the predation cycle into five stages: search, encounter, detection, attack, and eating. A predator enters a predation cycle under the probability to search, $\alpha(x)$; this is determined by the predator's hunger level, which in turn is influenced by digestion 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:

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

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,

$$a = \beta\gamma\varepsilon. \tag{7}$$

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 (1997*b*), 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

$$\alpha(x) = h(x). \tag{8}$$

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:

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

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

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

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

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

Inserting Eq. 11 into Eqs. 8 and 6 yields

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

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

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

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

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:

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

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,

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

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.

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

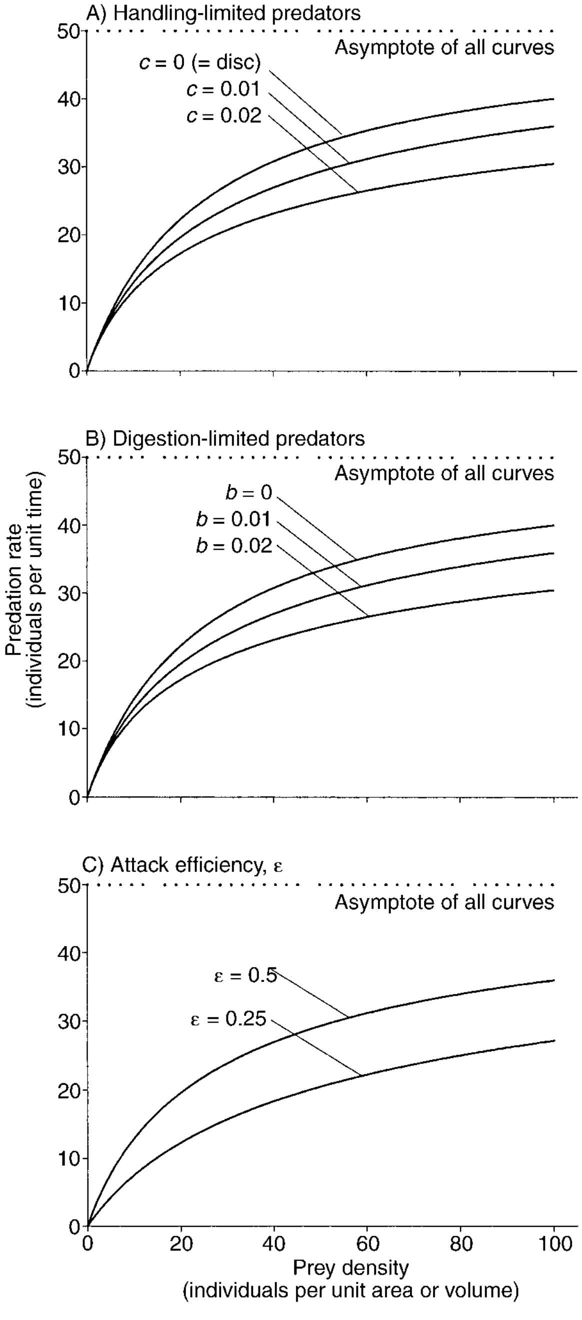

FIG. 3. Graphs of the SSS equation (Eq. 13). (A) Handling-limited predators. Model inputs were success rate $a = 2$, corrected handling time $b = 0.02$, and corrected digestion time $c = 0$, 0.01, or 0.02, respectively; thus, $b \geq c$. All curves are type II functional responses, and for all curves, 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.

←

(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 (1990*a*), 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 non-negligible 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 (1982*a*) directly measured the handling time of *Ochromonas* as $b = 20$ s. In addition, he performed long-term experiments (Fenchel 1982*b*): $1/y_{\max} = 19$ 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 predators (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$_i$ [± 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 $\hat{b} = \frac{1}{385}\sum_{i=1}^{6} \hat{b}_i n_i = 1.4$ 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 × 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.

Full and lazy herbivores

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The observation that animals spend most of their time resting or sleeping and comparably little time foraging is surprising when having in mind that foraging time influences energy input and thus, indirectly, fitness. Why animals don't forage for longer periods is usually explained by time constraints due to essential non-foraging activities, such as avoidance of predators or prevention of overheating. Herbers challenged this assumption by advocating that animals simply have no reason to forage more because they need no more time to reach satiation. By analyzing literature data from herbivorous molluscs, insects, birds, and mammals, we demonstrate the previously unrecognized broad validity of Herbers' hypothesis. Our finding suggests that herbivores are often released from time constraints and thus questions key assumptions of many studies, especially optimal foraging studies.

Given that foraging time influences energy input and thus, indirectly, fitness (1, 2), why spend, for example, mammals on average 61.5% of a 24 h-day or 14¾ h/d resting or sleeping (*N* = 222 species) and only 30.5% or 7½ h/d foraging (*N* = 120) (3; see also 4, 5)? Jeschke *et al.* (6) recently found a potential answer to this question. Their review of empirical data indicates that most animals need less time for handling, i.e. capturing and eating, one food item than for digesting it. Since digestion is a passive process, it does not prevent animals from searching for food or handling it, nor from avoiding predators or lying in the shadow, etc. Consequently, if food is abundant enough to be found quickly and if essential non-foraging activities do not take too much time, the foraging time of most species will, in accordance to Herbers' hypothesis (4), be determined by their physiological needs, not, as usually assumed (1, 2, 7-13), by the duration of essential non-foraging activities. In this study, we investigate how frequently this is actually the case.

Methods

Our approach is to compare observed animal feeding times from the literature to predicted values calculated under the assumption of Herbers' hypothesis. An animal's in this way predicted feeding time $\hat{t}_{feed}$, given as a fraction of time t, is the time it needs for handling one food item, b, multiplied by the number of food items it needs to consume during t in order to reach satiation, y_s:

$$\hat{t}_{feed} = b \cdot y_s. \tag{1}$$

Satiating food consumption rate y_s is the ratio of gut capacity g, which is the number of food items the gut of a satiated, i.e. *ad libitum* fed, animal holds, to t_g, which is the corresponding gut transit time. Accordingly,

$$\hat{t}_{feed} = b \cdot g / t_g. \tag{2}$$

For a given species, the handling time b, the satiating food consumption rate y_s, the gut capacity g, and the gut transit time t_g depend on the type of food consumed and vary within and between individuals. A trivial reason for this variability is the difference within and between individuals in body size, but a non-trivial one is the difference in energetic requirements (14-17). Mammalian females, for example, require much energy when lactating and thus need much food to reach satiation then. Therefore, when comparing our model to empirical data, it is necessary to use data that were obtained under similar conditions. Simplifying eq. 2 by replacing the ratio of gut transit time to gut capacity, t_g / g, by digestion time c gives

$$\hat{t}_{feed} = b / c. \tag{3}$$

For example, the yellow-bellied marmots (*Marmota flaviventris*) observed by Belovsky (10) at the National Bison Range, Montana, needed 3.40 min for digesting 1 g-dry mass of their diet, but only 0.425 min for handling it, i.e. for biting, chewing, and swallowing (Supporting Table 1, which is published on the PNAS web site, www.pnas.org, as is the other information supporting this paper). Hence, predicted feeding time $\hat{t}_{feed}$ = (0.425 min / g-dry mass) / (3.40 min / g-dry mass) = 0.125 = 12.5% of a 24 h-day or 3 h/d.

We calculated predicted feeding times $\hat{t}_{feed}$ for all 19 species for which we found the necessary data (one nectarivore and 18 herbivores) and compared them to the observed values t_{feed} (Fig. 1). Most of these values were obtained in summer (Supporting Table 1) and thus likely under good environmental conditions. The body mass of the animals ranged from 0.28 g (grasshoppers) to 636 kg [bison (*Bison bison*)], covering seven orders of magnitude. A few species in principle do not follow our model and were therefore excluded from our analysis: First, the rare consumers that need as much or more time for handling their food than for digesting it ($b \geq c$) (6). Second, pythons and similar predators adapted to rare meals that build up their digestive tract especially for each meal (18).

Results

The observed feeding times agree well with our predicted values. For all species, the mean difference between $\hat{t}_{feed}$ and t_{feed} is only 1.9 percentage points or 27 min/d (100% would equal 24 h per day), and the median, which is not so sensitive to outliers, is 0.6% or 9 min/d. To account for phylogenetic dependence between the data, we calculated standardized independent contrasts of $\hat{t}_{feed}$ and t_{feed} (see Supporting Fig. 5 for details). The correlation coefficient r between these contrasts is 0.821 ($P < 0.001$, SPSS 10.1.3, SPSS Inc. 2001). All feeding times except for the giant rams-horn snails (*Marisa cornuarietis*) and meadow voles (*Microtus pennsylvanicus*) were observed in the field. Excluding them from the analysis does not significantly change the result [mean $|\hat{t}_{feed} - t_{feed}|$ = 1.3% or 19 min/d, median $|\hat{t}_{feed} - t_{feed}|$ = 0.6% or 9 min/d, $r = 0.827$ ($P < 0.001$)]. For information on the relationship between feeding time and environmental temperature in the species analyzed here, see Supporting Text 1.

According to Fig. 1, all species except rams-horn snails spent similar portions of the day feeding [phylogenetically weighted mean excl. snails, beavers (*Castor canadensis*), and Rufous hummingbirds (*Selasphorus rufus*) (the latter two species were excluded because of incomparable data, see Supporting Table 1) = 15.5% or 3¾ h/d, range = 11.9 - 21.3% or 2¾ - 5¼ h/d]. The underlying reason becomes clear when eq. 3 is extended by allometric functions:

$$\hat{t}_{feed}(m) = \frac{b(m)}{c(m)} = \frac{\alpha_b m^{\beta_b}}{\alpha_c m^{\beta_c}} = \frac{\alpha_b}{\alpha_c} m^{\beta_b - \beta_c}, \tag{4}$$

where m is body mass and α_b, β_b, α_c, and β_c are allometric parameters. Since β_b is similar to β_c (Fig. 2), feeding time is independent of body mass (Fig. 3). A broader comparative analysis of herbivores by Belovsky (12) agrees with this result. Using ordinary least squares regression analysis, he found β_b to be -0.67. Furthermore, gut capacity g scaled as $m^{1.0}$ and gut transit time t_g as $m^{0.33}$ and given that $c = t_g/g$ (see above), $c \propto m^{0.33}/m^{1.0} \Rightarrow \beta_c = -0.67 \Rightarrow \beta_b = \beta_c$.

Discussion

We have shown that many herbivores naturally feed to satiation, with their feeding time depending on handling time, gut capacity, and gut transit time. Diamond *et al.* (19), whose data on Rufous hummingbirds are included in our study, are to our knowledge the only ones to have explicitly shown this for any species before. Our finding extends theirs to herbivores and thereby questions the validity of classical optimal foraging models (1, 2, 20-23) in which consumers cannot become satiated. It furthermore suggests that herbivores are often released from time constraints because such constraints would likely lead to trade offs in time allocation and thus to a non-satiating food consumption. However, this is certainly not always the case as food abundance and the time available to forage may allow herbivores to feed to satiation, but may not allow them to choose the most desirable diet. This could be the case if abundant or easily-handled food is only slowly digestible while quickly digestible food is rare or difficult to handle. Those optimal foraging models that consider satiation effects (7, 8, 11, 24) have to our knowledge only been applied with this scenario in mind, i.e. under the time constraint-assumption. Critically, this crucial assumption is not verified by these studies (Supporting Text 2, ref. 16). Some readers might object that pressure of time is a reasonable *a priori* assumption because 'lazy' animals are unlikely to be naturally selected. However, this objection is challenged theoretically by Wilson's principle of stringency (Fig. 4, ref. 25) and empirically by the observation that herbivores as well as carnivores are able to compensate for restricted food access, decreased food abundance, or increased food requirements by increasing their foraging time or effort (3, 6, 26-32). Even the assumption that foraging time is limited by sleeping time is doubtful, for the determinants of sleeping time as well as the function of sleep have remained elusive (33).

In conclusion, how frequently animals are pressed for time is at present unclear. Our results imply that at least herbivores are often not. Whether this is also true for carnivores should be investigated in future studies, as should the conditions leading to time constraints, e.g. scarce food (cf. caption below Fig. 4). Our results caution against routinely assuming that animals are pressed for time and recommend to consider that they can also be "full and lazy".

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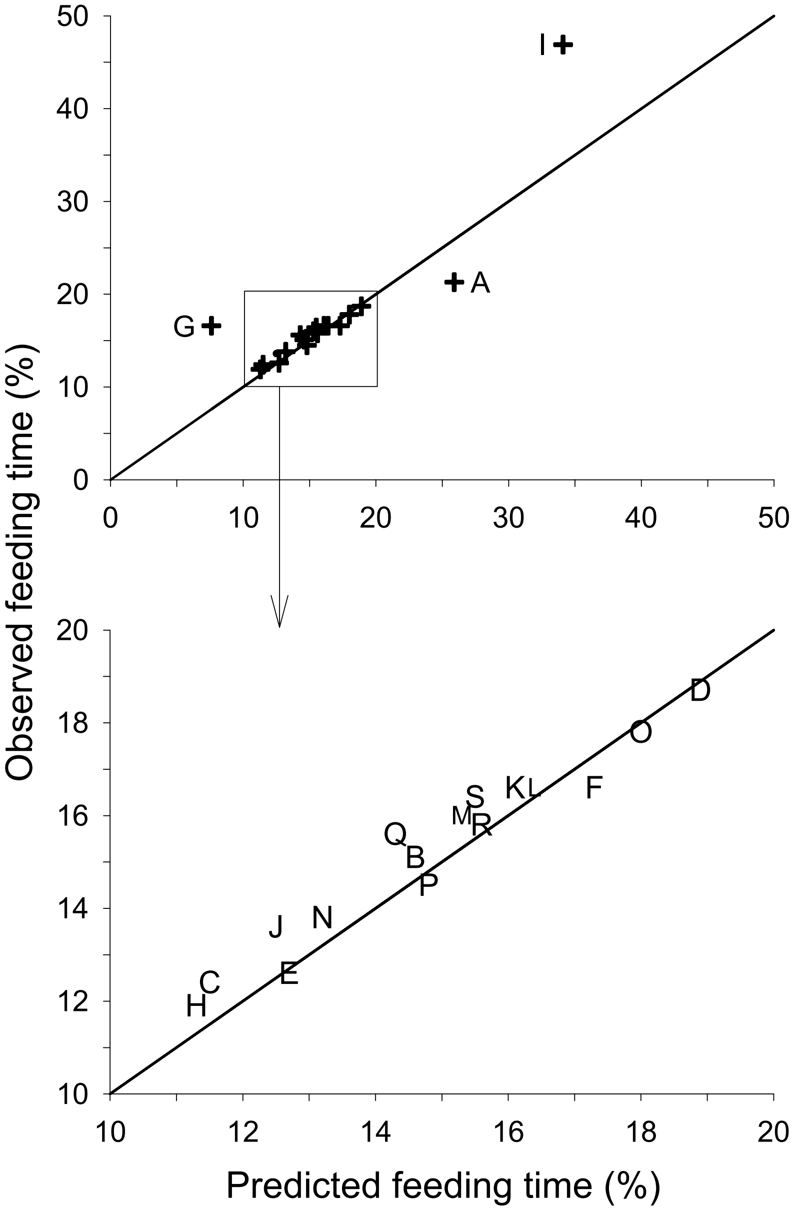

Fig. 1. Scatter plots of observed feeding times t_{feed} vs. predicted values $\hat{t}_{feed}$. The latter were calculated with eq. 3; for details and references, see Supporting Table 1. Both t_{feed} and $\hat{t}_{feed}$ are given as fractions of 24 h-days except for Rufous hummingbirds, where they are related to daylight hours. Letters indicate species: A) moose (*Alces alces*)^{T}, B) pronghorn antelope (*Antilocapra americana*)^{T}, C) bison (*Bison bison*)^{T}, D) beaver (*Castor canadensis*)^{T}, E) elk (*Cervus elaphus*)^{T}, F) undulant-winged grasshopper (*Circotettix undulatus*)^{T}, G) Carolina grasshopper (*Dissosteira carolina*)^{T}, H) snowshoe hare (*Lepus americanus*)^{M}, I) giant ramshorn snail (*Marisa cornuarietis*)^{C,M}, J) yellow-bellied marmot (*Marmota flaviventris*), K) red-legged locust (*Melanoplus femur-rubrum*)^{T}, L) migratory grasshopper (*Melanoplus sanguinipes*)^{T}, M) meadow vole (*Microtus pennsylvanicus*)^{C}, N) mule deer (*Odocoileus hemionus*)^{T}, O) white-tailed deer (*Odocoileus virginianus*)^{M}, P) bighorn sheep (*Ovis

canadensis)[T], Q) Rufous hummingbird (*Selasphorus rufus*), R) Columbian ground squirrel (*Spermophilus columbianus*), S) Rocky Mountain cottontail (*Sylvilagus nuttali*).

[C] captive animals

[M] given is mean $|\hat{t}_{feed} - t_{feed}|$, calculated from the values reported in Supporting Table 1

[T] negative correlation between daily activity time and temperature

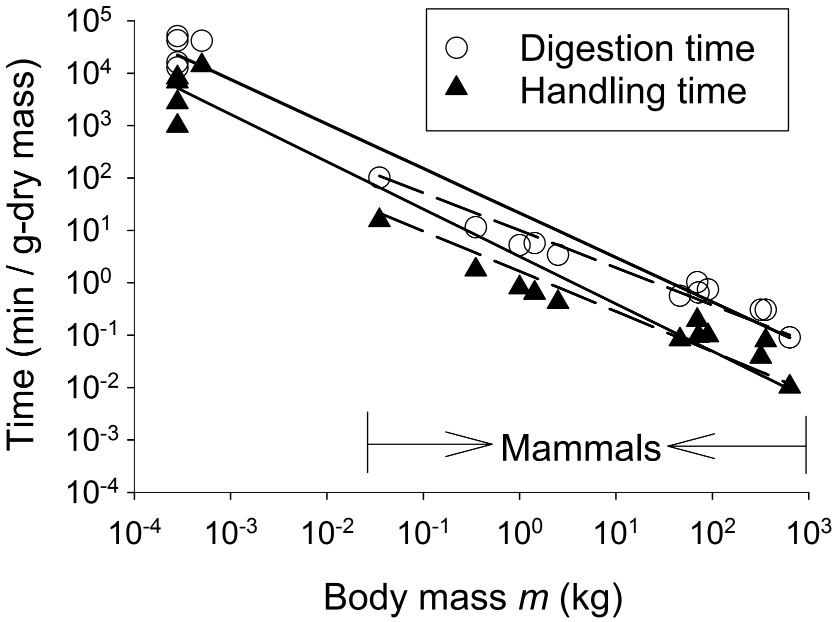

Fig. 2. Allometric relationships in herbivores between either handling time $\hat{b}$ (closed triangles) or digestion time $\hat{c}$ (open circles) and body mass *m*. Each symbol represents one species. Species included are as in Fig. 1, but beavers and Rufous hummingbirds were excluded because of incomparable data (see Supporting Table 1). Solid lines are OLSBISIC regressions (*o*rdinary *l*east *s*quares-*b*isector *i*ndependent *c*ontrasts regressions) for all species: $\tilde{b} = 3.19\ m^{-0.904}$, $r^2 = 0.880$ [OLSIC regression (*o*rdinary *l*east *s*quares *i*ndependent *c*ontrasts regression): $\tilde{b} = 3.62\ m^{-0.848}$, r^2 identical], $\tilde{c} = 21.49\ m^{-0.849}$, $r^2 = 0.926$ (OLSIC regression: $\tilde{c} = 23.13\ m^{-0.817}$); dashed lines are OLSBISIC regressions for mammals only: $\tilde{b} = 1.65\ m^{-0.766}$, $r^2 = 0.855$ (OLSIC regression: $\tilde{b} = 1.49\ m^{-0.727}$), $\tilde{c} = 10.02\ m^{-0.714}$, $r^2 = 0.943$ (OLSIC regression: $\tilde{c} = 9.51\ m^{-0.693}$). For data or information on independent contrasts regressions, see Appendices 1 or 2, respectively. For information on least squares-bisector regressions, see Babu & Feigelson (34).

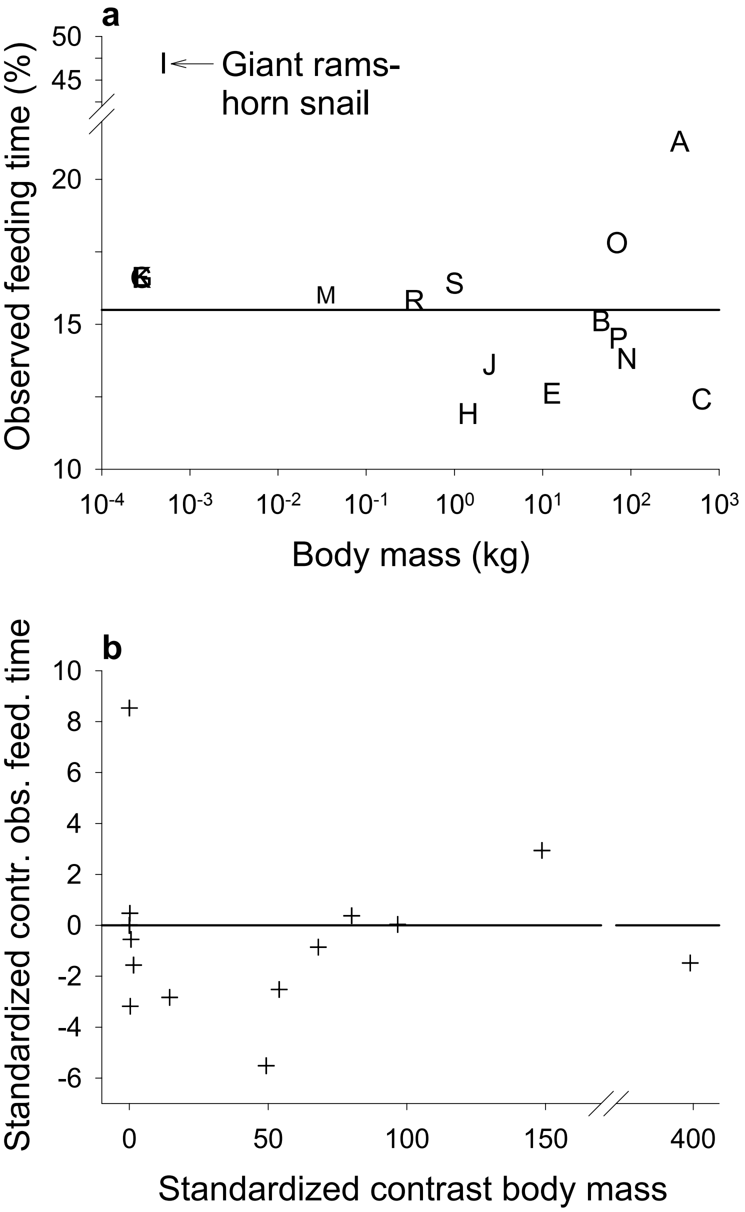

Fig. 3. For the species analyzed here, feeding time is independent of body mass. (*A*) Raw data given in Supporting Table 1; the letters are as in Fig. 1 and the solid line is the phylogenetically weighted mean feeding time excl. giant rams-horn snails (15.5% or 3¾ h/d); (*B*) Independent contrasts; for their calculation, see Supporting Fig. 5.

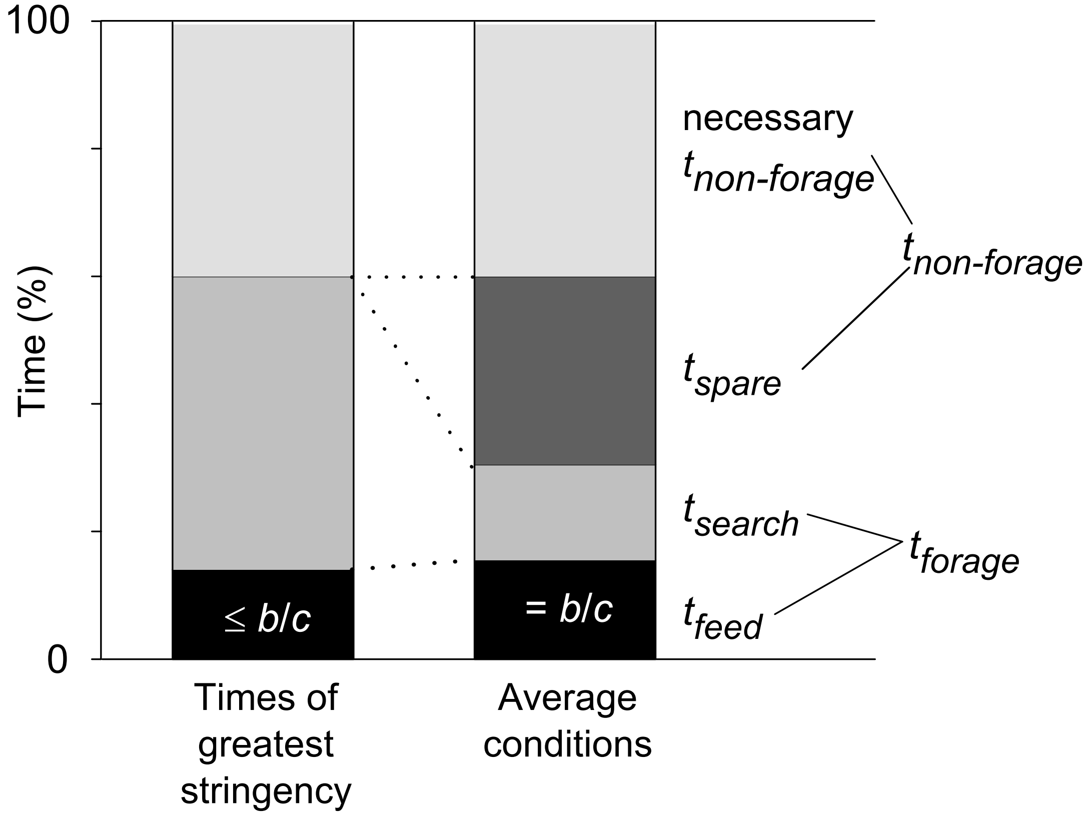

Fig. 4. Edward O. Wilson's principle of stringency (25): "Time-energy budgets evolve so as to fit to the times of greatest stringency", such as periods of low food abundance (e.g. severe winters), large food requirements (e.g. rearing of offspring), or greatest alternative demands (e.g. reproductive activities). For simplicity, energy-conserving mechanisms such as fat reserves are not considered. The given amounts of time spent for searching (t_{search}) and feeding (t_{feed}) under average conditions are, for mammals, realistic (3); other given amounts of time are arbitrary. Regarding birds, Ettinger & King (35) suggested the most stringent period for the female willow flycatchers (*Empidonax traillii*) they investigated had been the incubation phase. They estimated the spare time t_{spare} of these birds as 52.6% or 12½ h/d during the prenesting phase, 20.3% or 5 h/d during the nest-construction phase, and 25% or 6 h/d during the nestling phase.

The principle of stringency offers an evolutionary explanation for 'lazy' animals. It assumes that the fittest animals are those whose traits fit to the times of greatest stringency, especially those traits that determine their time budgets. As long as these traits cannot be adjusted to the environmental conditions as greatly and as rapidly as these conditions vary, animals are pressed for time during, but not outside the times of greatest stringency. Since these periods are rare, animals are seldom pressed for time. Indeed, the traits that determine one part of the time budget, feeding time t_{feed}, appear to be not sufficiently plastic. According to our study, these are handling time b and digestion time c, which is in turn determined by gut capacity g and gut transit time t_g.

