Toward a modular theory of trophic interactions

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This Supporting Information includes the following:

1. **Appendix S1.** Derivation of the functional response of predators from basic principles and its implications.
2. **Appendix S2.** Factorization of the functional response by separating steps of the predation cycle.
3. **Table S1.** Effect of body size and thermal niche on parameter values of the dynamic model described in the main text.
4. **Table S2.** Parameter values for the model represented in figure 3 of the main text.

Appendix S1. Derivation of the functional response of predators from basic principles and its implications

Summary

Here we define the basic steps of foraging, use these to revisit the derivation of the functional response of predators and arrive at a formulation of the single predator-single prey functional response that is more process explicit than the classic formulation (Holling 1959a). We then show how this formulation can be extended to situations with multiple prey or predators. Finally, we indicate briefly how the allometric trophic network (ATN) model approach (Otto et al. 2007, Berlow et al. 2009, Schneider et al. 2012) which links body size to underlying parameters of the functional response, fits with this revised formulation of the functional response.

1. Background

Solomon (1949) introduced the term 'functional response' to describe the change in the number of prey consumed by individual predators in response to 'increased availability of victims' (i.e. prey density) and Holling (1959b) identified three basic forms: a linear response, a saturating response and a sigmoid response (later termed type I, type II and type III, Fig S1). In the original mathematical derivation of the functional response (Holling, 1959a, based on a now classic experiment using sandpaper dishes), two main processes of foraging were considered: searching for prey, and handling of discovered prey. These led to the standard formulation of the saturating (type II) functional response (*FR*), for the number of prey killed per predator, replicated in many textbooks (e.g., Case 2000, Begon et al. 2005):

$$(SI\text{-}1) \qquad FR = \frac{aNT_{forage}}{1+ahN}$$

Here *a* was termed the 'discovery rate of prey' (or by later authors 'encounter rate' or 'attack rate'), while *h* is the 'handling time' of prey, *N* the density of prey, and T_{forage} the time available for foraging. Handling time can either be defined as (*i*) the average time to handle each *encountered* prey, or (*ii*) the average time to handle each *ingested* prey. As will be seen below, how handling time (*h*) is defined has important consequences for how the rest of the functional response equation should be formulated. For reasons outlined below, we advocate defining handling time in terms of the average time to handle each *ingested* prey.

Although highly influential (by capturing the essence of the saturating functional response and being able to replicate empirically observed data), this formulation is based on a series of simplifying assumptions that hampers development of quantitative, process-explicit models, where model parameters have been linked to species traits. More specifically, this formulation lumps a number of steps of the foraging process (predation cycle) that may need to be separated to see how parameters could be linked to traits. Here, we derive the functional response of predators from basic principles, essentially following T. J. Case (An illustrated guide to theoretical ecology, 2000, Ch. 11), but without lumping potentially important steps or assuming that all encountered prey are detected, decided upon, and successfully pursued

and subjugated. This leads to a modified, more explicit, and potentially more mechanistically useful formulation of the functional response relative to the classic formulation (Holling 1959a), with implications for how to develop the ATN model approach (Schneider et al. 2012) by including (additional) traits that are explicitly linked to different sequential parts of a predators foraging activity.
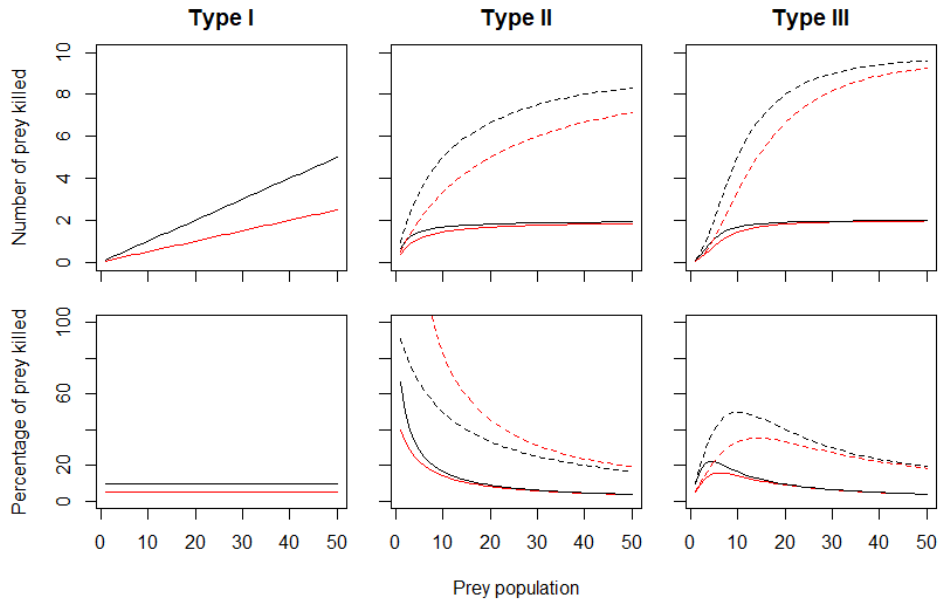
Fig S1. The three different functional responses and how they respond to different parameter values. The first row shows the number of prey consumed, while the second row shows the percentage of the prey population consumed. Black lines indicate an attack rate twice the magnitude of red lines (0.1 and 0.05 respectively for Type I and II, 0.01 and 0.05 respectively for Type III). Solid lines indicate a handling time five times the magnitude of dashed lines (0.5 and 0.1 respectively).

When foraging, a predator must (1) *search* for, (2) *detect,* (3) *decide* to exploit, (4) *pursue,* and (5) *subdue* a potential prey item, and then (6) *ingest,* (7) *digest,* and (8) *allocate* the immobilized prey to growth and reproduction (Fig. 1, main text). These eight steps can be aggregated into four stages; (I) Location, (II) Decision, (III) Attack and (IV) Consumption. In addition to simplifying for conceptual purposes, these four stages (with the exception of Decision, which tends to be overlooked) more closely match the way the predation process is broken up in the literature (e.g., Griffiths 1980, O'Brien et al. 1990, Jescke et al 2002, Vucic-Pestic et al 2011, Bateman et al. 2014). Many studies do break one or more of these stages into finer steps (and each of the eight steps we use have at least been mentioned by previous work), but for tractability, many studies implicitly do as we advocate here; omit steps, assume they equal one, and/or aggregate steps. The element that we advocate that these studies often miss is the explicit acknowledgement of which steps they are omitting or aggregating. The eight steps we use here are the coarsest division of the predation process that takes into account all steps we found mentioned in the literature. Although the predation process could be sliced into ever thinner pieces, the eight steps we present here are sufficiently specific that they capture each important element of a trophic interaction, and yet are sufficiently broad to apply to any type of trophic interaction, including predation,

herbivory, parasitism, and pollination. However, should further steps be necessary, by explicitly laying out our framework here it should be clear how to add steps as required.

The basic assumptions here, as with Holling (1959a) and Case (2000), are that predators, while foraging, move randomly in search of prey (or prey move randomly to encounter a sit-and-wait predator), and that the time available for searching for prey is negatively affected by the other activities of foraging. The more time that is spent on handling prey, the less is available for searching for new prey. These assumptions can be relaxed by appropriate formulations of relevant parameters, as discussed below. Thus, crucial to the derivation presented below is if and how the different activities of the predation cycle may affect one another. In general, one step will influence another step if (*i*) it determines the number of prey that will enter the next step (the flow-through rate from one step to another), or (*ii*) it affects the time available for the other step. Here, every step has the potential to affect the following step by controlling the number of prey that will enter the next step, and thus also the time that will be spent on handling prey in that step. Consequently, with a limited time for a predator to forage (T_{forage}, itself potentially a function of traits), the more time that is spent on one activity the less will be available for another. The time spent on searching is the most important for our derivation because this is the gateway to all subsequent activities of foraging; in other words, without searching there will be no prey to attack or consume. For the derivation of the functional response, we (and Holling 1959a and Case 2000) focus on how the time available for foraging is divided among the different activities of the predation cycle and, more specifically, how the time available for searching (T_{search}) is affected by the time spent handling prey in the other steps of the predation cycle.

