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# Mutually exclusive feeding yields Holling type III functional response

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## Abstract

1. Many generalist predators, including fish, insects and mammals, temporarily focus on their search behaviour and can switch between prey species. Flexible and rapid behavioural plasticity enables a predator to forage optimally, as guided by search image formation and prey switching in response to changing prey abundances.

2. More than half a century of studies have used Holling type III functional response to model the impact of this feeding behaviour on population dynamics, yet a mechanistic understanding for the pathway between individual behaviour and feeding rates remains poorly understood.

3. To understand this common feeding behaviour, we developed three mechanistic models using first-principles to provide direct derivations for the relationship between observed individual behaviour and feeding rates.

4. The derived models yield three novel, generalised functional responses for predators characterised by prey switching and mutually exclusive feeding (i.e. feeding is limited to one prey species at a time). We show how these functional responses act as Holling type III response, and how they can be used to predict predators' diet compositions.

5. Our results demonstrate that several behavioural forms of prey switching, as displayed in a wide range of predator species, consistently produce type III conforming functional responses.

**KEYWORDS**
adaptive feeding, predator–prey, prey switching, search image

## 1 | INTRODUCTION

Generalist predators have the ability to feed on a variety of prey, yet they often focus on one or a few prey species at a time (Cock, 1978). When the primary prey depletes or an alternative flourishes, these predators can shift their focus (Cornell, 1976). Interestingly, these "switching generalists" frequently consume prey species disproportionately to their relative abundances (Allen, 1988; Gendron, 1987; Greenwood & Elton, 1979). This flexible behaviour is known as prey switching, a form of adaptive feeding (Murdoch, 1969). Here, we explore the influence of prey switching on the predator's feeding rate across different prey species (i.e. 'functional response'), as well as on diet composition. Our focus is on situations where prey switching is driven by behavioural plasticity rather than ecological constraints or natural selection.

In assessing the consequences of prey switching on species interactions, biodiversity, and ecosystem functioning, it becomes crucial to understand how varying prey and predator abundances

impact predation rates (Abrams, 2010; Abrams & Matsuda, 2004). The key to this understanding is the functional response, which describes the predation rate between a specific predator and prey species in relation to their population abundances (Solomon, 1949). The functional response is unique to each predator–prey pair and is influenced by various behavioural and physiological characteristic, such as the prey's anti-predatory adaptations, the predator's diet preferences, attack and capture efficiency, and satiation level (DeLong, 2021). Commonly defined as the per capita rate of prey capture by an 'average' predator, functional response serves as an idealised model for an individual predator, incorporating information about the time the predator is expected to spend actively searching for a given prey species. During other activities, such as handling captured prey or seeking alternative prey species, active search of the focal prey is temporarily halted and curtailing the functional response towards that prey.

Holling (1959a, 1959b) classified functional responses based on the way predation rates change with increasing prey abundance. The three response types are: type I, a linear increase in predation rate; type II, saturating at high prey abundances due to the predator's limited handling capacity of captured prey (Holling, 1959b; Metz & Diekmann, 1986); and type III, an 'S'-shaped curve. Holling type III response has long been attributed to learning behaviour or prey switching, supported by experiments involving predators preying on two prey species (Holling, 1959a, 1959b; Murdoch, 1969). The intuitive idea is that when a prey becomes scarce, the predator switches to more abundant prey, resulting in the scarce prey being captured at a disproportionally lower rate.

Predator search behaviours are typically categorised as specialist, feeding exclusively on one prey species, or generalist, with several prey in their diet (e.g. Ali & Agrawal, 2012; Ceia & Ramos, 2015). Generalist predators can exhibit markedly different search behaviours depending on whether they feed on several prey species simultaneously or specialise on one prey species at a time. The latter scenario with prey switching implies that feeding on different prey species is mutually exclusive and the predator is alternating between them (Cornell, 1976). This mutually exclusive feeding can emerge from ecological constraints like spatial heterogeneity of prey species, where prey switching corresponds to moving between different patches (Holt, 1984). Yet, even when predators can potentially feed on several prey species simultaneously, focusing on a smaller subset might be advantageous due to varying anti-predator responses, physiological characteristics, and limitations in the predator's information processing (Cornell, 1976; Dukas, 2002).

In situations where prey possess distinct characteristics like complex camouflage patterns, using a fixed search behaviour for all prey can lead to suboptimal predation success. To overcome this, predators can adjust their search behaviour for different prey species (Ishii & Shimada, 2010), resulting in improved detection of preferred prey (Dukas, 2002; Punzalan et al., 2005). Such selective search behaviour for cryptic prey is called a 'search image' (Dawkins, 1971; Tinbergen, 1960). Search image inherently implies a trade-off between predation successes of preferred and non-preferred prey species (Garay et al., 2018), with the extreme case corresponding to mutually exclusive feeding, which is the focus of this study. A predator with an extreme search image may intentionally ignore potential non-preferred prey encounters, yet this behaviour could still yield higher net energy intake than opportunistic random searching without a search image (Garay et al., 2018). Such a search image can be formed rapidly and its maintenance requires constant reinforcement; otherwise the search image is disrupted (Dawkins, 1971; Ishii & Shimada, 2010). Numerous experiments on fish and birds have shown how successive encounters with the same prey species lead to significant improvements in feeding success, whereas delays in encounters impair these gains (Coolen et al., 2003; Croy & Hughes, 1991; Langley et al., 1996; Pietrewicz & Kamil, 1979). Prey encounter delays also affect predator satiation level, such that adjustments to feeding behaviour can be triggered by starvation. In an experiment, predatory mosquitofish (*Gambusia*) actively preferred feeding on smaller and more profitable prey, while only starved mosquitofish also fed on large prey, indicating that selective feeding was predominantly influenced by satiation level (Bence & Murdoch, 1986). Plastic search image formation is observed in various animals, including mammals and insects (for a review, see Ishii & Shimada, 2010).

A mechanistic understanding of the functional response requires a dynamic model that incorporates the behavioural properties of both predator and prey species that can affect the predation rate (Metz & Diekmann, 1986). We understand mechanistic modelling as a method to describe how individual-level observations translate to population-level dynamics. We consider a model 'mechanistic' when its parameters have a clear-cut interpretations in terms of individual behaviour (Geritz & Kisdi, 2012). This approach provides a mechanistic understanding of population dynamics based on elementary individual interactions, rather than density-dependent relationships alone. For switching predators that focus on one preferred prey at a time, the functional response depends on the proportion of time the predator allocates to feeding that prey.

The existing formulations of Holling's type III response have often lacked mechanistic depth, stemming from missing linkage between assumptions about individual-level processes (which are density-independent) and observed population-level dynamics (which exhibit nonlinear density-dependence; Baudrot et al., 2016; Real, 1977). Therefore, while justifications for Holling's type III response are intuitively sound, current formulations often struggle to provide a comprehensive mechanistic explanation for the parameters in the equation for Holling type III response (Uszko et al., 2020).

To address this gap, van Leeuwen et al. (2007, 2013) proposed a mechanistic derivation of functional responses based on the underlying processes of prey-switching feeding behaviour. Using this approach, van Leeuwen et al. (2007, 2013) developed a model that accounted for the dietary history of a generalist predator when simultaneously feeding on different prey species. The predator was most efficient in consuming prey which it successfully attacked previously, reflecting a form of learning behaviour. This behaviour resulted in Holling type III conforming functional response (van

Leeuwen et al., 2007, 2013). However, type III response has never been derived mechanistically based on mutually exclusive feeding.

In this study, we explore adaptive feeding behaviour when feeding on distinct prey species is mutually exclusive. We consider three feeding scenarios inspired by typical observations of search image formation; first, when prey switching is independent of dietary history; second, when only predators experiencing a delay between successive prey encounters are prone to prey switching; and third, when these predators with prey encounter delays act as temporal generalists and revert to specialised feeding upon satiation. We derive three mechanistic functional responses and investigate how they mirror Holling type III response characteristics. Finally, we examine how varying relative prey abundances and the number of prey species affects the predator's diet composition.

## 2 | METHODS

Prey switching manifests in various ways across animal species (Ishii & Shimada, 2010). We develop three distinct population dynamics models, henceforth referred to as M1, M2, and M3, each governed by unique sets of rules for predator feeding behaviour and thereby leading to differing functional responses. All models share the feature that a predator's adaptive feeding behaviour is guided by prey abundances, alongside potential genetic diet preferences, wherein switching is more likely towards abundant prey.