Supporting Table 1. Calculation of predicted feeding times

Species	Duration of observation (animal 24 h-days)	Body mass (kg)	Plant class *i*	$bulk_i$ (g-wet mass / g-dry mass)	$diet_i$	b_i (min / g-dry mass)	$\hat{b}$ (min / g-dry mass)	*dig. cap.* (g-wet mass / min)	$\hat{c}$ (min / g-dry mass)	$\hat{t}_{feed}$ (%)	t_{feed} (%)	$\lvert \hat{t}_{feed} - t_{feed} \rvert$ (%)
A) moose (1-3)	15.0 (summer)	358	terrestrial	4.04	0.75	0.09	0.07902	22.85	0.306	25.86	21.3	4.6
(*Alces alces*)			herbs	4.4	0.08	0.054						
			aquatics	20	0.18	0.04						
B) pronghorn antelope (4)	42.9 (summer)	46	monocots	1.64	0.02	0.207	0.08254	4.7	0.564	14.6	15.1	0.5
(*Antilocapra americana*)			dicots	2.67	0.98	0.08						
C) bison (4)	137.1 (summer)	636	monocots	1.64	0.99	0.01	0.01035	18.27	0.0903	11.5	12.4	0.9
(*Bison bison*)			dicots	2.67	0.01	0.045						
D) beaver (5)	5.0 (summer)	15	leaves	4.04	0.89	0.49	0.457	2.4	2.415	18.9	18.7	0.2
(*Castor canadensis*)			aquatics	20	0.11	0.19						
E) elk (4)	51.3 (summer)	318	monocots	1.64	0.64	0.029	0.03872	6.61	0.304	12.7	12.6	0.1
(*Cervus elaphus*)			dicots	2.67	0.36	0.056						
F) undulant-winged grasshopper (4)	7.5 (summer)	0.00028	monocots	1.64	0.96	2860	2768.8	0.000105	16011	17.3	16.6	0.7
(*Circotettix undulatus*)			dicots	2.67	0.04	580						
G) Carolina grasshopper (4)	7.5 (summer)	0.00028	monocots	1.64	0.85	1100	977	0.00014	12818	7.6	16.6	9.0
(*Dissosteira carolina*)			dicots	2.67	0.15	280						
H) snowshoe hare (6)	? (summer)	1.35	leaves	4.04	0.11	0.26	0.4798	0.766	5.766	8.3	9.1	0.8
(*Lepus americanus*)			herbs	4.4	0.88	0.49						
			fungus	10	0.01	2						
snowshoe hare	? (winter)	1.5	deciduous	2	0.79	0.8	0.8	0.374	5.628	14.2	14.6	0.4
			coniferous	2.5	0.21	0.8						
I) giant rams-horn snail; snail 4 (7)	1.0 (captive animals)	0.000501	*Ludwigia*	13430	0.94	15780	16087	0.324	42093	38.2	45.8	7.6
(*Marisa cornuarietis*)			*Vallisneria*	16900	0.06	20890						
giant rams-horn snail; snail 8	1.0 (captive animals)	0.000614	*Ludwigia*	13430	0.87	10100	9854.3	0.329	42192	23.4	45.8	22.4
			Vallisneria	16900	0.13	8210						
giant rams-horn snail; snail 14	1.0 (captive animals)	0.000655	*Ludwigia*	13430	0.98	14430	14371	0.329	41032	35.0	52.8	17.8
			Vallisneria	16900	0.02	11490						

giant rams-horn snail; snail 16	1.0 (captive animals)	0.000655	*Ludwigia*	13430	0.92	16630	16085.2	0.342	40081	40.1	43.1	3.0
			Vallisneria	16900	0.08	9820						
J) yellow-bellied marmot (4)	10.7 (summer)	2.5	monocots	1.64	0.11	1.52	0.4253	0.751	3.404	12.5	13.6	1.1
(*Marmota flaviventris*)			dicots	2.67	0.89	0.29						
K) red-legged locust (4)	7.5 (summer)	0.00028	monocots	1.64	0.22	10000	8198.2	0.000048	50904	16.1	16.6	0.5
(*Melanoplus femur-rubrum*)			dicots	2.67	0.78	7690						
L) migratory grasshopper (4)	7.5 (summer)	0.00028	monocots	1.64	0.29	6250	6881.9	0.0000564	42044	16.4	16.6	0.2
(*Melanoplus sanguinipes*)			dicots	2.67	0.71	7140						
M) meadow vole (4)	2.0 (captive animals)	0.035	monocots	1.64	0.45	21.17	15.56	0.0217	101.68	15.3	16.0	0.7
(*Microtus pennsylvanicus*)			dicots	2.67	0.55	10.97						
N) mule deer (4)	28.1 (summer)	90	monocots	1.64	0.09	0.18	0.0981	3.47	0.743	13.2	13.8	0.6
(*Odocoileus hemionus*)			dicots	2.67	0.91	0.09						
O) white-tailed deer; Montana (4)	23.4 (summer)	80	monocots	1.64	0.14	0.18	0.1112	3.33	0.758	14.7	14.1	0.6
(*Odocoileus virginianus*)			dicots	2.67	0.86	0.1						
white-tailed deer; Ontario (8, 9)	2.1 (early winter)	59	deciduous	1.85	0.94	0.28	0.2716	1.52	1.233	22.0	22.0	0.0
			coniferous	2.25	0.06	0.14						
white-tailed deer; Ontario	2.1 (mid winter)	59	deciduous	1.85	0.68	0.35	0.2892	1.52	1.301	22.2	22.0	0.2
			coniferous	2.25	0.32	0.16						
white-tailed deer; Ontario	2.1 (late winter)	59	deciduous	1.85	0.48	0.42	0.264	1.52	1.354	19.5	20.7	1.2
			coniferous	2.25	0.52	0.12						
P) bighorn sheep (4)	37.8 (summer)	72	monocots	1.64	0.26	0.128	0.09692	3.68	0.653	14.8	14.5	0.3
(*Ovis canadensis*)			dicots	2.67	0.74	0.086						
Q) Rufous hummingbird (*Selasphorus rufus*) (10, 11)	0.6 (summer)	≈ 0.004	-	-	-	-	0.588	-	4.1	14.3	15.6	1.3
R) Columbian ground squirrel (4)	4.8 (summer)	0.35	monocots	1.64	0.19	3.49	1.7728	0.218	11.350	15.6	15.8	0.2
(*Spermophilus columbianus*)			dicots	2.67	0.81	1.37						
S) Rocky Mountain cottontail (4)	4.6 (summer)	1	monocots	1.64	0.35	1.61	0.8105	0.441	5.237	15.5	16.4	0.9
(*Sylvilagus nuttali*)			dicots	2.67	0.65	0.38						

Estimated handling time $\hat{b} = \sum b_i \cdot diet_i$, where b_i is the handling time for plant class i and $diet_i$ is the relative frequency of plant class i in the species' diet (regarding to dry weights) (dimensionless). Estimated digestion time $\hat{c} = (\sum bulk_i \cdot diet_i) / dig.cap.$, where $bulk_i$ is the ratio of wet mass to dry mass in plant class i and *dig. cap.* is the species' digestive capacity. Predicted feeding time $\hat{t}_{feed} = \hat{b} / \hat{c}$ (eq. 3). Beaver: the given value for t_{feed} is actually t_{forage}, but $\hat{b}$ is corrected for this. Giant rams-horn snail: g-wet mass has to be replaced by mm^3. Rufous hummingbird: g-dry mass has to be replaced by foraging bout; t_{feed} and $\hat{t}_{feed}$ are related to daylight hours (6 a.m. to 8 p.m. ⇒ 14 h); the given value for t_{feed} is actually t_{forage} at a high flower density [Fig. 3 in Hixon *et al.* (10)], but $\hat{b}$ is corrected for this.

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Supporting Fig. 5. The phylogenetic tree underlying our analyses (1, 2), *v* are arbitrary branch lengths. We calculated the independent contrasts and the regressions with PDTREE (3-5). In case of regressions, we $\log_{10}$-transformed the data.

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Supporting Text 1. On the relationship between feeding time and environmental temperature. The observed feeding times given in Fig. 1 are mean values averaged over several days varying in temperature. In some of the studies analyzed here, animal activity time at single days was plotted against environmental temperature, giving further insights: Eleven species became less active with increasing temperature (see caption below Fig. 1), and three species were most active at intermediate temperatures [yellow-bellied marmots (*Marmota flaviventris*), white-tailed deer (*Odocoileus virginianus*), and Columbian ground squirrels (*Spermophilus columbianus*)]. The remaining five species were not analyzed (1-5).

Given that feeding time is correlated with activity time, these observations suggest that daily feeding time depended on temperature and may thus be limited by temperature. This interpretation is corroborated by Belovsky's study on snowshoe hares (*Lepus americanus*, 6) in which he showed that hourly and daily activity time in summer can be adequately predicted by a thermal balance model not accounting for digestion time.

However, since arctic species have severe problems with overheating in summer, the result for snowshoe hares should not be generalized. Furthermore, several weaknesses of the time constraint-interpretation of the correlations between daily activity time and environmental temperature exist. First, these correlations do not necessarily imply correlations between feeding time and temperature because the animals possibly just avoided unnecessary activities on unsuitably warm days. Second, a decreased daily feeding time would not necessarily imply a decreased daily food consumption because herbivores are able to compensate for restricted food access by increasing their foraging effort (7-10) and this may also be true for the animals analyzed here. According to Fig. 1, these species actually fed to satiation. Finally, if animals were pressed for time on hot days, this is not necessarily true for the other days (11).

1. Belovsky, G. E., & Jordan, P. A. (1978) *Theor. Pop. Biol.* **14**, 76-104.
2. Belovsky, G. E. (1984) *Am. Midl. Nat.* **111**, 209-222.
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Supporting Text 2. Why the validity of the time constraint-assumption is crucial for the application of existing optimal foraging models, explained in an exemplary fashion for Belovsky's linear programming model (1). This model predicts animal diets by constraints that are given as lines in an *n*-dimensional graph where *n* is the number of food types. In most studies, there have been two different food types, two relevant constraints (digestive capacity and maximum available feeding time) and the animals needed more time to fill their gut with energy-rich than with energy-poor food (2-4). In this situation, the predicted diet of an animal behaving as an energy maximizer, i.e. in a way that maximizes its energy intake rate (5), is equal to the ratio of the food types at the point of intersection between the digestive constraint-line and the maximum feeding time-line. Diets predicted in this or a similar way have been shown to very closely agree with observed ones (1-4, 6, 7), but Hobbs (8) and Huggard (9) found this predictive success to be statistically unlikely.

Similarly to Owen-Smith (10-12), we argue that this 'too good fit' has resulted from circularity in the way how linear programming models have been applied. Most often, researchers have simply inserted for the model parameter '*maximum* possible feeding time' the *observed* feeding time. They have justified this practice by claiming that the focal animals had been unable to spend more time feeding because of temperature constraints. Yet, if this claim and the assumption that the focal animals behaved as energy maximizers is invalid, the predicted diets are invalid as well, for they depend on the maximum feeding time-lines. Crucially, these invalidities cannot be made out as such because of the previously mentioned circularity.

A hypothetical example may help to explain this circularity. Imagine a man having dinner in a fast food restaurant that offers two meals, a hamburger with coke or chips with coke. A researcher wants to predict which and how many of them the man will buy and applies a linear programming model in the usual way. He has found that the digestible energy content of both meals is 1500 kJ and that the man needs 10 min for buying and eating the hamburger-meal and 8 min for the chips-meal. The researcher furthermore knows that the man is satiated after eating either two hamburger-meals (total energy content = 3000 kJ, total staying time =

20 min), one hamburger-meal and two chips-meals (4500 kJ, 26 min), or four chips-meals (6000 kJ, 32 min). He measures the time the man stays in the restaurant and assumes the man was unable to stay longer. He finally assumes the man behaves as an energy maximizer and predicts his dinner. Now, imagine the following four cases. First, both assumptions are valid; the predicted dinner will coincide with the chosen one and the analysis will be successful. Second, the time-constraint assumption is invalid, but the energy maximizer-assumption is valid, i.e. the man will stay for 32 min and will eat four chips-meals. Again, the predicted dinner will coincide with the chosen one. Furthermore, since the man has chosen the dinner with the highest energy content of all, the researcher has an indication for the invalidity of his time constraint-assumption. Third, the time-constraint assumption is valid, but the energy maximizer-assumption is invalid. Here, the predicted dinner will not coincide with the chosen one, and the researcher has an indication for the invalidity of his energy maximizer-assumption. Fourth, both assumptions are invalid. This is the problematic case because whatever the man will eat, the predicted dinner will coincide with the chosen one and the researcher therefore has no indication for the failure of his analysis.

In conclusion, our criticism is relevant for animals that are neither pressed for time nor energy-maximizing. Such a situation may appear quite frequently because animals are, according to our study, often released from time constraints and seem to frequently not behave as energy maximizers (11, 13-15), at least under good environmental conditions (16-24).

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Consumer-food systems: Why type I functional responses are exclusive to filter feeders

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ABSTRACT

The functional response of a consumer is the relationship between its consumption rate and the abundance of its food. A functional response is said to be of type I if consumption rate increases linearly with food abundance up to a threshold and is constant beyond. According to conventional wisdom, such type I responses are typical for filter feeders. However, the validity of this claim has never been tested. We review 815 functional responses from 235 studies, thereby showing that, indeed, type I responses have only been reported from filter feeders. On the other hand, 53% of the responses reported from filter feeders are not of type I.

These findings can be understood by considering the conditions that a consumer must fulfil in order to show a type I response: First, the *handling condition*: The consumer must have a negligibly small handling time (i.e. the time needed for capturing and eating a food item), or it must be able to search for and to capture food while handling other food. Second, the *satiation condition*: Unless its gut is filled completely, the consumer must search for food at a maximum rate with maximum effort. It thus has to spend much time on foraging (i.e. searching for food and handling it).

Our functional response review suggests only filter feeders sometimes meet both of these conditions. This suggestion is reasonable because filter feeders typically fulfil the handling condition and can meet the satiation condition without losing time, for they are, in contrast to non-filter feeders, able to simultaneously perform foraging and non-foraging activities, such as migration or reproduction. In our functional response review, the portion of filter feeders that actually fulfil the satiation condition appears to be 47%.

Key words: filter feeders, foraging time, predators, searching effort, suspension feeders, time budgets, type I functional responses, type II functional responses, type III functional responses, dome-shaped functional responses.

CONTENTS

I. INTRODUCTION

(1) Functional responses

The functional response of a consumer is the relationship between its consumption rate (i.e. mean number of food items or biomass consumed per consumer per unit of time) and the abundance or the biomass of its food, respectively (Solomon, 1949). The consumer can be a carnivore, herbivore, or parasite / parasitoid and its food prey, plants, or hosts, respectively.

Functional responses are important for population biologists, evolutionary biologists, ethologists, and physiologists. They attract population biologists because they link together different trophic levels. Long-term responses averaged over many individuals are useful here. Evolutionary biologists can utilize functional responses since these include the important fitness determinants energy intake and mortality risk. Evolutionary biologists are mainly interested in long-term responses of single individuals. Furthermore, also ethologists work with functional responses, for animal behaviour is often adaptive and thus influenced by energy intake or mortality risk. Ethologists primarily need short-term functional responses of single individuals. Finally and for obvious reasons, physiologists are interested in functional responses, too. They use short- as well as long-term responses of single individuals.

Theoretical ecologists have developed numerous functional response models (reviewed by Jeschke, Kopp & Tollrian, 2002). According to these models, functional responses are mainly affected by three consumer traits: success rate, handling time, and digestion time. The success rate is a parameter that summarizes a consumer's abilities to encounter (influenced by searching velocity and area or volume of perception), detect, and attack food items. Handling time is the time the consumer needs for attacking (including evaluating, pursuing, and catching; corrected for time wasted through unsuccessful attacks) and eating a food item. Finally, a consumer's digestion time is the gut transit time of a food item corrected for gut capacity, i.e. the number of food items that can be digested simultaneously.

Holling (1959) has categorized functional responses into three main types which he has termed type I, II, and III (Fig. 1). The type II is most common. Since it is also the simplest to simulate by a model (Jeschke *et al.*, 2002), it may be seen as the basic type of functional response. A type II response turns to type III if the consumer is able to learn (including training) or if it switches between food types, patches, or foraging tactics, e.g. from ambushing to cruising (reviewed by Jeschke *et al.*, 2002). Finally, a type I functional response has three characteristics: (1) a linearly rising part: below a certain threshold food abundance (i.e. the incipient limiting level), the consumption rate increases linearly with food abundance; (2) a constant part: above this threshold, the consumption rate is constant; and (3) a sharp transition between these two parts. If a functional response has all of these three characteristics, it is of type I; if it has two of them, it is of an intermediate type; and if it has only a linearly rising part or a constant part, we call it a "linear functional response" or a "constant functional response", respectively. If an empirical functional response is linear or constant, it is incomplete, i.e. the range of food abundance that was investigated or that occurs naturally is too small to allow a precise classification of the response as type I, II, or III.

(2) Filter feeders

According to conventional wisdom, type I functional responses are typical for filter feeders. This claim is probably based on Holling's early (1965) review of empirical functional responses. The only filter feeders included in it were crustaceans, and these showed type I functional responses. In the course of time, this observation might have been generalized to the given claim.

We here define filter feeders in a very broad sense. They include (1) suspension feeders (*sensu* Jørgensen, 1966), e.g. protozoans like *Stentor*, sponges, rotifers like *Brachionus*, bivalves like *Mytilus*, crustaceans like *Daphnia*, bryozoans, brachiopods, crinoids like *Antedon*, tunicates, tadpoles, or baleen whales; (2) trap-builders, e.g. carnivorous plants, hydromedusae, or web-building spiders; and (3) sediment filter feeders, e.g. lugworms or sea cucumbers like *Holothuria*. All other consumers are defined as non-filter feeders. Of course, the classification of a consumer as a filter feeder or a non-filter feeders is often subjective. In some taxa, the distinction is based on food particle size, e.g. in protozoans, rotifers, copepods, or euphausiids. Furthermore, several animals switch to a filter feeding foraging strategy at high food abundances only, e.g. the thalassinidean decapod *Upogebia* (Lindahl & Baden, 1997); we have classified them as filter feeders, too.

Filter feeders can only capture food particles that flow through, or over, their filtering system. While some species actively produce these currents (i.e. active filter feeders), others use already existing ones (i.e. passive filter feeders). All trap-builders are passive filter feeders, all sediment filter feeders are active filter feeders, and the large group of suspension feeders contains passive (e.g. crinoids) as well as active filter feeders (e.g. bivalves) (Jørgensen, 1966; LaBarbera, 1984; Riisgård & Larsen, 1995).

Some characteristics of filter feeders: (1) While searching for food, they are able to perform other activities, e.g. food capture, migration, or reproduction (Fig. 2). (2) They are also able to simultaneously capture several food items. (3) The food items they consume are relatively smaller than those of non-filter feeders. (4) Many of them are immobile or unable to move fast. (5) They are by far more abundant in aquatic than in terrestrial habitats. (6) Suspension feeders, which form the largest of the three groups that we have summarized as filter feeders, usually operate at small Reynolds numbers (LaBarbera, 1984).

The claim that type I functional responses are typical for filter feeders has never been tested or justified. By reviewing empirical functional responses from the literature, we reveal that, indeed, type I functional responses have only been reported from filter feeders. Yet, the majority of filter feeders does not show a type I response. To allow for a mechanistic understanding of these findings, we present the conditions that a consumer must fulfil in order to show a type I response.

II. METHODS

Table 1 summarizes 815 empirically derived functional responses from 235 studies; it is the only review since the 1970s (cf. Holling, 1965; Murdoch & Oaten, 1975; and Hassell, Lawton & Beddington, 1976). Since filter feeders are especially important for this study, we have listed all 365 functional responses from filter feeders that we are aware of. On the other hand, the given 450 functional responses from non-filter feeders have been chosen arbitrarily. In classifying functional responses, we usually follow the authors; exceptions are explicitly stated in Appendix A. If an author has not classified his or her functional response, we have done this by eye from the presented graph.

In order to gain an understanding of why consumers differ in their tendency to show type I functional responses, we classify in Table 1 consumers according to the degree of overlap between two of their activities: searching for food and handling it. These two activities are either mutually exclusive, partly overlapping, or completely overlapping.

Supplemental information on each functional response included in Table 1 is provided in Appendix A. It includes the consumer and the food species involved. Furthermore, since functional responses are also affected by the experimental conditions under which they are obtained (e.g. Ives *et al.*, 1999), Appendix A reports whether a response was obtained in the lab, in enclosures, or in the field, whether intra- or interspecifically competing consumers were present or not, whether alternative food was present or not, and whether the response includes satiation effects (long-term studies) or not (short-term studies). The spatial scale is usually small for laboratory studies, intermediate for enclosure experiments, and large for field studies.

III. RESULTS AND DISCUSSION

(1) The experimental conditions under which functional responses are obtained

The functional responses summarized in Table 1 have been measured under different experimental conditions (Table 2). In the next section, we will compare the frequency distributions of functional response types between non-filter feeders and filter feeders. We could obtain misleading results if these frequency distributions were greatly affected by the experimental conditions under which the functional responses have been obtained. This seems not to be the case, however: the frequency distribution of all data (i.e. mainly artificial experimental conditions) roughly matches that of field data (Fig. 3). This finding, furthermore, does not confirm Hassell *et al.*'s (1977) suggestion that type III functional responses are severely underrepresented in artificial laboratory studies.

(2) Are type I functional responses typical for filter feeders?

Yes, type I functional responses have only been reported from filter feeders (Fig. 3; the small fraction of type I responses reported from non-filter feeders corresponds to intermediate responses [e.g. type I/II responses] and to protozoans that consume only one food item per generation). On the other hand, the majority of filter feeders does not show a type I response.

(3) The conditions for a type I functional response

We will discuss these findings by considering the conditions that a consumer must fulfil in order to show a type I functional response. We thereby take into account the three consumer traits that mainly affect functional responses (see Introduction): success rate, handling time, and digestion time. A type I functional response requires that, below the ILL (incipient limiting level of food abundance, see Introduction), consumption rate is, besides food abundance, only determined by the consumer's success rate. In other words, below the ILL, neither the handling time nor the digestion time affects consumption rate. Above the ILL, though, one of these two consumer traits determines consumption rate, and this trait is digestion time (see, for example, Rigler [1961] for branchiopods, Frost [1972] for copepods, and Rothhaupt [1990] for rotifers). Hence, the handling time is either negligibly small or does not at all affect consumption rate (i.e. searching and handling are completely overlapping). The digestion time, on the other hand, must not influence consumption rate (i.e. the consumer must search for food at a maximum rate with maximum effort) below the ILL, but determines consumption rate above it. Above the ILL, the consumer has a completely filled gut and forages at a suppressed rate because it can only ingest as much food as it can digest per unit of time (see also Sjöberg, 1980).

In summary, a consumer must fulfil two conditions in order to show a type I functional response: First, the *handling condition*: The consumer must have a negligibly small handling time, or it must be able to search for and to capture food while handling other food. Second, the *satiation condition*: Unless its gut is filled completely, the consumer must search for food at a maximum rate with maximum effort. It thus has to spend much time on foraging (i.e. searching for food and handling it). For a more formal justification of these conditions, see Appendix B. The two conditions are necessary, not sufficient, i.e. a consumer showing a type I functional response must have met both conditions but a consumer meeting both conditions does not necessarily show a type I response. For example, if a consumer meets both conditions but additionally suffers from a swarming effect, its functional response will not be of pure type I but is expected to be type I dome-shaped. An exception to the conditions are consumers that consume only one food item during their lifetime, e.g. some protozoans. They show type I functional responses without fulfilling the two conditions. This is because, first, handling food does not prevent such a consumer from searching for its next meal since there is no next meal and, second, for the same reason, satiation cannot lower the searching effort of such a consumer.

Sjöberg (1980) has offered a further condition for a type I functional response (*digestion condition*): The consumer must be able to simultaneously digest many (ideally: an infinite number of) food items. This is in accordance with empirical data. For example, *Daphnia magna* typically show type I functional responses (Table 1) and are able to simultaneously digest 10^5 to 10^6 cells, depending on body size (Evers & Kooijman, 1989). As well as the other two conditions, the digestion condition implies that consumers are relatively large compared to their food. Consumers fulfilling the handling and the satiation condition should therefore automatically also meet the digestion condition. As we have mentioned in the Introduction, filter feeders are characteristically large compared to their food.

Holling (1966) has claimed that his invertebrate model produces type I functional responses when the “reactive field” of the consumer is constant (this corresponds to our satiation condition). However, simulations by ourselves (not shown) indicate that two additional conditions must be fulfilled for a type I functional response in the invertebrate model: handling time must be negligibly small (our handling condition), and consumers must be relatively large compared to their food. Thus, Holling’s invertebrate model is not in contradiction to our conditions for a type I functional response.

(4) Filter feeders vs. non-filter feeders

Combining the handling and the satiation condition with our finding that type I functional responses are restricted to filter feeders, it follows that all consumers evidently fulfilling both conditions are filter feeders. Indeed, the handling condition is - due to their characteristics given in the Introduction (1, 2, and 3) and according to Fig. 2 and Table 1 - generally fulfilled by filter feeders, but not by non-filter feeders. The satiation condition is hard to investigate directly. Appendix B, however, offers an indirect method: If a consumer fulfils the satiation condition, it should show a type I or an intermediate type I/II functional response, respectively, depending on whether or not it fulfils the handling condition. This statement refers to functional responses that include satiation effects. Those responses that include no satiation effects are by definition inappropriate for testing the validity of the satiation condition. Admittedly, the suggested method is hampered by the empirical difficulty to discriminate between type I/II and II responses. Moreover, it neglects consumer learning, switching, confusion, and other factors that can qualitatively alter the shape of a functional response. We apply the method with these drawbacks in mind. For non-filter feeders, type I/II functional responses that include satiation effects have almost never been reported (Appendix A). Hence, almost all non-filter feeders seem not to fulfil the satiation condition. On the contrary, about one half of the filter feeders appears to meet this condition. In conclusion, non-filter feeders usually show type II functional responses (Table 1, Fig. 3) since they neither fulfil the handling condition nor the satiation condition and because learning or switching effects leading to type III responses are infrequent. On the other hand, filter feeders typically meet the handling condition. They show type I functional responses when they additionally fulfil the satiation condition; they show type II responses when they decrease their filtration rate (i.e. searching effort) with increasing gut fullness in a strictly monotonic way; and they show type III responses when they reduce their filtration rate in times of low food abundances.

To fulfil the satiation condition, a consumer must spend much time on foraging. Figure 4 corroborates this statement. It illustrates that consumers showing type I responses (these fulfil the satiation condition) spend more time foraging (i.e. searching and handling) than consumers that show type II responses (these do not fulfil the satiation condition). Non-filter feeders are not able to simultaneously perform foraging and non-foraging activities, such as avoidance of top predators, migration, reproduction, or territorial behaviour. They likely would not have enough time for essential non-foraging activities, were they fulfilling the satiation condition. Filter feeders, on the other hand, can meet the satiation condition without becoming pressed for time. Why many of them do nevertheless not fulfil this condition may be clarified in future studies, e.g. by analyzing copepods. They show almost all imaginable types of functional response (Table 1) and are present in both marine and freshwater environments. According to Fig. 5 (see also Paffenhöfer & Stearns, 1988), copepod functional responses are qualitatively influenced by habitat type. Perhaps one or more factors coupled with habitat type ultimately determine the fulfilment of the satiation condition and consequently the type of functional response, e.g. the level or the variability of food abundance.

(5) The adaptive significance of type I functional responses

For a given success rate and digestion time, and at each food abundance, a consumer has a maximum consumption rate if it shows a type I functional response (replace digestion time by handling time if handling time is larger than digestion time). Compared to a type II response, the advantage is greatest at intermediate food abundances (Fig. 6). Combining this observation with our finding that filter feeders often show type I functional responses suggests that a filter feeding foraging strategy helps to increase consumption rate, especially at intermediate food abundances. Thus, besides an aquatic habitat and small food particles as an energy source (see Introduction), a third environmental condition favouring filter feeding may be an intermediate food abundance (more exactly and especially for passive filter feeders, not the food abundance should be intermediate, but the encounter rate with food, which is proportional to the product of food abundance and ambient velocity [see models reviewed by Jeschke *et al.* [2002]]). What the term "intermediate" means in practice depends on the characteristics of the focal consumer. For example, *Daphnia* spp. are more typical filter feeders than copepods: (1) Contrary to copepods, *Daphnia* have a foraging strategy, in which searching and handling are completely overlapping (see Appendix A). (2) They more often show type I functional responses (Table 1). (3) Their filtering system is less selective. Daphnids can therefore not avoid filamentous or toxic food particles. This disadvantage of an unconditional filter feeding foraging strategy counteracts its benefit of a higher consumption rate (according to Muck & Lampert [1984], mass-specific consumption rate of *Daphnia* exceeds that of *Eudiaptomus*). Moreover, the *Daphnia* filtering system has higher energetic demands than that of copepods (Schmink, 1996). It is hence expected to be adaptive at intermediate food abundances, the copepod one at low and high food abundances. This agrees with observations summarized by Muck & Lampert (1984; see also Mookerji *et al.*, 1998), that in oligotrophic and heavily eutrophic lakes and ponds, copepods usually dominate over daphnids, whereas in mesotrophic lakes and ponds, daphnids dominate over copepods. Similarly, copepods generally dominate in marine habitats which typically have a low food abundance. In freshwater copepods, an intermediate foraging strategy between *Daphnia* and marine copepods seems to have evolved: freshwater copepods collect food as marine copepods but fulfil the satiation condition as *Daphnia*. Finally, this pattern can be further affected by the higher susceptibility of *Daphnia* to predators (Mookerji *et al.*, 1998). This is because they are less agile than copepods. In summary, a filter feeding foraging strategy increases a consumer's energy input, especially at intermediate food abundances. On the other hand, it decreases the consumer's ability to select food, it increases its energy output by an amount that is roughly independent of food abundance, and it often increases the consumer's vulnerability to predators because it is frequently correlated with immobility or the inability to move fast (see Introduction). Our finding that type I functional responses are typical for filter feeders is thus not only important for population biologists but also for evolutionary ecologists.

IV. CONCLUSIONS

(1) Type I functional responses have only been reported from filter feeders. This is because only filter feeders sometimes meet both of the following conditions: *Handling condition*: The consumer must have a negligibly small handling time, or it must be able to search for and to capture food while handling other food. Filter feeders typically meet this conditions (Introduction, Table 1, Fig. 2). *Satiation condition*: Unless its gut is filled completely, the consumer must search for food at a maximum rate with maximum effort. It thus has to spend much time on foraging. Filter feeders can meet this condition without losing time because they are able to simultaneously perform foraging and non-foraging activities.

(2) On the other hand, more than every second functional response reported from filter feeders is not of type I. We explain this observation by a frequent non-fulfilment of the satiation condition which should be adaptive for filter feeders that, for example, consume food of a highly variable abundance.

(3) Non-filter feeders usually show type II functional responses since they normally neither fulfil the handling nor the satiation condition and because learning or switching effects leading to type III responses are infrequent. Non-filter feeders do not meet the handling condition, for their handling times are seldom negligibly small and, more importantly, they are characteristically not able to search for or to capture a food item while handling another

one. They are furthermore unable to simultaneously perform foraging and non-foraging activities and likely would not have enough time for essential non-foraging activities, were they fulfilling the satiation condition.

(4) An intermediate food abundance may favour a filter feeding foraging strategy because, all other things being equal, a consumer showing a type I functional response gains more energy per unit of time than one showing a type II response, and this difference is largest at an intermediate food abundance.