Of the eight steps of foraging identified here, only the second to sixth (detection to ingestion), directly affect the time available for searching, while the last, allocation, does not (in most cases). This is because when the predator is handling a prey item in any of step 2-6 it (normally) cannot search for new prey, while it can when in step 8 (but see Stouffer & Novak 2021 for a discussion of when this assumption may not apply. Such scenarios can be accounted for here by changing the formulation of t_{handle} (Eq. SI-10).). The effect of digestion (step 7) might be intermediate, or reach a threshold, with small amounts of prey to digest not significantly affecting foraging, but larger amounts effectively stopping a predator from searching for new prey. Digestion may also affect the time spent foraging (T_{forage}) by its effect on hunger (see Jeschke et al 2002 for how to integrate this into a model). Acknowledging these caveats, for the derivation below, we assume that only the first six steps of a predators' foraging are relevant, because the total time available for searching for prey will be negatively affected by the amount of time spent handling prey in step two to six, but not by step seven and eight. This assumption can easily be modified to the predation type in question.

2. Derivation of the functional response

Here, we focus on how to combine the steps of the predation cycle into a description of a 'single predator-single prey functional response', i.e. how the number of prey of one type (species) that one predator individual subjugates, changes with the abundance of the prey. This can then easily be expanded to include presence of alternative prey as well as effects of

multiple predators (e.g interference competition and fear of intraguild predation; see section 3.2-3.3 below).

The predation cycle starts with the activity of searching and here f_1 is the <u>proportion</u> of all prey individuals ($x_0 = x_{Tot}$) present within the area searched (scanned) by a predator that are encountered[1] per unit available search time. x_1 is the <u>number</u> of prey successfully searched for (encountered) per unit available search time. f_2 is the proportion of encountered prey that are detected, f_3 is the proportion of detected prey that the predator decides to pursue, f_4 is the proportion of decided upon prey that are successfully pursued and caught and f_5 is the proportion of caught prey that are successfully subjugated. Thus (per unit search time):

(SI-2)
$$\begin{cases} (2a): x_{Encountered} = x_1 = f_1 \cdot x_0 \\ (2b): x_{Detected} = x_2 = f_2 \cdot x_1 \\ (2c): x_{Decided} = x_3 = f_3 \cdot x_2 \\ (2d): x_{Pursued} = x_4 = f_4 \cdot x_3 \\ (2e): x_{Subdued} = x_5 = f_5 \cdot x_4 \end{cases}$$

The total number of prey individuals present (x_0) within the area searched (A_{search}) per unit available search time by a predator is simply: $x_0 = A_{search} \cdot N$ (where N is the density of prey)[2]. Thus, (assuming random movement of a predator species and/or its prey in a single uniform habitat) the number of individuals of the prey encountered per predator, χ_1, <u>per unit foraging time</u>, should depend on (*i*) the area scanned per unit available search time per predator (A_{search}), (*ii*) the density of prey (number of individuals per unit area, N), (*iii*) the encounter probability of present prey (f_1) and (*iv*) the proportion of foraging time spent searching, $\varphi_{search} = T_{search} / T_{forage}$, as:

(SI-3) $\qquad \chi_{Encountered} = \chi_1 = f_1 \cdot x_0 \cdot \varphi_{search} = f_1 \cdot A_{search} \cdot N \cdot \varphi_{search}$.

Note that from here and onwards we switch from "x_k", denoting the number of prey encountered/detected/decided on/pursued/subdued in step k per unit *search* time, to "χ_k", denoting step success per unit *foraging* time. The reason not all prey present within A_{search} are encountered may be because prey have access to safe hiding places (refuges) where they are completely hidden and thus safe from a predator. This may include differences in phenology or diurnal activity if prey are hidden and inactive while the predator is searching. The encounter probability (f_1) can therefore be interpreted as the proportion of prey that are out of hiding (i.e. $1 - f_1$ would be a measure of prey in safe refuges) and x_1 as the number of prey

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[1] The proportion of the individuals within the scanned area that a predator could potentially detect and kill. The predator and prey do not need to meet each other, be in physical contact with each other, or detect each other.

[2] If A_{search} equals the unit of area used to describe population abundance then $x_0 = N$.

which come within the sensory range of the predator, even if they are not necessarily detected.

Assuming that the predator is not perfectly efficient in detecting all the encountered prey, the detection probability (f_2) is the proportion of prey that are exposed (not in a safe refuge) that the predator detects[3]. This means that the number of prey individuals detected (per unit foraging time), χ_2, is[4]:

(SI-4) $\qquad \chi_2 = f_2 \cdot \chi_1 = f_1 \cdot f_2 \cdot A_{search} \cdot N \cdot \varphi_{search}$

We assume that the predator will decide to attack a proportion f_3 of all detected prey, that a proportion f_4 of these will be successfully pursued, and that a proportion f_5 of these will be subdued (generally killed in a predator-prey interaction). This means that (*a*) the number of prey individuals that a predator decides to pursue (χ_3), (*b*) the number of prey caught (χ_4), and (*c*) the number of prey subdued (χ_5), respectively, per predator (per unit foraging time), can be described as[5]:

(SI-5) $\qquad \begin{cases} (5a): & \chi_3 = f_3 \cdot \chi_2 = f_1 \cdot f_2 \cdot f_3 \cdot A_{search} \cdot N \cdot \varphi_{search} \\ (5b): & \chi_4 = f_4 \cdot \chi_3 = f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot A_{search} \cdot N \cdot \varphi_{search} \\ (5c): & \chi_5 = f_5 \cdot \chi_4 = f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search} \cdot N \cdot \varphi_{search} \end{cases}$

Because time available for searching, T_{search}, is dependent on the time taken to handle prey during other steps and therefore the number of prey a predator handles, it can be useful to express χ_5 in terms of the more consistent handling time. Although we in our contribution argue that $A_{search}, f_1, f_2, f_3, f_4$ and f_5, will be functions of species traits and settings when considering multiple predator-prey combinations and environmental conditions, for a given predator-prey combination (i.e. fixed traits) and consistent environmental conditions they will evaluate to constants and can be considered parameters (see Box 1 in the main text for further discussion). Thus, during the derivation of the functional response below, we assume the latter (i.e. the terms $A_{search}, f_1, f_2, f_3, f_4$ and f_5 are parameters that represent fixed average values across all predator individuals for particular predator-prey combination that are not affected by prey or predator abundance).

The time available for searching, T_{search}, is the amount of time left when total time for handling prey (T_{handle} = time for detection, decision, pursuit, subjugation and ingestion) has been subtracted from the total time spent foraging, T_{forage}:

(SI-6) $\qquad T_{search} = T_{forage} - T_{handle} = T_{forage} - T_{detect} - T_{decide} - T_{pursue} - T_{subjugate} - T_{ingest}$

If the total time for handling prey (T_{handle}) is a positive linear function of the number of prey to be handled in the respective steps, so that time available for searching (T_{search}) becomes a

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[3] In Case (2000) no distinction is made (as is here) between prey in refuges and exposed prey difficult to detect.

[4] In Case (2000) $f_1 \cdot f_2 \cdot A_{search}$ is denoted by a and termed 'the prey encounter rate'.