In M1, prey switching can occur whenever a predator is searching for prey. Switching mechanism activates upon sensing a nearby prey, even though an immediate attack is not possible. Subsequently, the predator continues in actively searching an opportunity to attack prey of this particular species. Thus, the predator's decision to switch its prey focus is predominantly influenced by the abundance of alternative prey species, impacting their likelihood of being detected, rather than the scarcity of the currently focused prey.

In M2, prey switching is restricted to predators that have had a sufficient delay in prey encounters. After such an encounter delay, the predator maintains focusing on the current prey species; however, if an opportunity arises by sensing the presence of another prey species, the predator may switch its focus. The predator's primary objective is to maintain the current search image, but should it prove unfruitful, it recognises the necessity of switching to avert starvation. This transition involves a swift change of search image akin to what is observed in numerous bird species (Dawkins, 1971; Langley et al., 1996). Importantly, this shift is rooted in the predator's existing memory of efficiently capturing other prey in its diet rather than in an extensive learning phase.

In M3, the predator's search image is disrupted after a delay in prey encounters, prompting it to seek any available prey with reduced capture efficiency. Such a temporal generalist forms its search image based on the next prey capture and proceeds preying on them. For example, in blue jays there was a 25% lower capture efficiency in the generalist state compared to when a specific search image was formed (Dukas & Kamil, 2001).

The model differences arise from the manner of search image formation, which is swift in M1 and M2. In M1, this occurs regardless of the time since the last prey encounter, whereas such a delay is a prerequisite for switching in M2 and M3. In M3, prey switching is further linked to learning behaviour, maximising capture efficiency towards any prey type after the second successive encounter. Though these model nuances might seem subtle, they yield notably distinct functional responses and feeding patterns.

We mechanistically derive functional responses using the modelling approach outlined by Metz & Diekmann, 1986. We begin by classifying a number of states to predator individuals and the manner of transitions between them. Individual states (i-states) refer to temporal conditions of an individual, reflecting behavioural differences and dictating which interactions it can undergo (e.g. searching or handling). Physiologically distinct individuals are considered different species or functional guilds. As such, individual differences arising from morphological properties, such as size, belong outside our definition of i-state. This 'bottom-up' approach deviates from phenomenological modelling, wherein all individuals of a species are treated identically, and bookkeeping is solely concerned in species' total population abundances but neglecting internal subpopulation compositions.

The ensemble of i-states, coupled with individual interactions, constitute the descriptive individual-behaviour model. We use this information to derive a dynamical model of ordinary differential equations for the population abundance changes within these i-states. Transitions between i-states are triggered by biological processes, either through interactions with others (second-order, e.g. a successful prey capture followed by transition to the handling state) or self-initiated processes (first-order, e.g. finishing handling a captured prey the consecutive transition back to the searching state).

Here, we utilise the standard timescale argument (Auger & Poggiale, 1996; Metz & Diekmann, 1986), which involves dividing population dynamics into fast and slow timescales. The focus is on the transitions among i-states on the short timescale, where relative changes in total population abundances are negligible. Thus, we can ignore details related to, for example predator birth, growth or mortality, enabling a focused analysis of behavioural factors relevant to feeding.

We address a general case with $n$ different prey species with population abundances $N_i$, $i = 1, 2, \ldots, n$, that are fed on by a predator species with abundance $P$. We further divide predators into different subpopulations based on their i-states. In each model, we denote the abundances of predators focusing their search or handling captured prey of species $i$ by $P_i^{(s)}$ and $P_i^{(h)}$, respectively. A predator searching for prey species $i$ captures them at the rate $\beta_i$ and has the mean handling time $h_i$ per captured prey item. Therefore, a predator handling a prey item of type $i$ finishes the process and transitions into the searching state at the per capita rate $1/h_i$. Both the capture rate and handling time by the predator are expected to depend allometrically on the prey's body size or their body-size ratio, but species-specific parametrisations are beyond the scope of this study. Further model-specific details are presented in the subsequent subsections. For an overview of all notations used in this study, see Table 1.

**TABLE 1** List of notations used in Models 1, 2 and 3.

| Symbol | Definition | Unit |
|---|---|---|
| $N_i$ | Prey species $i$ | No. of individuals/volume |
| $P_i^{(s)}$ | Predators searching for prey $i$ (temporal specialist) | No. of individuals/volume |
| $P_i^{(h)}$ | Predators handling a prey item of species $i$ | No. of individuals/volume |
| $\beta_i$ | Capture rate of prey $i$ | Volume×time$^{-1}$ |
| $h_i$ | Mean handling time of a prey $i$ | Time |
| *Specific to M1* | | |
| $a_i$ | Diet switch rate towards prey $i$ for searching predators | Volume×time$^{-1}$ |
| *Specific to M2* | | |
| $P_i^{(c)}$ | Predators searching for prey $i$ while hungry (temporal specialist) | No. of individuals/volume |
| $a_i$ | Diet switch rate towards prey $i$ for hungry predators | Volume×time$^{-1}$ |
| $c_i$ | Mean time of losing search image of prey $i$ after no capture | Time |
| *Specific to M3* | | |
| $P^{(c)}$ | Hungry predators searching for any prey (temporal generalist) | No. of individuals/volume |
| $c_i$ | Mean time of losing search image of prey $i$ after no capture | Time |
| $\omega_i$ | Scalar trade-off in capture rate of prey $i$ for temporal generalists | — |

The functional response of a predator to the prey species $i$, denoted $F_i(N_1, N_2, \ldots, N_n)$, is derived using the model's subpopulation equilibria for the i-states in which prey capture occurs. Commonly in the literature, this is the 'searching state', but for some of our models prey capture of a given prey species is associated with more than one i-state. Functional response to the prey species $i$ is then attained by taking the average of all i-states in which the predator captures those prey, weighted by their prey capture rates. For example, if the predator captures a prey species $i$ only when focusing their search for that prey and with the rate $\beta_i$, then the functional response equals $F_i(N_1, N_2, \ldots, N_n) = \beta_i N_i \widehat{P}_i^{(s)} / P$, where $\widehat{P}_i^{(s)}$ is the short timescale subpopulation equilibrium of those searching predators. This is how the functional response of Equation 3 is derived in our first modelling approach M1; the scenarios in which the predator captures a specific prey in several i-states are derived in the latter models M2 and M3 (Equations 7 and 12, respectively).

For each functional response, we explore the conditions on the predator behaviour under which it acts as Holling type II or III response (Holling, 1959b). In particular, we provide the general conditions that are independent of any fixed parameter values, but rather our results depend only on their relative values and the number of prey species in the predator's diet.

To investigate similarities with Holling's functional responses, recall that a type III response is characterised by an S-shaped curve. Any saturating functional response is a concave function for high prey abundances, and a type III response specifically involves an inflection point where the curve shifts from convex to concave. Using this insight, to determine if a functional response conforms to type III response, it suffices to investigate if it is a convex function for small prey abundances (van Leeuwen et al., 2007). Mathematically, this condition states that a functional response $F_i$ corresponds to a Holling type III response if $\partial^2 F_i(N_1, N_2, \ldots, N_n) / \partial N_i^2 > 0$ evaluated at $N_i \approx 0$, and a type II response otherwise. To compare our results with those of van Leeuwen et al. (2007, 2013) in the most transparent fashion, we explore the same three cases of prey abundances: first, if abundances of prey species $j = i$ are constant; second, if the total abundance of all prey species is constant, $N_{\text{total}} = \sum_{j=1}^{n} N_j$; and third, if abundances of prey species $j = i$ are relative to that of prey species $i$, $N_j = b_j N_i$. For each numerical example on the functional response shapes and the diet compositions, we extract the parameter values from van Leeuwen et al. (2007, 2013) whenever applicable. Notably, these parameter values are neither based on empirical observations nor are they intended to represent any particular species or ecosystem, but they are chosen with the aim of illustrating the overall nature our key findings.