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Table 1. *A review of empirical functional responses. References and information on the species investigated as well on the experimental conditions (see also Table 2) are given in Appendix A.*

** The symbol "+" means that searching and handling are mutually exclusive (while handling a food item, these consumers are not able to search for or to capture another one); "±" means that searching and handling are partly overlapping (while handling one or a few food items, these consumers are able to search for and to capture another one [Juliano, 1989]; exceptions are non-filter feeding planktivorous fishes which are, while handling a food item, partly able to search for but not to capture another one); and "-" means that searching and handling are completely overlapping (while handling one or many food items, these consumers are able to search for and to capture another one).*

*** The symbols "+" and "-" indicate whether or not a functional response of the corresponding type has been observed: "+" means that at least one has been observed, "-" means that none has been observed; only 'pure' types (I, II, or III) are relevant here, intermediate types not. The mostly observed type of functional response in each type of consumer is marked by a "‡" and highlighted by a grey background. The numbers in brackets indicate the corresponding numbers of observed functional responses; pure as well as intermediate types of functional response are relevant here. Dome-shaped functional responses have thereby been counted jointly, e.g. type II dome-shaped functional responses have been counted as type II functional responses. Intermediate type I/II functional responses have been counted as half type I and half type II. Other functional responses of an intermediate type have been considered analogously. Type I threshold functional responses have been classified as intermediate type I/III. Type I/II threshold functional responses have been classified as intermediate type I/II/III; they have been counted as one third type I, one third type II, and one third type III. Linear functional responses have been ignored because the underlying type of functional response is unknown; exceptions are linear threshold functional responses which have been counted as half unknown and half type III*

Type of consumer	Are searching and handling mutually exclusive?*	Observed types of functional response**		
		I	II	III
(1) Non-filter feeders				
(a) Carnivores				
(i) Non-queueing carnivores				
(α) Invertebrates	+	- (0)	**‡ (189)**	+ (28)
(β) Vertebrates	+	- (0)	**‡ (40)**	+ (11)
(ii) Planktivorous fishes	±	- (1)	**‡ (16)**	+ (2)
(iii) Queueing carnivores (e.g. *Notonecta* spp.)	±	- (0)	**‡ (15)**	+ (4)
(b) Herbivores				
(i) Invertebrates				
(α) Protozoans that consume only one food item per generation	Not relevant	**‡ (2)**	- (0)	- (0)
(β) Aquatic microphagous molluscs	±	- (1)	+ (2)	- (0)
(γ) Others	+	- (0)	**‡ (9)**	+ (5)
(ii) Vertebrates	±	- (9)	**‡ (69)**	+ (2)
(c) Parasites and parasitoids	+	- (0)	**‡ (23)**	+ (5)
(2) Filter feeders				
(a) Protozoans				
(i) Non-giants	±	- (3)	**‡ (22)**	+ (5)
(ii) Giants (e.g. *Stentor*)	-	+ (1)	- (0)	+ (3)

(b) Carnivorous plants	±	+ (3)	+ (1)	- (0)
(c) Cnidarians and ctenophores	-	- (5)	- (5)	+ (1)
(d) Rotifers	-	+ (16)	+ (17)	+ (6)
(e) Molluscs	-	**‡ (23)**	+ (14)	+ (3)
(f) Polychaets: arenicolids (lugworms)	-	- (0)	- (0)	**‡ (4)**
(g) Crustaceans				
(i) Branchiopods (e.g. *Artemia*, *Daphnia*)	-	**‡ (57)**	+ (19)	+ (2)
(ii) Copepods (e.g. *Acartia*, *Calanus*)	±	+ (30)	+ (32)	+ (28)
(iii) Euphausiids (e.g. *Euphausia superba*)	±	+ (2)	- (0)	**‡ (6)**
(iv) Thalassinidean decapods (e.g. *Upogebia*)	±	- (0)	- (0)	+ (1)
(h) Insect larvae: black flies	±	**‡ (4)**	- (1)	- (0)
(i) Bryozoans	-	**‡ (4)**	- (1)	- (0)
(j) Echinoderms: crinoids	-	- (0)	+ (1)	- (0)
(k) Tunicates				
(i) Ascidians	-	**‡ (6)**	+ (2)	- (0)
(ii) Thaliaceans	-	+ (2)	- (1)	- (0)
(l) Anuran larvae	-	- (0)	- (0)	**‡ (6)**

Table 2. *The experimental conditions under which the functional responses summarized in Table 1 have been obtained*

Experimental condition	Non-filter feeders				Filter feeders				All consumers		
Laboratory / enclosure / field	70%	22%	9		100%	0	0		83%	12	5
Competing consumers present / absent	28%	72%			87%	13%			55%	45%	
Alternative food present / absent	19%	81%			1	99%			11	89%	
Satiation effects included / excluded	62%	38%			84%	16%			72%	28%	

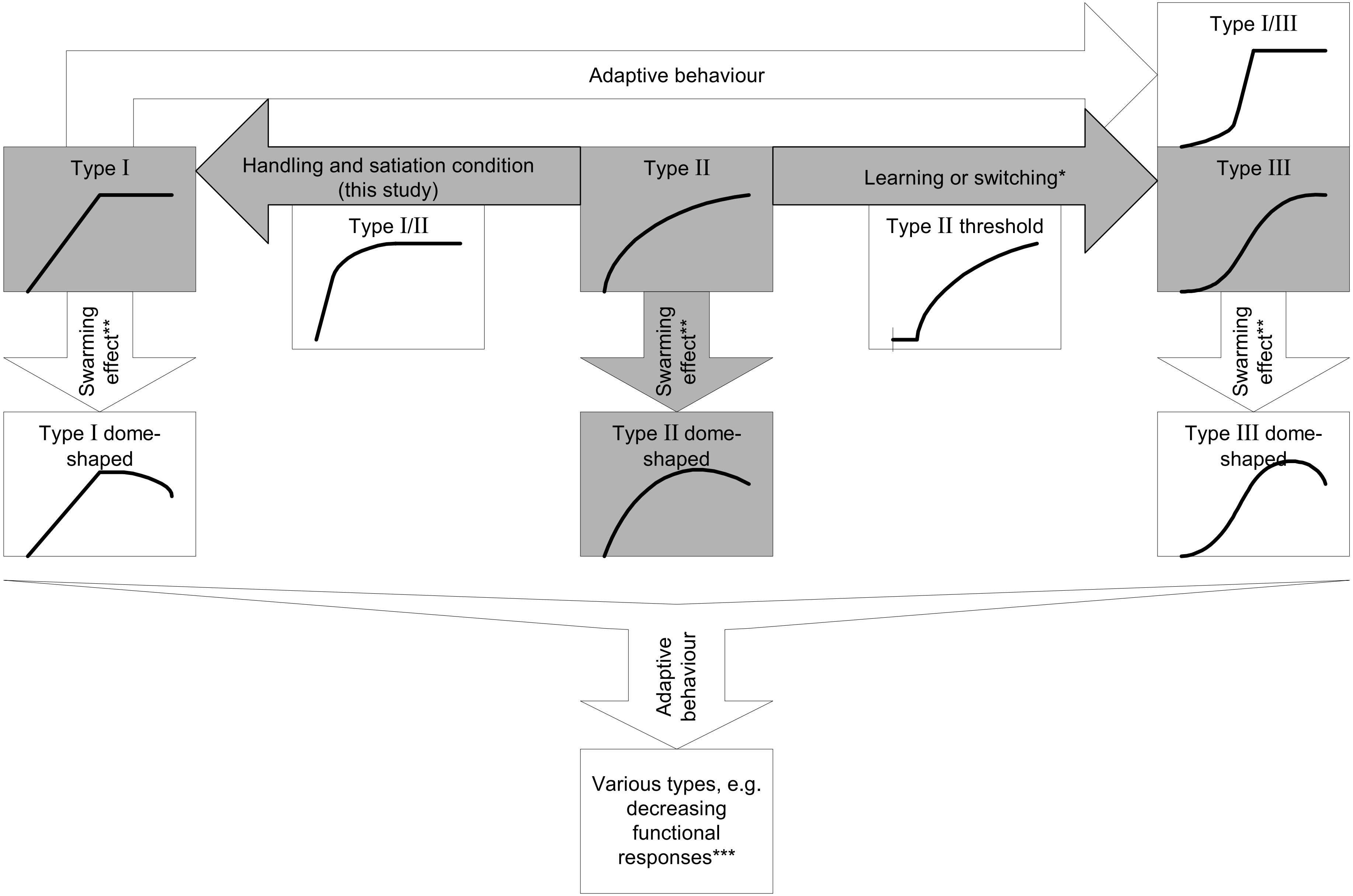

Type I/III
Adaptive behaviour
Type I
Handling and satiation condition (this study)
Type II
Learning or switching*
Type III
Type I/II
Type II threshold
Swarming effect**
Swarming effect**
Swarming effect**
Type I dome-shaped
Type II dome-shaped
Type III dome-shaped
Adaptive behaviour
Various types, e.g. decreasing functional responses***

Fig. 1. Types of functional response and the relationships between them. Types I, II, III, and II dome-shaped are highlighted because they are most common.

* Switching is often the result of adaptive behaviour.

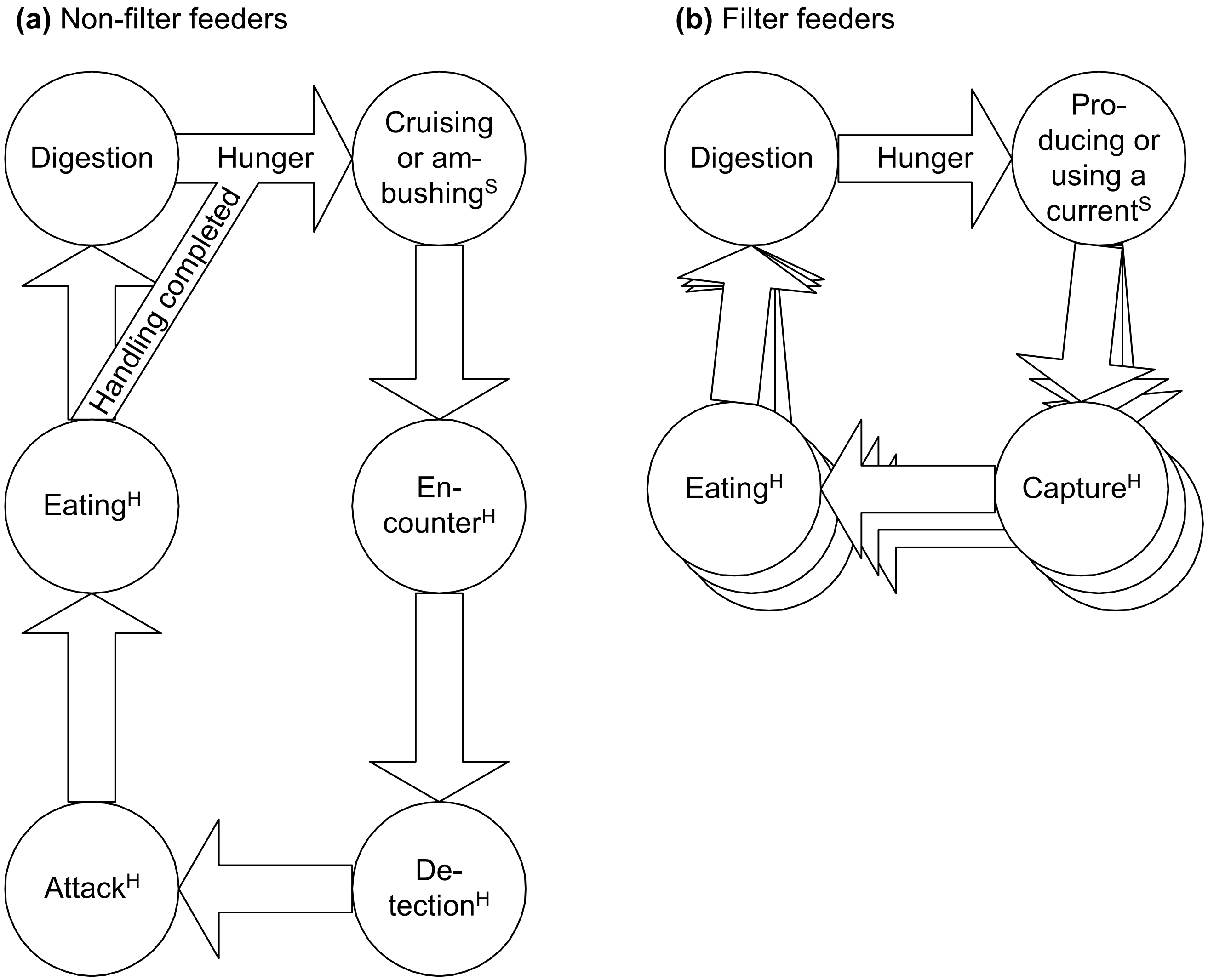
** That is consumer confusion, early-warning by individual prey in a flock, simultaneous active defence by a number of prey individuals, accumulation of toxic substances produced by food items, and clogging of consumer filters.

*** Reviewed by Jeschke *et al.* (2002)

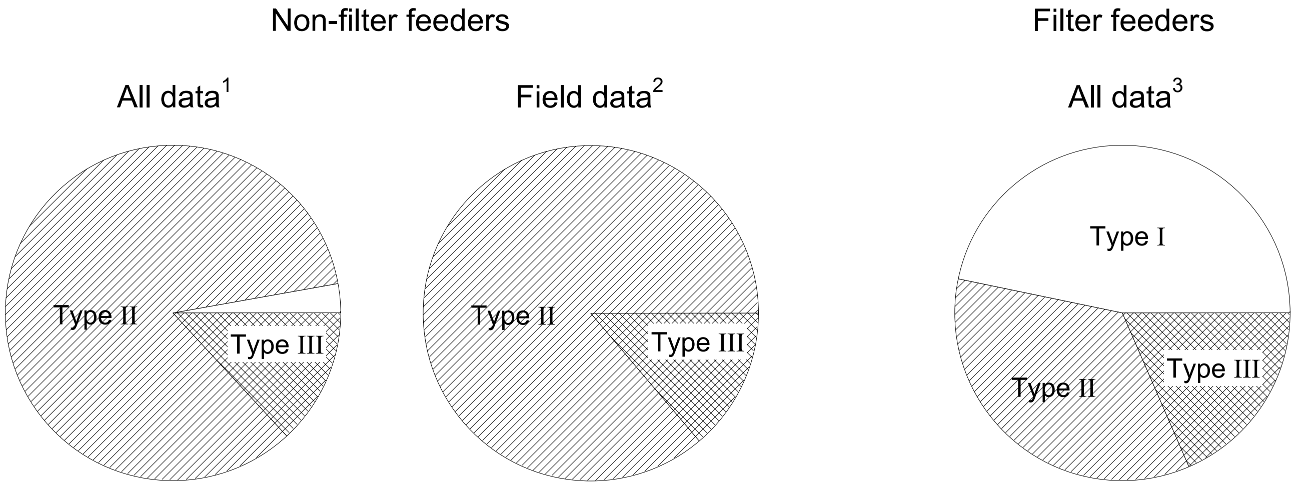
Fig. 2. A comparison of the foraging cycles of non-filter feeders and filter feeders (cf. Jeschke *et al.*, 2002). A non-filter feeder initiates a foraging cycle by actively seeking food (cruising consumers) or by sitting and waiting (ambushing consumers), whereas a filter feeder by producing a current through its filtering system (active filter feeders) or by placing its filtering system in an already existing current (passive filter feeders). Furthermore, filter feeders but not non-filter feeders are able to simultaneously handle several food particles (for more details, see Table 1). Both types of consumers initiate a new foraging cycle when they are sufficiently hungry, but non-filter feeders must have finished their last meal before.

[S] For the corresponding type of consumer, this activity is meant by the general term “searching for food”.

[H] For the corresponding type of consumer, this activity is a part of the handling process.


(a) Non-filter feeders
Digestion
Hunger
Cruising or ambushing^S
Handling completed
Eating^H
Encounter^H
Attack^H
Detection^H
(b) Filter feeders
Digestion
Hunger
Producing or using a current^S
Eating^H
Capture^H

(a) Dome-shaped functional responses counted jointly*


Non-filter feeders

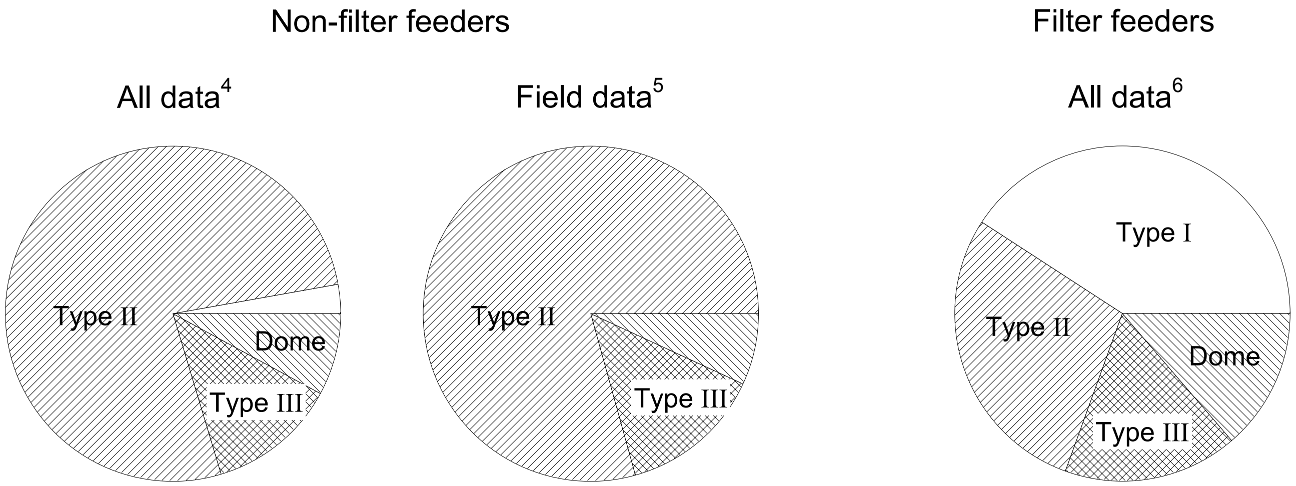
Filter feeders

All data[1]

Field data[2]

All data[3]

(b) Dome-shaped functional responses counted separately


Non-filter feeders

Filter feeders

All data[4]

Field data[5]

All data[6]

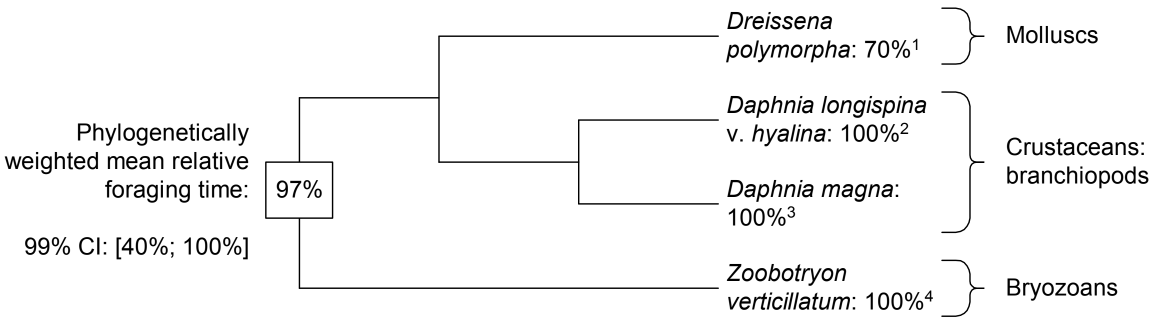
Fig. 3. Summary of Table 1. It can be seen that type I functional responses are exclusive to filter feeders. Furthermore, whilst type II responses are most common for non-filter feeders, type I responses are most common for filter feeders.

* For example, type II dome-shaped functional responses have been counted as type II functional responses.

Data corresponding to the pie charts: [1]$N_{\text{type I}}$ = 12 (2.8%), $N_{\text{type II}}$ = 361.5 (84.1%), $N_{\text{type III}}$ = 56.5 (13.1%), N_{linear} = 20.0, N_{total} = 450.0; [2]$N_{\text{type I}}$ = 0.0, $N_{\text{type II}}$ = 25.0 (86.2%), $N_{\text{type III}}$ = 4.0 (13.8%), N_{linear} = 7.0, N_{total} = 36.0; [3]$N_{\text{type I}}$ = 153.8 (46.8%), $N_{\text{type II}}$ = 114.3 (34.8%), $N_{\text{type III}}$ = 60.8 (18.5%), N_{linear} = 36.0, N_{total} = 365.0; [4]$N_{\text{type I}}$ = 12 (2.8%), $N_{\text{type II}}$ = 330.5 (76.9%), $N_{\text{type III}}$ = 53.5 (12.4%), $N_{\text{dome-shaped}}$ = 34.0 (7.9%), N_{linear} = 20.0, N_{total} = 450.0; [5]$N_{\text{type I}}$ = 0.0, $N_{\text{type II}}$ = 23.0 (79.3%), $N_{\text{type III}}$ = 4.0 (13.8%), $N_{\text{dome-shaped}}$ = 2.0 (6.9%), N_{linear} = 7.0, N_{total} = 36.0; [6]$N_{\text{type I}}$ = 134.3 (40.8%), $N_{\text{type II}}$ = 94.3 (28.7%), $N_{\text{type III}}$ = 55.3 (16.8%), $N_{\text{dome-shaped}}$ = 45.0 (13.7%), N_{linear} = 36.0, N_{total} = 365.0

Intermediate types of functional response have been included and have been counted as in Table 1.

(a) Consumers that show type I functional responses



(b) Consumers that show type II functional responses

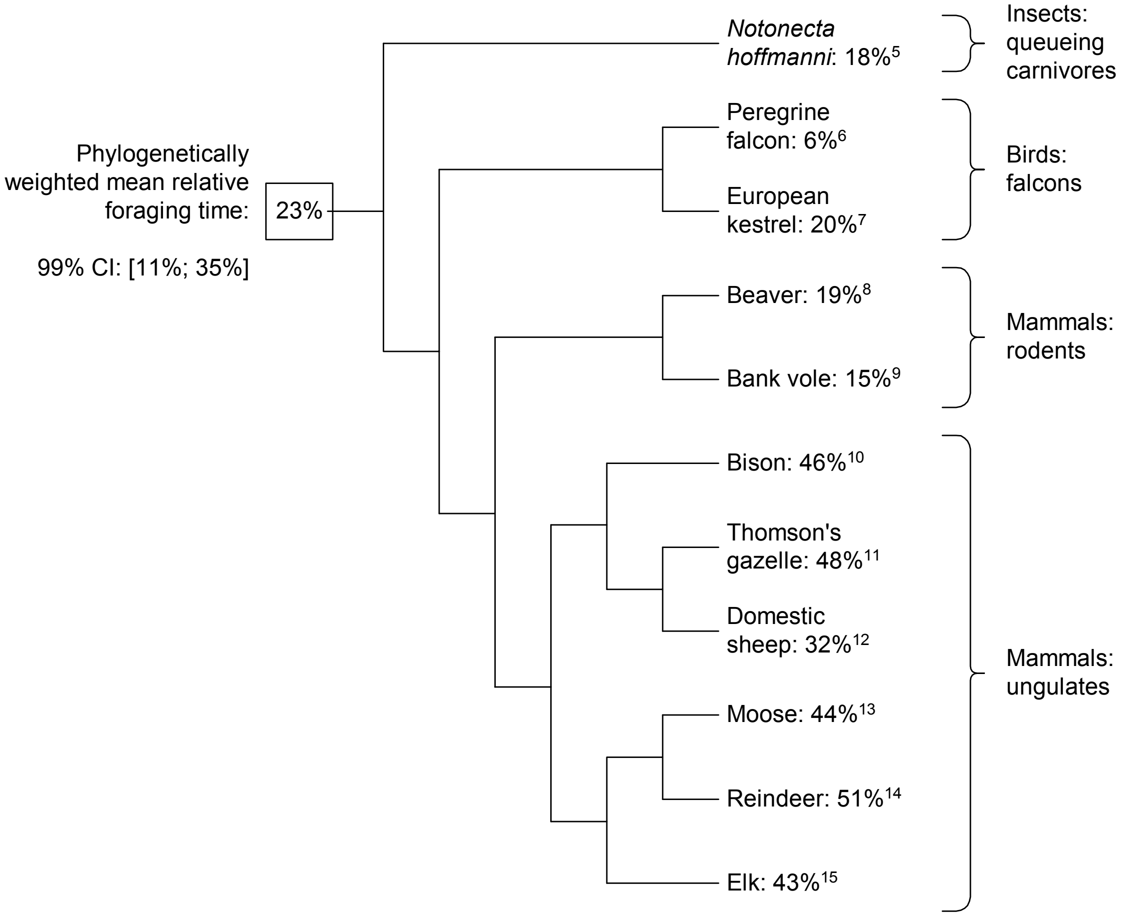


Fig. 4. A comparison of foraging times between consumers that show type I functional responses and consumers that show type II responses (foraging time is the time spent searching for food and handling it; foraging times are related to a 24 h-day). It can be seen that type I functional response consumers spend more time foraging than type II ones.

The phylogenies are based on Pérez-Barbería & Gordon (1999*a*, *b*) and Maddison (2001). We have calculated the means and the confidence intervals with independent contrasts analyses (Felsenstein, 1985; Garland *et al.*, 1993; Garland, Midford & Ives, 1999) by using Pagel's (1992) arbitrary branch lengths and arcsine transformed data (Sokal & Rohlf, 1995).

Notes on foraging times and corresponding references: [1]Shell opening time (Walz, 1978); [2]Nauwerck (1959); [3]Porter, Gerritsen & Orcutt (1982); [4]Bullivant (1968); [5]moving time (Sih, 1992); [6]*Falco peregrinus*, reviewed by McGowan (1997); [7]*Falco tinnunculus*, females ≈17.9% (4.6% flight-hunting + 2.0% flying incl. soaring + ≈11.3% perch-hunting [= halve of total perching time]), males ≈21.2% (6.7% flight-hunting + 3.8% flying incl. soaring + ≈10.7% perch-hunting [= halve of total perching time]), Masman, Daan & Dijkstra (1988); [8]*Castor canadensis*, Belovsky (1984); [9]*Clethrionomys glareolus*, reviewed by Ashby (1972); [10]*Bison bison*, sum of searching time (i.e. moving time, 34%) and cropping time (12%) Belovsky & Slade (1986); [11]*Gazella thomsonii*, sum of searching time (i.e. moving time, 12%) and cropping time (36%), Walther (1973); [12]*Ovis aries*, average of values reported from Allden & Whittaker (1970; ≈31%) and reviewed by Trudell & White (1981; ≈30%, ≈35%); [13]*Alces alces*, sum of searching time (i.e. moving time, 23%) and cropping time (21%), Belovsky & Jordan (1978); [14]*Rangifer tarandus tarandus*, average of values reported from Trudell & White (1981; 53% [sum of searching time (i.e. moving time, 27%) and cropping time (26%)]) and reviewed by Trudell & White (1981; 49%); [15]*Cervus elaphus*, sum of searching time (i.e. moving time, 30%) and cropping time (13%), Belovsky & Slade (1986).

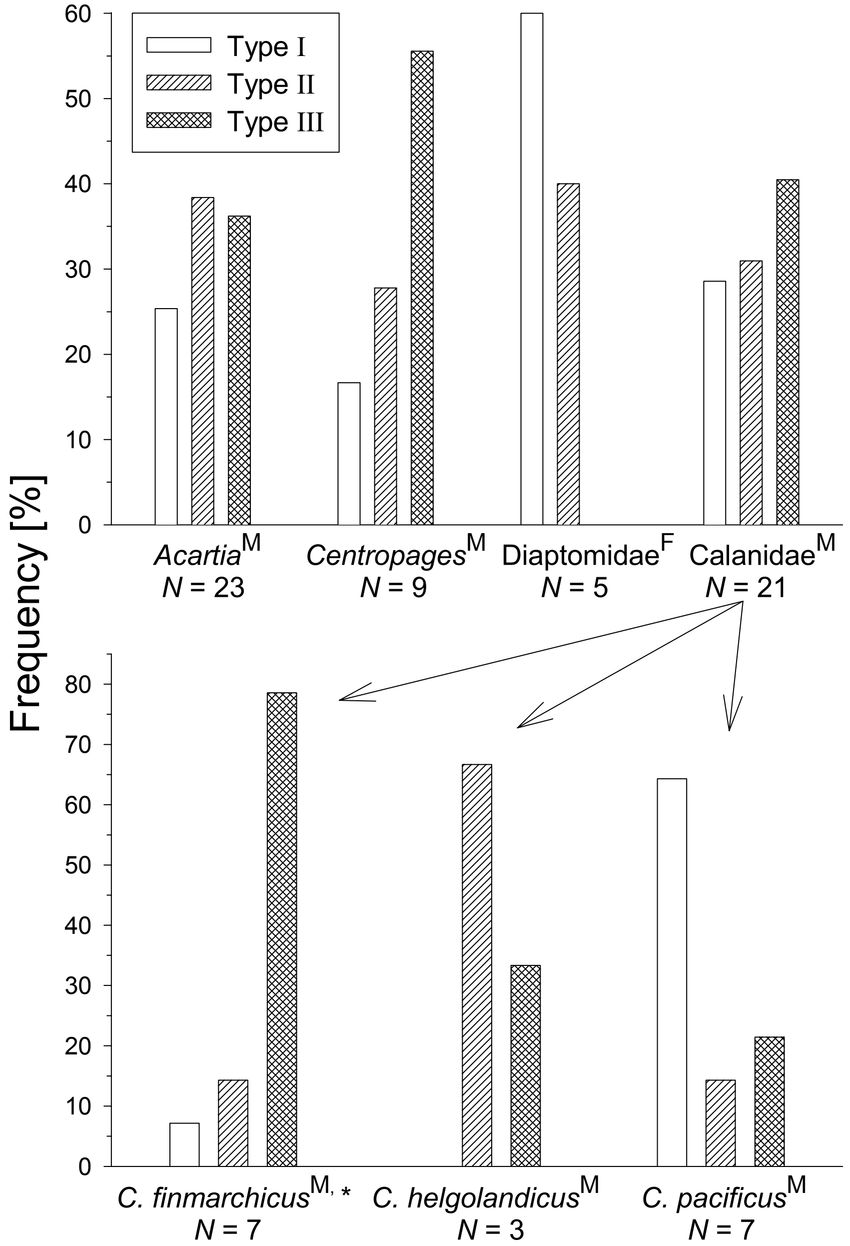


Fig. 5. Functional response types of calanoid copepods depending on phylogeny and habitat type (^{F}freshwater, ^{M}marine). It can be seen that most marine copepods usually show type II or III functional responses (*Acartia*: type II or III; *C. finmarchicus*: type III [$*P < 0.05$, χ^2-Test

against uniform distribution, 2 df]; *C. helgolandicus*: type II or III; *Centropages*: type III), whereas *C. pacificus* and freshwater copepods usually show type I functional responses.

Data are from Table 1; *Acartia* species: *A. clausi*, *A. erythraea*, *A. hudsonica*, and *A. tonsa*; *Centropages* species: *C. chierchiae*, *C. hamatus*, *C. typicus*, and *C. yamadai*; Diaptomidae: *Diaptomus oregonensis*, *Diaptomus sicilis*, and *Eudiaptomus gracilis*; Calanidae: *Calanus finmarchicus*, *Calanus helgolandicus*, *Calanus pacificus*, *Calanus plumchrus*, *Calanus sinicus*, and *Calanoides carinatus*. Dome-shaped functional responses have been excluded. Intermediate types of functional response have been included and have been counted as in Table 1.