[5] In Case (2000) it is assumed that all encountered prey are detected, deemed suitable and profitable to pursue and successfully subjugated (=killed), i.e. $f_2 = f_3 = f_4 = f_5 = 1$.

negative linear function of the number of prey to be handled, this will result in a saturating type II functional response. A sigmoid type III functional response may occur if, for example, f_2, detection, is positively related to prey abundance. Assuming that total time for detection, decision, pursuit, subjugation and ingestion all are linearly related to the average times to (*i*) detect each encountered prey individual (t_2), (*ii*) decide on each detected prey individual (t_3), (*iii*) pursue each decided upon prey (t_4), (*iv*) subjugate each caught prey (t_5) and (*v*) ingest each subjugated (killed) prey respectively (t_6), then:

(SI-7)
$$\begin{cases} (7a): T_{detect} = t_2 \cdot \chi_1 \cdot T_{forage} \Rightarrow \varphi_{detect} = \dfrac{T_{detect}}{T_{forage}} = t_2 \cdot \chi_1 \\[2em] (7b): T_{decide} = t_3 \cdot \chi_2 \cdot T_{forage} \Rightarrow \varphi_{decide} = \dfrac{T_{decide}}{T_{forage}} = t_3 \cdot \chi_2 \\[2em] (7c): T_{pursue} = t_4 \cdot \chi_3 \cdot T_{forage} \Rightarrow \varphi_{pursue} = \dfrac{T_{pursue}}{T_{forage}} = t_4 \cdot \chi_3 \\[2em] (7d): T_{subjugate} = t_5 \cdot \chi_4 \cdot T_{forage} \Rightarrow \varphi_{subjugate} = \dfrac{T_{subjugate}}{T_{forage}} = t_5 \cdot \chi_4 \\[2em] (7e): T_{ingest} = t_6 \cdot \chi_5 \cdot T_{forage} \Rightarrow \varphi_{ingest} = \dfrac{T_{ingest}}{T_{forage}} = t_6 \cdot \chi_5 \end{cases}$$

Note that T_k is the *total* time required for step k (and has the units of 'total time') and thus increases as the number of prey entering that step increases. t_k, in contrast, is the *average* time taken for step k per prey individual "handled" in step k (and thus has units of time per prey). Since

(SI-8) $\chi_{k+1} = f_{k+1} \times \chi_k \Leftrightarrow \chi_k = \dfrac{\chi_{k+1}}{f_{k+1}},$

equation SI-7 can be reformulated, all as functions of χ_5:

(SI-9)
$$\begin{cases} (9a): T_{detect} = \dfrac{t_2}{f_2 \cdot f_3 \cdot f_4 \cdot f_5} \cdot \chi_5 \cdot T_{forage} \\[2em] (9b): T_{decide} = \dfrac{t_3}{f_3 \cdot f_4 \cdot f_5} \cdot \chi_5 \cdot T_{forage} \\[2em] (9c): T_{pursue} = \dfrac{t_4}{f_4 \cdot f_5} \cdot \chi_5 \cdot T_{forage} \\[2em] (9d): T_{subjugate} = \dfrac{t_5}{f_5} \cdot \chi_5 \cdot T_{forage} \\[2em] (9e): T_{ingest} = t_6 \cdot \chi_5 \cdot T_{forage} \end{cases}$$

Eqs. SI-9*a* – SI-9*e* can be collected to describe the total foraging time <u>not</u> spent on searching, but that is spent on handling prey, as a function of the 'average handling time' (t_{handle}):

$$T_{handle} = T_{detect} + T_{decide} + T_{pursue} + T_{subjugate} + T_{ingest} =$$

(SI-10)
$$= \left(\frac{t_2}{f_2 \cdot f_3 \cdot f_4 \cdot f_5} + \frac{t_3}{f_3 \cdot f_4 \cdot f_5} + \frac{t_4}{f_4 \cdot f_5} + \frac{t_5}{f_5} + t_6 \right) \cdot \chi_5 \cdot T_{forage} =$$

$$= t_{handle} \cdot \chi_5 \cdot T_{forage}$$

Here t_{handle} is the average handling time <u>per ingested prey</u> (= the time that on average has been spent on detection, decision, pursuit, subjugation and ingestion to result in one ingested prey). Note that t_2 (detection) and t_3 (decision) include the time for 'negative detections' and 'negative decisions', respectively, and similarly that t_4, t_5 and t_6 include the time for unsuccessful pursues, unsuccessful subjugations and incomplete ingestion respectively. Inserting Eq. SI-10 into Eq. SI-6 yields:

(SI-11) $\quad T_{search} = T_{forage} - t_{handle} \cdot \chi_5 \cdot T_{forage} = T_{forage} \left(1 - t_{handle} \cdot \chi_5 \right) \Rightarrow \varphi_{search} = 1 - t_{handle} \cdot \chi_5$

Now, inserting Eq. SI-11 into Eq. SI-5c gives:

(SI-12)
$$\chi_5 = f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search} \cdot N \cdot \varphi_{search} =$$
$$= f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search} \cdot N \cdot \left(1 - t_{handle} \cdot \chi_5 \right) =$$
$$= f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search} \cdot N +$$
$$- f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search} \cdot N \cdot t_{handle} \cdot \chi_5$$

Rearranging Eq. SI-12 results in a somewhat familiar expression for a saturating type II functional response, expressed <u>per unit available foraging time</u>:

(SI-13) $\quad \chi_5 = \dfrac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search} \cdot N}{1 + f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search} \cdot t_{handle} \cdot N}$

Thus, expressing the functional response (*FR*) as the number of prey killed per predator <u>per unit total time</u>, T_{Tot}, (where $\varphi_{forage} = T_{forage}/T_{Tot}$):

(SI-14) $\quad FR = \chi_5 \cdot \varphi_{forage} = \dfrac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search} \cdot N \cdot \varphi_{forage}}{1 + f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search} \cdot t_{handle} \cdot N}$

Eq. SI-14 is <u>the general relationship for the functional response of every foraging process that can be decomposed into the basic steps outlined in Fig. 1, main MS,</u> assuming (*i*) that the number of prey to be handled in every step is a cumulative proportion of the prey being handled in the preceding steps (= Eq. SI-5), (*ii*) that total handling time in every step is linearly related to the average time to handle a single prey individual in each step (= Eq. SI-7) and (*iii*) that $A_{search}, f_1, f_2, f_3, f_4$ and f_5 are constants and with t_{handle} defined as in Eq. SI-10.

2.1. ALTERNATIVE FORMULATION OF THE FUNCTIONAL RESPONSE BY AGGREGATING STEPS OF THE PREDATION CYCLE INTO STAGES

Instead of using all eight steps, we can simplify the derivation by using only the four stages Location, Decision, Attack, and Consumption. Using only four stages may be appropriate in some cases, but limits the ability to link different traits to particular parameters and so, in general, we recommend starting from all eight steps and then deciding to remove those steps which are least relevant. However, because previous research frequently utilizes groupings of steps similar to these four stages, we present this option here for comparison with that research. Eq. SI-14 can be rewritten (and simplified) by grouping the steps *search* and *detect* into the stage of Location and grouping the steps *pursuit* and *subjugation* into Attack. That is, denoting $A_{search} \cdot f_1 \cdot f_2$ with γ_{Loc}, and $f_5 \cdot f_4$ with γ_{Att}, SI-Eq. 14 reads:

(SI-15) $$FR = \chi_5 \cdot \varphi_{forage} = \frac{\gamma_{Loc} \cdot f_3 \cdot \gamma_{Att} \cdot N \cdot \varphi_{forage}}{1 + \gamma_{Loc} \cdot f_3 \cdot \gamma_{Att} \cdot t_{handle} \cdot N}$$

3. Implications of more explicit formulation of functional response

3.1. COMPATIBILITY WITH CLASSIC HOLLING FORMULATION AND EXISTING ATN MODEL APPROACH

How the foraging cycle of a predator is split into stages or steps and how handling time is defined, have important implications for the final formulation of the functional response equation, and should depend on the type of predator considered. Essentially, there are two ways to reach the classic Holling equation (SI-1) from our modular functional response (SI-14). Either we assume that attack rate, *a*, from SI-1 is the aggregate of the success of each step (i.e. $a = f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5$), OR we assume that $f_2 = f_3 = f_4 = f_5 = 1$, and that $a = f_1$. In the latter case, it does not matter how handling time is defined. In the former case, however, SI-14 can only be equivalent to SI-1 if handling time is defined as the average handling time per *ingested* prey (taking failures in each step into account, Eq. SI-10), not per *located* prey. It may seem like a trivial difference, but here we demonstrate its implications.