We also investigate the relationship between diet breadth (i.e. the number of prey species in the predator's diet) and diet composition. In the spirit of (van Leeuwen et al., 2007), we use a functional response, $F_i$, to quantify the relative representation of the focal prey in the diet composition. Without loss of generality, we consider prey species 1 as the focal prey and the alternative prey are each introduced by artificially partitioning the population of prey species 2, $N_2$, into equally sized compartments. Hence, the proportion of the focal prey remains unchanged in the presence of any arbitrary $n-1$ number of alternative prey species. Let $\eta$ describe the proportion of

the focal prey, $\eta = N_1 / (N_1 + N_2)$. The total proportion of alternative prey is $1 - \eta$ and it comprises $n - 1$ species with identical properties, each of which has the proportion $(1 - \eta)/(n - 1)$. Then, the proportion of the focal prey in the diet composition as dependent on the relative abundance and the diet breadth is

$$\phi(\eta) = \frac{F_1\left(\overbrace{\eta}^{\text{prey 1}}, \overbrace{(1-\eta)/(n-1), \ldots, (1-\eta)/(n-1)}^{\text{prey 2 to } n; n-1 \text{ copies}}\right)}{\sum_{j=1}^{n} F_j(\eta, (1-\eta)/(n-1), \ldots, (1-\eta)/(n-1))}. \tag{1}$$

Whenever $\phi(\eta) > \eta$ ($\phi(\eta) < \eta$), the focal prey is over-represented (under-represented) in the diet as it is being fed at a rate that is disproportionally greater (lower) than its relative abundance. The diet switching point, $\phi(\eta^*) = \eta^*$, is the critical proportion of the focal prey at which it switches from being under- to over-represented in the predator's diet.

To provide further information about the relationship between diet switching and diet breadth, we categorise diet switching into two classes: 'accelerated' if $\eta^* < 1/n$, and conversely 'delayed' if $\eta^* > 1/n$. This definition seamlessly links disproportionally high feeding on the focal prey with the number of prey species in the predator's diet, providing additional insight about when the predator switches to predominantly feed on the focal prey. In particular, it informs whether the focal prey should be most prevalent to trigger switching. An accelerated diet switch can be understood as the focal prey being the predator's genetically preferred source of food, while a delayed diet switch signifies the focal prey acting as a substitute when the preferred food becomes rare. Given our assumption that non-focal prey have the same proportions, an accelerated (delayed) diet switch implies that the focal prey is the least (most) abundant species when the switch occurs. To illustrate, if $\eta^* = 0.20$ in the presence of three prey species, the switch is accelerated as it happens when the focal prey comprises 20% of the total, while each of the two non-focal prey make up 40%. Similarly, maintaining the same diet switch point value in the context of six prey species results in delayed switching. This is due to the fact that the focal prey is most abundant, accounting for 20%, while each of the five non-focal prey contribute 16% each.

## 3 | THEORY AND RESULTS

### 3.1 | Model 1

In M1, we assume that a searching predator can switch between several prey species but can only feed on one at a time. Following the capture and handling of a prey, the predator resumes focused searching for prey of the same species but may also switch to another type. Notably, this mutually exclusive feeding behaviour sets our model derivation apart from that of van Leeuwen et al. (2007, 2013), where the assumption was that the searching predator feeds simultaneously on different prey species. Top panel of Figure 1 illustrates the individual-level transitions behind our derivation of M1. We neglect any possible effect of dietary history, resulting in equal per capita rate of switching to any specific prey regardless of the current focus. Furthermore, the predator may switch even to a prey that is distinctively of poorer quality or lower abundance. This potential for switching persists regardless of the currently focused prey's characteristics. In our later models, we introduce constraints to limit the incidence of switching.

When a predator currently focusing its search for prey species $i$ switches to species $j$, it retains searching but simply has a different focus. The population level rate at which a predator switches the focus to prey species $j$ is proportional to its abundance $N_j$ and to the predator's per capita switching rate $a_j$ towards that species. On the population-level, the transition from a searching state of prey species $i$ to species $j$ occurs at the rate $a_j N_j$. This combines both the rate at which a predator senses the presence of a prey individual and the probability of switching based on that information.

The dynamical model for the change of predator population abundances in these i-states is described by

$$\dot{P}_i^{(s)} = + \overbrace{a_i N_i \sum_{j=i} P_j^{(s)} - P_i^{(s)} \sum_{j=i} a_j N_j}^{\text{prey switching}} - \overbrace{\beta_i N_i P_i^{(s)}}^{\text{prey capture}} + \overbrace{h_i^{-1} P_i^{(h)}}^{\text{finish handling}}$$

$$\dot{P}_i^{(h)} = + \beta_i N_i P_i^{(s)} - h_i^{-1} P_i^{(h)}. \tag{2}$$

The resulting functional response of the predator to the prey species $i$ equals to the population-level capture rate of that prey divided by the overall predator population $P$,

$$F_i(N_1, N_2, \ldots, N_n) = \beta_i N_i \frac{\widehat{P}_i^{(s)}}{P} = \frac{a_i \beta_i N_i^2}{\sum_{j=1}^{n} a_j N_j (1 + \beta_j h_j N_j)}, \tag{3}$$

where $\widehat{P}_i^{(s)}$ is the subpopulation equilibrium of the predators focusing their search for that prey. For further details of the dynamical system and the derivation of the functional response, see Appendix A. In the simplest case with only one prey present, the functional response reduces to the standard form of Holling type II response, $F = \beta N / (1 + \beta h N)$.

We now explore the three cases of prey abundances, as outlined in section "Methods", to see when the functional response of Equation 3 acts as Holling type II or type III response (Figure 2, top row). First, when prey species $j = i$ are present with constant abundances, the functional response is a convex function of prey species $i$ at zero abundance given that the predator has positive switching rate to it, $a_i > 0$, and also to at least one other prey species, $a_j > 0$. Therefore, the above functional response displays type III behaviour whenever the predator exercises prey switching (Figure 2, dashed line). This results applies even when handling times are arbitrarily
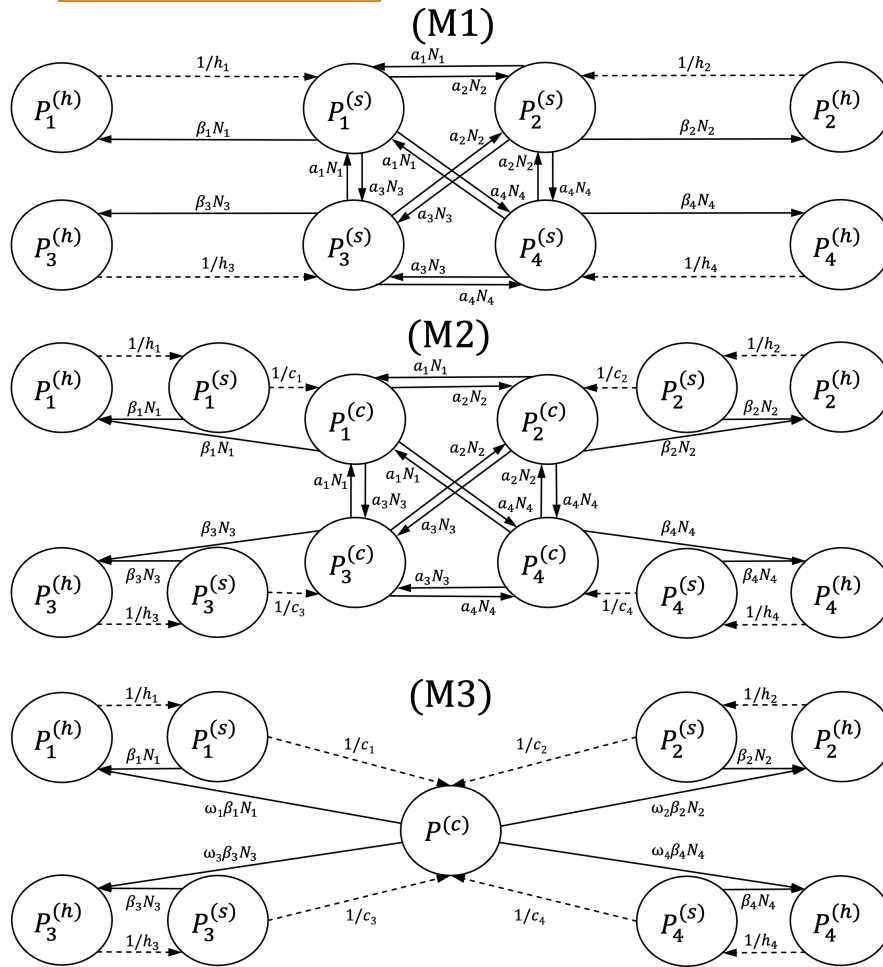
**FIGURE 1** Diagrams depicting the three behavioural models developed here. Nodes represent different predator states, characterised by current activity and focused prey (subindex). Solid arrows indicate second-order state transitions that depend on the predator's per capita rates and prey abundances. Dashed arrows indicate first-order state transitions that depend on the mean handling time of a prey item ($h_i$) or the mean time of becoming hungry after handling ($c_i$).

small, $h_i \approx 0$ for all $i$, demonstrating that the sigmoidal, type III curve is an integral characteristic of the functional response of Equation 3.