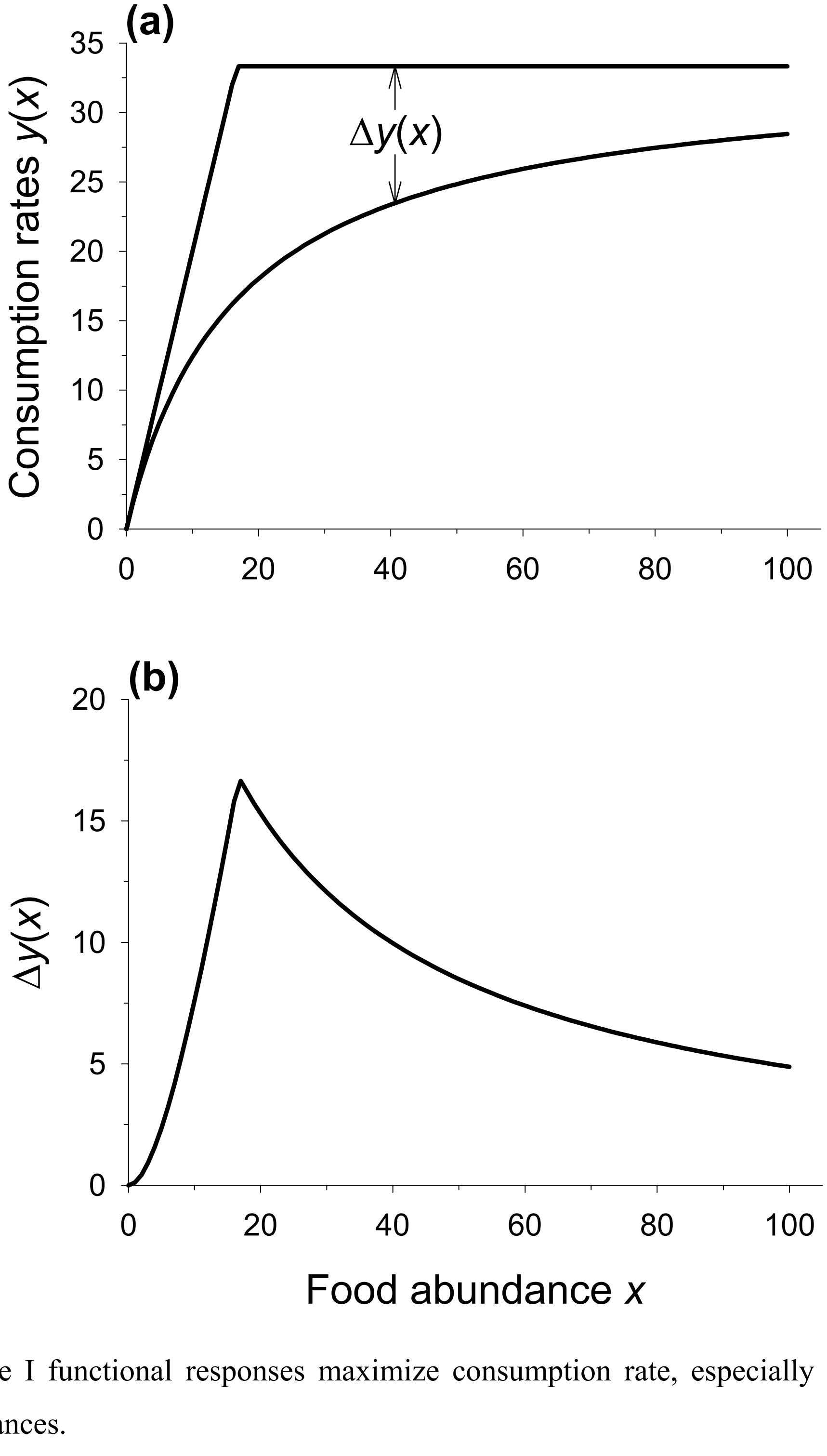


Fig. 6. Type I functional responses maximize consumption rate, especially at intermediate food abundances.

VII. APPENDIX A: SUPPLEMENTARY INFORMATION ON TABLE 1

References and information of the species investigated and on the experimental conditions ("lab": experiments performed in the laboratory, "enclosure": enclosure experiments, "field": field data; "c +": intra- or interspecifically competing consumers were present [valid for field data], "c -": competing consumers were absent, i.e. only one individual of the focal consumer species was present; "f +": alternative food was present [valid for field data], "f -": alternative food was absent; "s +": with more or less natural satiation effects [long-term experiments or with consumers that had been adapted to the food abundance], "s -": with unnaturally low satiation effects [short-term experiments with consumers that had not been adapted to the food abundance or when consumption rate is given per foraging time instead of total time]).

(1) Non-filter feeders

(a) Carnivores

(i) Non-queueing carnivores (searching and handling are mutually exclusive according to Holling [1966])

(α) Invertebrates

Type II (*N* = 168 functional responses): Clark (1963; field, s +: *Syrphus* sp. – *Cardiaspina albitextura*), Morris (1963; lab, c -, f -, s +: *Podisus maculiventris* – *Hyphantria cunea* [defenceless or free to defend]), Holling (1966; lab, c -, f -, s - or + [1, 2, 4, 6, 8, 10, 12, 14, or 16 h]: *Hierodula crassa* – *Musca domestica*), Lasker (1966; lab, c -, f -, s +: *Euphausia pacifica* – *Artemia salina*), Murdoch (1969; lab, c +, f +, s +: *Acanthina spirata* – *Balanus glandula*, *A. spirata* – *Mytilus edulis*, *T. emarginata* – *M. edulis*; lab, c +, f -, s +: *A. spirata* – *M. edulis*, *Thais emarginata* – *M. edulis*), Tostowaryk (1972; lab, c -, f -, s -: *Podisus modestus* [3rd instars] – *Neodiprion pratti banksianae* [inactive: 2nd instars], *P. modestus* [4th instars] – *N. p. banksianae* [inactive: 3rd instars], *P. modestus* [adults] – *N. p. banksianae* [active: 5th instars; inactive: 5th instars], *P. modestus* [2nd instars] – *Neodiprion swainei* [active: 1st instars], *P. modestus* [3rd instars] – *N. swainei* [inactive: 2nd instars], *P. modestus* [4th instars] – *N. swainei* [active: 2nd instars; inactive: 2nd instars], *P. modestus* [5th instars] – *N. swainei* [active: 3rd instars], *P. modestus* [adults] – *N. swainei* [active: 3rd, 4th , or 5th instars; inactive: 4th instars]), Murdoch & Marks (1973; lab, c -, f +, s +: *Coccinella septempunctata* – *Aphis fabae*), Fedorenko (1975; enclosure, c -, f -, s +: *Chaoborus americanus* – *Diaptomus kenai*, *C. americanus* – *Diaptomus tyrelli* [7, 13, or 19° C], *Chaoborus trivittatus* – *Diaphanosoma* sp., *C. trivittatus* [3rd instars] - *D. kenai*, *C. trivittatus* [young 4th instars] - *D. kenai*, *C. trivittatus* [old 4th instars] - *D. kenai* [13 or 14° C], *C. trivittatus* [2nd instars] - *D. tyrelli* [11, 17, or 22° C], *C. trivittatus* [3rd instars] - *D. tyrelli*, *C. trivittatus* [4th instars] - *D. tyrelli* [7 or 13° C]), Thompson (1975; lab, c -, f -, s +: *Ischnura elegans* [8th instars] – *Daphnia magna* [1.10, 1.44, or 1.70 mm length], *I. elegans* [9th instars] – *D. magna* [1.10, 1.44, 1.70, or 2.30 mm length], *I. elegans* [10th instars] – *D. magna* [1.10, 1.44, 1.70, 2.30, or 2.93 mm length], *I. elegans* [11th instars] – *D. magna* [1.10, 1.44, 1.70, 2.30, or 2.93 mm length], *I. elegans* [12th instars] – *D. magna* [1.10, 1.44, 1.70, 2.30, or 2.93 mm length]), Hassell *et al.* (1977; lab, c -, f -, s -: *C. septempunctata* - *Brevicoryne brassicae* [5th instars]), Thompson (1978; lab, c -, f -, s +: *I. elegans* – *D. magna* [5, 8, 12, 16, 20, or 27.5° C]), Akre & Johnson (1979; lab, c -, f + [equal densities of alternative prey] or -, s +: *Anomalagrion hastatum* – *D. magna*, *A. hastatum* – *Simocephalus vetulus*), Smyly (1979; lab, c +, f -, s +: *Chaoborus flavicans* – *Ceriodaphnia quadrangula*, *C. flavicans* – *Chydorus sphaericus*, *C. flavicans* – *Diaptomus gracilis*), Hewett (1980; lab, c -, f -, s +: *Didinium nasutum* – *Paramecium aurelia*, *D. nasutum* – *Paramecium jenningsi*, *D. nasutum* – *Paramecium multimicronucleatum*), Longstaff (1980; lab, c -, f -, s + or -: *Pergamasus crassipes* [males] – *Onychiurus armatus*, *P. crassipes* [females] – *O. armatus*), Vinyard & Menger (1980; lab, c -, f -, s +: *C. americanus* – *Cyclops vernalis*, *C. americanus* – *Diaptomus birgei*, *C. americanus* – *Diaptomus leptopus*, *C. americanus* – *Daphnia pulex* [1.0, 1.5, or 2.0 mm], *C. americanus* – *Daphnia rosea* [1.0, 1.5, or 2.0 mm]), Eveleigh & Chant (1981; lab, c -, f -, s +: *Amblyseius degenerans* [protonymphs] – *Tetranychus pacificus*, *A. degenerans* [deutonymphs] – *T. pacificus*, *A. degenerans* [adults] – *T. pacificus*, *Phytoseiulus persimilis* [protonymphs] – *T. pacificus*, *P. persimilis* [deutonymphs] – *T. pacificus*, *P. persimilis* [adults; experiment 1, day 1 or experiment 2] – *T. pacificus*; lab, c -, f -, s -: *A. degenerans* [protonymphs] – *T. pacificus*, *A. degenerans* [deutonymphs] – *T. pacificus*, *P. persimilis* [protonymphs] – *T. pacificus*, *P. persimilis* [deutonymphs] – *T. pacificus*), Sherr, Sherr & Berman (1983; lab, c +, f -, s +: *Monas* sp. – *Chlorobium phaeobacteroides*, *Monas* sp. – *Escherichia coli*, *Monas* sp. – isolate 1, *Monas* sp. – *Salmonella typhimurium* 635B+), Ohman (1984; lab, c +, f -, s +: *E. pacifica* – *Pseudocalanus* sp.), Spitze (1985; lab, c -, f +, s +: *C. americanus* – *D. pulex* [0.8, 1.1, 1.4, or 1.7 mm]; lab, c -, f -, s +: *C. americanus* [3rd instars] –

D. pulex [0.8, 1.1, or 1.4 mm], *C. americanus* [4th instars] – *D. pulex* [0.8, 1.1, 1.4, 1.7, or 2.0 mm]), Lipcius & Hines (1986; lab, c -, f -, s +: *Callinectes sapidus* – *Mya arenaria* [mud]), Stuart (1986; lab, c -, f -, s +: *Euphausia lucens* – *Acartia africana*, *E. lucens* - *Engraulis encrasicholus*), Colton (1987; lab, c -, f + or -, s +: *Enallagma aspersum* – *Diaptomus spatulocrenatus*, *E. aspersum* – *Simocephalus serrulatus*), Turchin & Kareiva (1989; field, s -: *Hippodamia convergens* - *Aphis varians*), Eggleston (1990*a*; lab, c -, f -, s +: *C. sapidus* [males] - *Crassostrea virginica* [15, 25, or 35 mm shell height]), Soluk (1993; lab, c +, f -, s +: *Agnetina captitata* – *Ephemerella subvaria*), Jeschke & Tollrian (2000; lab, c -, f -, s +: *Chaoborus obscuripes* – *D. pulex* [2nd instars of typical morph, 2nd instars of neckteeth morph, or 3rd instars of typical morph]), Gaymer, Himmelman & Johnson (2001; lab, c -, f -, s +: *Asterias vulgaris* – *M. edulis*, *Leptasterias polaris* – *M. edulis*), Mohaghegh, De Clercq & Tirry (2001; lab, c -, f -, s +: *P. maculiventris* – *Spodoptera exigua* [18 or 23° C], *Podisus nigrispinus* – *S. exigua* [18° C]), Sell, van Keuren & Madin (2001; lab, c +, f -, s +: *Centropages typicus* – *Calanus finmarchicus* [eggs, 6° C], *Metridia lucens* – *C. finmarchicus* [nauplii, 9° C] [The authors have classified their curve as linear.]), J. Jeschke (*personal observation*; lab, c -, f -, s -: *C. obscuripes* – *D. obtusa*), M. Kredler (*personal communication*; lab, c -, f -, s +: *Libellula depressa* – *D. magna*), E. Parawas & I. Fritz (*personal communication*; lab, c -, f -, s -: *Aeshna* sp. – *D. magna*); reviewed by Holling (1965; lab: *Acheta domesticus* – *M. domestica*, *Acilius semisulcatus* – mosquito larvae, *Corixa* sp. – mosquito larvae, *Lethocerus* sp. – tadpoles), Murdoch & Oaten (1975; *Exenterus canadensis* – sawfly larvae, *Nemeritus* sp. – moth larvae, *Pisaster* sp. – turban snails, *Pleolopus basizonus* – sawfly cocoons), Hassell *et al.* (1976; *Anthocoris confusus* – *Aulacorthum* sp., *Harmonia axyridis* – *Aphis craccivora*, *Linyphia triangularis* – *Drosophila* sp., *Macrocyclops albidus* – *Paramecium* sp.), Hassell (1978; lab, f -, s +: *Phytoseiulus persimilis* – *Tetranychus urticae* [eggs or deutonymphs]; ?: *Harmonia axyridis* – *Aphis craccivora*), Fujii, Holling & Mace (1986; *Typhlodromus occidentalis* – *Tetranychus telarius*); **type II dome-shaped** ($N = 20$): Mori & Chant (1966; lab, c -, f -, s + [no, 1 d, or 5 d starvation]: *P. persimilis* – *T. urticae* [33%, 76%, or 100% relative humidity]), Haq (1967; lab, c +, f -, s +: *Metridia longa* – *Artemia* sp., *M. lucens* – *Artemia* sp.), Tostowaryk (1972; lab, c -, f -, s -: *P. modestus* [3rd instars] – *N. p. banksianae* [active: 2nd instars], *P. modestus* [4th instars] – *N. p.*

banksianae [active: 3rd instars], *P. modestus* [5th instars] – *N. p. banksianae* [active: 4th instars], *P. modestus* [2nd instars] – *N. swainei* [active: 2nd instars], *P. modestus* [3rd instars] – *N. swainei* [active: 2nd instars]), Vinyard & Menger (1980; lab, c -, f -, s +: *C. americanus* – *Moina hutchinsoni*), Williamson (1984; lab, c -, f -, s +: *Mesocyclops edax* – *Asplanchna priodonta*, *M. edax* – *Brachionus calyciflorus*), S. Hübner (*personal communication*; lab, c -, f -, s -: *Chaoborus crystallinus* – *D. pulex*); **type II roller-coaster-shaped** (A dome-shaped functional response where at very high prey densities, consumption rate increases again.) (*N* = 1): S. Hübner (*personal communication*; lab, c -, f -, s +: *Aeshna cyanea* – *D. magna*)

Type III (*N* = 26): Murdoch (1969; lab, c +, f +, s +: *Acanthina spirata* – *Balanus glandula*, *A. spirata* – *Mytilus edulis*), Akre & Johnson (1979; lab, c -, f + [complementary densities of alternative prey], s +: *Anomalagrion hastatum* – *Daphnia magna*, *A. hastatum* – *Simocephalus vetulus*), Vinyard & Menger (1980; lab, c -, f -, s +: *Chaoborus americanus* – *Holopedium gibberum* [1.0 or 2.0 mm]), Eveleigh & Chant (1981; lab, c -, f -, s +: *Phytoseiulus persimilis* [adults; experiment 1, day 5] – *Tetranychus pacificus*), Lipcius & Hines (1986; lab, c -, f -, s +: *Callinectes sapidus* – *Mya arenaria* [sand]), Stuart (1986; lab, c -, f -, s +: *Euphausia lucens* – *Artemia* sp.), Eggleston (1990*b*; lab, c -, f -, s +: *C. sapidus* [females] – *Crassostrea virginica* [35 mm shell height]), DeBlois & Leggett (1991; lab, c +, f -, s +: *Calliopius laeviusculus* – *Mallotus villosus* [three different conditions: 7° C and 8 h, 14.5° C and 8 h, or 14.5° C and 24 h]), Soluk (1993; lab, c +, f -, s +: *Agnetina captitata* – *Baetis tricaudatus*), Pilditch & McClatchie (1994; lab, c +, f + or -, s +: *Nyctiphanes australis* – *Acartia ensifera* and *Acartia jiletti*), Agarwala *et al.* (2001; lab, c -, f -, s +: *Menochilus sexmaculatus* – *Aphis craccivora*), Mohaghegh *et al.* (2001; lab, c -, f -, s +: *Podisus maculiventris* – *Spodoptera exigua* [27° C], *Podisus nigrispinus* – *S. exigua* [23 or 27° C]), Sell *et al.* (2001; lab, c +, f -, s +: *Metridia lucens* – *Calanus finmarchicus* [eggs, 6° C]); reviewed by Hassell *et al.* (1977; lab, c -, f -, s -: *Coccinella septempunctata* – *Brevicoryne brassicae* [1st instars]; ?: *Cyclops bicuspidatus* – *C. bicuspidatus* [nauplii or copepodites], *C. bicuspidatus* - cladocerans), Begon, Harper & Townsend (1996; *Aphelinus thomsoni* – *Drepanosiphum platanoidis*); **type III dome-shaped** (*N* = 2): Nelmes (1974; lab, c -, f -, s -: *Prionchulus punctatus* –

Aphelenchus avenae); reviewed by Hassell *et al.* (1977; *C. bicuspidatus* – *Diaptomus* sp.)

Linear (i.e. incomplete, not classifiable functional response) (*N* = 8): Murdoch & Marks (1973; lab, c -, f +, s +: *Coccinella septempunctata* – *Acyrthosiphon pisum*), Eggleston (1990*b*; lab, c -, f -, s +: *Callinectes sapidus* [males or females] – *Crassostrea virginica* [25 mm shell height]), Sell *et al.* (2001; lab, c +, f -, s +: *Centropages typicus* – *Calanus finmarchicus* [eggs, 11° C; nauplii, 6 or 11° C], *Metridia lucens* – *C. finmarchicus* [nauplii, 6 or 13° C])

(β) Vertebrates

Type II (*N* = 38): Brönmark, Malmqvist & Otto (1984; lab, c -, f -, s +: *Salmo trutta* - *Velia caprai*), Ranta & Nuutinen (1985; lab, c -, f -, s -: *Triturus vulgaris* [10, 13, 18, or 37 mm] - *Daphnia longispina*, *T. vulgaris* [10, 13, 18, or 37 mm] – *D. magna*), Wanink & Zwarts (1985; lab, c -, f -, s +: *Haematopus ostralegus* - *Scrobicularia plana*), Corbett & Newsome (1987; field, s +: *Canis familiaris dingo* – *Amphibolurus nuchalis*, *C. f. dingo* – *Bos taurus*, *C. f. dingo* – *Oryctolagus cuniculus*, *C. f. dingo* – small mammals), Korpimäki & Norrdahl (1991; field, s +: *Asio flammeus* – *Microtus* spp., *Asio otus* – *Microtus* spp., *Falco tinnunculus* – *Microtus* spp. [The authors have classified their curves as linear.]), Soluk (1993; lab, c -, f -, s +: *Cottus bairdi* – *Baetis tricaudatus*, *C. bairdi* – *E. subvaria*), Dale, Adams & Bowyer (1994; field, s +: *Canis lupus* - *Rangifer tarandus caribou*), Messier (1994; field, s +: *C. lupus* - *Alces alces*), O'Donoghue *et al.* (1998; field, s +: *Lynx canadensis* – *Lepus americanus*), Nielsen (1999; field, s +: *Falco rusticolus* – *Lagopus mutus*), Redpath & Thirgood (1999; field, s +: *Falco peregrinus* – *Lagopus lagopus scoticus*), Salamolard *et al.* (2000; field, s +: *Circus pygargus* – *Microtus arvalis*), Anderson (2001; lab, c +, f -, s +: *Paralabrax clathratus* – *Brachyistius frenatus* [none, low, medium, or high levels of habitat structure]), E. Röttinger (*personal communication*; lab, c -, f -, s +: *Triturus alpestris* [20.8 or 25.8 mm length, 400 or 600 mL medium] – *D. obtusa*); reviewed by Holling (1965; field: *Dendroica castanea* – *Choristoneura fumiferana*, *Parus major* – *Acantholyda nemoralis*), Piersma, de Goeij & Tulp (1993; lab: *Calidris canutus* – *Cerastoderma edule*, *C. canutus* – *Macoma balthica* [1 or 3 cm deep]); **type II dome-shaped** (*N* = 2): Treherne & Foster

(1982; field, s -: *Sardinops sagax – Halobates robustus*), Burger & Gochfeld (2001; field, s -: *Crotophaga ani – Eunica monima*)

Type III (*N* = 11): Holling (1959*a*; lab, c -, f +, s +: *Blarina brevicauda talpoides – Neodiprion sertifer*, *Peromyscus leucopus – N. sertifer* [dog biscuits as alternative food; sand depth = 10, 15, 20, or 25 mm], *P. leucopus – N. sertifer* [sunflower seeds as alternative food], *Sorex cinereus cinereus – N. sertifer*), Horwood & Goss-Custard (1977; field, s +: *Haematopus ostralegus – Cerastoderma edule*), Pech *et al.* (1992; field, s +: *Vulpes vulpes – Oryctolagus cuniculus*), Redpath & Thirgood (1999; field, s +: *Circus cyaneus – Lagopus lagopus scoticus*), Burger & Gochfeld (2001; field, s -: *Crotophaga ani – Aphrissa statira* and *Phoebis trite*)

(ii) Planktivorous fishes (For example, three-spined sticklebacks [*Gasterosteus aculeatus*] feeding on *Daphnia* spp. Visser & Reinders [1981] divided a stickleback's handling into external [i.e. catching prey] and internal handling [i.e. swallowing and transporting to the stomach]. While handling internally, the fish is able to search for prey. In other words, searching and handling are partly overlapping. Note: While handling internally, most non-filter feeding carnivores are actually able to search for prey. We have ignored this point for simplicity and because internal handling time is usually negligibly small compared to external handling time.)

Type I/II (*N* = 1): LeBrasseur *et al.* (1969; lab, c +, f -, s -: *Oncorhynchus keta*– Anomura)

Type II (*N* = 9): LeBrasseur *et al.* (1969; lab, c +, f -, s -: *Oncorhynchus gorbuscha* [34 or 90 mm] – *Calanus plumchrus*, *Oncorhynchus keta - C. plumchrus*), Visser & Reinders (1981; lab, c -, f -, s -: *Gasterosteus aculeatus – Daphnia magna*), Townsend & Risebrow (1982; lab, c -, f -, s -: *Abramis brama – D. magna* [1.25 Lux]), Bence & Murdoch (1986; lab, c -, f -, s -: *Gambusia affinis – D. magna* [large]), Ehlinger (1989; lab, c +, f -, s -: *Notemigonus crysoleucas – Daphnia pulex*); reviewed by Holling (1965; lab: *Cyprinus carpio* – nonliving food, *Rutilus rutilus caspicus* – chironomid larvae); **type II dome-shaped** (*N* = 6): LeBrasseur *et al.* (1969; lab, c +, f -, s -: *O. gorbuscha - Microcalanus* sp.), Bence & Murdoch (1986; lab, c -, f -, s -: *G. affinis – D. magna* [small or small and large]), M. Kredler (*personal communication*; lab, c -, f -, s -: *G. aculeatus* [small or medium] – *D. magna*); reviewed by Young *et al.* (1994; lab, s -: *Alburnus alburnus – D. magna*)

Type III (*N* = 1): Townsend & Risebrow (1982; lab, c -, f -, s -: *A. brama – D. magna* [low light level]); **Type III dome-shaped** (*N* = 1): M. Kredler (*personal communication*; lab, c -, f -, s -: *G. aculeatus* [large] – *D. magna*)

(iii) Queueing carnivores (e.g. *Notonecta* spp.) (searching and handling are partly overlapping according to Bailey [1985] and to Juliano's [1989] review)

Type II (*N* = 15): Ellis & Borden (1970; lab, c -, f -, s -: *Notonecta undulata – Aedes aegypti*), Hassell *et al.* (1977; lab, c -, f -, s +: *Notonecta glauca – Asellus aquaticus* [8 mm]), Fox & Murdoch (1978; lab, c -, f -, s + or -: *Notonecta hoffmanni* [small or large] – *Culex quinquefasciatus*), Chesson (1989; lab, c -, f +, s -: *N. hoffmanni – Culex pipiens* [0, 5, 10, or 20 *Daphnia pulex* as alternative prey; 0 or 5 *Drosophila* sp. as alternative prey]), Streams (1994; lab, c -, f -, s -: *N. undulata – N. undulata* [2nd instars]); reviewed by Holling (1965; lab: *Notonecta* sp. – mosquito larvae), Hassell *et al.* (1976; *N. glauca – Daphnia* sp.)

Type III (*N* = 4): Hassell *et al.* (1977; lab, c -, f -, s +: *Notonecta glauca – Asellus aquaticus* [4 mm]), Chesson (1989; lab, c -, f +, s -: *Notonecta hoffmanni – Culex pipiens* [10 *Drosophila* sp. as alternative prey]), Streams (1994; lab, c -, f -, s -: *Notonecta undulata – N. undulata* [1st instars]); reviewed by Hassell *et al.* (1977; lab, c -, f -, s +: *Plea atomaria – Aedes aegypti*)

(b) Herbivores

(i) Invertebrates

(α) Protozoans that consume only one food item per generation

Type I (*N* = 2): Hansen & Nielsen (1997; lab, c +, f -, s +: *Fragilidium subglobosum – Ceratium tripos*), Jakobsen & Hansen (1997; lab, c +, f -, s +: *Gymnodinium* sp. – *Rhodomonas salina*)

(β) Aquatic microphagous molluscs (Searching and handling are partly overlapping in aquatic microphagous molluscs, because these consumers are able to simultaneously capture several food particles with their radula.)

Type I/II (*N* = 1): Tahil & Juinio-Menez (1999; lab, c -, f -, s +: *Haliotis asinina – Acanthophora specifera*, *Hypnea valentiae*, and *Laurencia papillosa* [The authors have classified their curve as type I.])

Type II (*N* = 1): Sommer (1999; lab, c -, f -, s +: *Littorina littorea* – algae)

(γ) Others

Type II (*N* = 7): Strom (1991; lab, c +, f -, s +: *Gymnodinium* sp. – *Isochrysis galbana*), Hansen (1992; lab, c +, f -, s -: *Gyrodinium spirale – Heterocapsa triquetra*), Strom & Buskey (1993; lab, c +, f -, s +: *Oblea rotunda – Ditylium brightwellii*, *O. rotunda – Dunaliella tertiolecta*), Jeong & Latz (1994; lab, c +, f -, s +: *Protoperidinium* cf. *divergens – Gonyaulax polyedra*); reviewed by Begon, Harper & Townsend (1990; slugs – *Lolium perenne*, *Tyria jacobaeae – Senecio jacobaea*); **type II dome-shaped** (*N* = 1): Jeong & Latz (1994; lab, c +, f -, s +: *Protoperidinium crassipes – G. polyedra*)

Type II threshold (*N* = 2): Caron *et al.* (1985; lab, c +, f + or -, s +: *Paraphysomonas imperforata – Phaeodactylum tricornutum*)

Type III (*N* = 4): Kamiyama (1997; lab, c +, f -, s +: *Favella azorica - Heterocapsa circularisquama*, *F. azorica – Heterocapsa triquetra*, *Favella taraikensis – H. triquetra*); reviewed by Hassell *et al.* (1977; *Calliphora vomitora* – sugar droplets)

(ii) Vertebrates (While chewing, a vertebrate herbivore is able to search for its next bite [Spalinger, Hanley & Robbins, 1988; Spalinger & Hobbs 1992; Laca, Ungar & Demment, 1994; Parsons *et al.*, 1994; Farnsworth & Illius, 1996, 1998; Hirakawa, 1997]. It is also able to simultaneously capture [i.e. bite] several food items [Ungar & Noy-Meir, 1988; Spalinger *et al.*, 1988; Laca *et al.*, 1994; Parsons *et al.*, 1994; Shipley *et al.*, 1994]. In other words, searching and handling are partly overlapping.)

Type I/II (*N* = 18): Allden & Whittaker (1970; enclosure, c -, f -, s -: *Ovis aries* [adults or lambs] – *Bromus* spp., *Lolium rigidum*, and *Trifolium subterraneum*), Black & Kenney (1984; enclosure, c -, f -, s -: *O. aries – L. rigidum*), Wickstrom *et al.* (1984; enclosure, f +, s -: *Cervus elaphus nelsoni* – grasses, *Odocoileus hemionus hemionus* - grasses), Hudson & Watkins (1986; enclosure, c +, f -, s -: *C. e. nelsoni* – grasses [summer or fall]), Renecker & Hudson (1986; enclosure, c +, f +, s -: *Alces alces* – plants [January] [The authors have classified their curve as type II.]), Short

(1986; enclosure, c +, f -, s +: *Macropus rufus* – plants [The author has classified his curve as type II.]), Spalinger *et al.* (1988; enclosure, c -, f -, s -: *Odocoileus hemionus sitkensis* – *Coptis aspleniifolia*, *O. h. sitkensis* – *Rubus pedatus*, *O. h. sitkensis* – *Tsuga heterophylla*), Shipley & Spalinger (1995; enclosure, c -, f -, s -: *A. alces* [yearlings] – *Acer rubrum*, *Odocoileus virginianus* [fawns or yearlings] – *A. rubrum*), Fritz, Durant & Guillemain (2001; enclosure, c -, f -, s -: *Anas platyrhynchos* ["FrB"] – pellets [medium], *A. platyrhynchos* ["FrB", "MBB"] – pellets [large] [The authors have classified their curves as type II.])