For a consumer with a very simple foraging behaviour, such as sedentary filter feeders (e.g. sponges and bivalves), the processes of detection, decision, pursuit and subjugation may be irrelevant so that $f_2 = f_3 = f_4 = f_5 \approx 1$ and $t_2 = t_3 = t_4 = t_5 \approx 0$. This implies that $t_{handle} \approx t_6$ (i.e. the average time to ingest a captured food particle) and means that Eq. 14 simplifies to (with $A_{search} = 1$):

(SI-16) $$FR = \chi_5 \cdot \varphi_{forage} = \frac{f_1 \cdot N \cdot \varphi_{forage}}{1 + f_1 \cdot t_{consume} \cdot N}$$

This recovers the classic Holling equation perfectly. However, in many cases, predators have a more complex foraging behaviour where detection, decision, pursuit and/or subjugation are separate processes in the foraging cycle, clearly distinguishable from consumption (so that $f_2 \neq f_3 \neq f_4 \neq f_5 < 1$ and $t_2 \neq t_3 \neq t_4 \neq t_5 > 0$). In these cases, the full version of the functional response equation (Eq. SI-14) provides a more realistic representation of the ingestion rate of

these predators. This will also aid in linking species traits in a more nuanced way to parameters of the functional response. Here it is important to also note that handling time as defined in Eq. SI-14 (where $t_{handle,1} = \dfrac{t_2}{f_2 \cdot f_3 \cdot f_4 \cdot f_5} + \dfrac{t_3}{f_3 \cdot f_4 \cdot f_5} + \dfrac{t_4}{f_4 \cdot f_5} + \dfrac{t_5}{f_5} + t_6$), is the average handling time <u>per ingested prey</u>. This is the sum of the time it takes for a predator to detect, decide on, pursue, subjugate and ingest a prey item. The time for each of these activities increases as the proportions of prey not detected, decided on, pursued, and subjugated increases. In the ecological literature, however, handling time is often not clearly defined (i.e. what it includes and/or what the prey unit is) or sometimes (e.g., Case 2000) defined as the average handling time <u>of each encountered prey</u>. The latter definition, which here corresponds to:

(SI-17) $t_{handle,2} = t_2 + t_3 \cdot f_2 + t_4 \cdot f_2 \cdot f_3 + t_5 \cdot f_2 \cdot f_3 \cdot f_4 + t_6 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5$

is the sum of the proportion of foraging time it takes for a predator to identify, detect, decide on, pursue, subjugate and ingest each *encountered* prey. The smaller the proportion of success for each step, the smaller $t_{handle,2}$ becomes, relative to $t_{handle,1}$. The definition of handling time (as the average time to handle each encountered or the average time to handle each killed prey) is crucial because this has important consequences for how the rest of the functional response equation is formulated. Defining handling time as in Eq. SI-17 leads to a functional response formulation significantly different from Eq. SI-14:

(SI-18) $FR = \chi_5 \cdot \varphi_{forage} = \dfrac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot A_{search} \cdot N \cdot \varphi_{forage}}{1 + f_1 \cdot A_{search} \cdot t_{handle,2} \cdot N}$

If $f_2 f_3 f_4 f_5$ does not equal one, then SI-18 is not equivalent to SI-1, because $f_1 \neq f_1 f_2 f_3 f_4 f_5$ and thus they cannot both be denoted with a. In most real situations (for predators which are not passive filter-feeders), $f_2 f_3 f_4 f_5 < 1$, illustrating that if handling time is defined as $t_{handle,2}$ above, the classic Holling expression is a simplification based on potentially unrealistic assumptions.

Because Eq. SI-14 is a more explicit formulation of the functional response than Eq. SI-1, it allows species traits to more easily be linked to parameters of the functional response (see below). Attempts in this direction have already been developed, most notably within the framework of the ATN model approach (Otto et al. 2007, Berlow et al. 2009, Schneider et al. 2012). We argue, however, that, although laudable, this effort now needs to be developed (and possibly also adjusted depending on how handling time is defined). More specifically, Vucic-Pestic et al. (2011) and Schneider et al. (2012) argued that a in Eq. SI-1 could be described as the product of two processes: 'success' × 'encounter', with Eq. SI-1 interpreted as (with $T_{forage} = 1$):

(SI-19) $FR = \dfrac{\text{'encounter'} \cdot \text{'success'} \cdot N}{1 + \text{'encounter'} \cdot \text{'success'} \cdot \text{'handling time'} \cdot N}$

Encounter was argued to depend on predator and prey speed, and Schneider et al. (2012) suggested that is should scale allometrically with predator (W_j) and prey (W_i) body size as:

$a_0 W_i^{0.25} W_j^{0.25}$ (where a_0 is a scaling constant). *Success* was argued to describe the predators'

'ability to subdue prey of different sizes' and suggested to scale as $\left(\dfrac{W_j/W_i}{R_{opt}}\right) e^{\left(1-\frac{W_j/W_i}{R_{opt}}\right)^{\theta}}$

(where R_{opt} is the optimal predator-prey body mass ratio of the predator, and θ a constant determining the width of the success curve). *Handling time* was the time required for processing and digesting one prey item', and suggested to scale as $h_0 W_i^{0.25} W_j^{-0.25}$. It is unclear if this means the average handling time <u>per encountered prey</u> or the average handling time <u>per ingested prey</u> (see above for mathematical definitions). As discussed above, how handling time is defined is crucial since it affects how the rest of the functional response equation is formulated (either as Eq. SI-14 or SI-18). If handling time is defined as the average time per *encountered* prey, then we would expect to only see "encounter" in the denominator of SI-19. The ATN model approach clearly represents a significant and important step towards linking parameters of predator-prey models to species traits and several studies have used this approach to parameterize models that attempt to replicate observed predator-prey dynamics, either from controlled experiments (Schneider et al. 2012, 2014, Jonsson et al. 2018) or from field surveys (Curtsdotter et al. 2019). If γ_{Loc} and γ_{Att} in Eq SI-16 are interpreted as 'encounter' and 'success', respectively, in Schneider et al. (2012), and f_3 is assumed to equal unity, Eq. SI-20 (the Schneider et al. formulation) is identical to Eq. SI-14 (our more detailed formulations of the functional response, with $\varphi_{forage} = 1$).

