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Optimal foraging strategy to balance mixed diet by generalist consumers: a simulation model

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Abstract

Animals of a wide range of taxonomic groups mix various food sources to achieve a nutritionally balanced diet. The strategies they adopt to balance multiple nutrients depend on their availability in the environment. Behavioural and physiological adaptations to forage for nutrient-differing food sources have rarely been investigated in respect to nutrient availability in the environment. We developed a simulation model to explore the strategy consumers should adopt in response to the abundance of two nutritionally complementary food types. Results show that (1) consumers should invest more effort in detecting the scarce resource; (2) there is an optimized negative relationship between effort foragers should allocate to find the two types of food; (3) consumers should exhibit higher selectivity when the proportion of food types in the habitat deviates from their optimal ratio in the diet. These findings have important implications for pest control using predators that benefit from plant-based food supplements.

1. Introduction

Nutritional ecologists have long acknowledged the benefits of a mixed diet for generalist consumers (House, 1969; Waldbauer & Friedman, 1991). Combining foods of different nutritional values allows consumers to balance their nutrient intake (Pulliam, 1975; Westoby, 1978; Waldbauer & Friedman, 1991). Consequently, mixed diets have a positive influence on various aspects of an animal's life history and performance, such as growth, fecundity and longevity (Simpson et al., 2004; Lee et al., 2008; Warbrick-Smith et al., 2009; Jensen et al., 2012; Le Couteur et al., 2016; Piper et al., 2017), which are well documented in a wide range of generalist consumers (Bernays et al., 1994). Indeed, there is ample evidence of animals that actively mix various food sources in their diet to achieve a target nutrient balance, in what is often termed 'dietary self-selection' (Waldbauer & Friedman, 1991; Simpson et al., 2004; Simpson & Raubenheimer, 2012). Such behaviour is ubiquitous and has been described in consumers as different as herbivores (Bernays et al., 1994; Behmer, 2009; Warbrick-Smith et al., 2009; Wang et al., 2010; Cui et al., 2018), carnivores (Mayntz et al., 2005, 2009; Jensen et al., 2012), and omnivores (which mix plant and prey food sources; Lee et al., 2008; Coogan et al., 2014; Balestrieri et al., 2019), belonging to a wide range of taxa, from arthropods to primates.

Despite the recognized importance of balancing the intake of multiple resources, classic optimal foraging theory generally assumes that animals aim to maximize a single foraging currency, typically energy gain (Pyke et al., 1977; Stephens & Krebs, 1986; Raubenheimer & Simpson, 2018; Morehouse et al., 2020). The need to integrate nutrient balance into the study of animal foraging was pointed out long ago (Pulliam, 1975; Westoby, 1978), yet such integration has been advanced only more recently (Simpson & Raubenheimer, 2012; Raubenheimer & Simpson, 2018; Morehouse *et al.*, 2020). An important contribution was the introduction of the Geometric Framework for nutrition (Simpson & Raubenheimer, 2012; Raubenheimer & Simpson, 2018). This framework aims at combining (1) the nutritional requirements of animals (represented as a target point within a multidimensional nutritional space), (2) the diet components that are available in the environment, and (3) the influence of these on animals' physiology, behaviour, life history and ecology (Raubenheimer & Simpson, 1993; Simpson & Raubenheimer, 1993). However, despite this important advancement,

animal optimal foraging for multiple complementary foods is understudied and still remains poorly understood (Morehouse et al., 2020).