Type II (*N* = 58): Arnold & Dudzinski (1967; enclosure, c +, f -, s +: *Ovis aries* – *Phalaris tuberosa* and *Trifolium subterraneum*), Allden & Whittaker (1970; enclosure, c -, f -, s -: *O. aries* [yearlings] – *Bromus* spp., *Lolium rigidum*, and *T. subterraneum*), Trudell & White (1981; field, s +: *Rangifer tarandus tarandus* – *Salix* spp., *R. t. tarandus* – lichens), Short (1985; enclosure, c +, f -, s +: *Macropus rufus* – plants, *Oryctolagus cuniculus* - plants, *O. aries* - plants), Renecker & Hudson (1986; enclosure, c +, f +, s -: *Alces alces* – plants [July or October]), Lundberg (1988; lab, c -, f -, s -: *Clethrionomys glareolus* – *Salix myrsinifolia*), Belovsky (1990; enclosure, c -, f -, s -: *Molothrus ater* – *Panicum miliaceum*), Lundberg & Danell (1990; enclosure, c -, f -, s -: *A. alces* – *Betula pubescens*), Fryxell & Doucet (1993; enclosure, c +, f -, s +: *Castor canadensis* - *Populus tremuloides* [one size or different sizes]), Fryxell *et al.* (1994; enclosure, c +, f -, s +: *C. canadensis* – *Alnus rugosa*, *C. canadensis* – *P. tremuloides*), Shipley & Spalinger (1995; enclosure, c -, f -, s -: *A. alces* [calves] – *Acer rubrum*), Wilmshurst, Fryxell & Hudson (1995; enclosure, c -, f -, s -: *Cervus elaphus* - pasture), Wilmshurst, Fryxell & Colucci (1999; enclosure, c -, f -, s -: *Gazella thomsoni* – *Cynodon dactylon*), Bergman, Fryxell & Gates (2000; enclosure, c -, f -, s -: *Bison bison athabascae* ["Cygnus", "Elvis", "Jean-Louis", "Mo", "Scruffy", or "Tokisa"] – *Carex atherodes*), Fritz *et al.* (2001; enclosure, c -, f -, s -: *Anas platyrhynchos* ["FbB", "FBB", "FNB", "FrB", "FRB", "MbB", "MBB", "MrB", "MRB", "MVB"] – pellets [small], *A. platyrhynchos* ["FbB", "FBB", "FNB", "FRB", "MbB", "MBB", "MRB", "MVB"] – pellets [medium], *A. platyrhynchos* ["FbB", "FBB", "FNB", "FRB", "MbB", "MrB", "MRB", "MVB"] – pellets [large]), Fortin, Fryxell & Pilote (2002; field, s -: *B. bison* - pasture [growing season or winter]); reviewed by Arnold & Dudzinski (1967; enclosure, c +, f -, s +: *O. aries* [2-year-olds or adults] – *Phalaris tuberosa* and *T. subterraneum*), Fujii *et al.* (1986; *Columba palumbus* – wheat and barley), Spalinger

& Hobbs (1992; *A. alces* - ?, *B. bison* – pasture); **type II dome-shaped** (*N* = 1): Owen-Smith (1994; enclosure, c +, f -, s +: *Tragelaphus strepsiceros* – plants)

Type II threshold (*N* = 1): Short (1986; enclosure, c +, f -, s +: *Macropus fuliginosus* – plants)

Type III (*N* = 1): Fryxell & Doucet (1993; enclosure, c +, f +, s +: *Castor canadensis - Populus tremuloides*)

Linear (*N* = 12): Batzli, Jung & Guntenspergen (1981; lab, f +, s -: *Lemmus sibericus* - monocots; enclosure, f +, s -: *L. sibericus* – monocots [early summer 1976, late summer 1976, or early summer 1977]), Trudell & White (1981; field, s -: *Rangifer tarandus tarandus – Betula nana*, *R. t. tarandus – Carex aquatilis*, *R. t. tarandus – Eriophorum vaginatum*, *R. t. tarandus* – forbs), Åström, Lundberg & Danell (1990; enclosure, c -, f -, s -: *Alces alces – Betula pubescens* and *Sorbus aucuparia*), Andersen & Sæther (1992; field, s +: *A. alces* [calves or cows] - plants), Rowcliffe, Sutherland & Watkinson (1999; field, s -: *Branta bernicla bernicla – Enteromorpha intestinalis* and *Ulva lactuca*)

(c) Parasites and parasitoids

Type II (*N* = 23): Messenger (1968; lab, c -, f -, s +: *Praon exsoletum – Therioaphis trifolii* [10, 12.8, 15.6, 21.1, 23.9, or 26.7° C]), Elliott (1983; lab, c -, f + or - or field, s +: *Agriotypus armatus – Silo pallipes*), Runjie, Heong & Domingo (1996; lab, c -, f -, s +: *Cardiochiles philippinensis - Cnaphalocrocis medinalis* [25, 28, 30, 33, or 35° C]), Tillman (1996; enclosure, c +, f -, s +: *Cardiochiles nigriceps – Heliothis virescens*, *Microplitis croceipes – H. virescens*), Ives *et al.* (1999; lab, c +, f -, s -: *Aphidius ervi – Acyrthosiphon pisum*); reviewed by Hassell *et al.* (1976; *Dahlbominus fuscipennis – Neodiprion sertifer*, *Nasonia vitripennis – M. domestica*), Hassell *et al.* (1977; lab, c -, f -, s +: *Aphidius uzbeckistanicus – Metapolophium dirhodum*), Elliott (1983; field, s +: *A. armatus – S. pallipes*), Fujii *et al.* (1986; *D. fuscipennis – Neodiprion decontei*), Begon *et al.* (1996; *Pleolophus basizonus – N. sertifer*)

Type III (*N* = 5): reviewed by Hassell *et al.* (1976; *Encarsia formosa – Trialeurodes vaporariorum*), Hassell *et al.* (1977; lab, c -, f -, s +: *Aphidius uzbeckistanicus – Hylopteroides humilis*; ?: *Nemeritis canescens* [2nd, 3rd, or 4th instars] – *Cadra* sp.)

(2) Filter feeders

(a) Protozoans (For filter feeding protozoans, searching means concentrating food particles from the environment. Handling is enclosing a food item in a membrane-covered vacuole [i.e. phagocytosis]. In most filter feeding protozoans ["non-giants"], searching and handling are partly overlapping because these consumers are able to handle [i.e. to phagocytise] several food items simultaneously. The exact number of food items thereby depends on the size of the 'mouth' [peristome]. In case of an exceptionally large mouth ["giants", e.g. *Stentor*], searching and handling are completely overlapping. References: Heinbokel [1978], Fenchel [1980*a*, *b*, 1987].)

(i) Non-giants

Type I/II (*N* = 3): Curds & Cockburn (1968; lab, c +, f -, s +: *Tetrahymena pyriformis – Klebsiella aerogenes*), Heinbokel (1978; lab, c +, f -, s +: *Eutintinnus pectinis – Dunaliella tertiolecta*, *Isochrysis galbana*, and *Monochrysis lutheri*, *Helicostomella subulata – D. tertiolecta* and *I. galbana*); **type I/II dome-shaped** (*N* = 3): Verity (1985; lab, c +, f -, s +: *Tintinnopsis vasculum – Dicrateria inornata* [5, 10, or 15° C])

Type II (*N* = 16): Fenchel (1980*a*; lab, c +, f + [two different concentrations of alternative food], s -: *Colpidium colpoda* – latex beads; lab, c +, f -, s -: *Cyclidium* sp. – latex beads [0.357 or 1.09 µm], *Glaucoma scintillans* – latex beads), Fenchel (1980*b*; lab, c +, f -, s -: *Colpidium campylum* – latex beads), Verity (1985; lab, c +, f -, s +: *Tintinnopsis acuminata – Isochrysis galbana* [25° C]), Jonsson (1986; lab, c +, f -, s -: *Lohmanniella spiralis* – latex beds [2.87, 5.7, or 14.4 µm]), Grover (1990; lab, c +, f -, s +: *Paraphrysomonas vestita vestita – Nitzschia acicularis*, *P. v. vestita – Nitzschia palea*), Verity (1991; lab, c +, f -, s +: *Strobilidium* cf. *spiralis – Pseudobodo* cf. *tremulans* [cultured on bacteria]), Jakobsen & Hansen (1997; lab, c +, f -, s +: *Balanion comatum – Rhodomonas salina*), Müller & Schlegel (1999; lab, c +, f -, s +: *Strobilidium lacustris – Cryptomonas* sp.); reviewed by Fenchel (1987; *Halteria grandinella* – latex beads); **type II dome-shaped** (*N* = 3): Scott (1985; lab, c +, f -, s +: *Strombidium* sp. – *Pavlova (Monochrysis) lutheri*), Verity (1985; lab, c +, f -, s +: *T. acuminata – I. galbana* [15 or 20° C])

Type III (*N* = 5): Verity (1991; lab, c +, f -, s +: *Strobilidium* cf. *spiralis – Isochrysis galbana*, *S.* cf. *spiralis – Pseudobodo* cf. *tremulans* [cultured on picoplankton], *Tintinnopsis dadayi – Katodinium rotundatum*, *T. dadayi –*

Paraphysomonas sp. [cultured on picoplankton or bacteria] [The author has classified his curves as type II.])

Linear (*N* = 2): Heinbokel (1978; lab, c +, f -, s +: *Tintinnopsis* cf. *acuminata* – *Isochrysis galbana* and *Monochrysis lutheri*), Müller & Schlegel (1999; lab, c +, f -, s +: *Histiobalantium bodamicum* – *Cryptomonas* sp.)

(ii) Giants (e.g. *Stentor*)

Type I (*N* = 1): Wenzel & Liebsch (1975; lab, c +, f -, s +: *Stentor coeruleus* – *Tetrahymena pyriformis*)

Type III (*N* = 3): reviewed by Murdoch & Oaten (1975; *Stentor* sp. – *Chlamydomonas* sp., *Stentor* sp. – *Euglena* sp., *Stentor* sp. – *Tetrahymena* sp.)

(b) Carnivorous plants (Searching and handling are partly overlapping in carnivorous plants that are able to simultaneously capture a low number of prey [e.g. as in the experiments summarized below where small plant fractions were used]. These activities are, in contrast, completely overlapping in carnivorous plants that are able to simultaneously capture a high number of prey.)

Type I (*N* = 2): Harms & Johansson (2000; lab, c -, f -, s +: *Utricularia vulgaris* – *Polyphemus pediculus* [experiments from 1995/1997 or 1999] [The authors have classified their curves as type II.])

Type I/II (*N* = 2): Harms & Johansson (2000; lab, c -, f -, s +: *Utricularia vulgaris* – *Eucyclops serrulatus* [experiments from 1995/1997 or 1999] [The authors have classified their curves as type II.])

(c) Cnidarians and ctenophores

Type I/II (*N* = 10): Daan (1986; lab, c -, f -, s +: *Sarsia tubulosa* [umbrella height = 3, 4, 5, 6, 7, 8, 9, 10, 11, or 12 mm] - copepods)

Type III (*N* = 1): H. Stibor & N. Tokle (*personal communication*; lab, c -, f -, s +: *Sarsia* sp. – *Temora* sp.)

(d) Rotifers (searching and handling are completely overlapping according to Jørgensen [1966])

Type I (*N* = 9): Chotiyaputta & Hirayama (1978; lab, c +, f -, s -: *Brachionus plicatilis* – *Chlamydomonas* sp. [growing or senescent]), Schlosser & Anger (1982; lab, c +, f -, s

-: *B. plicatilis – Saccharomyces cerevisiae*), Rothhaupt (1990; lab, c +, f -, s +: *Brachionus calyciflorus – Cyclotella meneghiniana*, *B. calyciflorus* - *Monoraphidium minutum*, *Brachionus rubens – Chlamydomonas reinhardii*, *B. rubens – M. minutum*), Rothhaupt & Lampert (1992; lab, c +, f -, s +: *B. rubens – M. minutum*), Mohr & Adrian (2000; lab, c +, f -, s +: *B. calyciflorus – Tetrahymena pyriformis*); **type I superfluous feeding** (Above a certain extremely high food abundance, searching effort [i.e. clearance or filtration rate] does not further decrease with increasing food abundance but remains constant. The consumption rate, therefore, increases again.) (*N* = 2): Walz & Gschloessl (1988; lab, c +, f -, s +: *Brachionus angularis – Coccomyxa* sp., *B. angularis – Stichococcus bacillaris*)

Type I/II (*N* = 5): Chotiyaputta & Hirayama (1978; lab, c +, f -, s -: *Brachionus plicatilis – Olisthodiscus* sp.), Rothhaupt (1990; lab, c +, f -, s +: *Brachionus rubens – Chlamydomonas sphaeroides*, *B. rubens – Cyclotella meneghiniana* [The author has classified the latter curves as type II.], *B. rubens – Chlorella minutissima* [The author has classified the curve as type I.]), Hansen, Wernberg-Møller & Wittrup (1997; lab, c +, f -, s +: *B. plicatilis – Rhodomonas baltica* [The authors have classified their curve as type II.]); **type I/II superfluous feeding** (*N* = 4): Yúfera & Pascual (1985; lab, c +, f -, s +: *B. plicatilis* [90-170 µm] – *Nannochloropsis oculata*, *B. plicatilis* [90-170 µm] – *Nannochloris maculata*, *B. plicatilis* [90-170 or 160-250 µm] – *Nannochloris oculata*)

Type II (*N* = 7): Starkweather & Gilbert (1977; lab, c +, f -, s +: *Brachionus calyciflorus* - *Rhodotorula glutinis*), Rothhaupt (1990; lab, c +, f -, s +: *B. calyciflorus – Chlamydomonas sphaeroides*), Hansen *et al.* (1997; lab, c +, f -, s +: *Brachionus plicatilis – Thalassiosira fluviatilis*), Navarro (1999; lab, c +, f -, s +: *Brachionus rotundiformis – Nannochloropsis oculata* [live or freeze-dried]), Mohr & Adrian (2000; lab, c +, f -, s +: *B. calyciflorus – Coleps* sp., *Brachionus rubens – T. pyriformis*); **type II dome-shaped** (*N* = 5): Starkweather & Gilbert (1977; lab, c +, f -, s +: *B. calyciflorus* - *Euglena gracilis*), Yúfera & Pascual (1985; lab, c +, f -, s +: *B. plicatilis* [90-170 µm] – *Nannochloropsis gaditana*), Rothhaupt (1990; lab, c +, f -, s +: *B. calyciflorus – Micractinium pusillum*, *B. rubens – C. sphaeroides*, *B. rubens – M. pusillum*)

Type III (*N* = 4): Pilarska (1977; lab, c +, f -, s +: *Brachionus rubens – Chlorella vulgaris*), Awaïss, Kestemont & Micha (1992; lab, c +, f -, s +: *Brachionus calyciflorus – Saccharomyces cerevisiae*), Navarro (1999; lab, c +, f -, s +: *Brachionus plicatilis – Nannochloropsis oculata* [live or freeze-dried]); **type III dome-shaped** (*N* = 2): Halbach & Halbach-Keup (1974; lab, c +, f -, s +: *B. calyciflorus – Chlorella* *pyrenoidosa*), Awaïss *et al.* (1992; lab, c +, f -, s +: *B. calyciflorus – Dictyosphaerium chlorelloides*)

Linear (*N* = 4): Starkweather, Gilbert & Frost (1979; lab, c +, f -, s +: *Brachionus calyciflorus – Aerobacter aerogenes*), Schlosser & Anger (1982; lab, c +, f -, s -: *Brachionus plicatilis – Dunaliella* sp. [18° C with rotation, 23.5° C with rotation, or 23.5° C without rotation])

(e) Molluscs (Searching and handling are completely overlapping according to Jørgensen [1955, 1966, 1990], Crisp, Yule & White [1985], Sprung & Rose [1988], and Ward *et al.* [1993]: Filter feeding molluscs search for food by pumping water through their gills. They then handle caught food particles by transferring them via the labial palps [bivalves] or the radula [gastropods] to the mouth where they are ingested.)

Type I (*N* = 8): Ali (1970; lab, c +, f + or -, s +: *Hiatella arctica – Phaeodactylum tricornutum*), Foster-Smith (1975; lab, f -, s -: *Cerastoderma edule* – aluminum particles [grade 1], *C. edule* - *P. tricornutum*, *Mytilus edulis – P. tricornutum*), Walz (1978; lab, c +, f -, s +: *Dreissena polymorpha – Nitzschia actinastroides*), Sprung & Rose (1988; lab, c +, f -, s +: *D. polymorpha – Chlamydomonas reinhardii*), Clausen & Riisgård (1996; lab, c +, f -, s +: *M. edulis – Rhodomonas* sp.); **type I dome-shaped** (*N* = 8): Foster-Smith (1975; lab, f -, s -: *Venerupis pullastra – Isochrysis galbana*, *V. pullastra – P. tricornutum*), Wilson (1980; lab, c +, f -, s +: *Ostrea edulis* [larvae] – *Dunaliella tertiolecta*), Widdows, Fieth & Worrall (1979; lab, c -, f -, s +: *M. edulis* [3, 5, or 7 cm] – particles), Dorgelo & Smeenk (1988; lab, c +, f -, s -: *D. polymorpha – Chlamydomonas eugametos*); reviewed by Monakov (1972; *Valvata piscinalis – Scenedesmus* sp.)

Type I/II (*N* = 10): Ali (1970; lab, c +, f + or -, s +: *Hiatella arctica – Isochrysis galbana*), Tenore & Dunstan (1973; lab, c +, f -, s +: *Crassostrea virginica – Skeletonema costatum* and other algae, *Mytilus edulis – S. costatum* and other algae), Jespersen & Olsen (1982; lab, c +, f -, s +: *M. edulis* [five different sizes] – *I. galbana* and *Monochrysis lutheri*), Bayne *et al.* (1989; lab, c +, f -, s +: *M. edulis – I. galbana* and *Phaeodactylum tricornutum* [The authors have classified their curve as type II.])

Type I/III (*N* = 1): Riisgård & Randløv (1981; lab, c +, f -, s +: *Mytilus edulis – Phaeodactylum tricornutum*); **type I/III dome-shaped** (*N* = 2): Wilson (1980; lab, c +, f -, s +: *Ostrea edulis* [larvae] – *Isochrysis galbana*; lab, c -, f -, s +: *O. edulis* [spat] – *I. galbana*)

Type II (*N* = 6): Crisp *et al.* (1985; lab, c +, f -: *Ostrea edulis – Pavlova lutheri*), Hansen & Ockelmann (1991; lab, c +, f -, s +: *Philine aperta* [135, 159, 217, 244, or 330 µm] – *Isochrysis* cf. *galbana*); **type II dome-shaped** (*N* = 3): Tenore & Dunstan (1973; lab, c +, f -, s +: *Mercenaria mercenaria – Skeletonema costatum* and other algae), Wilson (1980; lab, c -, f -, s +: *O. edulis* [spat] – *Dunaliella tertiolecta*); reviewed by Monakov (1972; *Sphaerium corneum – Chlorella* sp.)

Type III (*N* = 1): reviewed by Monakov (1972; *Bithynia tentaculata – Scenedesmus* sp.)

Linear (*N* = 3): Thompson & Bayne (1974; lab, c -, f -, s -: *Mytilus edulis – Tetraselmis suecica*), Foster-Smith (1975; lab, f -, s -: *Cerastoderma edule* – aluminium particles [grade 2], *M. edulis – I. galbana*)

(f) Polychaets: arenicolids (lugworms) (searching and handling are completely overlapping according to Hobson [1967])

Type III (*N* = 4): Taghon & Greene (1990; lab, c -, f -, s +: *Abarenicola pacifica* – particles [experiment L3 or L4]), Taghon, Greene & Bard (1990; lab, c -, f -, s +: *A. pacifica* – particles [artificial or natural sediments])

(g) Crustaceans

(i) Branchiopods (e.g. *Artemia*, *Daphnia*) (Searching and handling are completely overlapping according to Jørgensen [1966], Lampert [1987], Fryer [1991], and Schmink [1996]. For example, *Daphnia* spp. search for food by pumping water through the filter meshes of their appendages; integrated in this pumping-and-filtering process is the transport of collected food particles to the food groove. *Daphnia* then handle food particles by transporting them to the mouth, processing them by the mandibles, and, finally, swallowing them.)

Type I (*N* = 46): Ryther (1954; lab, c +, f -, s +: *Daphnia magna* [fed detritus and bacteria prior to experiments] – *Chlorella vulgaris* [growing]; lab, c +, f -, s -: *D. magna – C. vulgaris* [growing]), Rigler (1961; lab, c +, f -, s +: *D. magna – Saccharomyces cerevisiae*), McMahon & Rigler (1963; lab, c -, f -, s +: *D. magna – C. vulgaris*, *D. magna – S. cerevisiae*), Reeve (1963; lab, c +, f -, s +: *Artemia salina – Chlorella stigmatophora*, *A. salina – Dunaliella tertiolecta*, *A. salina – Phaeodactylum tricornutum* [six different ages]), McMahon (1965; lab, c +, f -, s +: *D. magna* [1.25, 1.91, 2.56, 2.72, 3.05, 3.25, or 3.54 mm] – *C. vulgaris, D. magna –*

S. cerevisiae [20, 24, or 28° C]), McMahon & Rigler (1965; lab, c +, f -, s +: *D. magna – C. vulgaris*, *D. magna – Escherichia coli, D. magna – S. cerevisiae*, *D. magna – Tetrahymena pyriformis*), Geller (1975; lab, c +, f -, s +: *Daphnia pulex* [10° C and 1 mm, 10° C and 2 mm, 10° C and 3 mm, 15° C and 1 mm, 15° C and 2 mm, 15° C and 3 mm, 20° C and 2 mm, or 25° C and 2 mm] – *Scenedesmus acutus*), Hayward & Gallup (1976; lab, c +, f -, s +: *Daphnia schødleri – Ankistrodesmus* sp.), Kersting & van der Leeuw (1976; lab, c +, f -, s +: *D. magna – C. vulgaris*), Horn (1981; lab, c +, f -, s +: *Daphnia hyalina – Scenedesmus quadricauda*), Muck & Lampert (1984; lab, c +, f -, s +: *Daphnia longispina – S. acutus* [7 or 19° C], *D. longispina – Staurastrum* cf. *planctonicum* [19° C], *D. longispina – Eudiaptomus gracilis* [7 or 19° C]), Ganf & Shiel (1985; lab, c +, f -, s -: *Ceriodaphnia quadrangula – Ankistrodesmus falcatus*), Rothhaupt & Lampert (1992; lab, c +, f -, s +: *Daphnia pulicaria – S. acutus*), Dierckens *et al.* (1997; lab, c +, f -, s +: *Branchipus schaefferi* [males] – *E. coli*); **type I dome-shaped** (*N* = 2): Dierckens *et al.* (1997; lab, c +, f -, s +: *Streptocephalus torvicornis* [males or females] – *E. coli*)

Type I/II (*N* = 18): Ryther (1954; lab, c +, f -, s -: *Daphnia magna – Scenedesmus quadricauda* [growing]), McMahon (1965; lab, c +, f -, s +: *D. magna – Saccharomyces cerevisiae* [5, 10, 15, 33, or 35° C]), Sorokin (1966; lab, c +, f -, s +: *Daphnia pulex – Chlorococcum* sp.), Burns & Rigler (1967; lab, c +, f -, s +: *Daphnia rosea – Rhodotorula glutinis*), Crowley (1973; lab, c +, f -, s +: *D. pulex* – particles), Chisholm, Stross & Nobbs (1975; lab, c +, f -, s +: *Daphnia middendorffiana – Chlamydomonas reinhardii*), DeMott (1982; lab, c +, f -, s +: *Bosmina longirostris – C. reinhardii*, *D. rosea – C. reinhardii*), Porter *et al.* (1982; lab, c +, f -, s +: *D. magna – C. reinhardii* [The authors have classified their curves as type II.]), Holm, Ganf & Shapiro (1983; lab, c +, f -, s +: *D. pulex – Aphanizomenon flos-aquae*), Hopp & Horn (1984; lab, f -, s +: *Daphnia hyalina* [1, 1.5, or 2 mm] – *S. quadricauda*), Evers & Kooijman (1989; lab, c +, f -, s +: *D. magna – Scenedesmus subspicatus* [The authors have classified their curves as type II.])

Type II (*N* = 9): Ryther (1954; lab, c +, f -, s +: *Daphnia magna* [fed *Chlorella vulgaris* prior to experiments] – *C. vulgaris* [growing]; lab, c +, f -, s -: *D. magna – C. vulgaris* [senescent], *D. magna* - *Navicula pellicosa* [growing or senescent], *D. magna – Scenedesmus quadricauda* [senescent]), Geller (1975; lab, c +, f -, s -: *Daphnia pulex – Scenedesmus acutus*), Downing & Peters (1980; enclosure, c +, f -, s +: *Sida crystallina* – small (< 35 µm) particles); reviewed by Monakov (1972; *Daphnia longispina – Chlorococcum* sp., *D. pulex – Chlorococcum* sp.)

Type II threshold (*N* = 1): King & Shiel (1993; lab, c +, f -, s +: *Daphnia carinata – Melosira granulata*)

Type III (*N* = 1): Ganf & Shiel (1985; lab, c +, f -, s -: *Daphnia carinata – Ankistrodesmus falcatus*)

Linear (*N* = 8): Muck & Lampert (1980; lab, c +, f -, s +: *Daphnia longispina – Scenedesmus acutus* [7 or 19° C], *D. longispina – Staurastrum* cf. *planctonicum* [7 or 19° C], *D. longispina – Stichococcus minutissimus* [7 or 19° C]), Muck & Lampert (1984; lab, c +, f -, s +: *D. longispina – S.* cf. *planctonicum* [7° C]), Dierckens *et al.* (1997; lab, c +, f -, s +: *Branchipus schaefferi* [females] – *Escherichia coli*)

(ii) Copepods (e.g. *Acartia*, *Calanus*) (Searching and handling are partly overlapping according to Koehl & Strickler [1981], Paffenhöfer, Strickler & Alcaraz [1982], Strickler [1982], Price, Paffenhöfer & Strickler [1983], Yule & Crisp [1983], Vanderploeg & Paffenhöfer [1985], Price & Paffenhöfer [1986*a*, *b*], Paffenhöfer & Stearns [1988], Schmink [1996], and Bundy & Vanderploeg [2002]: Searching is producing a water current towards the body here. The handling process consists of capturing a food item, transporting it to the mandibles, processing it with the mandibles, and, finally, swallowing it. Food item capture is passive in the case of small items and active for large ones. Accordingly, filter feeding copepods are able to simultaneously capture small items but not large ones. They are also able to search for and to capture a food item while transporting and eating another one.)

Type I (*N* = 15): Richman (1966; lab, c +, f -, s -: *Diaptomus oregonensis – Chlamydomonas reinhardii*, *D. oregonensis* - *Chlorella vulgaris*), Nassogne (1970; lab, c +, f -, s +: *Euterpina acutifrons – Gymnodinium* sp., *E. acutifrons – Platymonas suecica*), Frost (1972; lab, c +, f -, s +: *Calanus pacificus – Centric* sp., *C. pacificus – Coscinodiscus angstii*, *C. pacificus – Coscinodiscus eccentricus*, *C. pacificus – Thalassiosira fluviatilis*), Bartram (1980; lab, c +, f -, s +: *Acartia tonsa* and *Paracalanus parvus – T. fluviatilis*), Deason (1980; lab, c +, f -, s +: *Acartia hudsonica – Skeletonema costatum* [5° C]), Uye (1986; lab, c +, f -, s +: *Acartia erythraea – Chattonella antiqua*, *Calanus sinicus – C. antiqua*, *Centropages yamadai – C. antiqua*, *P. parvus – C. antiqua*, *Pseudodiaptomus marinus – C. antiqua*); **type I dome-shaped** (*N* = 6): Schnack (1983; lab, c +, f -, s +: *Calanus* *helgolandicus – Thalassiosira partheneia*), Muck & Lampert (1984; lab, c +, f -, s +: *Eudiaptomus gracilis – Scenedesmus acutus* [7° C; males or females], *E. gracilis* - *Stichococcus minutissimus* [7° C]), Houde & Roman (1987; lab, c +, f -, s -: *A. tonsa* – *Thalassiosira weissflogii* [growing or senescent] [The authors have classified their curves as type II.])

Type I/II (*N* = 6): Nassogne (1970; lab, c +, f -, s +: *Euterpina acutifrons – Phaeodactylum tricornutum*), Gaudy (1974; lab, c +, f -, s +: *Centropages typicus – Dunaliella* sp.), Muck & Lampert (1984; lab, c +, f -, s +: *Eudiaptomus gracilis – Scenedesmus acutus* [19° C; males or females]), Houde & Roman (1987; lab, c +, f -, s -: *Acartia tonsa – Amphidinium carteri* [experiment 1 or 2] [The authors have classified their curves as type II.])