   On the one hand, suggesting how trophic interaction strengths may be affected by body sizes, the approach of Schneider et al (2012) represents a significant step forward by showing how 'success', 'encounter' and handling time may quantitatively be linked to predator and prey body sizes. This will be very useful for future research. On the other hand, we show here that unless handling time is defined as in Eq. SI-10, and f_3 assumed to equal unity, Eq. SI-14 cannot be recovered from Eq. SI-19. Furthermore, by aggregating steps search and detect into 'location' and steps pursuit and subjugation into 'success' important details on how various species traits affect different parts of the foraging of a predator may be obscured

3.2. MULTIPLE SPECIES

The presence of other species can affect trophic interactions in a number of different ways (Terry et al. 2017, Jonsson et al. 2018) and the dynamic model and functional response we describe above can easily be extended to include some effects of multiple prey and/or predators. As examples of such effects, (*i*) the time spent handling one prey species will usually leave less time to handle other prey species (see e.g. Koen-Alonso, 2007) (*ii*) the chance of encountering prey may increase if the prey's response to a second predator makes them more visible to the focal predator (e.g. Losey & Denno, 1998; Prasad & Snyder, 2010), thus affecting f_1), (*iii*) predators may decrease the proportion of time they spend foraging if they are avoiding their own predators or interfering with other predators (e.g. Preisser et al. 2007), thus affecting φ_{forage} and/or φ_{search}, and (*iv*) predators may strategically choose one

prey species over another based on their nutritional needs and the availability of alternate prey (e.g. McCluney & Sabo, 2009; Razeng and Watson, 2015), thus affecting f_3. Each of these effects, and others, can be incorporated into a model by making the appropriate terms of the general model (i.e. φ_{forage}, φ_{search}, f_k, t_k, A_{search}) a function of the presence of other species. Here we explicitly demonstrate this for handling multiple resources (3.2.1), predator interference (3.2.2), and fear of predation (3.2.3).

3.2.1. MULTIPLE PREY

If the predator has several different prey types (species) to choose from, this can affect the predator's foraging in many ways. The predator may develop preferences for different prey or become more experienced at handling a particular prey depending on their abundances. This could be incorporated in the functional response by allowing one or more of the probability parameters (i.e. f_1 - f_5), and/or the time components of t_{handle} (i.e. $t_2 - t_6$), to be functions of prey abundance. This has the capacity of turning a type II functional response into a type III functional response. However, the simplest and most straightforward effect of multiple prey on the foraging of a predator is its effect on searching time (see Koen-Alonso, 2007).

If additional prey only affect the time available to predator j for searching for prey (with m different prey types available to predator j) and assuming that the predator searches for all prey at the same time, Eq. SI-14 can easily be extended to account for multiple prey (note that this is not always the case (Stouffer & Novak 2021), and what follows could be parameterized differently to account for different scenarios). This is done in the traditional way by adding an expression for the time spent handling other prey items (species) to the denominator of the functional response equation. To show this, first, modify the expression for available search time (Eqs. SI-6 & SI-7) by taking time to handle all types of prey into account (here, R_j is the set of resource species to species j):

$$T_{search} = T_{forage} - \sum_{m \in R_j} T_{handle,m} = T_{forage} - \sum_{m \in R_j} \left(t_{handle,m} \cdot \chi_{m,5} \cdot T_{forage} \right) =$$

(SI-20)

$$= T_{forage} \left(1 - \sum_{m \in R_j} \left(t_{handle,m} \cdot \chi_{m,5} \right) \right)$$

Now, inserting Eq. SI-20 into Eq. SI-6c (and observing that components of f_1 - f_5 are predator-prey specific) gives (per unit foraging time):

(SI-21)

$$\chi_{i,j,5} = f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot A_{search,i,j} \cdot N_i \cdot \varphi_{search} =$$

$$= f_{5,i,j} \cdot f_{4,i,j} \cdot f_{3,i,j} \cdot f_{2,i,j} \cdot f_{1,i,j} \cdot A_{search,i,j} \cdot N_i \cdot \left(1 - \sum_{m \in R_j} \left(t_{handle,m,j} \cdot \chi_{m,j,5} \right) \right) =$$

$$= f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot A_{search,i,j} \cdot N_i \cdot \left(\begin{array}{c} 1 - t_{handle,i,j} \cdot \chi_{i,j,5} + \\ - \sum_{m \neq i} \left(t_{handle,m,j} \cdot \chi_{m,j,5} \right) \end{array} \right) =$$

$$\left[\begin{array}{c} \chi_{m,j,5} = \dfrac{\chi_{i,j,5}}{\chi_{i,j,5}} \cdot \chi_{m,j,5} = \chi_{i,j,5} \cdot \dfrac{\chi_{m,j,5}}{\chi_{i,j,5}} = \\[2mm] = \chi_{i,j,5} \cdot \dfrac{f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot f_{4,m,j} \cdot f_{5,m,j} \cdot A_{search,m,j} \cdot N_m \cdot \varphi_{search}}{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot A_{search,i,j} \cdot N_i \cdot \varphi_{search}} = \\[2mm] = \chi_{i,j,5} \cdot \dfrac{f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot f_{4,m,j} \cdot f_{5,m,j} \cdot A_{search,m,j} \cdot N_m}{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot A_{search,i,j} \cdot N_i} \end{array} \right]$$

$$= A_{search,i,j} \cdot N_i \cdot f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot$$

$$\cdot \left(\begin{array}{c} 1 - t_{handle,i,j} \cdot \chi_{i,j,5} + \\ - \sum_{m \neq i} \left(t_{handle,m,j} \cdot \chi_{i,j,5} \cdot \dfrac{f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot f_{4,m,j} \cdot f_{5,m,j} \cdot A_{search,m,j} \cdot N_m}{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot A_{search,i,j} \cdot N_i} \right) \end{array} \right) =$$

$$= A_{search,i,j} \cdot N_i \cdot f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot$$

$$\cdot \left(1 - \chi_{i,j,5} \cdot \sum_{m \in R_j} t_{handle,m,j} \cdot \dfrac{f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot f_{4,m,j} \cdot f_{5,m,j} \cdot A_{search,m,j} \cdot N_m}{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot A_{search,i,j} \cdot N_i} \right) =$$

$$= A_{search,i,j} \cdot N_i \cdot f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} +$$

$$- \chi_{i,j,5} \cdot \sum_{m \in R_j} t_{handle,m} \cdot f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot f_{4,m,j} \cdot f_{5,m,j} \cdot A_{search,m,j} \cdot N_m$$

Rearranging Eq. SI-21 (and multiplying by φ_{forage}) results in an expression for a saturating type II functional response with multiple prey (per unit total time):

(SI-22) $\quad FR = \chi_{i,j,5} \cdot \varphi_{forage} = \dfrac{A_{search,i,j} \cdot N_i \cdot f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot \varphi_{forage}}{1 + \sum_{m \in R_j} \left(t_{handle,m,j} \cdot f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot f_{4,m,j} \cdot f_{5,m,j} \cdot A_{search,m,j} \cdot N_m \right)}$

.

Now, $A_{search,i,j} \neq A_{search,m,j}$ if mobility of prey m is different from that of prey i. Thus, if mobility of prey m is NOT different from that of prey i (so that $A_{search,i,j} = A_{search,m,j} = A_{search}$) and with $A_{search} = 1$ this simplifies to:

$$(\text{SI-23}) \quad FR = \chi_{i,j,5} \cdot \varphi_{forage} = \frac{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot N_i \cdot \varphi_{forage}}{1 + \sum\limits_{m \in R_j} \left(f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot f_{4,m,j} \cdot f_{5,m,j} \cdot t_{handle,m,j} \cdot N_m \right)} .$$

The implication of this is that in a 'multiple prey species situation', differences in mobility of the different prey species become important, since they affect the encounter rates between the predator and the different prey species and need to be accounted for.