Second, when the total abundance of all prey is constant, the functional response is a convex function of prey species $i$ at zero abundance under the same condition as in the first case, and hence results in type III behaviour (Figure 2, dot-dashed line). Third, if the abundances of prey species $j = i$ are relative to that of prey species $i$, the functional response is a concave function of prey species $i$ at zero abundance, and hence conforms to type II response (Figure 2, solid line).

We now investigate the role of diet breadth and relative prey abundances for feeding on the focal prey, species 1, assuming without the loss of generality that alternative prey have identical characteristics as species 2. Using the functional response of Equation 3 and the relative prey abundances, we solve the focal prey's proportion in the predator's diet composition, which gives

$$\phi(\eta) = \frac{a_1 \beta_1 \eta^2}{a_2 \beta_2 (n-1)^{-1} (1-\eta)^2 + a_1 \beta_1 \eta^2}. \tag{4}$$

From this expression, we see that diet broadening via increasing the number of prey species, $n$, contributes to decreasing the term $a_2 \beta_2 (n-1)^{-1} (1-\eta)^2$ in the denominator. This leads to increasing the overall expression of Equation 4 and hence more pronounced feeding on the focal prey (Figure 3, top row). Diet broadening from two to three (four) prey species leads up to 100% (200%) relative increase in feeding on the focal prey (Figure 4, top row). This result shows that

even if the relative abundance of the focal prey would be fixed, the feeding rate on that prey can dramatically change when increasing the number of alternative prey species.

Biologically, this result can be explained by deconstructing the chain of transitions behind prey switching and capture events. Recall that the predator focuses on one prey species at a time, and that prey switching rates are directly proportional to their abundances. When artificially partitioning non-focal prey into smaller population compartments, the focal prey's abundance remains unaffected, thereby maintaining an unaltered prey capture and switching rate towards the focal prey unlike for the non-focal prey. In the simplest case of broadening the diet from two to three prey species, these rates are halved. Switching and consecutively capturing a non-focal prey constitutes to a second-order interaction, which leads to the overall rate being only one quarter of the original.

Specifically, at each point of the interaction chain in the above example, diet broadening lowers the probability of capturing a non-focal prey. For a predator currently focusing its search for prey species 2, the probability that the next event is capturing a prey of that type, instead of switching to prey species 1, is $\beta_2 N_2 / (\beta_2 N_2 + a_1 N_1)$. When broadening the diet to three prey species and halving the abundance of species 2, this probability becomes $0.5\beta_2 N_2 / (0.5\beta_2 N_2 + a_1 N_1 + a_3 N_3)$, where in the denominator the last term corresponds to switching to prey species 3. This further simplifies into $\beta_2 N_2 / (\beta_2 N_2 + 2a_1 N_1 + a_2 N_2)$, which is always lower than in the case of two prey species.

**FIGURE 2** The three functional responses to the focal prey $(F_1)$ when a second prey species is present. All functional responses are Holling type III conforming when the second prey's abundance is constant, $N_2 = 2$, or when the total abundance of both prey is constant, $N_1 + N_2 = 15$. Parameters: $\beta_1 = 1, \beta_2 = 0.4, h_1 = h_2 = 0.5, a_1 = 1, a_2 = 2, \omega_1 = \omega_2 = 0.5, c_1 = c_2 = 10$. (Left column) The dotted meshes represent functional response values for varying prey abundances, while the lines represent three special cases. (Right column) Mappings of the plots into two dimensions for small prey abundances.
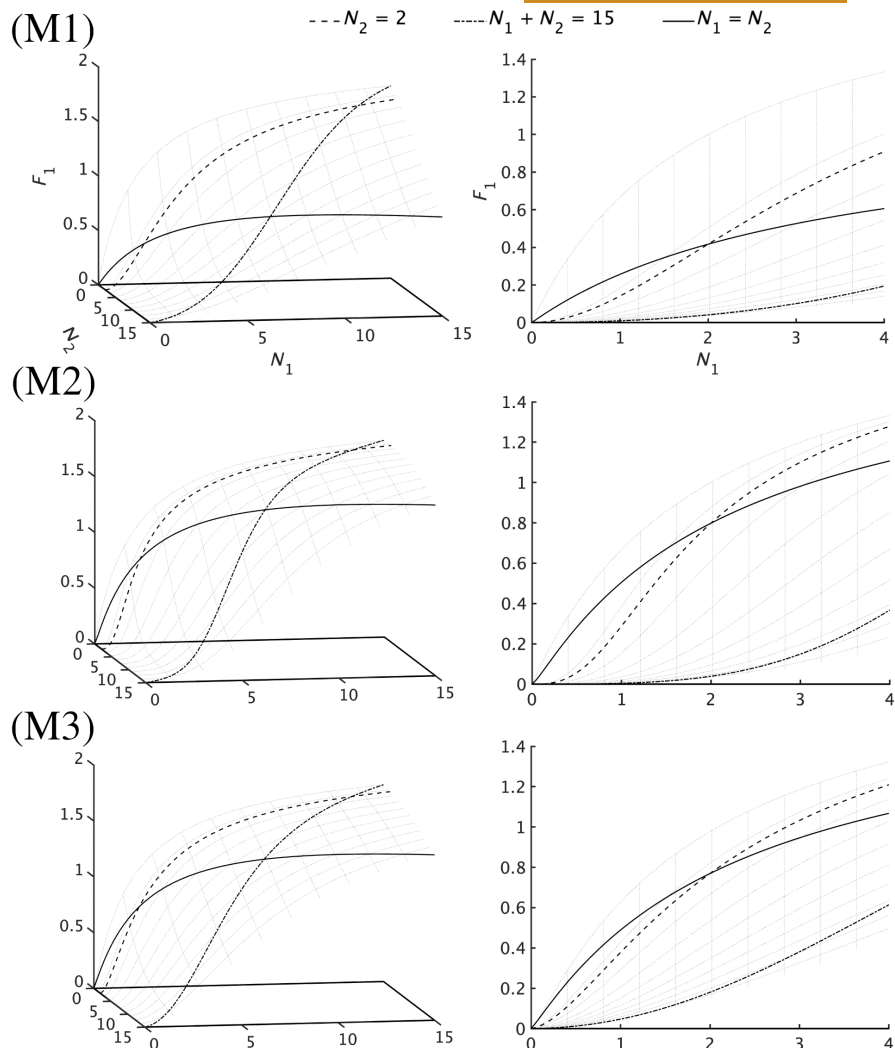


Similarly, for a predator searching for prey species 1, the probability of switching to prey species 2 is $a_2 N_2 / (\beta_1 N_1 + a_2 N_2)$, which via diet broadening decreases into $a_2 N_2 / (2\beta_1 N_1 + a_2 N_2)$. Conversely, the probability of capturing prey species 1 remains unchanged at $\beta_1 N_1 / (\beta_1 N_1 + a_2 N_2) = \beta_1 N_1 / (\beta_1 N_1 + 0.5a_2 N_2 + 0.5a_3 N_3)$. In conclusion, diet broadening amplifies feeding on the focal prey species 1.

Next, we use the functional response of Equation 3 to solve the critical proportion of the focal prey associated with diet switching, which results in

$$\eta^* = \frac{a_2 \beta_2}{a_1 \beta_1 (n-1) + a_2 \beta_2}. \tag{5}$$

The above diet switching point always decreases with diet broadening, such that higher count of prey species in the overall diet accelerates the switch to the focal prey being over-represented. Accelerated diet switch occurs whenever $a_1 \beta_1 > a_2 \beta_2$, otherwise diet switch is delayed.

## 3.2 | Model 2

In M2, we extend M1 to encompass the influence of dietary history, achieved by limiting prey switching to situations involving delays in prey encounters. We regard prey switching as an option a predator might employ when it becomes hungry or the focused prey appears difficult to find. The center panel of Figure 1 illustrates the individual-level transitions behind our derivation of M2.