Type I threshold (*N* = 4): Parsons, LeBrasseur & Fulton (1967; lab, c +, f -, s +: *Calanus pacificus* [and euphausiid furcilia] – nanoplankton, *Pseudocalanus minutus* - microplankton [The authors have classified their curves as type II threshold.]), Gamble (1978; lab, c +, f -, s +: *Calanus finmarchicus – Chaetoceros* spp. and other phytoplankton [date: 25 April – 2 May]), O'Connors, Biggs & Ninivaggi (1980; lab, c +, f -, s +: *Temora longicornis – Rhizosolenia delicatula* and small flagellates); **type I/III** (*N* = 3): Roman (1977; lab, c +, f -, s +: *Acartia tonsa – Nitzschia closterium*), Deason (1980; lab, c +, f -, s +: *Acartia hudsonica – Skeletonema costatum* [10 or 15° C])

Type I/II threshold (*N* = 7): O'Connors *et al.* (1980; lab, c +, f -, s +: *Temora longicornis – Leptocylindrus danicus*, *Cerataulina pelagica*, *Skeletonema costatum*, and *Asterionella japonica*, *T. longicornis – Rhodomonas* spp., *S. costatum*, and *Thalassionema nitschiodes*, *T. longicornis – S. costatum* and *Prorocentrum* sp.), Durbin & Durbin (1992; lab, c +, f -, s +: *Acartia hudsonica – Thalassiosira constricta* [4, 8, 12, or 16° C])

Type II (*N* = 18): Haq (1967; lab, c +, f -, s +: *Metridia longa – Dunaliella* sp.), Esaias & Curl (1972; lab, c +, f -, s +: *Acartia clausi – Gonyaulax acatenella* [low capacity for bioluminescence]), Gaudy (1974; lab, c +, f -, s +: *Calanus helgolandicus – Lauderia borealis*), Schnack (1983; lab, c +, f -, s +: *Calanoides carinatus – Scrippsiella trochoidea*, *C. carinatus – Thalassiosira partheneia*, *C. helgolandicus – S. trochoidea*, *Centropages chierchiae* - *S. trochoidea*, *C. chierchiae – T. partheneia*, *Temora stylifera – S. trochoidea*, *T. stylifera – T. partheneia*), Vanderploeg, Scavia & Liebig (1984; lab, c +, f -, s +: *Diaptomus sicilis –*

Chlamydomonas spp.), Houde & Roman (1987; lab, c +, f -, s -: *Acartia tonsa – Hymenomonas carterae*), Paffenhöfer & Stearns (1988; lab, c +, f -, s +: *Paracalanus sp. – Thalassiosira weissflogii*), Verity & Smayda (1989; lab, c +, f -, s +: *Acartia hudsonica – Skeletonema costatum*, *A. tonsa – S. costatum* [solitary cells or colonies]), Hansen, Tande & Berggreen (1990; lab, c +, f -, s -: *Calanus finmarchicus – Thalassiosira nordenskioeldii*), Dutz (1998; lab, c +, f -, s +: *A. clausi – Rhodomonas baltica*); **type II dome-shaped** (*N* = 6): Haq (1967; lab, c +, f -, s +: *Metridia lucens – Dunaliella* sp.), Esaias & Curl (1972; lab, c +, f -, s +: *Calanus pacificus – Gonyaulax catenella* [low capacity for bioluminescence]), Smayda (1973; lab, c +, f -, s +: *A. clausi – S. costatum* [4 or 10° C]), Gaudy (1974; lab, c +, f -, s +: *Centropages typicus – Ditylium brightwellii*, *T. stylifera – D. brightwellii*)

Type II threshold (*N* = 4): Parsons *et al.* (1967; lab, c +, f -, s +: *Centropages typicus* [and euphausiid furcilia] – microplankton), Parsons *et al.* (1969; lab, c +, f -, s +: *Calanus pacificus – Thalassiosira* spp., *Calanus plumchrus* [3rd and 4th stage] – *Skeletonema costatum* and microflagellates), Esaias & Curl (1972; lab, c +, f -, s +: *Acartia clausi – Gonyaulax acatenella* [high capacity for bioluminescence]); **type II dome-shaped threshold** (*N* = 1): Esaias & Curl (1972; lab, c +, f -, s +: *C. pacificus – G. catenella* [high capacity for bioluminescence])

Type III (*N* = 16): Corner, Head & Kilvington (1972; lab, c +, f -, s +: *Calanus helgolandicus - Biddulphia sinensis*), Gaudy (1974; lab, c +, f -, s +: *Centropages typicus – Asterionella japonica*, *C. typicus – Lauderia borealis*, *C. typicus – Phaeodactylum tricornutum*, *C. typicus – Skeletonema costatum*, *Acartia clausi – P. tricornutum*), Kjørboe, Møhlenberg & Nicolajsen (1982; lab, c +, f -, s +: *Centropages hamatus – Ditylium brightwellii*), Kjørboe, Møhlenberg & Hamburger (1985; lab, c +, f -, s +: *Acartia tonsa – Rhodomonas baltica*), Paffenhöfer & Stearns (1988; lab, c +, f -, s +: *A. tonsa – Thalassiosira weissflogii*), Hansen *et al.* (1990; lab, c +, f -, s +: *Calanus finmarchicus – Phaeocystis pouchetii* [ESD (equivalent spherical diameter) = 30 – 100 µm or ESD > 100µm], *C. finmarchicus – Porosira glacialis*; lab -, s -: *C. finmarchicus – P. pouchetii*, *C. finmarchicus – P. glacialis*), Gismervik & Andersen (1997; lab, c +, f -, s +: *A. clausi – Strobilidium undinum*, *A. clausi – T. weissflogii*); **type III dome-shaped** (*N* = 2): Gaudy (1974; lab, c +, f -, s +: *C. helgolandicus – S. costatum*), Verity & Smayda (1989; lab, c +, f -, s +: *Acartia hudsonica – P. pouchetii*)

Linear (*N* = 14): Fuller (1937; lab, c +, f -, s +: *Calanus finmarchicus – Nitzschia closterium*), Gauld (1951; lab, c ±, f -, s +: *C. finmarchicus* [3rd, 4th, or 5th stages] – *Chlamydomonas* sp., *Centropages hamatus – Chlamydomonas* sp., *Temora longicornis – Chlamydomonas* sp.), Parsons *et al.* (1969; lab, c +, f -, s +: *Calanus plumchrus* [5th stage] – *Skeletonema costatum* and microflagellates), Dagg *et al.* (1980; lab, c +, f -, s +: *Calanus chilensis* – particles, *Centropages brachiatus* – particles, *Eucalanus inermis* – particles), Dagg & Grill (1980; lab, c +, f -, s +: *Centropages typicus* – particles), Muck & Lampert (1980; lab, c +, f -, s +: *Eudiaptomus gracilis – Scenedesmus acutus* [7 or 19° C]), Muck & Lampert (1984; lab, c +, f -, s +: *E. gracilis – Stichococcus minutissimus* [19° C])

Linear threshold (*N* = 3): Roman (1977; lab, c +, f -, s +: *Acartia tonsa – Fucus vesiculosus*), Gamble (1978; lab, c +, f -, s +: *Calanus finmarchicus – Chaetoceros* spp. and other phytoplankton [date: 8 May – 15 May]), Vanderploeg *et al.* (1984; lab, c +, f -, s +: *Diaptomus sicilis* – lake seston)

See also Fig. 5

(iii) Euphausiids (e.g. *Euphausia superba*) (Here, searching and handling are partly overlapping in three of the four different foraging modes documented in the literature. In foraging mode 1, euphausiids pump-and-filter water with their feeding baskets; captured food particles are formed to a food bolus; and pumping-and-filtering is stopped for ingesting the food bolus [Antezana, Ray & Melo, 1982; Hamner *et al.*, 1983; Boyd, Heyraud & Boyd, 1984; Schmink, 1996]. In foraging mode 2, which is performed in case of low food abundances, they sieve the water with their feeding baskets, closing it when enough food has been accumulated [Schmink, 1996]. In foraging mode 3, while swimming just beneath the surface, they "hold one branch of each antennule out of the water" [Hamner *et al.*, 1983] to capture floating particles from the surface film. In foraging modes 1, 2, and 3, euphausiids can simultaneously capture food items but cannot capture a food item while ingesting another. In foraging mode 4, filter feeding euphausiids rake algae off ice [Hamner *et al., 19*83; Schmink, 1996], i.e. searching and handling are mutually exclusive.)

Type I (*N* = 1): Boyd *et al.* (1984; lab, c -, f -, s +: *Euphausia superba* - algae)

Type I threshold (*N* = 1): Parsons *et al.* (1967; lab, c +, f -, s +: *Euphausia pacifica* - microplankton [The authors have classified their curve as type II threshold.])

Type III (*N* = 4): Boyd *et al.* (1984; lab, c -, f -, s +: *Euphausia superba* – ciliates), Ohman (1984; lab, c +, f -, s +: *Euphausia pacifica – Thalassiosira angstii*), Stuart (1986; lab, c +, f -, s +: *Euphausia lucens – Thalassiosira weissflogii*), Pilditch & McClatchie (1994; lab, c +, f -, s +: *Nyctiphanes australis – Chaetoceros gracilis* [The authors have classified their curve as type II.])

Linear threshold (*N* = 2): Parsons *et al.* (1967; lab, c +, f -, s +: *Euphausia pacifica* - nanoplankton), McClatchie (1986; lab, c +, f -, s -: *Thysanoessa raschii – Chaetoceros gracilis*)

(iv) Thalassinidean decapods (e.g. *Upogebia*) (searching and handling are partly overlapping according to Lindahl & Baden [1997])

Type III (*N* = 1): Lindahl & Baden (1997; lab, c -, f -, s -: *Upogebia deltaura – Artemia salina*)

(h) Insect larvae: black flies (searching and handling are partly overlapping according to Schröder [1980*a*], Merritt & Wallace [1981], and Hart & Latta [1986])

Type I (*N* = 3): Schröder (1980*b*; lab, c +, f -, s -: *Odagmia ornata – Nitzschia actinastroides* [current velocity = 31, 42, or 104 cm/s])

Type I/II (*N* = 2): Hart & Latta (1986; lab, c +, f -, s -: *Prosimulium mixtum* / *fuscum* – pollen of *Corylus californica* [10 or 120 min])

(i) Bryozoans (searching and handling are completely overlapping according to Riisgård & Manríquez [1997])

Type I (*N* = 3): Bullivant (1968; lab, c -, f -, s +: *Zoobotryon verticillatum – Dunaliella tertiolecta*, *Z. verticillatum – Monochrysis lutheri*, *Z. verticillatum – Phaeodactylum tricornutum*)

Type I/II (*N* = 2): Bullivant (1968; lab, c -, f -, s +: *Zoobotryon verticillatum – Cricosphaera carterae* [The author has classified his curve as type I.]), Lisbjerg & Petersen (2001; lab, c -, f -, s +: *Electra crustulenta – Rhodomonas* sp.)

(j) Echinoderms: crinoids (searching and handling are completely overlapping according to Jørgensen [1966])

Type II dome-shaped (*N* = 1): Leonard (1989; lab, c -, f -, s -: *Antedon mediterranea* – *Hymenomonas elongata*)

(k) Tunicates

(i) Ascidians (searching and handling are completely overlapping according to Goldschmid [1996])

Type I (*N* = 6): Robbins (1983; lab, c +, f -, s -: *Ascidiella scabra* – Fuller's earth; lab, c -, f -, s -: *Ciona intestinalis* – Fuller's earth [5, 10, or 15° C]), Petersen & Riisgård (1992; lab, c +, f -, s +: *C. intestinalis* [small or large] – *Rhodomonas* sp.)

Type II (*N* = 2): Petersen, Schou & Thor (1995; lab, c +, f -, s +: *Ciona intestinalis* – *Rhodomonas* sp. and particulate organic matter [experiment 2 or 3])

(ii) Thaliaceans (searching and handling are completely overlapping according to Goldschmid [1996])

Type I dome-shaped (low consumption rate at high food abundances probably caused by "clogging" [see Harbison & Gilmer (1976), Harbison, McAlister & Gilmer (1986)]) (*N* = 1): Andersen (1985; lab, c +, f -, s +: *Salpa fusiformis* [blastozooids] – *Phaeodactylum tricornutum* [The author has classified his curve as type II.])

Type I/II (*N* = 1): Andersen (1985; lab, c +, f -, s +: *Salpa fusiformis* [oozooids] – *Phaeodactylum tricornutum* [The author has classified his curve as type II.])

(l) Anuran larvae (searching and handling are completely overlapping according to Kenny [1969])

Type III (*N* = 6): Seale & Wassersug (1979; lab, c -, f -, s +: *Rana sylvatica* – *Chlorella pyrenoidosa*), Seale & Beckvar (1980; lab, c -, f -, s +: *Bufo woodhousei fowleri* – *Anabaena sphaerica*, *Hyla crucifer* – *A. sphaerica*, *Rana catesbeiana* – *A. sphaerica* [The authors have classified their curves as type II threshold.]), Seale (1982; lab, c -, f -, s -: *Rana pipiens* – *Saccharomyces cerevisiae*, *Xenopus laevis* – *S. cerevisiae* [The author has classified her curves as type II threshold])

VIII. APPENDIX B: A FORMAL JUSTIFICATION OF THE TWO CONDITIONS FOR A TYPE I FUNCTIONAL RESPONSE

(1) Searching and handling are mutually exclusive

A basic functional response model that has been designed for consumers for which the processes searching for food and handling it are mutually exclusive is the SSS equation (Jeschke *et al.*, 2002). An underlying assumption is that the consumer's searching effort ($\alpha(h) = \alpha(h(x))$ =) $\alpha(x)$ [$0 \le \alpha(x) \le 1$], when it is currently not handling food, equals its hunger level $h(x)$:

$$\alpha(x) = h(x) = 1 - c\,y(x), \tag{A1}$$

where x is food abundance and $y(x)$ is consumption rate. For the dimensions in SI units of all parameters given in this section, see Jeschke *et al.* (2002), except for food abundance x: its dimension is 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. It is not, as wrongly given in Jeschke *et al.* [2002], individuals/m^2 or individuals/m^3, respectively. To allow correct cancellation of units, the unit "individuals" must either be excluded from or included in the dimensions of all relevant parameters. Since we, the authors of Jeschke *et al.* [2002], have given the dimensions in SI units, "individuals" was excluded from all dimensions. Without asking us, however, somebody has changed the dimension of food abundance x to individuals/m^2 or individuals/m^3, respectively, but let the other dimensions unchanged.

In eq. A1, searching activities are assumed to increase linearly with hunger level. Searching effort is the product of searching probability (of a consumer that is currently not handling food) and searching intensity. Hence, for consumers that do not vary the intensity of searching (this is more or less true for cruising carnivores), searching effort equals searching probability.

Here, we want to make a more flexible and therefore more realistic assumption for searching effort $\alpha(x)$:

$$\alpha(x) = \frac{dh(x)}{1+(d-1)h(x)} = \frac{d(1-cy(x))}{1+(d-1)(1-cy(x))}, \tag{A2}$$

where c is the (corrected) digestion time of the consumer and d [$0 \le d < \infty$] is a dimensionless shape parameter (Figs. A1a, b, c): for $d = 1$, eq. A2 is identical to eq. A1 (the graph of $\alpha(h(x))$ is linear, see Fig. A1a); for $d < 1$, $\alpha(x)_{A2} \le \alpha(x)_{A1}$ (the graph of $\alpha(h(x))$ is accelerating); and for $d > 1$ (which may be valid for most consumers), $\alpha(x)_{A2} \ge \alpha(x)_{A1}$ (the graph of $\alpha(h(x))$ is decelerating).

Using eq. A2 instead of A1 leads to the following functional response equation:

$$y(x)=\begin{cases}\dfrac{d(1+ax(b+c))-\sqrt{d(4acx+d(1+ax(b-c))^2)}}{2c(d(1+abx)-1)} & c>0, x\neq\dfrac{1-d}{abd}\\ \dfrac{ax}{1+abx} & c=0, x\neq\dfrac{1-d}{abd}\\ \dfrac{1-d}{b+c(1-d)} & x=\dfrac{1-d}{abd}\end{cases}, \tag{A3}$$

where *a* is the consumer's success rate and *b* is its (corrected) handling time. For the SSS equation and eq. A3, the gradients at the origin and the asymptotic maximum consumption rates are identical:

$$\begin{aligned}&\frac{dy(0)}{dx}=a\\ &\lim_{x\to\infty}\; y(x)=\min\left(\frac{1}{b},\frac{1}{c}\right).\end{aligned} \tag{A4}$$

As the SSS equation, eq. A3 generally produces type II functional responses (Fig. A1d). In case of large values for the shape parameter *d*, however, eq. A3 produces type I-like curves. This results from a step-like relationship between searching effort and hunger level (Fig. A1a). For the limiting case $d\to\infty$, this relationship (eq. A3) becomes a real step function:

$$\begin{aligned}&\alpha(x)=\begin{cases}1 & x\leq x^*\\ \dfrac{1}{ax(c-b)} & x>x^*\end{cases}\\ &\text{with } x^*=\frac{1}{a(c-b)}.\end{aligned} \tag{A5}$$

The functional response eq. A3 then simplifies to

$$\begin{aligned}&y(x)=\begin{cases}\dfrac{ax}{1+abx} & x\leq x^*\\ \dfrac{1}{c} & x>x^*\end{cases}\\ &\text{or}\\ &y(x)=\min\left(\frac{ax}{1+abx},\frac{1}{c}\right).\end{aligned} \tag{A6}$$

The gradients at the origin and the asymptotic maximum consumption rates of the SSS equation, eq. A3, and eq. A6 are identical (see eq. A4). Equation A6 can also be derived by extending the disc equation by a digestive capacity constraint (Schmitz, 1995).

Depending on handling time *b*, eq. A6 produces functional responses of type I, I/II, or II (Fig. A2). Since eq. A6 is based on the assumption that $d\to\infty$, all curves have a sharp transition between their rising and their constant part (if there is a constant part at all). (1) For $b=0$, handling time does not affect consumption rate. The functional response therefore has a linearly rising part ($x \leq x^*$). Above the incipient limiting level ($x > x^*$), digestion time limits consumption rate which is constant here. Thus, the functional response is of type I. (2) For $0 < b < c$, handling time gradually decreases the slope of the curves in their rising part, and the rising part is therefore not linear. However, the curves do have a constant part determined by digestion time. Thus, these curves are intermediate between type I and II. (3) Finally, for $b \geq c$, handling time gradually decreases the slope of the curve in its rising part. The rising part is therefore not linear. In addition, no constant part exists because consumption rate becomes limited by handling time before it can be limited by digestion time (mathematically, x^* is negative and has therefore no biological meaning). Thus, the curve is of type II.

In summary, when searching and handling are mutually exclusive, a consumer must fulfil two necessary but not sufficient conditions to show a type I functional response: (1) *Handling condition*. It must have a negligibly small handling time ($b = 0$). (2) *Satiation condition.* Unless its gut is filled completely, it must search for food at a maximum rate with maximum effort ($d \rightarrow \infty$).

(2) Searching and handling are completely overlapping

If searching and handling are completely overlapping, the consumer is able to search for and to capture food while handling other food. Therefore, its handling time does not affect its consumption rate. The handling condition for a type I functional response must therefore be extended as follows: The consumer must have a negligibly small handling time, *or* it must be able to search for and to capture food while handling other food.

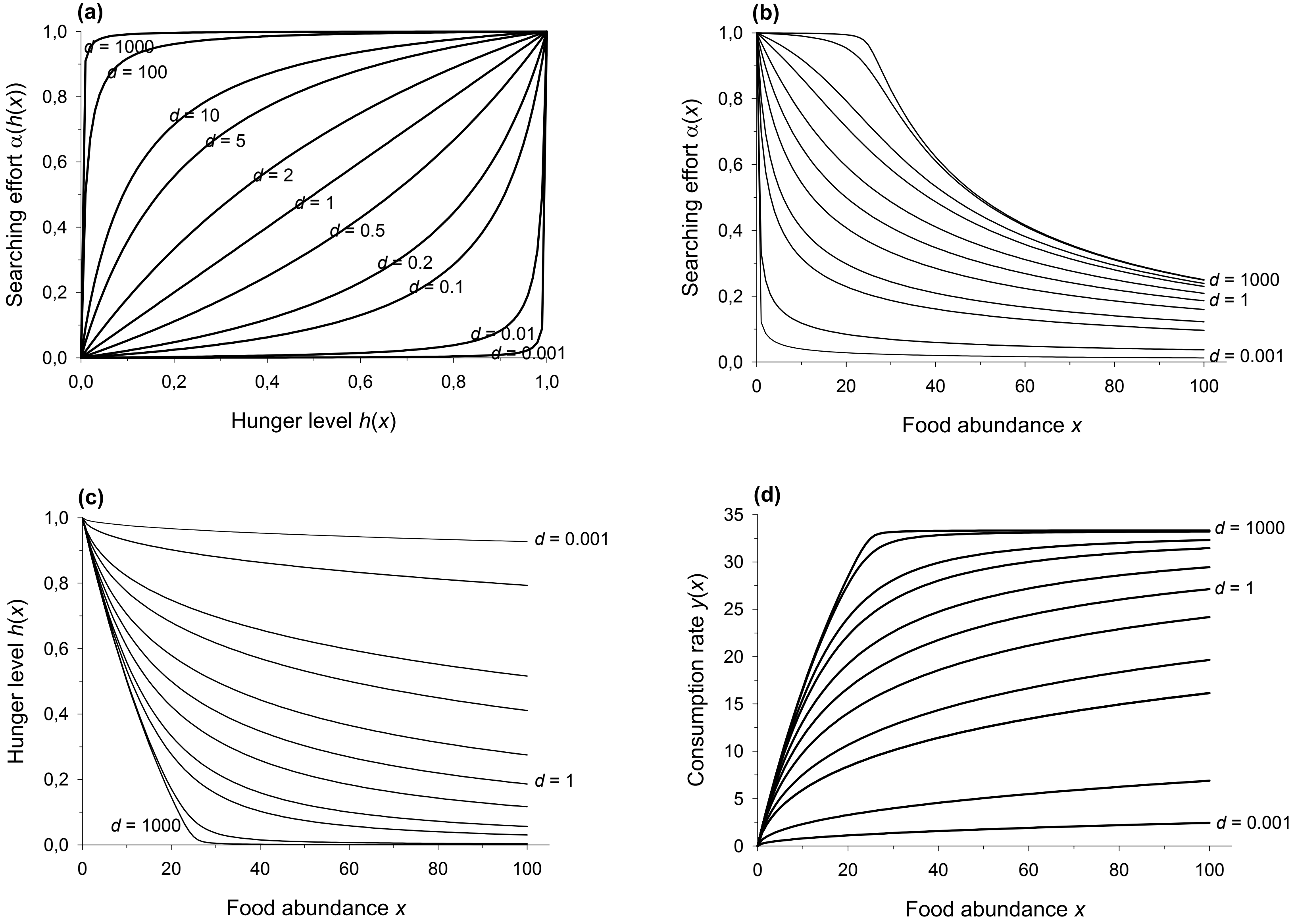

(a)
Searching effort α(h(x))
Hunger level h(x)
1,0
0,8
0,6
0,4
0,2
0,0
0,0
0,2
0,4
0,6
0,8
1,0
d = 1000
d = 100
d = 10
d = 5
d = 2
d = 1
d = 0.5
d = 0.2
d = 0.1
d = 0.01
d = 0.001
(b)
Searching effort α(x)
Food abundance x
1,0
0,8
0,6
0,4
0,2
0,0
0
20
40
60
80
100
d = 1000
d = 1
d = 0.001
(c)
Hunger level h(x)
Food abundance x
1,0
0,8
0,6
0,4
0,2
0,0
0
20
40
60
80
100
d = 0.001
d = 1
d = 1000
(d)
Consumption rate y(x)
Food abundance x
35
30
25
20
15
10
5
0
0
20
40
60
80
100
d = 1000
d = 1
d = 0.001

Fig. A1. Graphical representations of eqs. A2 (**a**, **b**) and A3 (**c** [note that $h(x) = 1 - c\,y(x)$], **d**) with different values for the shape parameter d. In **a**, d determines the gradient at the origin. For $d = 1$, eq. A2 is identical to A1 and consequently, eq. A3 is identical to the SSS equation. In **d**, it can be seen that eq. A3 generally produces type II functional responses. For large values of d, however, these become type I-like. This results from a step-like relationship between searching effort and hunger level (**a**). Other model inputs: success rate $a = 2$, handling time $b = 0.01$, digestion time $c = 0.03$.

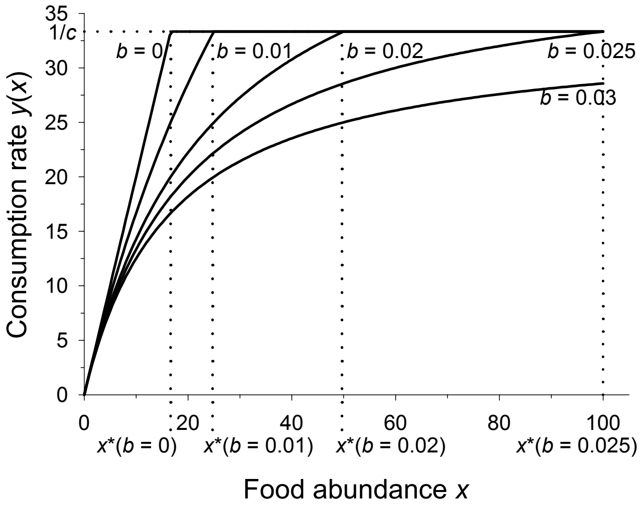


Fig. A2. A continuum (handling time $b = 0.01, 0.02, 0.025$) between type I ($b = 0$) and type II ($b = 0.03$) functional responses (according to eq. A6). It can be seen that, if searching and handling are mutually exclusive (this is assumed by eq. A6), a consumer can only show a type I functional response, if its handling time is negligibly small. Other model inputs: success rate $a = 2$, digestion time $c = 0.03$. For $b = c$ (= 0.03 here), eq. A6 equals the disc equation (Holling, 1959*b*: $y(x) = (ax) / (1 + abx)$). The incipient limiting levels x^* are according to eq. A6: $x^*(b = 0) = 16.67$, $x^*(b = 0.01) = 25$, $x^*(b = 0.02) = 50$, and $x^*(b = 0.025) = 100$. For all curves, asymptotic maximum consumption rate is 33.33 (eq. A4).

Correlates and Consequences of Predator Confusion

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ABSTRACT

When confronted by a swarm of their prey, many predators become confused and are thus less successful in their attacks. It is unknown how widespread this confusion effect is and largely unknown which predator or prey traits facilitate or impede it. We therefore performed corresponding experiments in the predator-prey systems *Aeshna cyanea* (Odonata) – *Daphnia magna* (Crustacea), *Libellula depressa* (Odonata) – *D. magna*, *Chaoborus obscuripes* (Diptera) - *Daphnia obtusa*, and *Triturus alpestris* (Alpine newt) – *D. obtusa*. We combine our results with literature data and find that predators have become confused in 70% of the 20 predator-prey systems studied to date. Tactile predators appear to be generally susceptible, whereas visual predators seem susceptible only if their prey is highly agile. This difference arguably results from the superiority of the latter in singling out individual prey. To allow a better understanding of the ecological, ethological, and evolutionary consequences of predator confusion, we examine its effects on functional responses. We theoretically and empirically show that the widespread assumption confusion would let a functional response become dome-shaped is not necessarily true. The response can alternatively remain qualitatively unchanged and is affected only in a quantitative way. Thus, a non-dome-shaped response is no indication for the absence of predator confusion.

Introduction

When and why do organisms aggregate? At present, we naturalists cannot offer a short answer to this question. We can only list examples where we know or think to know the answer and thereafter sort these examples (Fig. 1). This approach provides us with several categories of reasons for gregariousness, one being a defensive function. The present study focuses on one mechanism behind such a defensive function: the confusion effect which is present if predators that are confronted with a swarm of their prey are restricted by their neuronal abilities, causing them to be less successful in their attacks (references are given below Fig. 1 and Table 1).

Experimental work investigating whether a certain predator suffers from confusion is rare compared to the popularity of this concept and has mainly been restricted to two biological taxa, fishes and birds (Table 1). In an effort to expand the availability of empirical work on this subject, we performed experiments in the four predator-prey systems *Aeshna cyanea* (Odonata) – *Daphnia magna* (Crustacea), *Libellula depressa* (Odonata) – *D. magna*, *Chaoborus obscuripes* (Diptera) - *Daphnia obtusa*, and *Triturus alpestris* (Alpine newt) – *D. obtusa*. We combine our results with data available from the literature in order to investigate, first, whether or not predator confusion is a widespread phenomenon and, second, which predator or prey traits facilitate or impede it. To our knowledge, neither question has been addressed before.

In addition, to allow for a better understanding of the ecological, evolutionary, and ethological consequences of predator confusion, we examine its effects on predator functional responses, i.e. on the relationships between predation rate and prey density (Solomon 1949). Functional responses are usually classified by their shape into three main classes: type I (predation rate increases linearly with prey density up to a threshold and is constant beyond), type II (the increase is decelerating), or type III (the increase is sigmoid) (Holling 1959*a*, Jeschke et al., submitted). Functional responses can help us understanding population dynamics because they link together different trophic levels. They may also reveal evolutionary insights since they include the important fitness determinants energy intake and mortality risk. Lastly, they may shed light on animal behavior, for this is often adaptive and thus influenced by energy intake or mortality risk. On the basis of our review of empirical data on predator confusion and our own experiments, we develop the first functional response model on this subject. We qualitatively and quantitatively compare the functional responses simulated by this model to the ones we measured in our experiments, thereby revealing new insights into the effects of predator confusion on functional responses and demonstrating the high predictive power of our model.

Materials and Methods

THE FREQUENCY AND THE CORRELATES OF PREDATOR CONFUSION

Our experiments

In each of our four predator-prey systems, we transferred a single predator to a defined number of *Daphnia*, thereby confronting it with a large range of prey densities, up to those occurring naturally in swarms (cf. Malone and McQueen 1983, Davies 1985, Kvam and Kleiven 1995). In each experiment, we counted the number of attacks as well as the number of prey eaten and calculated predator attack efficiency as the ratio of the latter to the former. Since *Libellula* larvae did not always eat the prey they successfully attacked and thus killed, we additionally counted the number of these “wasteful kills” (Johnson et al. 1975) and added it to the number of prey eaten. To investigate whether a predator species becomes confused due to *Daphnia* swarms, we tested whether attack efficiency is negatively correlated with prey density by performing one-tailed rank correlation tests with Spearman’s correlation coefficient r_{Sp}. All statistical analyses were carried out with SPSS for Windows 10.1.3 (SPSS Inc. 2001). The predators were caught in southern Bavarian ponds, and the prey came from laboratory cultures that originated from such ponds. Furthermore, all experiments were performed at room temperature and experimental time began with the first attack of the predator. Except for *T. alpestris* – *D. obtusa*, eaten prey were not replaced. In the following, we give additional information on the organisms used and experimental conditions specific to each of our four predator-prey systems.