3.2.2. PREDATOR INTERFERENCE

Predators can interact in many different ways, for example indirectly via resource competition, directly via interference competition or by affecting the behaviour of one another (e.g. due to 'fear of predation'). Indirect resource competition (where consumption of prey species *i* by predator species *j* reduces the availability of prey species *i* to predator species *m*, and vice versa) will immediately be covered by a predator-prey model based on Eq. SI-14 and expanded to multiple species where several predators feed on the same prey type. Focusing on predator interference (where predators interact physically) and assuming that it only affects a predator's foraging by reducing the time available for searching, this can easily be accommodated in Eq. SI-14 (as mentioned above, however, interference may affect time for foraging as well, or instead). We do this in a similar way as accounting for multiple prey, by describing the decrease in available search time due to contacts with intra- and/or interspecific competitors. This results in an expression for a saturating type II functional response with multiple interacting predators. First, modify the expression for available search time (Eq. SI-6 and SI-7) by taking time to interfere with other predators into account (here, I_j is the set of species that species *j* has interference competition with):

$$(\text{SI-24})$$
$$T_{search} = T_{forage} - T_{handle,i,j} - \sum_{m \in I_j} T_{interfere,m,j} =$$

$$= T_{forage} - T_{handle,i,j} - \sum_{m \in I_j} \left(t_{interfere,m,j} \cdot \chi_{m,j,Interfere} \cdot T_{forage} \right)$$

Here, $\chi_{m,j,Interfere}$ is the number of individuals of species *m* that an individual of species *j* interferes with per unit time. Here it is assumed that for interference between predator species *j* and *k* to occur, the predator needs to encounter, detect and decide to interfere with the other species (while no steps similar to pursuit and immobilization should occur for interference). Now, inserting Eq. SI-24 into Eq. SI-6c (and performing the same steps as in Eq. SI-21 gives (per unit total time):

$$(\text{SI-25}) \quad FR = \chi_{i,j,5} \cdot \varphi_{forage} = \frac{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot A_{search,i,j} \cdot N_i \cdot \varphi_{forage}}{1 + \left(\begin{array}{l} f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot t_{handle,i,j} \cdot A_{search,i,j} \cdot N_i + \\ + \sum\limits_{m \in I_j} \left(f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot t_{interfere,m,j} \cdot A_{search,m,j} \cdot N_m \right) \end{array} \right)}$$

Similarly as above for multiple prey, $A_{search,i,j} \neq A_{search,m,j}$ if mobility of predators m that predator j interferes with is different from that of prey i. Conversely, if mobility of predators m is NOT different from that of prey i (so that $A_{search,i,j} = A_{search,m,j} = A_{search}$) and with $A_{search} = 1$ this simplifies to:

$$(SI\text{-}26) \quad FR = \chi_{i,j,5} \cdot \varphi_{forage} = \frac{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot N_i \cdot \varphi_{forage}}{1 + \left(\begin{array}{l} f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot t_{handle,i,j} \cdot N_i + \\ + \sum_{m \in I_j} \left(f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot t_{interfere,m,j} \cdot N_m \right) \end{array} \right)}$$

The implication of this is that in a 'multiple predator species situation' with interference taking place, differences in mobility of the different predator species become important, and need to be accounted for, since they affect the encounter rates between focal predator and the other predator species it interferes with.

To summarize, the result of interference competition is described as a time loss on search time. Replacing $f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot t_{interfere,m,j} \cdot A_{search,m,j}$ with the parameter $c_{m,j}$, results in a general reformulation of Eq. 26, for the effect of intra- and interspecific interference competition that is the same as that used for intraspecific competition in the ATN model (with $A_{search,i,j} = 1$):

$$(SI\text{-}27) \quad FR = \chi_{i,j,5} \cdot \varphi_{forage} = \frac{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot N_i \cdot \varphi_{forage}}{1 + \sum_{m \in I_j} \left(c_{m,j} \cdot N_m \right) + f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot t_{handle,i,j} \cdot N_i},$$

suggesting that $c_{m,j}$ could be related allometrically to body size as in Schneider et al. (2012).

If predator interference also has other (secondary) effects on a predator's foraging, such as increasing the risk of physical injuries, this could also affect one or more of the probability components f_1- f_5), and/or the time components of t_{handle} (i.e. $t_2 - t_6$). This development is, however, outside the scope of this paper.

3.2.3. FEAR OF PREDATION

'Fear of predation' is when the presence of a predator affects the behaviour of another predator (e.g. due to intraguild predation) or prey species. The effect of this should be more complex than the simple one described above as a result of interference competition, since it can be expected that the effect is not only on the time available for searching in both species. Instead, it could be assumed that the effect is a reduction in the time available for searching in one species (due to induced inactivity and hiding in the one experiencing the 'fear of predation'), but a decrease in the encounter rate in the other species (due to less exposed prey for the one causing the 'fear of predation'). Assuming increasing encounters with individuals of species j causes a linear increase in the time species i spends hiding, the effect on species i's foraging can either be described as a direct decrease in the proportion of time spent foraging (φ_{forage}) or as a decrease in available search time (T_{search}). Here we take the latter

approach and modify the expression for available search time (Eq. SI-7) by subtracting time spent hiding ($t_{inactive,m,j}$) from each individual of species m of the set P_j of species inducing fear in species j.

(SI-28)
$$T_{search} = T_{forage} - T_{handle,i,j} - \sum_{m \in P_j} T_{inactive,m,j} =$$
$$= T_{forage} - T_{handle,i,j} - \sum_{m \in P_j} \left(t_{inactive,m,j} \cdot \chi_{m,j,Fear} \cdot T_{forage} \right).$$

Here, $\chi_{m,j,Fear}$ is the number of individuals of species m, that upon meeting an individual of species j induces inactivity in species j, due to fear of predation, per unit foraging time. Here it is assumed that for inactivity of species j due to fear of predation from species m to occur, species j needs to encounter, detect and decide to become inactive for a period of time (while no steps similar to pursuit and immobilization should occur for fear of predation). Now, inserting Eq. SI-28 into Eq. SI-6c (and performing the same steps as in Eq. SI-21 gives:

(SI-29) $FR = \chi_{i,j,5} \cdot \varphi_{forage} = \dfrac{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot A_{search,i,j} \cdot N_i \cdot \varphi_{forage}}{1 + \left(\begin{array}{l} f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot t_{handle,i,j} \cdot A_{search,i,j} \cdot N_i + \\ + \sum\limits_{m \in P_j} \left(f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot t_{inactive,m,j} \cdot A_{search,m,j} \cdot N_m \right) \end{array} \right)}.$

Similarly as above for interference and multiple prey, $A_{search,i,j} \neq A_{search,m,j}$ if mobility of predators m that induces fear in predator j is different from that of prey i. Conversely, if mobility of predators m is NOT different from that of prey i (so that $A_{search,i,j} = A_{search,m,j} = A_{search}$) and with $A_{search} = 1$ this simplifies to:

(SI-30) $FR = \chi_{i,j,5} \cdot \varphi_{forage} = \dfrac{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot N_i \cdot \varphi_{forage}}{1 + \left(\begin{array}{l} f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot t_{handle,i,j} \cdot N_i + \\ + \sum\limits_{m \in P_j} \left(f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot t_{inactive,m,j} \cdot N_m \right) \end{array} \right)}$

The implication of this is that in a 'fear of predator situation', differences in mobility of the different predator species become important, since they affect the encounter rates between focal predator and the other predator species that induces fear of predation behaviour and need to be accounted for. To summarize, the result of 'fear of predation' is as above described as an added time loss on search time. Replacing $f_{1,m,j} \cdot f_{2,m,j} \cdot f_{3,m,j} \cdot t_{inactive,m,j} \cdot A_{search,m,j}$ with $b_0 \times \rho_j$, results in a general formulation for the effect of 'fear of predation' on the species experiencing it, and would recover the basic formulation in Laubmeier et al. (2018):

(SI-31)
$$FR = \chi_{i,j,5} \cdot \varphi_{forage} =$$
$$= \dfrac{f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot N_i \cdot \varphi_{forage}}{1 + \sum\limits_{m \in P_j} \left(b_0 \cdot \rho_j \cdot N_m \right) + f_{1,i,j} \cdot f_{2,i,j} \cdot f_{3,i,j} \cdot f_{4,i,j} \cdot f_{5,i,j} \cdot t_{handle,i,j} \times N_i},$$

suggesting that this could be modelled as in Laubmeier et al. (2018).