To regulate nutritional intake and maintain a target balanced diet, animals are expected to be able to evaluate the nutritional quality of their food, assess their own nutritional state and respond to deficits or surpluses of specific nutrients. Physiological mechanisms allowing for these abilities have been shown in various study systems (reviewed by Simpson & Raubenheimer, 2012; Walker et al., 2017; Simpson et al., 2018). For example, experiments on locusts have shown that, when deprived of protein, the concentration of free amino acids in the blood falls, causing elevated responsiveness of taste receptors to amino acids (Simpson & Raubenheimer, 2012). The response to nutritional imbalance may be both behavioural and physiological, and can take place either pre-, during or post-ingestion; animals may forage for specific nutrients, choose which foods and nutrients to ingest, and even change the rate at which ingested nutrients are processed (Behmer, 2009; Simpson & Raubenheimer, 2012). For example, a study on locusts that were fed diets with imbalanced protein-carbohydrate ratios showed reduced levels of digestive enzymes for nutrients present in excess in the diet (Clissold et al., 2010).

The optimal strategies adopted for foraging, feeding and ingesting multiple nutrients depend not only on the animal's target nutrient balance, but also on the availability and relative abundance of nutrients in the environment (Behmer et al., 2003; Morehouse et al., 2020). Natural selection should favour animals with strategies that are adjusted to nutrient availability in the environment, allowing these consumers to reach their target nutrient balance most efficiently. For all costs being equal, we expect therefore that, for example, (1) natural selection should favor animals that are able to perceive vital diet components that are rare in the environment from a larger distance, compared to other more abundant components. Indeed, genetic variability has been demonstrated in the area an animal can perceive while searching for resources (Wajnberg & Colazza, 1998), demonstrating that such a trait can be subject to natural selection; (2) when choosing which foods to ingest, individuals should defend their target balanced diet more strictly if it differs from the relative abundance of essential nutrients in the environment (Kay, 2002); and, (3) once consumed, the rate at which different food types and nutrients are processed may also influence the ability of an animal to reach its target balanced diet (Raubenheimer & Simpson, 1998; Simpson & Raubenheimer,

2012), which may vary under different nutrient abundances in the environment. However, the behavioural and physiological adaptations to foraging and feeding on multiple, nutrient-differing food sources have rarely been investigated in the context of nutrient availability in the environment.

In the present study, we developed a theoretical approach of a model system comprised of consumers that forage for two complementary foods. The consumers are able to sense their own nutritional state and adjust the food type on which they focus accordingly, to reach a target balance. To test the aforementioned predictions regarding foraging, feeding and food processing strategies that natural selection should favour, we explored how absolute and relative availability of complementary food resources is likely to influence (1) the effort a forager should optimally allocate to find each resource type, (2) how strictly they should adhere to their target balanced diet, and (3) how long they should optimally process consumed foods. Toward these objectives, we developed a spatially explicit Monte Carlo simulation model in which consumers must balance their diet to reach a target ratio between two separate complementary food sources. Using a genetic algorithm, we explored the optimal strategy consumers should adopt under different absolute and relative abundances of the two complementary foods in their environment. We used this framework to advance our understanding of the behavioural and physiological adaptations that are expected for an animal to optimally negotiate changes in resource availability in their environment. Implication of the obtained insight to biological pest control is also discussed.

2. Methods

2.1. General framework

To identify the optimal strategy consumers should adopt when foraging and feeding on complementary resources, we developed a spatially explicit simulation (Monte Carlo) model in which a single animal is simulated following a discrete time process. To simplify the model description, we hereafter refer to the complementary resources as prey and plant foods. The consumers in the model therefore represent omnivores, as an example of animals mixing food sources that differ extremely in nutritional value and spatial and temporal availability. However, the model could equally represent a wide range of consumer types.

The foraging environment is represented as a 2D square grid (1000×1000) in which the location of plant and prey food items is drawn randomly (Poisson distributions). Each cell of the grid can contain either one plant item, one prey item, or no food item. The overall plant and prey abundance in the environment is determined by two parameters that remain fixed throughout each simulation. For this, each plant or prey item that is consumed reappears randomly somewhere else in the grid to avoid depletion. Another version of the model was developed with an aggregated distribution of the location of prey in the grid instead, but the results obtained were qualitatively similar to those obtained with a random distribution. So only results with prey randomly distributed over the grid are presented here. Each animal stores consumed food items in its gut, and must target an optimal proportion of plant food in its gut, defined as p^*, to maximize its overall fitness output, e.g., by producing more progeny, having a higher longevity, etc. For this, at each time step during the entire simulation process, the foraging animal increases its overall fitness by a value β (arbitrary unit) defined by the following equation, in which p is the proportion of plant among all food items currently present it its gut:

$$\beta = \begin{cases} \frac{p}{p^*} & \text{if } p < p^* \\ \frac{(p-1)}{(p^*-1)} & \text{if } p \geqslant p^* \end{cases} \tag{1}$$