Aeshna cyanea (Odonata) – *Daphnia magna*. Larvae of *A. cyanea* are visual predators that can switch between an ambush and a cruising foraging tactic (Pritchard 1965). We used pre-fed larvae with five individuals at each prey density except at 200 where we used four. The prey were 3rd and 4th instar *D. magna*, the experimental volume was 280 mL and the duration 2 min.

Libellula depressa (Odonata) – *Daphnia magna.* Larvae of *L. depressa* are ambush predators that hunt their prey by visual and tactile means (Pritchard 1965). Here we worked with pre-fed larvae (mean length = 13 mm) and used six individuals at each prey density except at 100 where we used five. We worked with 4th juvenile instar to 2nd adult instar *D. magna* in an experimental volume of 200 mL and a duration of 10 min.

Chaoborus obscuripes (Diptera) - *Daphnia obtusa* (Crustacea). Kvam and Kleiven (1995) suggested that daphnids sometimes form swarms in order to defend themselves against *Chaoborus* larvae. In our experiments, we used pre-starved 4th instar larvae (mean length = 11.6 mm), ten individuals at each prey density. For these tactile hunting ambush predators, we defined an attack as a jerky movement directed to a near prey (Duhr 1955, Swift and Fedorenko 1975, Smyly 1979). To standardize the *Daphnia* to an equal size, we sieved them and used those that passed a 500 µm gauze but were retained by a 200 µm one. The experimental volume was 40 mL and the duration 30 min.

Triturus alpestris (Amphibia: Caudata; Alpine newt) – *Daphnia obtusa*. Alpine newt larvae are visually hunting and apply a cruising foraging tactic (RT, personal observation). We used pre-fed newts (mean length = 25.8 mm), six individuals at each *Daphnia* density except at 60 and 100 where we used five. The experimental volume was 400 mL and the duration 10 min.

The comparative analysis

To investigate whether predator confusion is a widespread phenomenon and which predator or prey traits facilitate or impede it, we must combine the results of our experiments with those of previous studies, for which we searched the databases BIOSIS and ISI Web of Science. In these studies, together with those cited therein, we have found data from 19 predator-prey systems, in addition to our four making a total of 23 systems (Table 1).

Since predator confusion might correlate to the degree of prey agility (Eibl-Eibesfeldt 1962, Humphries and Driver 1970, Ohguchi 1981), we tried to quantify this trait. It must be related to the agility of the predator’s prey-catching organ and should ideally include speed, acceleration, and maneuverability (see also Howland 1974). The degree of prey position predictability (where the prey will be in the next moment) is indirectly included in prey maneuverability because these should be negatively correlated. Data are scarce, however, especially for maneuverability. When possible, we calculated relative prey agility as relative prey speed (i.e. prey escape speed divided by predator attack speed) or relative prey acceleration (i.e. prey escape acceleration divided by predator attack acceleration). Otherwise, we classified relative prey agility subjectively.

THE EFFECTS OF PREDATOR CONFUSION ON FUNCTIONAL RESPONSES

The model

To allow for a better understanding of the ecological, ethological, and evolutionary consequences of predator confusion, we develop a corresponding functional response model. It is based on the SSS equation (Jeschke et al. 2002):

$$y(x)=\begin{cases}\dfrac{\left(1+ax(b+c)-\sqrt{1+ax\left(2(b+c)+ax(b-c)^2\right)}\right)t}{2abcx} & a,b,c,x>0\\ \dfrac{atx}{1+abx} & b>0, c=0\\ \dfrac{atx}{1+acx} & b=0, c>0\\ atx & b=c=0\\ 0 & a=0 \quad \text{or} \quad x=0\end{cases}$$

with success rate $a=\beta\gamma\delta\varepsilon$ (1)

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

where β is the encounter rate between a searching predator and a single prey item [dimension in SI units: m^2 sec^{-1} for two-dimensional, e.g. terrestrial, habitats; m^3 sec^{-1} for three-dimensional, e.g. aquatic, habitats]; γ is the probability that the predator detects encountered prey [dimensionless]; δ is the probability that the predator attacks detected prey [dimensionless]; ε is the efficiency of attack [dimensionless]; c is the digestion time per prey item [sec]; t is total time [sec], i.e. the length of the time interval of interest, e.g. one day or the duration of an experiment; t_{att} is attacking time per prey item [sec]; t_{eat} is eating time per prey item [sec]; x is prey density [m^{-2} or m^{-3}, respectively]; and y is the number of prey eaten [dimensionless].

To simulate the functional response of a predator that shows a confusion effect, the constant ε in the SSS equation has to be replaced by an attack efficiency $\varepsilon(x)$ that is free to decrease with increasing prey density x. The empirical data summarized in Table 1 as well as Krakauer's (1995) neural network model indicate that in predators showing a confusion effect, this decrease is decelerating and that attack efficiency mostly does not fall below a minimum value which corresponds to complete confusion:

$\varepsilon(x) = \exp(-\varepsilon_s x) \cdot (\varepsilon_{max} - \varepsilon_{min}) + \varepsilon_{min}$, (2)

where ε_{max} (= $\varepsilon(0)$) is the maximum efficiency of attack [dimensionless]; ε_{min} (= $\lim_{x\to\infty} \varepsilon(x)$) is the minimum efficiency of attack [dimensionless]; and ε_s [dimensionless] is a shape parameter that regulates the curve's decrease with increasing prey density x (Fig. 2). If ε_{min} is zero, eq. 2 simplifies to: $\varepsilon(x) = exp\ (-\varepsilon_s\ x) \cdot \varepsilon_{max}$. For example, this simplified equation is applicable to peregrine falcons (*Falco peregrinus*) preying on redshanks (*Tringa totanus*) (Cresswell 1994).

Analysis of empirical functional responses

To empirically investigate how predator confusion affects functional responses, we analyzed the responses of those predators that showed a confusion effect. We thereby fitted a logistic regression model to the number of prey eaten vs. prey density (Trexler et al. 1988, Hosmer and Lemeshow 1989, Juliano 1993, Sokal and Rohlf 1995, Jeschke and Tollrian 2000). Furthermore, in order to check whether the number of prey eaten decreased at high prey densities (i.e. broad sense dome-shaped response, otherwise type II response), we compared the mean number of prey eaten at high densities to that at intermediate ones via *t*-tests (for unequal variances if necessary).

The predictive power of the model

To allow a quantitative evaluation of our model, it must be adapted to the experimental conditions. Two main assumptions underlying our model are that prey density and predator hunger level are constant (Jeschke et al. 2002). These assumptions are more or less valid in the field, but are usually violated in laboratory studies, including this one, where eaten prey are normally not replaced and the predators are often pre-starved (reviewed by Jeschke et al., submitted). Therefore, by allowing prey density to decrease and the hunger level to vary, we extend the steady-state satiation (SSS) equation (eq. 1) to the satiation model (eqs. A1, A2, A3; Appendix 1). We combine the satiation model with eq. 2, which simulates predator confusion, and compare it to the functional response from the predator-prey system where the necessary data to parameterize the model are available: *Chaoborus obscuripes* - *Daphnia obtusa* (for model parameter values, see Appendix 2).

Results

THE FREQUENCY AND THE CORRELATES OF PREDATOR CONFUSION

Our experiments

Aeshna cyanea preying on *Daphnia magna* ($r_{Sp} = -0.784$, $P < 0.001$) as well as *Chaoborus obscuripes* preying on *Daphnia obtusa* ($r_{Sp} = -0.630$, $P < 0.001$) showed a confusion effect, whereas *Libellula depressa* preying on *D. magna* ($r_{Sp} = 0.242$, i.e. attack efficiency increased with prey density here) and *Triturus alpestris* preying on *D. obtusa* (r_{Sp} = -0.108, P = 0.210) did not (Fig. 3). For both predators suffering from confusion, the relationship between attack efficiency and prey density agrees with the usual pattern considered in eq. 2: the decrease in attack efficiency is decelerating and attack efficiency apparently does not fall below a minimum value.

The comparative analysis

Three of the 23 predator-prey systems summarized in Table 1 are excluded from our analysis because of ambiguous results. In the remaining 20 systems, the overall frequency of confusion is 70%.

The occurrence of predator confusion appears to be influenced by both the mode of prey detection and the degree of prey agility. A hypothetical a posteriori model predicting the occurrence of confusion based on these two traits is outlined in Fig. 4. The prediction of this model is correct for 18 of the 20 predator-prey systems (= 90%). Predators that do not actively detect their prey should not become confused at all. This agrees with empirical data from the carnivorous plant *Utricularia vulgaris* and the passively filter feeding copepod *Acartia tonsa*. Conversely, both tactile predators investigated so far, *Chaoborus obscuripes* and the nematode *Prionchulus punctatus*, showed a confusion effect. In visual predators, finally, confusion seems to correlate to the degree of prey agility (see also Eibl-Eibesfeldt 1962, Humphries and Driver 1970, and Ohguchi 1981): while the frequency of confusion is 92% for highly agile prey (N = 12), it is only 25% for slightly agile prey (N = 4), and the correlation between the occurrence of confusion in visual predators and the degree of prey agility (low or high) is significant ($P < 0.01$, r_{Sp} = 0.667, one-tailed Spearman rank correlation test).

THE EFFECTS OF PREDATOR CONFUSION ON FUNCTIONAL RESPONSES

Theoretical results

The analysis of our model revealed that predator confusion can affect a functional response in three different ways (Fig. 5). First, the response can become dome-shaped in the narrow sense, i.e. at high prey densities, prey uptake decreases towards zero. Second, the response can become roller-coaster-shaped (this is a new type of functional response), i.e. at high prey densities, prey uptake decreases but stops decreasing before it becomes zero and rises again to reach a plateau. For most species, however, this plateau probably lies beyond naturally occurring prey densities. These two response types may be summarized as dome-shaped in the broad sense, i.e. prey uptake decreases at high prey densities. Third, the functional response can remain qualitatively unchanged and is affected only quantitatively: type II remains type II but the plateau is lowered and is reached earlier. The conditions leading to each of these three types of functional response are outlined in Fig. 6.

Empirical results

The functional responses of the predators that showed a confusion effect in our experiments are given in Fig. 7. Larval *Aeshna cyanea* showed a roller-coaster-shaped response: at high prey densities, prey uptake decreased but stopped decreasing before it became zero (the difference in the number of prey eaten between intermediate prey densities [50, 100, 150] and high prey densities [200 and 250] is significant [$P < 0.01$, one-tailed *t*-test]). The maximum number of prey eaten in 2 min was 8.6 (at prey density 100). The functional response of *Chaoborus obscuripes* preying on *Daphnia obtusa* may be classified as type II because the predation rates that were observed at the two highest prey densities do not significantly differ ($P = 0.308$, one-tailed *t*-test for unequal variances). The maximum number of prey eaten in 30 min was 10.5 (at prey density 50).

The predictive power of the model

As shown in Fig. 7a, the functional response of *Chaoborus obscuripes* preying on *Daphnia obtusa* predicted by our model agrees well with the observed one: $r = 0.612$, $r_{Sp} = 0.664$ ($P < 0.001$, two-tailed). These values are similar to those of a logistic regression fit of the empirical data: $r = 0.624$, $r_{Sp} = 0.647$ ($P < 0.001$, two-tailed). Some readers might object that three of the ten parameter values given in Appendix 2 depend on *Daphnia* body length and this is only approximate because the daphnids were sieved for the experiments. However, our model is insensitive to changes in *Daphnia* body length. Using 0.8 mm for *Daphnia* body length instead of 0.7 mm results in $r = 0.610$ (instead of 0.612) and r_{Sp} remains constant. Thus, the predictive power of our model appears to be high.

Discussion

THE FREQUENCY OF PREDATOR CONFUSION

Predator confusion appears to be a widespread phenomenon, as it is observed in 70% of the 20 predator species investigated to date. However, a problem of such a comparative analysis is the bias of the underlying data. Positive results are more likely to be published than negative ones. Therefore, the ‘true’ frequency of predator confusion is probably lower than

70%. Restricting the analysis to data free of publication bias, i.e. our four predator-prey systems, reduces the frequency to 50%, though this is a small sample size.

TACTILE VS. VISUAL PREDATORS

We found that tactile predators seem generally susceptible to confusion, whereas visual predators seem susceptible only if their prey is highly agile. The finding for tactile predators is again hampered by a small sample size, but assuming its validity, we must address the question where the difference between tactile and visual predators comes from. Confusion has been empirically (Ohguchi 1981, Landeau and Terborgh 1986) and theoretically (Krakauer 1995) shown to decrease if a prey swarm includes odd individuals. Thus, confusion appears to decrease when it is easier for a predator to single out individual prey. Predators surely differ in their ability to do so, and our findings suggest that visual predators are in this regard superior over tactile ones. This suggestion makes sense first because singling out an individual means to detect one or more differences between this and other members of the swarm. Second, the probability to detect such differences increases with the amount of information provided by the sensory organs per unit of time, which is known to be larger for eyes than for mechanoreceptors (Dusenbery 1992).

An objective evaluation of the suggestion that visual predators are better able to single out individual prey than tactile ones may be possible, though not easy. One option is to look at a predator's probability of attack δ (see above and Jeschke et al. 2002), which is the ratio of the number of attacks launched by the predator per unit of time to the number of prey items it encounters and detects per unit of time, corrected for satiation, handling, and simultaneous encounters (for predators such as *Chaoborus* larvae or lions that are unable to simultaneously attack several individuals; cf. Jeschke et al., submitted). Assuming that visual predators are better than tactile ones in singling out prey, δ will decrease with swarm density for visual predators but will be roughly independent of swarm density for tactile predators. Although δ can hardly be measured, one can estimate the relationship between δ and prey density for thoroughly investigated predator-prey systems, e.g. for our *Chaoborus-Daphnia* system. The parameterized satiation model (Appendices 1, 2) is able to adequately predict the *Chaoborus* functional response in this system (Fig. 7a) as well as the relationship between *Chaoborus* attack rate and *Daphnia* density (Fig. 8). In this model, the probability of attack δ is independent of prey density, supporting the suggestion that tactile predators are inferior to visual ones in their ability to single out individual prey.

IMPLICATIONS FOR FUNCTIONAL RESPONSES

In this study, we have provided the first functional response model that includes predator confusion (cf. Jeschke et al. 2002). As suggested by the quantitative agreement of our model to the empirical data, the consideration of success rate, handling time, digestion time, and swarming effects that reduce predator foraging success (cf. Fig. 1) is sufficient to adequately predict a laboratory functional response. While success rate is important for all predator-prey systems under all experimental conditions, the relative importance of the three other factors is variable. For example, handling time is especially important in short-term experiments, whereas digestion time is especially important in long-term experiments. In the field (and elaborate laboratory experiments), additional determinants important to a functional response are learning, switching, and adaptive behavior (reviewed by Jeschke et al. 2002).

According to conventional wisdom, confusion and other effects that reduce foraging success (cf. Fig. 1) let functional responses become dome-shaped (Young et al. 1994, Watt and Chapman 1998). We have both theoretically and empirically shown that they can also remain qualitatively unaffected. This finding is for example important to the following three topics:

- *Functional responses used as indicators.* According to our finding, a non-dome-shaped response indicates neither the presence nor absence of swarming effects that reduce foraging success (cf. Fig. 1). On the other hand, a dome-shaped response in the broad sense indicates that at high prey densities, the predator either shows such a swarming effect or avoids unpalatable prey due to learning (Holling 1965, see also Heinrich and Vogt 1980 and Brönmark et al. 1984).
- *How common are swarming effects that reduce foraging success?* Such swarming effects must be more common than dome-shaped responses in the broad sense. This finding resolves the apparent paradox that dome-shaped responses are rarer than swarming effects (cf. Jeschke et al., submitted).
- *Fitting functional responses*. Type II responses have mostly been fitted with either the disc equation (Holling 1959*b*), the random predator equation (Royama 1971, Rogers 1972), or the Gause-Ivlev equation (Gause 1934, Ivlev 1961). Regression equations obtained in this way include one parameter that represents the maximum number of prey eaten. For example, in the disc and the random predator equation, the parameter “handling time” t_h is the reciprocal value of the maximum number of prey eaten. Our results demonstrate that the term “handling time” is misleading: real handling time and the parameter t_h have little in common (see also Fox and Murdoch 1978, Abrams 1990, Caldow and Furness 2001, and Jeschke et al. 2002). This is because the maximum number of prey eaten is naturally

determined by many factors including handling time, digestion time, learning, switching, adaptive behavior, and - as shown here - swarming effects that reduce foraging success. These factors are amalgamated by the parameter t_h in an unknown way. Therefore, the value of the parameter t_h obtained by fitting an empirical functional response cannot be biologically interpreted.

OUTLOOK

This study is intended as a step towards an understanding of the mechanisms behind predator confusion and its ecological, evolutionary, and ethological consequences. In an effort to motivate others to join us on this way, we close with suggestions for future research. First, our comparison of the influence of the mode of prey detection and the degree of prey agility on the occurrence of predator confusion may be extended by considering further potentially important animal traits, such as the size of the prey relative to the predator's prey-catching organ (relatively smaller prey allow less precise attacks) or the amount of change in light reflection from the prey's bodies (Treherne and Foster 1981). Such a comparison may for example reveal counter-adaptations of predators that prevent them from becoming confused. Second, since our finding that tactile predators seem especially susceptible to confusion is hampered by a small sample size, we suggest to investigate whether it holds for tactile predators other than *Chaoborus* and *Prionchulus*. Third, given the confirmation of this finding, the difference between tactile and visual predators in the susceptibility to confusion needs further exploration. Although we have provided indirect support of our suggestion that tactile predators are inferior to visual ones in their ability to single out individual prey, this suggestion remains speculative. Finally, our functional response model may serve as a basis for predator-prey population models and adaptive behavior models that include the confusion effect, e.g. models that simulate predators foraging in a patchy environment where each patch consists of one prey swarm.

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Appendix 1: The satiation model

In this section, we extend the steady-state satiation (SSS) equation (eq. 1) to the satiation model. For this extension, we must refer to the functional response model that underlies the SSS equation (Jeschke et al. 2002):

$$\frac{\mathrm{d}y(t)}{\mathrm{d}t}=\frac{h(t)ax(t)}{1+h(t)abx(t)}, \qquad \text{(A1)}$$

for success rate a and handling time b, see eq. 1. The number of prey eaten $y(t)$ is obtained by integration. In the satiation model, prey density has an initial value $x(0)$ and is decreased by predation:

$$x(t)=x(0)-y(t). \qquad \text{(A2)}$$

Furthermore, predator hunger level $h(t)$ is allowed to vary. Hunger level is the proportion of empty volume of the part of the gut that is responsible for feelings of hunger and satiation. For most predator species, this is the stomach or the crop; $h = 0$ means no hunger, i.e. full gut, and $h = 1$ means 100% hunger, i.e. empty gut. The hunger level has an initial value $h(0)$, is increased by digestion and decreased by ingestion. For extreme parameter values, it is necessary to define the process of digestion for hunger levels beyond the interval [0; 1]. Therefore,

$$\frac{\mathrm{d}h(t)}{\mathrm{d}t}=\begin{cases}\dfrac{1}{t_{dig}}-s\dfrac{\mathrm{d}y(t)}{\mathrm{d}t} & h(t)<0\\[2ex] \dfrac{1-h(t)}{t_{dig}}-s\dfrac{\mathrm{d}y(t)}{\mathrm{d}t} & 0\le h(t)\le 1\\[2ex] -s\dfrac{\mathrm{d}y(t)}{\mathrm{d}t} & h(t)>1,\end{cases} \qquad \text{(A3)}$$

where s is the satiation per prey item, i.e. the reciprocal capacity of the hunger-determining part of the gut; for example, if the stomach capacity of a human is equal to 10 potatoes, then $s = 0.1$. A negative value for h means that the predator caught a prey item too large to eat whole. The predator will feed to satiation and store the rest until being hungry again. When the whole prey item is gone, h will again be positive. On the other hand, a value of h larger than 1 means that the predator is starving. The complete satiation model consists of the coupled eqs. A1, A2, and A3.

Appendix 2: The satiation model (eqs. A1, A2, A3, 2) parameter values for our experiments in the *Chaoborus-Daphnia* system

Parameter	Value	Source
Encounter rate β	0.21 min^{-1}	Giguère et al. (1982), Dodson and Ramcharan (1991)[1]
Product of detection probability γ and attack probability δ	0.46	Giguère et al. (1982)
Maximum attack efficiency ε_{max}	0.48	This study[2]
Minimum attack efficiency ε_{min}	0.12	This study[2]
Shape parameter ε_s	0.051	This study[2]
Initial hunger level $h(0)$	1	This study
satiation per *Daphnia* s	0.095	This study[3]
Chaoborus handling time b	0.023 min	Pastorok (1981)[4]
Chaoborus digestion time t_{dig}	447 min	Giguère (1986)[5]
Duration of an experiment	30 min	This study

Notes:

1) $$\beta = v \cdot \pi \cdot \left(\frac{60 \cdot R' \cdot L_t}{2 \cdot 10^6 \cdot V} \right),$$ (A4; Giguère et al. 1982)

where v is the *Daphnia* swimming velocity, R' is the *Chaoborus* encounter field radius, L_t is the *Chaoborus* encounter field length, and V [L] is the experimental volume.

Daphnia swimming velocity v has been calculated as

$v = 2.444 +$ *Daphnia* length [mm] $\cdot\ 0.853$. (A5)

We have obtained eq. A5 by linearly regressing ($r = 0.844$) empirical data given by Dodson and Ramcharan (1991).

Chaoborus encounter field radius R' has been computed as

$R' =$ *Chaoborus* length [mm] $\cdot\ (2.2 / 14.8) +$ *Daphnia* length [mm] $/ (1.75 \cdot 2)$.

(A6; Giguère et al. 1982)

Finally, *Chaoborus* encounter field length L_t has been calculated as

$L_t =$ *Chaoborus* length [mm] $+ 2 R'$. (A7; Giguère et al. 1982)

Here, experimental volume $V = 0.040$ L, *Chaoborus* length = 11.59 mm and *Daphnia* length ≈ 0.7 mm, giving $v = 3.04$, $R' = 1.92$, and $L_t = 15.44$.

2) See Fig. 3a

3) The given value is the reciprocal observed maximum number of prey eaten (= 10.5). This estimation is possible because no complete digestion took place during our short-term experiments.

4) $b = 0.0203 \cdot \exp(\textit{Daphnia}\ \text{length} \cdot 2.74) / 60$ (A8; Pastorok 1981)

5) $t_{dig} = (5.538 + 4.140 \cdot \textit{Daphnia}\ \text{length [mm]}^{2.17}) \cdot 60$ (A9)

We have obtained eq. A9 by linearly regressing (r = 0.925) empirical data given by Giguère (1986),

$t_{dig} = (5.538 + 696.903 \cdot \textit{Daphnia}\ \text{mass [µg]}) \cdot 60$, (A10)

and by replacing *Daphnia* body mass with body length (reviewed by Giguère 1986),

$\textit{Daphnia}\ \text{mass [µg]} = 0.00594 \cdot \textit{Daphnia}\ \text{length [mm]}^{2.17}$. (A11)

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Table 1: A review of empirical data on the confusion effect

Predator	Prey detection	Prey	Relative prey agility[1]	Confusion? observed (pred.)[2]
1) Carnivorous plants				
Utricularia vulgaris	None	*Polyphemus pediculus* (Crustacea)	Low	-[3] (-)
2) Nematodes				
Prionchulus punctatus	Tactile	*Aphelenus avenae* (Nematoda)	Low	+[4] (+)
3) Mollusks: cephalopods				
Loligo vulgaris (squid)	Visual	*Atherina* spp. (Pisces)	High	+[5] (+)
Sepia officinalis (cuttlefish)	Visual	*Mugil* spp. (mullet)	High	+[5] (+)
4) Crustaceans				
Acartia tonsa	None (filtering)[6]	*Gyrodinium fissum* (Flagellata)	Low	-[6] (-)
5) Insects				
a) Odonate larvae				
Aeshna cyanea	Visual[7]	*Daphnia magna* (Crustacea)	Low[8]	+[9] (-)
Aeshna juncea	Visual[7]	*D. magna* (small / medium / large)	Low[8]	+ / - / -[10] (-)
Libellula depressa	Visual (and tactile)[7]	*D. magna*	Low[8]	-[9] (-)
b) Dipteran larvae				
Chaoborus obscuripes	Tactile[11]	*Daphnia obtusa*	Low[12]	+[9] (+)
6) Fishes				
Aequidens pulcher (blue acara cichlid)	Visual	*Poecilia reticulata* (guppy)	High	+[13] (+)

Ambloplites rupestris (rock bass)	Visual	*Semotilus atromaculatus* (creek chub)	High	?[14] (+)
Esox lucius (pike)	Visual	Cyprinids[15]	High[16]	+[5] (+)
Micropterus salmoides (largemouth bass)	Visual	*Hybognathus nuchalis* (silvery minnow)	High[17]	+[18] (+)
Morone americana (white perch)	Visual	*Fundulus diaphanus* (banded killifish)	High	?[19] (+)
Perca fluviatilis (perch)	Visual	*Poecilia vivipara* (guppy)	High[20]	+[5] (+)
Sardinops sagax	Visual	*Halobates robustus* (ocean skater)	High[21]	+[22] (+)
7) Amphibians: newts				
Triturus alpestris (Alpine newt)	Visual	*D. obtusa*	Low[23]	-[9] (-)
8) Birds				
Accipiter gentilis (goshawk)	Visual	*Columba palumbus* (woodpigeon)	High[24]	+[25] (+)
Accipiter nisus (sparrow hawk)	Visual	*Tringa totanus* (redshank)	High	+[26] (+)
Falco columbarius (merlin)	Visual	*Callidris minutilla* (least sandpiper)	High	?[27] (+)
Falco peregrinus (peregrine falcon)	Visual	*Tringa totanus* (redshank)	High[28]	+[26] (+)
Motacilla spp. (wagtails)	Visual	Scatophagids (Insecta: Diptera)	High	+[29] (+)
9) Mammals				
Panthera leo (lion)	Visual	Ungulates	High[30]	-[31] (+)

The overall frequency of predator confusion is $p = 0.70 \pm 0.102$ (mean ± SE, $N = 20$ [ambiguous results ("?") have been excluded], 95% CI: [0.50; 0.90], binomial distribution); predictions based on Fig. 4 are correct in 18 cases (= 90%).

Notes and references: **(1)** If corresponding data is available, we have calculated relative prey agility as relative prey speed (i.e. mean or maximum prey escape speed divided by mean or maximum predator attack speed, respectively) or relative prey acceleration (i.e. maximum prey escape acceleration divided by maximum predator attack acceleration). Otherwise, we have classified relative prey agility subjectively. **(2)** The predictions are based on Fig. 4. **(3)** Englund and Harms (2001); **(4)** Nelmes (1974); **(5)** Neill and Cullen (1974); **(6)** Paffenhöfer and Stearns (1988); **(7)** Pritchard (1965); **(8)** relative prey speed ≈ 0.25 (mean *Daphnia* escape speed ≈ 0.1 m sec^{-1} [Brewer et al. 1999], mean odonate larva attack speed ≈ 0.4 m sec^{-1} [Pritchard 1965]); **(9)** this study; **(10)** counted as "-" in the calculation of p, Hirvonen and Ranta (1996); **(11)** Duhr (1955); **(12)** relative prey speed ≈ 0.02 (mean *Daphnia* escape speed ≈ 0.1 m sec^{-1} [Brewer et al. 1999], mean *Chaoborus* attack speed ≈ 4.5 m sec^{-1} [estimation based on *Chaoborus* attacking time given by Pastorok 1981]); **(13)** Krause and Godin (1995); **(14)** Krause et al. (1998); **(15)** mostly *Alburnus alburnus* (bleak) and *Leuciscus leuciscus* (dace); **(16)** maximum pike attack speed = 4.0 m sec^{-1}, maximum pike attack acceleration = 120 m sec^{-2} (Harper and Blake 1990); **(17)** maximum bass attack speed = 1.0 m sec^{-1} (reviewed by Harper and Blake 1990); **(18)** Landeau and Terborgh (1986); **(19)** Morgan and Godin (1985); **(20)** maximum perch attack speed = 1.15 m sec^{-1}, maximum perch attack acceleration = 24 m sec^{-2} (reviewed by Harper and Blake 1990); **(21)** mean ocean skater escape speed = 0.28 m sec^{-1} (Treherne and Foster 1981); **(22)** Foster and Treherne (1981), Treherne and Foster (1982); **(23)** mean *Daphnia* escape speed ≈ 0.1 m sec^{-1} (Brewer et al. 1999); **(24)** maximum goshawk attack speed = 30 m sec^{-1} (Alerstam 1987); **(25)** Kenward (1978); **(26)** Cresswell (1994); **(27)** Page and Whitacre (1975); **(28)** maximum peregrine attack speed = 44 m sec^{-1}, maximum peregrine attack acceleration = 5 m sec^{-2} (Peter and Kestenholz 1998); **(29)** Davies (1977); **(30)** relative prey speed = 1.2 (maximum prey escape speed = 19 m sec^{-1} [*Connochaetes taurinus* (wildebeest): 22 m sec^{-1}; *Equus* spp. (zebras): 19 m sec^{-1}; *Syncerus caffer* (buffalo): 16 m sec^{-1}; reviewed by Garland 1983], maximum lion attack speed = 16 m sec^{-1} [reviewed by Garland 1983]), relative prey acceleration = 0.6 (maximum prey escape acceleration = 5.3 m sec^{-2} [wildebeest: 5.6 m sec^{-2}; zebra: 5.0 m sec^{-2}; Elliott et al. 1977], maximum lion attack acceleration = 9.5 m sec^{-2} [Elliott et al. 1977]); **(31)** Van Orsdol (1984).