Suppose that $c_i$ is the mean delay in prey captures after which a searching, satiated predator becomes hungry. A searching predator focusing on prey $i$ transitions to the hungry state at the per capita rate $1/c_i$, and these predators' population abundance is denoted by $P_i^{(c)}$. A hungry predator resumes searching for its focused prey and maintains the same capture success. However, it is also prone to prey switching. If the predator captures the focused prey $i$ while hungry, it transitions to the handling state and this satiated predator is no longer prone to switching. A hungry predator switches its focus on another prey species $j$ at the per capita rate $a_j$, similarly as in M1. Following such a switch, the predator remains hungry but now focuses its search on a different prey foci, signifying that it has sensed the presence of prey species $j$ but has not yet captured one. Further back-and-forth switching may occur between different prey focuses until an actual prey capture occurs.

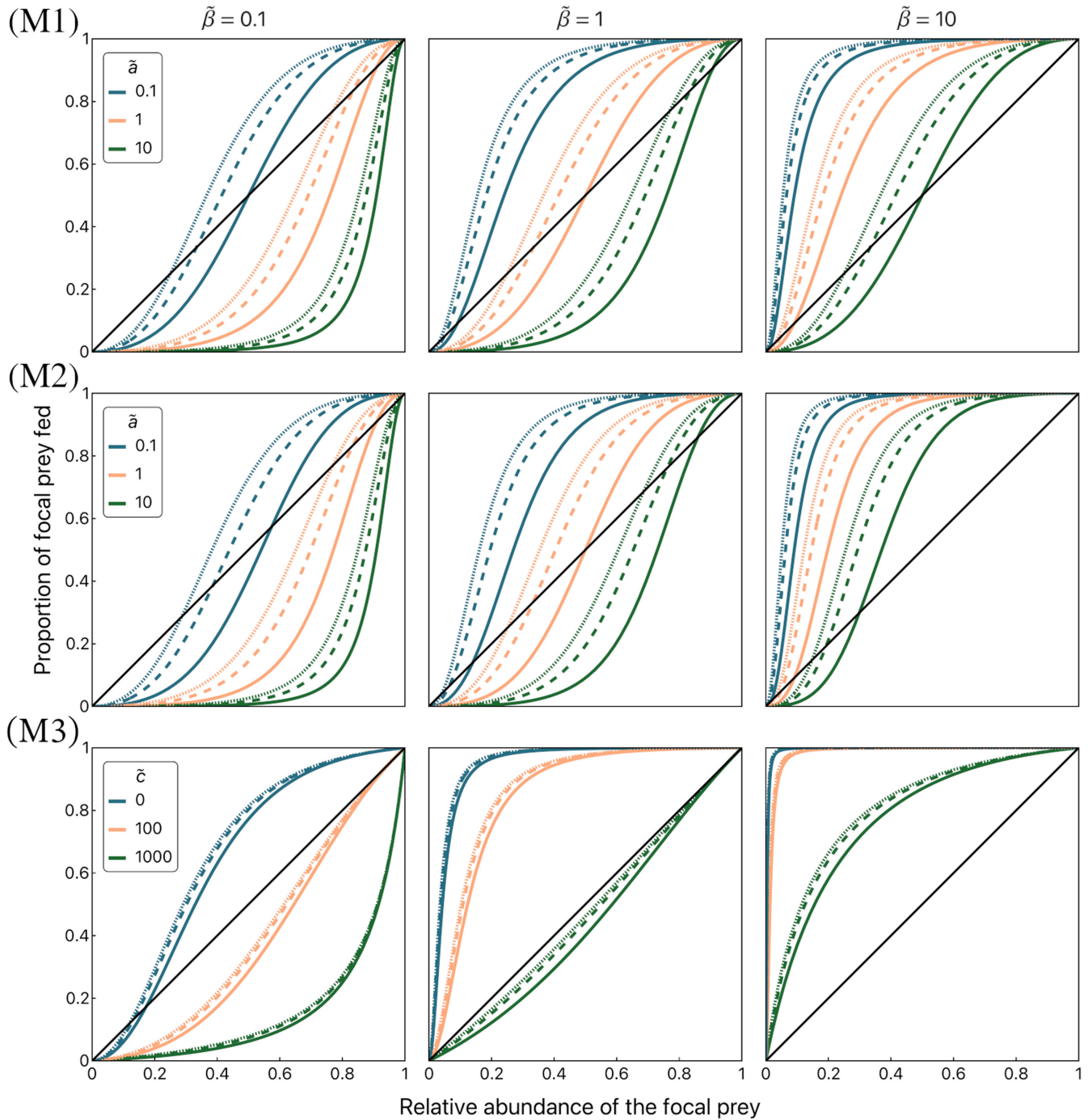The dynamical model for the change of predator population abundances in these i-states is described by

**FIGURE 3** The role of diet breadth and relative abundances on feeding the focal prey. Intersections with the diagonal line correspond to diet switching points. The panels represent different parametrisation cases of predation ratios between the focal and alternative prey, $\tilde{\beta}$, while coloured lines represent additional parametrisation cases of adaptive feeding behaviour: prey switching rate, $\bar{a}$ (Models 1 & 2), and mean delay in prey captures after which switching can occur, $\bar{c}$ (Model 3). Solid, dashed and dotted lines represent diet breadth of two, three, and four prey species, respectively. Parameters: $\bar{\beta} = \beta_1 / \beta_2$, $\bar{a} = a_1 / a_2$, $\bar{c} = c_1 / c_2$, where $a_2 = \beta_2 = c_2 = 1$.

$$\dot{P}_i^{(s)} = - \overbrace{c_i^{-1}P_i^{(s)}}^{\text{become hungry}} - \overbrace{\beta_i N_i P_i^{(s)}}^{\text{prey capture}} + \overbrace{h_i^{-1}P_i^{(h)}}^{\text{finish handling}}$$

$$\dot{P}_i^{(c)} = + c_i^{-1}P_i^{(s)} \beta_i N_i P_i^{(c)} + \overbrace{a_i N_i \sum_{j=i} P_j^{(c)} - P_i^{(c)} \sum_{j=i} a_j N_j}^{\text{prey switching}} \quad (6)$$

$$\dot{P}_i^{(h)} = + \beta_i N_i \left( P_i^{(s)} + P_i^{(c)} \right) - h_i^{-1}P_i^{(h)}.$$