If the gut is empty, however, there is no fitness increment. The contribution to fitness is maximal when $p = p^*$, as predicted by Simpson et al. (2004). Varying the value of p^* enables the simulation of animals with different nutritional needs.

At the beginning of each simulation (i.e., at the beginning of its life), the simulated animal is 'released' in the center of the grid, with nothing in its gut, and starts searching for food items to be consumed. An animal having an actual value of p below p^* will search for plant food items, and the same regarding p value above p^* and prey consumption. At each time step, the animal moves at a distance drawn from a Normal distribution with average 5.0 and standard deviation 2.0 (in cell numbers). Its moving direction is also drawn from a Normal distribution with an average corresponding to the direction of the closest searched food item perceived, and SD equal to $60 \times \beta$, where β is as defined by eq. (1) above. Hence, when the animal's gut content is far from p^*, the animal walks in a rather straight line towards the food item from the type needed to balance its diet, but starts to wander more

when its gut content approaches p^* and the need to balance its diet is less urgent. Such influence of nutritional state on movement patterns has been demonstrated in several systems (Simpson et al., 2006; Bazazi et al., 2011; Lihoreau et al., 2017).

At each time step, the animal can perceive all plant and prey items between its location and a maximal distance RD_{plant} and RD_{prey}, respectively (i.e., 'Reactive Distance', see Yano, 1978; Roitberg, 1985; Bruins et al., 1994; Wajnberg & Colazza, 1998). Larger RD values represent a larger effort allocated by the animal to find a resource type. The closest food item of the type for which the animal is searching determines the average of the Normal distribution used to define the walking direction (see above). Hence, the animal will move preferentially to the closest food item of the food type it is searching. If no food item is perceived at a given time step during the walking behaviour, the animal keeps on using the same walking strategy as used in the previous time step.

During its walking behaviour, if the simulated animal perceives a food item located within a radius of 15 cells around its current location and if this perceived food item is not the one the animal is looking for, it will still be consumed with a probability γ, providing that there is enough room in its gut (see below). The probability γ is defined by:

$$\gamma = \begin{cases} \left(\frac{p}{p^*}\right)^c & \text{if } p < p^* \\ \left(\frac{(p-1)}{(p^*-1)}\right)^c & \text{if } p \geqslant p^* \end{cases} \tag{2}$$

Hence, a non-searched food item has a higher probability of being consumed if the animal is close to p^*, and c defines its level of choosiness, i.e., the willingness of consuming a food item that will distance the animal further from its optimal balanced diet p^*. The higher the value of c, the higher the selectivity level of the simulated foraging animal and thus the lower is the probability it will consume non-searched food items encountered.

A maximum number of 100 food items can be stored in the animal's gut. Therefore, after a given food item remains in the gut for a given time t (i.e., food processing time; equal for plant and prey items), it disappears.

The longevity of the simulated animal cannot exceed 2000 time steps. However, if no food item is found after 100 time steps, the animal dies. This amount of time before death is increased by 20 time steps if a plant or a prey item is found and consumed. After this time increment has passed, and if the animal is still alive, the time before death is reset to its initial value of 100.