Finally, assuming that 'fear of predation' also has an effect on the species causing it, we need to find a way to describe this. The simplest assumption is probably that this results in a decrease in the encounter rate the species experiencing 'fear of predation' (due to inactivity and/or hiding behaviour of the prey). This development is also outside the scope of this paper.

4.   References

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Appendix S2. Factorization of the functional response by separating steps of the predation cycle.

Remembering the definition of t_{handle} (Eq. SI-10), the full composite functional response (Eq. SI-14) can be factorized to give main text Eq. 12 as follows:

(SI-32)

$$FR = \chi_5 \cdot \varphi_{forage} = \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{1 + f_1 f_2 f_3 f_4 f_5 \cdot t_{handle} \times N \cdot A_{search}} =$$

$$= \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{1 + f_1 f_2 f_3 f_4 f_5 \times \left(\dfrac{t_2}{f_2 f_3 f_4 f_5} + \dfrac{t_3}{f_3 f_4 f_5} + \dfrac{t_4}{f_4 f_5} + \dfrac{t_5}{f_5} + t_6 \right) \cdot N \cdot A_{search}} =$$

$$= \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{1 + \left(f_1 \cdot t_2 + f_1 f_2 \cdot t_3 + f_1 f_2 f_3 \cdot t_4 + f_1 f_2 f_3 f_4 \cdot t_5 + f_1 f_2 f_3 f_4 f_5 \cdot t_6 \right) \cdot N \cdot A_{search}} = \left[\xi_0 = N \cdot A_{search} \right] =$$

$$= \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{1 + f_1 \cdot t_2 \cdot \xi_0 + f_1 f_2 \cdot t_3 \cdot \xi_0 + f_1 f_2 f_3 \cdot t_4 \cdot \xi_0 + f_1 f_2 f_3 f_4 \cdot t_5 \cdot \xi_0 + f_1 f_2 f_3 f_4 f_5 \cdot t_6 \cdot \xi_0} =$$

$$= \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{\left(1 + f_1 \cdot t_2 \cdot \xi_0 \right) \cdot \left(1 + \frac{f_1 f_2 \cdot t_3 \cdot \xi_0}{1 + f_1 \cdot t_2 \cdot \xi_0} + \frac{f_1 f_2 f_3 \cdot t_4 \cdot \xi_0}{1 + f_1 \cdot t_2 \cdot \xi_0} + \frac{f_1 f_2 f_3 f_4 \cdot t_5 \cdot \xi_0}{1 + f_1 \cdot t_2 \cdot \xi_0} + \frac{f_1 f_2 f_3 f_4 f_5 \cdot t_6 \cdot \xi_0}{1 + f_1 \cdot t_2 \cdot \xi_0} \right)} = \left[\xi_1 = \frac{f_1 \cdot \xi_0}{1 + f_1 \cdot t_2 \cdot \xi_0} \right] =$$

$$= \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{\left(1 + f_1 \cdot t_2 \cdot \xi_0 \right) \cdot \left(1 + f_2 \cdot t_3 \cdot \xi_1 \right) \cdot \left(1 + \frac{f_2 f_3 \cdot t_4 \cdot \xi_1}{1 + f_2 \cdot t_3 \cdot \xi_1} + \frac{f_2 f_3 f_4 \cdot t_5 \cdot \xi_1}{1 + f_2 \cdot t_3 \cdot \xi_1} + \frac{1 f_2 f_3 f_4 f_5 \cdot t_6 \cdot \xi_1}{1 + f_2 \cdot t_3 \cdot \xi_1} \right)} = \left[\xi_2 = \frac{f_2 \cdot \xi_1}{1 + f_2 \cdot t_3 \cdot \xi_1} \right] =$$

$$= \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{\left(1 + f_1 \cdot t_2 \cdot \xi_0 \right) \cdot \left(1 + f_2 \cdot t_3 \cdot \xi_1 \right) \cdot \left(1 + f_3 \cdot t_4 \cdot \xi_2 \right) \cdot \left(1 + \frac{f_3 f_4 \cdot t_5 \cdot \xi_2}{1 + f_3 \cdot t_4 \cdot \xi_2} + \frac{f_3 f_4 f_5 \cdot t_6 \cdot \xi_2}{1 + f_3 \cdot t_4 \cdot \xi_2} \right)} = \left[\xi_3 = \frac{f_3 \cdot \xi_2}{1 + f_3 \cdot t_4 \cdot \xi_2} \right] =$$

$$= \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{\left(1 + f_1 \cdot t_2 \cdot \xi_0 \right) \cdot \left(1 + f_2 \cdot t_3 \cdot \xi_1 \right) \cdot \left(1 + f_3 \cdot t_4 \cdot \xi_2 \right) \cdot \left(1 + f_4 \cdot t_5 \cdot \xi_3 \right) \cdot \left(1 + \frac{f_4 f_5 \cdot t_6 \cdot \xi_3}{1 + f_4 \cdot t_5 \cdot \xi_3} \right)} = \left[\xi_4 = \frac{f_4 \cdot \xi_3}{1 + f_4 \cdot t_5 \cdot \xi_3} \right] =$$

$$= \frac{f_1 \cdot f_2 \cdot f_3 \cdot f_4 \cdot f_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}}{\left(1 + f_1 \cdot t_2 \cdot \xi_0 \right) \cdot \left(1 + f_2 \cdot t_3 \cdot \xi_1 \right) \cdot \left(1 + f_3 \cdot t_4 \cdot \xi_2 \right) \cdot \left(1 + f_4 \cdot t_5 \cdot \xi_3 \right) \cdot \left(1 + f_5 \cdot t_6 \cdot \xi_4 \right)} =$$

$$\frac{f_1}{1 + f_1 \cdot t_2 \cdot \xi_0} \cdot \frac{f_2}{1 + f_2 \cdot t_3 \cdot \xi_1} \cdot \frac{f_3}{1 + f_3 \cdot t_4 \cdot \xi_2} \cdot \frac{f_4}{1 + f_4 \cdot t_5 \cdot \xi_3} \cdot \frac{f_5}{1 + f_5 \cdot t_6 \cdot \xi_4} \cdot N \cdot A_{search} \cdot \varphi_{forage} =$$

$$\psi_1 \cdot \psi_2 \cdot \psi_3 \cdot \psi_4 \cdot \psi_5 \cdot N \cdot A_{search} \cdot \varphi_{forage}$$

Here, $\psi_k = \dfrac{f_k}{1 + f_k \cdot t_{k+1} \cdot \xi_{k-1}}$ can be interpreted as 'the proportional functional response of one step of the predation cycle' with ξ_{k-1} being 'the number of prey entering step k from step k-1 per unit aggregated step time up until step k-1' and ξ_k thus being the rate of prey successfully handled in step k). Thus, ψ_k can be understood as 'the realized proportion of prey handled in step k when handling in the following step is taken into account' (since in a conveyer belt

system, to avoid pile-up/overflow, the numbers that can be processed in one station will ultimately be limited by the process rate in the following station).