The resulting functional response of the predator to the prey species $i$ equals to the population-level capture rate of that prey species divided by the overall predator population $P$. Unlike in the functional response of Equation 3 for M1, here the predator captures the prey species $i$ in two i-states: the searching state and the hungry state. Therefore, the functional response is the sum of the capture rates in both of these states,
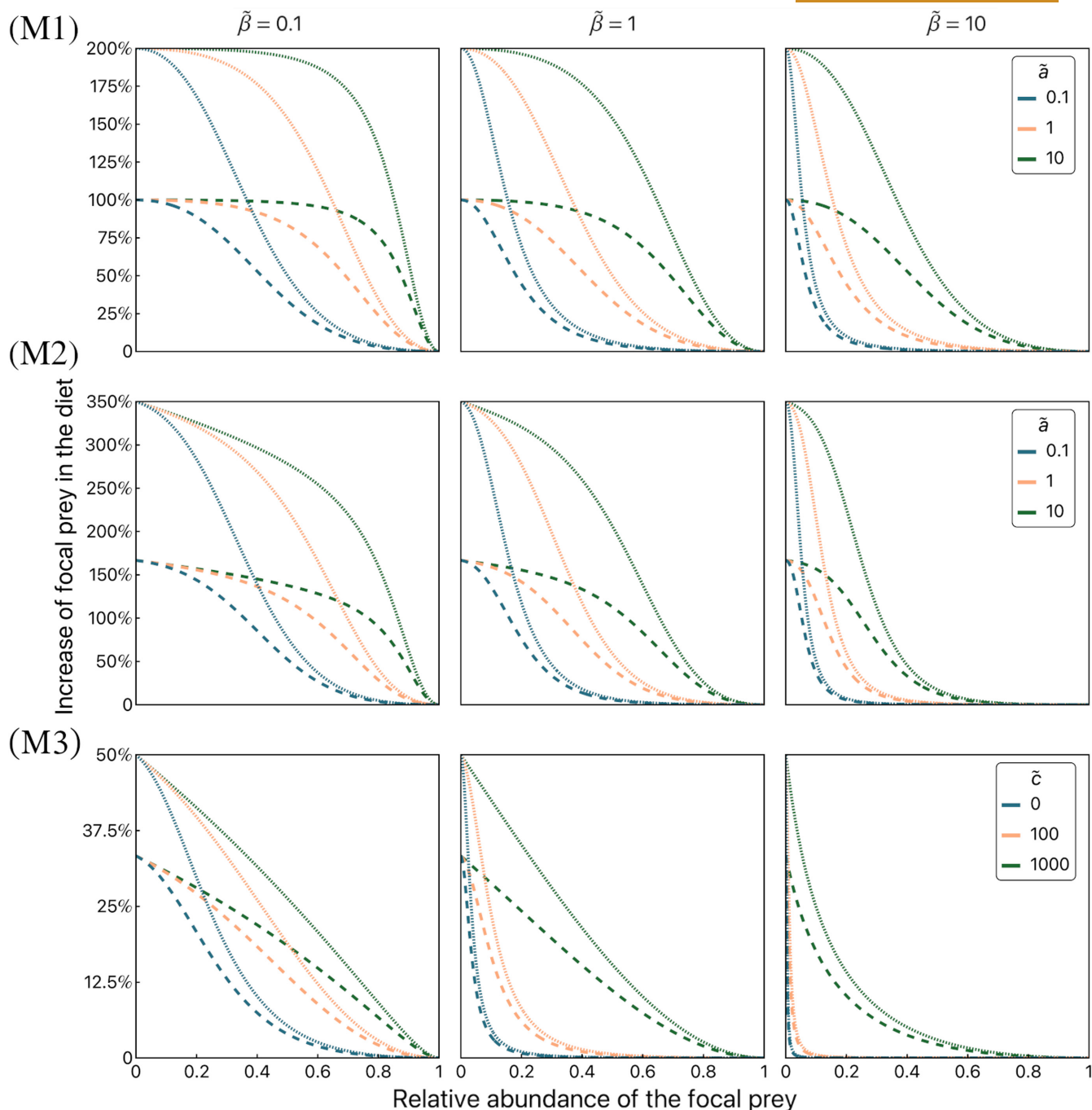
**FIGURE 4** Relative increases in feeding on the focal prey due to diet broadening. In all three models, this effect is amplified under relatively small focal prey abundances. The panels represent the same parametrisation cases as described in Figure 3. Dashed (dotted) lines represent relative changes in feeding on the focal prey in cases of three (four) prey species when compared against the case with only two prey species. Parameters: $\bar{\beta} = \beta_1 / \beta_2$, $\bar{a} = a_1 / a_2$, $\bar{c} = c_1 / c_2$, where $a_2 = \beta_2 = c_2 = 1$.

$$F_i(N_1, N_2, \ldots, N_n) = \beta_i N_i \frac{\widehat{P}_i^{(s)} + \widehat{P}_i^{(c)}}{P} = \frac{a_i \beta_i \left(1 + c_i \beta_i N_i\right) N_i^2}{\sum_{j=1}^{n} a_j N_j \left(1 + c_j \beta_j N_j\right)\left(1 + \beta_j h_j N_j\right)},$$

(7)

where $\widehat{P}_i^{(s)}$ and $\widehat{P}_i^{(c)}$ are the subpopulation equilibria of the searching and hungry predators. For further details of the dynamical system and the derivation of the functional response, see Appendix B. In the simplest

case with only one prey being present, the functional response reduces to the standard Holling type II form, $F = \beta N / (1 + \beta h N)$.

We now explore the three cases of prey abundances to see when the functional response of Equation 7 conforms to Holling type III response (Figure 2, center row). In the two cases of when the abundances of prey species $j = i$ or the total abundance of all prey is constant, the functional response of Equation 7 conforms

to type III response (Figure 2, dashed and dot-dashed lines). This is similar as with the functional response of Equation 3 corresponding to M1.

In the third case if the abundances of prey species $j$ are relative to that of prey species $i$, the functional response conforms to type III response if

$$c_i > \frac{a_i\beta_i h_i + \sum_{j=i} a_j b_j^2 (c_j + h_j)\beta_j}{\beta_i \left(\sum_{j=i} a_j b_j\right)}. \tag{8}$$

High $c_i$ values indicate stronger resilience against starvation, whereupon prey switching is limited to situations when the focal prey abundance is low. Consequently, this pattern gives rise to the 'S'-shape of the type III response. Noteworthy, however, is that this shape can be remarkably difficult to detect from the figure alone (Figure 2, solid line). The 'S'-shape becomes evident when $c_i$ value is vastly greater than other parameters, or when non-focal prey abundances are substantially smaller compared to the focal prey. Conversely, low $c_i$ values prompt the predator to switch away from the focal prey even when its abundance is relatively high. From the above equation, it can be observed that combination of low $c_i$ and high $c_j$ values hinders the emergence of Holling type III behaviour. Strong resilience against starvation while feeding on non-focal prey (high $c_j$) makes switching to the focal prey less likely.

We now investigate the role of diet breadth and relative prey abundances for the feeding on the focal prey. The focal prey's proportion in the diet is

$$\phi(\eta) = \frac{a_1\beta_1\eta^2(1 + c_1\beta_1\eta)}{a_2\beta_2(1-\eta)^2(n-1)^{-1}\left(1 + c_2\beta_2(1-\eta)(n-1)^{-1}\right) + a_1\beta_1\eta^2(1 + c_1\beta_1\eta)}. \tag{9}$$

From this expression, we see that diet broadening contributes to more pronounced feeding on the focal prey (Figure 3, centre row). Diet broadening from two to three (four) prey species leads up to 167% (350%) relative increase in feeding on the focal prey (Figure 4, centre row). Therefore, even when the focal prey's relative abundance remains unchanged, varying the number of prey species available for the predator can have a significant impact on the diet composition.

The underlying biological mechanism driving this outcome mirrors that of M1. Specifically, the sequence of successive interactions that the predator must engage in with the same prey species becomes less likely as the non-focal prey are partitioned into smaller compartments. However, M2 introduces an additional layer to this interaction by imposing the constraint that prey switching behaviour is confined to hungry predators. To elaborate, the potential for a predator to switch feeding on a non-focal prey necessitates a sufficient delay in capturing the focal prey. After this delay, the predator retains the ability to capture the focal prey which would obviate the need for switching. Consequently, in M2 the window of opportunity for prey switching towards rarer prey narrows significantly as the relative differences between prey abundances increase. This

explains why diet broadening yields more pronounced relative increases in feeding on the focal prey in comparison to M1.

The critical proportion of the focal prey associated with diet switching is

$$\eta^* = \left((1-n)\sqrt{a_2^2\beta_2^2 + a_1\beta_1(n-1)^2 + 2a_1a_2\beta_1\beta_2(n-1+2c_2\beta_2 + 2c_1(n-1+c_2\beta_2)\beta_1)}\right.$$
$$\left. + a_2\beta_2(n-1+2c_2\beta_2) + a_1(n-1)^2\beta_1\right)/2\left(a_2c_2\beta_2^2 - a_1c_1\beta_1^2(n-1)^2\right). \tag{10}$$

The above diet switching point always decreases with diet broadening. Accelerated diet switch occurs whenever $n < \left(a_1c_1\beta_1^2 - a_2c_2\beta_j^2\right)/\left(a_2\beta_2 - a_1\beta_1\right)$, otherwise diet switch is delayed.

## 3.3 | Model 3

In M3, we consider an alternative to M2 by assuming that hungry predators can feed simultaneously on different prey. After capturing a prey while hungry, the predator focuses on that prey species until a delay in prey captures renews the hunger. This temporal generalist behaviour is traded off for capture efficiency, potentially leading to lower net energy intake, but in this way the predator might avert starvation. Thus, in this model predators exhibit characteristics of both temporal specialists and generalists, as they alternate between these two behaviour modes as influenced by their satiation level. Hungry predator's ability to capture prey of any species effectively replaces prey switching rate $a_i$ of M1 and M2, causing switching to occur via direct confrontation with prey rather than sensing its vicinity. The bottom panel of Figure 1 illustrates the individual-level transitions behind our derivation of M3.

The population abundance of predators in the hungry i-state is $P^{(c)}$, in which state prey capture of species $i$ is traded off by a dimensionless scaling parameter $\omega_i \in [0, 1]$, yielding the per capita capture rate $\omega_i\beta_i$. The parameter $\omega_i$ thus describes the degree to which predation efficiency is decreased without a search image.