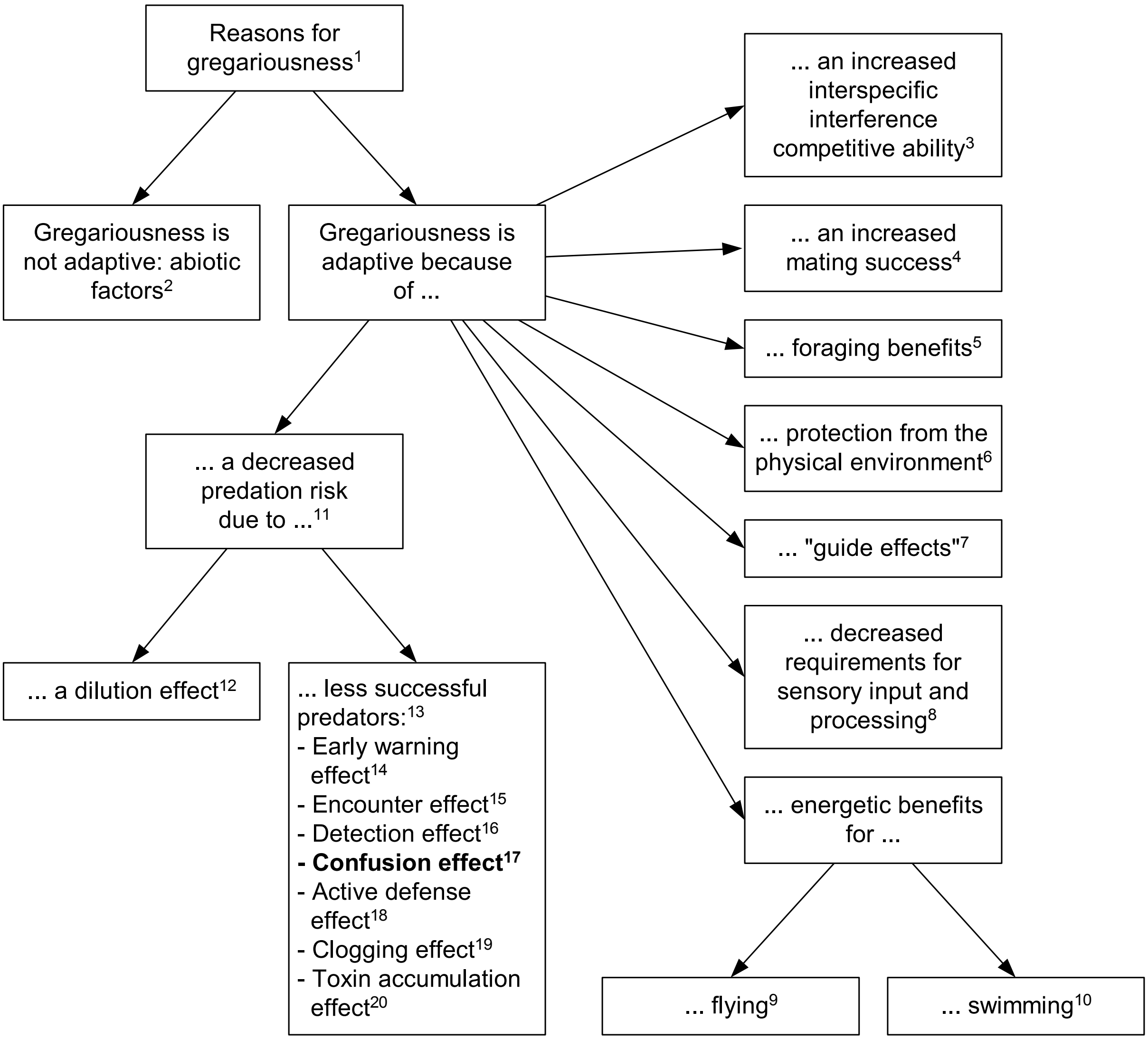


Figure 1: When and why organisms aggregate. Notes and references: **(1)** Alexander (1974), Heinrich and Vogt (1980), Brönmark et al. (1984), Choe and Crespi (1997), Folt and Burns (1999), Olupot and Waser (2001), and most of the other references given in this caption. **(2)** Potential disadvantages of gregariousness are an increase in intraspecific competition (e.g. in bryozoans: Buss 1981), in transmission of diseases and ectoparasites (e.g. in prairie dogs: Hoogland 1979), or in predation risk (e.g. in krill: baleen whales sieve them because they aggregate). For abiotic factors leading to non-adaptive gregariousness, see Levin and Segel (1976), Malone and McQueen (1983), Abraham (1998), Parrish and Edelstein-Keshet (1999), and Young et al. (2001). **(3)** For example, in bryozoans (Buss 1981); **(4)** e.g. in palolo worms; **(5)** Miller (1922), Packer and Ruttan (1988), Uetz (1989), Fryxell (1991); **(6)** e.g. in harvestmen (Wagner 1954); **(7)** e.g. in spiny lobsters (Childress and Herrnkind 2001); **(8)** Kavanau (2001); **(9)** Lissaman and Shollenberger (1970); **(10)** Weihs (1973). **(11)** Mussels have been shown to aggregate in response to the presence of predators (Reimer and Tedengren 1997, Côté and Jelnikar 1999). **(12)** See Hamilton (1971), Treisman (1975), Foster

and Treherne (1981), Treherne and Foster (1982), Folt (1987), Turchin and Kareiva (1989), and Riipi et al. (2001). **(13)** In more detail, predators are less successful at one or more stages of their predation cycle (Jeschke et al. 2002). For previous reviews on such effects, see Bertram (1978), Vulinec (1990), and Caro and Fitzgibbon (1992). **(14)** That is, approaching predators are detected either with a higher probability or earlier from a prey flock than from a single prey item (Miller 1922, Eibl-Eibesfeldt 1962, Pulliam 1973, Treisman 1975, Kenward 1978, Lazarus 1979, Treherne and Foster 1980, 1981, Ydenberg and Dill 1986, Godin et al. 1988, Uetz and Hieber 1994, Watt and Chapman 1998, Uetz et al. 2002). **(15)** That is, the number of encounters between a predator and a prey item per time unit (i.e. the encounter rate) is lower in case of grouped prey (Englund and Harms 2001). **(16)** "The [detection] effect favours being in a group by decreasing the probability of detection by a predator: detection does not increase in direct proportion to group size (a group of 200 gazelles is not 200 times as likely to be detected by a lion as is a solitary individual)." (Inman and Krebs 1987) See also Treisman (1975); for empirical examples, see Uetz and Hieber (1994) and Riipi et al. (2001). Note that Inman and Krebs (1987) and, in reference to them, Uetz and Hieber (1994) ignored the encounter effect sensu this study and termed the detection effect sensu this study "encounter effect". Since the latter effect relates to predator detection probability rather than predator-prey encounter rate, we feel the change in nomenclature to be justified. **(17)** This is the issue of this study. The effect is present if predators that are confronted with a swarm of their prey are restricted by their neuronal abilities, causing them to be less successful in their attacks (Allen 1920, Miller 1922, Welty 1934, Eibl-Eibesfeldt 1962, Humphries and Driver 1970, Esaias and Curl 1972, Milinski and Curio 1975, Milinski and Heller 1978, Gillett et al. 1979, Milinski 1979, 1990, Ohguchi 1981, Williamson 1984, Krakauer 1995, and see Table 1). (**18**) That is, grouped prey are more effective at actively defending themselves. A prominent example for the active defense effect are muskoxen (*Ovibos moschatus*): When threatened by wolves, they "gather into a defensive formation with an array of powerful horns facing the predators and with vulnerable animals in the middle." (Bertram 1978) References: Mori and Chant (1966), Tostowaryk (1972), and Andersson and Wiklund (1978). **(19)** A clogging effect is present if the filters of filter feeders clog in case of highly abundant food particles (Harbison and Gilmer 1976, Harbison et al. 1986). **(20)** That is, predators suffer from an accumulation of prey-specific toxins (Halbach and Halbach-Keup 1974).

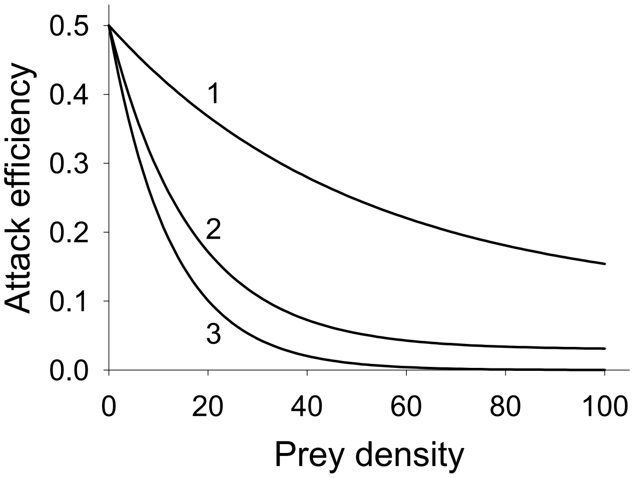


Figure 2: Graphical representation of eq. 2; parameter values for curve 1: maximum attack efficiency ε_{max} = 0.5, minimum attack efficiency ε_{min} = 0.1, shape parameter ε_s = 0.02; parameter values for curve 2: ε_{max} = 0.5, ε_{min} = 0.03, ε_s = 0.06; parameter values for curve 3: ε_{max} = 0.5, ε_{min} = 0, ε_s = 0.08.

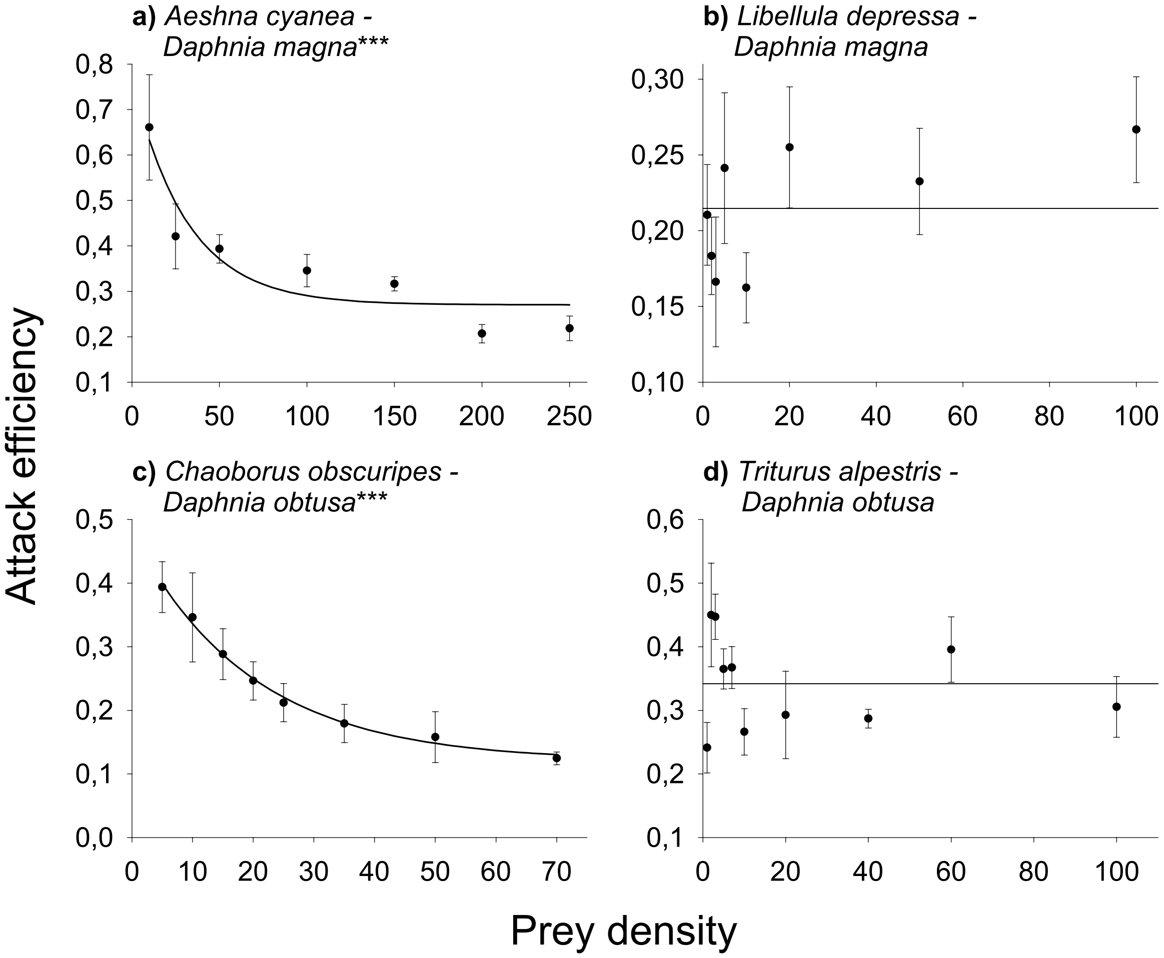


Figure 3: An empirical test of the presence of predator confusion in four predator-prey systems; ***attack efficiency is significantly correlated with prey density ($P < 0.001$, one-tailed Spearman rank correlation test); solid lines in **a** and **c** are non-linear regression fits (cf. eq. 2), in **b** and **d** they are mean attack efficiencies.

a) *Aeshna cyanea - Daphnia magna*, $V = 280$ mL, attack efficiency $\varepsilon(x) = exp\ (-0.051x) \cdot (0.48 - 0.12) + 0.12$ ($r = 0.619$, $r_{Sp} = 0.630$).

b) *Libellula depressa – Daphnia magna*, $V = 200$ mL, mean attack efficiency $\overline{\varepsilon} = 0.21$.

c) *Chaoborus obscuripes - Daphnia obtusa*, $V = 40$ mL, attack efficiency $\varepsilon(x) = exp\ (-0.032x) \cdot (0.77 - 0.27) + 0.27$ ($r = 0.727$, $r_{Sp} = 0.784$).

d) *Triturus alpestris – Daphnia obtusa*, $V = 400$ mL, mean attack efficiency $\overline{\varepsilon} = 0.34$.

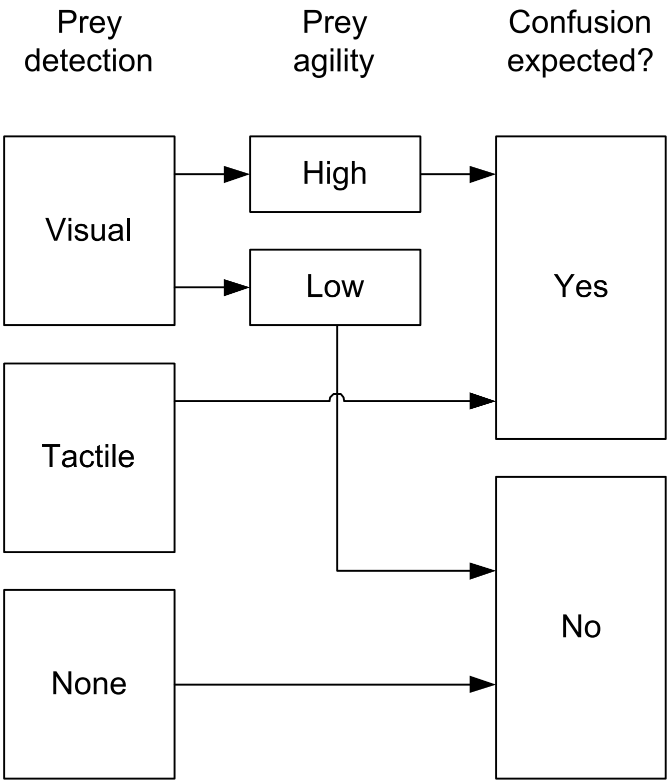
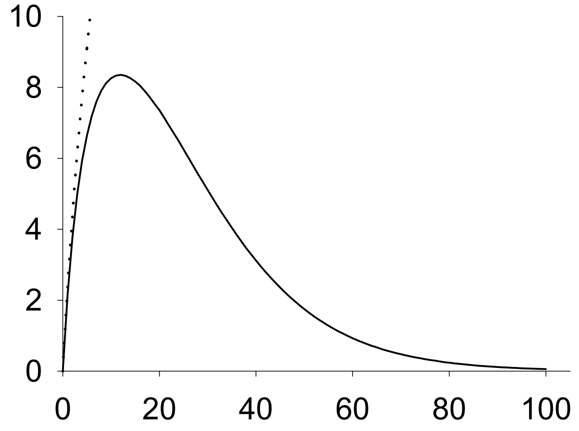
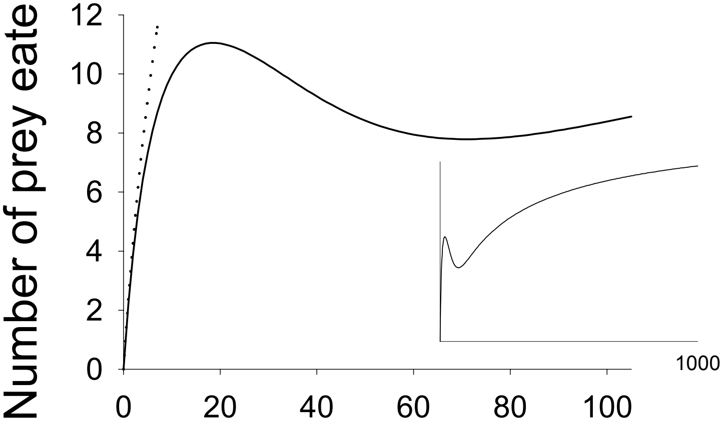


Figure 4: Predicting predator confusion: a hypothetical a posteriori model which is based on the comparative analysis given in Table 1.

a) Dome-shaped in the narrow sense



b) Roller-coaster-shaped



c) Type II

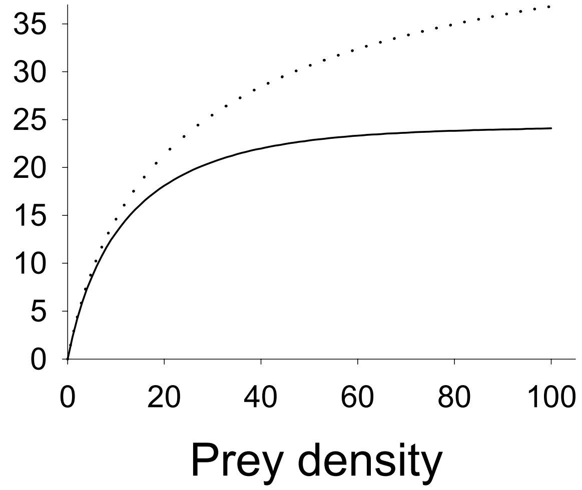


Figure 5: How predator confusion affects the functional response, theoretical results part I. Solid lines refer to functional responses including confusion; dotted lines correspond to responses without confusion (these are all of type II); parameter values: encounter rate $\beta = 10$, detection probability $\gamma = 0.5$, attack probability $\delta = 1$, digestion time $c = 0.02$, total time $t = 1$, attacking time $t_{att} = 0.001$, and eating time $t_{eat} = 0.01$.

a) Type II becomes dome-shaped in the narrow sense; parameter values are equal to curve 3 in Fig. 2: maximum attack efficiency $\varepsilon_{max} = 0.5$, minimum attack efficiency $\varepsilon_{min} = 0$, shape parameter $\varepsilon_s = 0.08$.

b) Type II becomes roller-coaster-shaped; parameter values are equal to curve 2 in Fig. 2: $\varepsilon_{max} = 0.5$, $\varepsilon_{min} = 0.03$, $\varepsilon_s = 0.06$. The plateau of a roller-coaster-shaped response (insert) lies for most species probably beyond the range of naturally occurring prey densities.

c) Type II remains type II but the plateau is lowered and is reached earlier; parameter values are equal to curve 1 in Fig. 2: $\varepsilon_{max} = 0.5$, $\varepsilon_{min} = 0.1$, $\varepsilon_s = 0.02$.

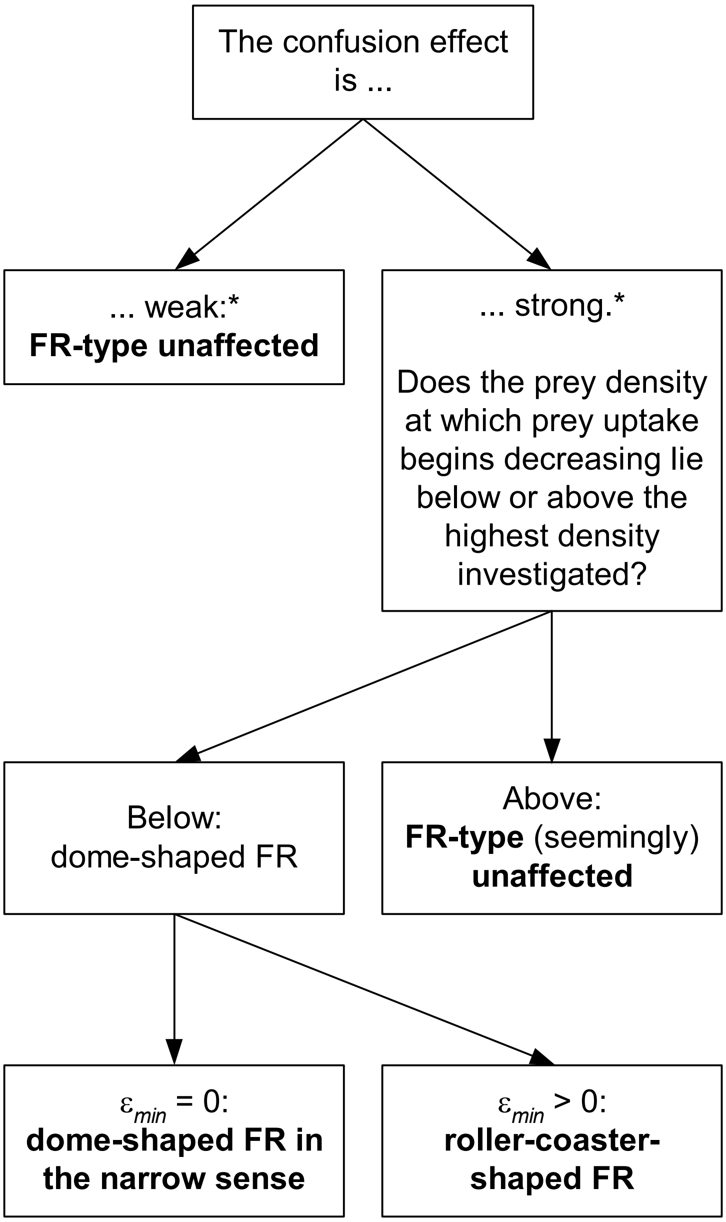


Figure 6: How predator confusion affects the functional response, theoretical results part II. Note: *A confusion effect is called "strong" here if either minimum attack efficiency $\varepsilon_{min} = 0$ or the ratio of maximum to minimum attack efficiency, $\varepsilon_{max}/\varepsilon_{min}$, is high. For $\varepsilon_{min} > 0$, we mathematically define a weak or strong confusion effect due to the complexity of our model only for the simplified case handling time $b = 0$. If $\varepsilon_{min} > 0$ and $b = 0$, the functional response remains type II, i.e. the confusion effect is weak, if $\varepsilon_{max}/\varepsilon_{min} \leq \exp(2) + 1 \Leftrightarrow \varepsilon_{max}/\varepsilon_{min} \leq 8.39$. Otherwise the response becomes roller-coaster-shaped, i.e. the confusion effect is strong. The derivation of this inequality is available from JMJ upon request.

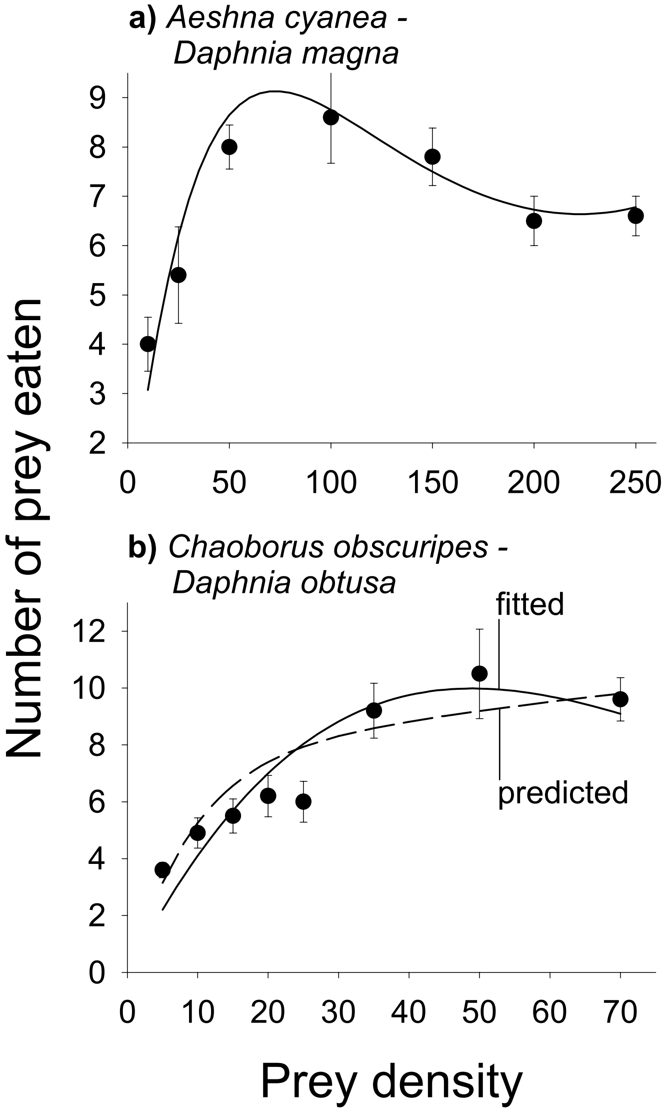


Figure 7: How predator confusion affects the functional response, empirical results; circles are means ± SE, solid lines are logistic regression fits.

a) *Aeshna cyanea - Daphnia magna*, $T = 2$ min, $V = 280$ mL, logistic regression fit: $y = [\exp(-0.60272 - 0.02151x + 0.000038x^2) \cdot x] / [1 + \exp(-0.60272 - 0.02151x + 0.000038x^2)]$.

b) *Chaoborus obscuripes - Daphnia obtusa*, $T = 30$ min, $V = 40$ mL, logistic regression fit ($r = 0.624$, $r_{Sp} = 0.647$): $y = [\exp(-0.10634 - 0.02565x) \cdot x] / [1 + \exp(-0.10634 -$

0.02565x)], dashed line: satiation model (correlation between predicted and observed values: r = 0.612, r_{Sp} = 0.664; eqs. A1, A2, A3, 2; parameter values are given in Appendix 2).

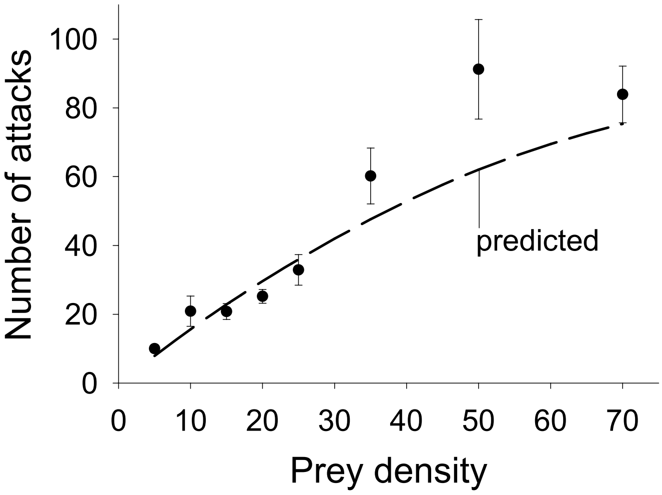


Figure 8: The number of attacks launched by *Chaoborus obscuripes* (means ± SE) depending on *Daphnia obtusa* density; T = 30 min, V = 40 mL. The line has been computed with the satiation model (correlation between predicted and observed values: $r = 0.778$, $r_{Sp} = 0.856$; eqs. A1, A2, A3, 2; parameter values are given in Appendix 2).

Lebenslauf

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Veröffentlichungen und Manuskripte in Vorbereitung

Jeschke, J.M.; Tollrian, R. In Vorbereitung. Correlates and consequences of predator confusion.

Jeschke, J.M.; Tollrian, R. Eingereicht. Full and lazy herbivores.

Jeschke, J.M.; Kopp, M.; Tollrian, R. Eingereicht. Consumer-food systems: Why type I functional responses are exclusive to filter feeders.

Jeschke, J.M.; Kopp, M.; Tollrian, R. 2002. Predator functional responses: discriminating between handling and digesting prey. *Ecological Monographs* 72, 95-112.

Kopp, M.; Jeschke, J.M.; Gabriel, W. 2001. Exact compensation of stream drift as an evolutionary stable strategy. *Oikos* 92, 522-530.

Jeschke, J.M.; Tollrian, R. 2000. Density-dependent effects of prey defences. *Oecologia* 123, 391-396.

Symposien und Workshops

12/2001	British Ecological Society Winter Meeting University of Warwick, Großbritannien Titel des Vortrags: „Why type I functional responses are exclusive to filter feeders“
09/2001	2. Workshop „Chronoethologie – Chronoökologie“ IZW Berlin
03/2001	7th Meeting of PhD Students in Evolutionary Biology Bernried bei München Titel des Vortrags: „Conditions for a type I functional response“
07/2000	Ecological Society of America Annual Meeting Snowbird, Utah, USA Titel des Vortrags: „Predator functional responses: discriminating between handling and digesting prey“
03/2000	6th Meeting of PhD Students in Evolutionary Biology Vaalbeek, Belgien Titel des Vortrags: „Predator functional responses: discriminating between handling and digesting prey“
09/1999	Vth International Symposium on Cladocera Plön Titel des Vortrags: „Density-dependent effects of prey defenses”
07/1999	Workshop „Evolutionary Biology“ Guarda, Schweiz Lehrkörper: Dieter Ebert, John Maynard Smith, Richard Lenski, Rolf Hoekstra
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Weitere Kenntnisse

Berufliche Kenntnisse	Vergleichende Analysen: Erfahrung im Sammeln und Auswerten von Daten (→ Statistik) Statistik: Erfahrung in der Durchführung gewöhnlicher und außergewöhnlicher Methoden, z.B. reduced major axis-Regression, logistische Regression, Meta-Analyse, independent contrasts-Analyse; verwendete Software: SPSS, SYSTAT Modellierung: Erfahrung mit Mathcad, Stella und Turbo Pascal
Sprachkenntnisse:	Englisch (sehr gut)
Sonstiges:	Führerschein Klasse 3

München, den 08.11.2002