To get a further understanding of the meaning of ψ_k and ξ_k above, the revised composite formulation of the functional response (Eq. SI-14) can be factorized along a different route, by remembering that

$$\frac{T_{search}}{T_{search}+T_2+T_3+T_4+T_5+T_6}=\frac{T_{search}}{T_{forage}}=\varphi_{search}=\frac{1}{1+f_1\cdot f_2\cdot f_3\cdot f_4\cdot f_5\cdot t_{handle}\cdot N\cdot A_{search}}\ .$$

Thus:

(SI-33)

$$FR=\chi_5\cdot\varphi_{forage}=\frac{f_1\cdot f_2\cdot f_3\cdot f_4\cdot f_5\cdot N\cdot A_{search}\cdot\varphi_{forage}}{1+f_1\cdot f_2\cdot f_3\cdot f_4\cdot f_5\cdot t_{handle}\cdot N\cdot A_{search}}=$$

$$=\frac{T_{Search}}{T_{Search}+T_2+T_3+T_4+T_5+T_6}\cdot f_1\cdot f_2\cdot f_3\cdot f_4\cdot f_5\cdot N\cdot A_{search}\cdot\varphi_{forage}=$$

$$=\left[T_{forage}=T_{Search}+T_2+T_3+T_4+T_5+T_6\right]=$$

$$=\frac{T_{Search}\cdot\left(T_{Search}+T_2\right)\cdot\left(T_{Search}+T_2+T_3\right)\cdot\left(T_{Search}+T_2+T_3+T_4\right)\cdot\left(T_{Search}+T_2+T_3+T_4+T_5\right)}{\left(T_{Search}+T_2\right)\cdot\left(T_{Search}+T_2+T_3\right)\cdot\left(T_{Search}+T_2+T_3+T_4\right)\cdot\left(T_{Search}+T_2+T_3+T_4+T_5\right)\cdot T_{forage}}\cdot$$

$$\cdot f_1\cdot f_2\cdot f_3\cdot f_4\cdot f_5\cdot N\cdot A_{search}\cdot\varphi_{forage}=$$

$$=\left[\frac{T_{Search}}{T_{Search}+T_2}\cdot f_1\right]\left[\frac{T_{Search}+T_2}{T_{Search}+T_2+T_3}\cdot f_2\right]\left[\frac{T_{Search}+T_2+T_3}{T_{Search}+T_2+T_3+T_4}\cdot f_3\right]\cdot$$

$$\cdot\left[\frac{T_{Search}+T_2+T_3+T_4}{T_{Search}+T_2+T_3+T_4+T_5}\cdot f_4\right]\cdot\left[\frac{T_{Search}+T_2+T_3+T_4+T_5}{T_{forage}}\cdot f_5\right]\cdot N\cdot A_{search}\cdot\varphi_{forage}=$$

$$=\zeta_1\cdot\zeta_2\cdot\zeta_3\cdot\zeta_4\cdot\zeta_5\cdot N\cdot A_{search}\cdot\varphi_{forage}$$

This implies that $\zeta_k=\psi_k$ or more specifically:

(SI-34)
$$\zeta_k=\frac{T_{Search}+\ldots+T_k}{T_{Search}+\ldots+T_{k+1}}\cdot f_k=\psi_k=\frac{f_k}{1+f_k\cdot t_{k+1}\cdot\xi_{k-1}}$$

That $\zeta_k=\psi_k$ can be verified by noting that $\xi_k=\dfrac{T_{forage}\cdot\chi_k}{\displaystyle\sum_1^k T_i}$ and inserting this into Eq. SI-32.

This second factorization of the functional response suggests two alternative or complementary interpretations of $\dfrac{\psi_k}{f_k}$:

(SI-35)
$$\frac{\psi_k}{f_k}=\frac{1}{1+f_k\cdot t_{k+1}\cdot\xi_{k-1}}=\frac{\zeta_k}{f_k}=\frac{T_{Search}+\ldots+T_k}{T_{Search}+\ldots+T_{k+1}}\ .$$

That is, either (*i*) as the 'realized success function' of step *k*' (= the proportion of the intrinsic handling probability (f_k) that is realized'), or (*ii*) as 'the proportion of foraging time from step 1 (= searching) to step *k*+1 that is available for steps 1 to *k*, (in other words, the proportion of foraging time from step 1 to step *k*+1 that is <u>not</u> 'used' by step *k*+1).

From the exercise above it can also be seen how χ_k (in Eqs. SI-3-5) is related to ξ_k:

$$(\text{SI-36}) \qquad \xi_k = \left. \chi_k \middle/ \frac{1}{T_{forage}} \cdot \sum_1^k T_i \right. = \frac{\chi_k}{\varphi_{T_{search} \to T_k}} = x_k \cdot \frac{T_{search}}{\sum_1^k T_i}$$

This means that while χ_k is the rate of prey handling in step *k* <u>per unit foraging time</u>, ξ_k is the rate of prey handling in step *k* per unit step time up until step *k*.

To summarize, the proportional functional responses (ψ_k) above, factored out from the composite functional response, correspond to and have a similar meaning and form as the well-known 'prey risk functions' (i.e. *FR/N*, or the proportion of prey killed per predator) of a type II or type III functional response, albeit describing the realized predator success rate and prey risk for individual foraging steps.

Table S1. Effect of body size and thermal niche on parameter values of the dynamic model described in the main text.

Parameter	Effect	Explanation	Factor
A_{search}	$B_C^{0.25}$	Larger predators can cover more area when searching. This is scaled by metabolic rate. Prey are stationary. Based on ATN	Body size
f_1, f_2, f_4, f_5	1	Assuming stationary aphid prey which do not flee, all prey within the area searched will be encountered and detected, and all prey decided upon will be successfully pursued and subdued	NA
f_3	$\dfrac{B_C}{B_N R_{opt}} e^{1-\frac{B_C}{B_N R_{opt}}}$	Predators will decide to attack prey close to their optimal prey size. Equation based on the Ricker function.	Body size
t_{2-5}	0	Time for prey to detect and decide upon prey, and pursue and subjugate stationary aphid prey which they have encountered is sufficiently minimal that we can set these to zero to simplify our model.	NA
t_6	$\dfrac{B_N}{B_C}$	Larger prey take longer to handle and larger predators are faster at handling prey.	Body size
φ_{forage}	$\dfrac{1}{\sigma\sqrt{2\pi}} e^{-\left(\frac{temp-\mu}{2\sigma^2}\right)}$	Predators spend more time foraging when closer to the optimum of their thermal niche. Based on the probability density function for a normal distribution	Temperature

1: Banks, H. T. et al. (2016) Parameter Estimation for an Allometric Food Web Model. (Technical Report No. CRSC-TR16-03), CRSC Technical Reports. CRSC-TR16-03, Center for Research in Scientific Computation, North Carolina State University, Raleigh, May., Raleigh.

NA: Not applicable.

Table S2. Parameter values for the model represented in figure 3 of the main text.

Parameter	Value
B_C	*Bembidion lampros* = 1.61 mg *Trechus secalis* = 1.96 mg *Agonum dorsale* = 10.53 mg *Pterostichus vernalis* = 9.55 mg
B_N	*R. padi* = 0.1550mg
R_{opt}	118 (from Jonsson et al 2018)[1]
σ	*Bembidion lampros* = 9.9 °C *Trechus secalis* = 5.7 °C *Agonum dorsale* = 9 °C *Pterostichus vernalis* = 7.2 °C
μ	*Bembidion lampros* = 23.5 °C *Trechus secalis* = 15.6 °C *Agonum dorsale* = 19.9 °C *Pterostichus vernalis* = 31.0 °C
temp	10-35°C
N	10 individuals

1: Jonsson, T. et al. (2018) Predictive power of food web models based on body size decreases with trophic complexity. *Ecology Letters* 21: 702–712.