The dynamical model for the change of predator population abundances in these i-states is described by

$$\dot{P}_i^{(s)} = -\overbrace{\sum_{j=1}^{n} c_i^{-1} P_i^{(s)}}^{\text{become hungry}} - \overbrace{\sum_{j=1}^{n} \omega_j\beta_i N_i P_i^{(s)}}^{\text{prey capture}} + \overbrace{h_i^{-1} P_i^{(h)}}^{\text{finish handling}}$$
$$\dot{P}^{(c)} = +\sum_{j=1}^{n} c_j^{-1} P_j^{(s)} - \sum_{j=1}^{n} \omega_j\beta_j N_j P^{(c)}$$
$$\dot{P}_i^{(h)} = +\beta_i N_i\left(P_i^{(s)} + \omega_i P^{(c)}\right) - h_i^{-1} P_i^{(h)}. \tag{11}$$

The resulting functional response of the predator to the prey species $i$ equals the capture rate of that prey species divided by the overall predator population $P$. The predator captures the prey species $i$ in two different i-states: searching state and the hungry state corresponding to simultaneous feeding. Therefore, the functional response is given by

$$F_i(N_1, N_2, \dots, N_n) = \beta_i N_i \frac{\left(\hat{P}_i^{(s)} + \omega_i \hat{P}^{(c)}\right)}{P} = \frac{\omega_i\beta_i N_i(1 + c_i\beta_i N_i)}{1 + \sum_{j=1}^{n}\omega_j\beta_j N_j(h_j + c_j(1 + \beta_j h_j N_j))}, \tag{12}$$

where $\widehat{P}_i^{(s)}$ and $\widehat{P}^{(c)}$ are the subpopulation equilibria, respectively, of the searching and hungry, temporal generalist predators. For further details of the dynamical system and the derivation of the functional response, see Appendix C.

We could say that a predator is unequipped for simultaneous feeding if $\sum_{j=1}^{n} \omega_j < 1$. Conversely, a predator thrives in simultaneous feeding if $\sum_{j=1}^{n} \omega_j \geq 1$. This simple definition, however, fails to account for the overall performance that also depends on prey capture rates and prey abundances, but it can provide a useful premise when considering its parametrisation. The simplest parametrisation assumes equally divided attention between all prey species, $\omega_i \equiv 1/n$, in which case temporal generalist's predation efficiency decreases linearly with diet broadness.

In the simplest case of only one prey being present, the above functional response reduces into $F = \omega\beta N(1 + c\beta N)/(1 + \omega\beta N(h + c(1 + \beta hN)))$. Note that in the absence of other prey species, the scalar term $\omega$ for the prey capture rate in the hungry state, can no longer be reasonably interpreted as the trade-off factor associated with temporal generalist behaviour. Instead, in the case of a single prey, it could be better understood as the predator's decreased prey capture success while hungry or near starvation. Additionally, this functional response never reduces to the standard Holling type II form, unlike the other two functional responses we derived earlier (Equations 3 and 7). Even in the absence of alternative prey species, Equation 12 is a convex function conforming to type III behaviour if $c > \omega h/(1 - \omega)$. Indeed, this can be explained as the predator losing their learned skills in prey capture after sufficient delay in prey captures. If the predation efficiency's trade-off is too crude in that unlearned state, it leads to type III response at low prey abundances. Therefore, Holling type III behaviour is possible already in the absence of alternative prey, which as far as we are aware, has never before been presented with mechanistic underpinning.

We now explore the three cases when alternative prey species are present to see under which conditions the functional response of Equation 12 conforms to Holling type III response (the bottom row of Figure 2). First, when any prey species $j = i$ are present with constant abundances, the functional response conforms to type III response if

$$c_i > \frac{\omega_i h_i}{1 - \omega_i + \sum_{j=i} \beta_j N_j \left( h_j + c_j \left( 1 + \beta_j h_j N_j \right) \right)}. \tag{13}$$

Second, when the total abundance of all prey abundances is constant, the functional response conforms to type III response if

$$c_i > \frac{-\omega_i \beta_i h_i + \sum_{j=i} \omega_j \beta_j \left( h_j + c_j (1 + 2\beta_j h_j (N_{\text{total}} - \sum_{k=i,j} N_k)) \right)}{\beta_j \left( \omega_j - 1 - \sum_{j=1} \omega_j \beta_j (N_{\text{total}} - \sum_{k=i,j} N_k)(h_j + c_j(1 + \beta_j h_j (N_{\text{total}} - \sum_{k=i,j} N_k))) \right)}. \tag{14}$$

Third, if the abundances of prey species $j = i$ are relative to that of prey species $i$, the functional response conforms to type III response if

$$c_i > \frac{\beta_i h_i \omega_i + \sum_{j=i} b_j \beta_j \omega_j (c_j + h_j)}{\beta_i (1 - \omega_i)}. \tag{15}$$

In conclusion, the functional response of Equation 12 can act as Holling type III response for all three cases of prey abundances. This occurs if either $c_i$ is sufficiently large, such that the predator remains satiated for a long time after a prey capture; or if $\omega_i$ is sufficiently small, such that the generalist behaviour is strongly traded off for capture efficiency.

We now investigate the role of diet breadth and relative prey abundances for the feeding on the focal prey. Assume that the trade-off of prey capture in the temporal generalist state is the same for all prey species, $\omega_i \equiv \omega$. The focal prey's proportion in the diet is

$$\phi(\eta) = \frac{\beta_1 \eta (1 + c_1 \beta_1 \eta)}{\beta_2 (n-1)^{-1} (1 - \eta) \left( 1 + c_2 \beta_2 (n-1)^{-1} (1 - \eta) \right) + \beta_1 \eta (1 + c_1 \beta_1 \eta)}. \tag{16}$$

From this expression, we see that diet broadening contributes to more pronounced feeding on the focal prey (Figure 3, bottom row). Diet broadening from two to three (four) prey species leads up to 33% (50%) relative increase in feeding on the focal prey (Figure 4, bottom row). This effect is considerably smaller than in M1 and M2, in which the relative increase is up to 200% and 350%, respectively.

The underlying mechanism driving this outcome remains consistent with that of M1 and M2. However, the main biological distinction that sets M3 apart is the predator's simultaneous feeding ability of all prey while hungry, rather than having to first switch a specific prey before being able to capture them. This streamlining of consecutive interactions causes the relative changes in feeding patterns to be substantially smaller than in M1 and M2. We predict that variations in the number of available prey species will result in more pronounced alterations in the diet composition when feeding is mutually exclusive rather than simultaneous.

The critical proportion of the focal prey associated with diet switching is

$$\eta^* = \frac{\beta_1(1-n) + \beta_2(n - 1 + c_2 \beta_2)}{c_1 \beta_1^2 (n-1) + c_2 \beta_2}. \tag{17}$$

It corresponds to an admissible population proportion, that is $\eta^* \in [0, 1]$, if $c_1 > (\beta_2 - \beta_1)/\beta_1^2$ and $c_2 > (1 - n)(\beta_2 + \beta_1)/\beta_2^2$. Whenever these conditions are satisfied, diet switching point decreases with diet broadening, otherwise the focal prey is always over-represented in the predator's diet composition. The bottom row of Figure 3 demonstrate this result, in which diet switch only occurs for sufficiently high values of $c_1$ and/or $\beta_1$. Accelerated diet switch occurs whenever $n < (c_1 \beta_1^2 - c_2 \beta_2^2)/(\beta_2 - \beta_1)$, otherwise diet switch is delayed.

## 4 | DISCUSSION

In this study, we utilised mechanistic modelling to explore the impact of a predator's adaptive feeding behaviour on functional response and diet composition. Specifically, we focused on prey switching, a phenomenon linked to search image formation and mutually exclusive feeding behaviour

(Ishii & Shimada, 2010). We developed three models based on different patterns of search behaviour in switching generalists, including when delays between successive prey encounters have to precede switching (Figure 1). Our analysis revealed that predator's diet diversity, quantified by the number of prey species fed on, positively correlated with the focal prey's proportion in the predator's diet. Furthermore, we derived three novel functional responses that all followed a Holling type III pattern (Holling, 1959b). Our findings aligned with the hypothesis that prey switching as characterised by mutually exclusive feeding is linked to type III response, which has been long supported by empirical observations and now validated by our mechanistic theory (Murdoch, 1969). Previous mechanistic modelling attempts of deriving functional responses for adaptive feeding behaviour have been limited to simultaneous search for different prey species (van Leeuwen et al., 2007, 2013).

We investigated the impact of diet broadening on feeding towards a focal prey by artificially dividing alternative prey populations into smaller compartments with identical characteristics while maintaining the focal prey unchanged. All our three models predicted that introducing additional prey resulted in elevated feeding of the focal prey (Figures 3 and 4). Although this finding may overestimate the role of diet broadening, it nonetheless provides valuable qualitative insight. This phenomenon can be understood by considering a scenario in which a predator is currently focusing its searching for alternative prey whose population is divided into smaller compartments. As the number of alternative prey populations increases, the likelihood of the predator capturing an alternative prey instead of switching to the focal prey diminishes. In the limit of infinitely many yet arbitrarily rare alternative prey populations, the predator switches to the focal prey with certainty.

Despite the shared Holling type III pattern characterising all three mechanistic functional responses, the conditions dictating its occurrence were model-specific. The simplest model (M1) exhibited type III behaviour irrespective of parameter choices, manifesting whenever the total prey abundance or that of non-focal prey remained constant. In the more complex model (M2), which restricted switching to hungry predators, type III pattern materialised in ways analogous to those of M1. While the modifications in M2 may appear modest, they led to the manifestation of type III pattern also when prey abundances were relative to each other. This hinged on the predator's resilience to starvation when focusing on the focal prey, which hindered (promoted) prey switching under high (low) focal prey abundances. Consequently, type III responses appear more probable in switching generalists whose feeding behaviour is influenced by encounter frequency with the focused prey species, rather being entirely random. The third model (M3) deviated from M2 by triggering prey switching through direct attacks. In this case, the occurrence of type III pattern always depended on the predator's capability to endure starvation, regardless of relationships between prey abundances. Therefore, for temporal generalists whose search image deteriorates swiftly following periods of no prey encounters, the functional response is less likely to follow type III pattern.

Earlier approaches to modelling adaptive feeding behaviour by van Leeuwen et al. (2007, 2013) employed similar mechanistic modelling

techniques to derive functional response for generalist predators. However, while we assumed mutually exclusive feeding on different prey with switching corresponding to search image formation of cryptic prey, earlier studies assumed simultaneous feeding on conspicuous prey guided by learning behaviour. Specifically, van Leeuwen et al. (2007, 2013) addressed prey switching based on observations that certain predators are more efficient at feeding on prey they had captured previously. These studies implemented this feature through memory-dependent parameters, specifically predation success and handling efficiency, which were assumed to increase with successive encounters involving similar prey. Thus, both modelling approaches address adaptive feeding behaviour but within distinct ecological contexts.

Despite the differing assumptions about feeding behaviour, these two theories yield similar Holling type III conforming functional responses (Holling, 1959b). To ensure comparability, we used identical parameter values whenever possible, as done in van Leeuwen et al. (2007, 2013). As a result, the functional response shapes are similar when varying population abundances (Figure 2). Both formulations feature prey abundances in squares $(N_i^2)$ in the numerator of the functional response and in squares and linear terms $(N_i)$ in the denominator, which appears to be an essential feature for the functional response of any switching generalist. Together our mechanistic model theory and that of van Leeuwen et al. (2007, 2013) capture a wide range of empirically observed switching generalists' feeding behaviours.

The key qualitative distinctions between these two theories become evident when considering the second-order terms involving two distinct prey $(N_i N_j)$, which are absent in each of our three responses but consistently present in those of van Leeuwen et al. (2007, 2013). This is to be expected since in our theory, any successive interactions corresponding to prey capture always involve the same species. To transition from handling prey of species $i$ to that of species $j$, predators must traverse a sequence of state transitions that involve interactions beyond prey capture itself. These include switching of prey focus (M1) or disruption of the search image due to delays in prey captures (M2, M3). In contrast, in the theory of van Leeuwen et al. (2007, 2013), such intermediate transitions are unnecessary, as a generalist predator can immediately move to capture prey of species $j$ after finishing handling a prey of species $i$. This streamlined chain of state transitions is likely the main cause for the emergence of second-order terms involving distinct prey.

We underline that our functional responses, similarly to those of van Leeuwen et al. (2007, 2013), never have the exact form of Holling type III response, in which all terms involving prey abundances appear in square terms and is formulated as

$$F_i(N_1, N_2, \ldots, N_n) = \frac{\beta_i N_i^2}{1 + \sum_{j=1}^{n} \beta_j h_j N_j^2}. \qquad (18)$$

Across our three functional responses, prey abundances consistently appear in both linear and square terms (Equations 3 and 12), with an additional instance where prey abundances feature in a third-order term ($N_i^3$, see Equation 7). Whenever any parameter combinations yield these higher-order terms, all lower-order terms

are also present. We suspect that it is impossible to find a clear-cut and biologically meaningful mechanistic derivation for the classical form of Holling type III response.

Whether the functional responses of the present study or those of van Leeuwen et al. (2007, 2013) is a better modelling choice for a predator species ultimately hinges on that predator's observed search behaviour. The functional responses of van Leeuwen et al. (2007, 2013) might be more appropriate for predators whose prey share similar characteristics, whereupon search image formation is weak or undetectable. Conversely, when prey are cryptic rather than conspicuous, mutually exclusive feeding is more commonly observed (Dawkins, 1971; Ishii & Shimada, 2010; Tinbergen, 1960), and in such scenarios our functional responses offer considerably more realistic mechanistic underpinning. The subsequent choice between our three functional responses (Equations 3, 7 and 12) depends on the finer details of search image formation, such as predator satiation level.

While both the present study and the works of van Leeuwen et al. (2007, 2013) offer a wide range of functional responses originating from underlying behavioural models of feeding, neither of these models have yet undergone wide empirical testing in real-world study systems. While the models meticulously account for intricate details about individual behaviour, the gap lies in the absence of information about plausible parameter value ranges applicable to natural systems. Furthermore, empirical grounding for many parameters introduced in this study remains lacking. Beyond the mean handling time of prey items and per capita prey capture rates, the key model-specific parameters include the per capita diet switching rate between prey species, $a_i$ (M1 & M2); the mean time after which search image is disrupted, $c_i$ (M2 & M3); and finally the trade-off between temporal generalist and specialist feeding efficiency, $\omega_i$ (M3). To assess how our results on the Holling type III functional response shapes and diet-switching behaviour might manifest in natural settings, it becomes crucial to first conduct experiments to estimate these values for potential study species. This would ensure that the mechanistically derived functional responses realistically capture the individual behaviour of the study species.

We assumed that feeding on different prey species is mutually exclusive, it is improbable that a predator's ability to detect and attack different prey species adheres to such strict criteria in reality. When several prey share similar characteristics, the search image might extend to groups of similar prey rather than being limited to one only (Robledo-Ospina et al., 2022). Although we loosely used the term prey 'species' throughout this study, that term can be also understood as a functional guild comprising similar prey. Particularly, if a predator feeds on similar prey species at equivalent prey capture rate and possess identical handling times, then our models can be readily used for this purpose. However, if either of these characteristics are expected to differ between simultaneously fed prey, then an extension would necessitate a mechanistic development based on these assumptions.

In conclusion, we investigated generalist predators switching between distinct prey species, based on mutually exclusive feeding behaviour, in three intentionally simplistic mechanistically founded models. Although these models omit intricate ontogenetic, spatial or ecosystem-specific structures in favour of biologically relevant generalist predator behavioural traits, they offer a wide applicability across taxa. Most notably, our results confirm the long-standing hypothesis that Holling type III functional response shape, which has been widely employed in ecological models since its conceptualisation in late 1950s (Holling, 1959b), can indeed be explained by the adaptive feeding behaviour. In the process, however, our results also propose that the original form of Holling type III response is unfortunately erroneous. While it is equally admissible that the type-III conforming functional responses developed in this study cannot encompass all possible biological scenarios, we firmly believe that these findings can serve as a cornerstone for a lineage of ecological modelling that underscores the significance of mechanistic foundations.

## AUTHOR CONTRIBUTIONS

Sami O. Lehtinen conceived the ideas, designed the methodology and conducted the analysis; Sami O. Lehtinen and Tommi A. Perälä designed the figures; Sami O. Lehtinen led the writing of the manuscript. All authors contributed to interpreting the results, drafting and revising the article, and gave final approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

## DATA AVAILABILITY STATEMENT

Data available from the Zenodo digital repository: https://zenodo.org/record/7303982#.ZCGFyi8RppS.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix A.** Mechanistic derivation of Model 1.

**Appendix B.** Mechanistic derivation of Model 2.

**Appendix C.** Mechanistic derivation of Model 3.