We assumed that a foraging animal that invests more energy to maintain higher values of RD_{plant}, RD_{prey}, t (food processing time), and c (level of choosiness), will have, as a result, less energy to invest in its survival. Hence, the total longevity of the simulated animal was actually:

$$2000 \times \left(1 - \left(\frac{RD_{plant}}{RD_{plant\_max}}\right)^3\right) \times \left(1 - \left(\frac{RD_{prey}}{RD_{prey\_max}}\right)^3\right)$$
$$\times \left(1 - \left(\frac{t}{t_{max}}\right)^3\right) \times \left(1 - \left(\frac{c}{c_{max}}\right)^3\right) \qquad (3)$$

Where RD_{plant_max}, RD_{prey_max}, t_{max} and c_{max} are the maximal possible values for the four parameters, i.e., 200, 200, 2000 and 50.0, respectively. Table 1 lists the most important parameters of the model, with their meaning and the values used in the simulations.

2.2. Optimization procedure

The values of the parameters RD_{plant}, RD_{prey}, t and c that maximize the overall fitness of the simulated animals in each environmental situation were determined by means of a genetic algorithm. Such a numerical optimization method has been used regularly to solve several ecology problems, including for the behavioural ecology of foraging insects (Hancock & Milner-Gulland, 2006; Hoffmeister & Wajnberg, 2008; Ruxton & Beauchamp, 2008; Wajnberg et al., 2012, 2013). This approach is used to find optimal or close to optimal solutions to problems, even difficult ones, in a flexible way (Sumida et al., 1990; Huse et al., 1999).

A population of 100 chromosomes was used, each coding for four genes corresponding to the four parameters RD_{plant}, RD_{prey}, t and c whose values were used to compute the fitness of each simulated animal using the algorithm described above. To explore new solutions in the optimization process, genes on chromosomes at each generation were randomly modified using a mutation rate of 2.5% and chromosomes were rearranged using a recombination rate of 60%. At each generation, chromosomes leading to lower fitness for the simulated foraging animals were eliminated and replaced by the offspring of those leading to higher fitness levels. The entire process was repeated over 1000 cycles leading to stable optimized solutions (Forrest, 1993; Hoffmeister & Wajnberg, 2008) for all the explored environmental situations. Since the algorithm used to simulate the strategy of the foraging animals is highly stochastic, the fitness of each chromosome was estimated

Table 1.

List of the most important parameters of the model with the values used.

Parameters	Meaning/values used
Grid size	1000×1000
Plant abundance	50, 100, 200, 400, 800
Prey abundance	50, 100, 200, 400, 800
p	Current proportion of plant in the gut of the animal.
p^*	The optimal value of p for a given foraging species (0.2, 0.5, 0.8)
Longevity of the simulation animal	A maximum of 2000 time steps, reduced in proportion to higher RD_{plant}, RD_{prey}, t, and c values.
Maximal number of food items that can be stored in the gut	100
Average linear walking speed	5.0 cell units
SD of linear walking speed	2.0 cell units
RD_{plant}	Maximal distance from which the animal is able to perceive a plant item.
RD_{prey}	Maximal distance from which the animal is able to perceive a prey item.
t	Food processing time. The time a food item remains in the animal's gut before disappearing.
c	Level of choosiness defining the probability of a food item that is encountered but not searched for to be consumed.
Survival time without food	Survival time of an animal that does not find any food item. 100 time steps.
Increase in survival time after food intake	20 additional time steps are granted for each consumed plant or prey item.

Parameters RD_{plant}, RD_{prey}, t, and c were optimized by means of a genetic algorithm (see text).

each time by the average of 5 independent simulation runs of the same gene combination using different randomly drawn prey and plant item locations. To avoid reaching local optima, the entire optimization process was repeated 100 independent times for each environmental situation. The optimization process was entirely repeated for all combinations of all possible values of (1) prey abundance, (2) plant abundance, and (3) optimal proportion of plant food in the gut, p^* (i.e., for species exhibiting different levels of omnivory), representing a design consisting of $5 \times 5 \times 3 = 75$ situations (see Table 1).

3. Results

Primarily plant-feeders ($p^* = 0.8$) maximized their fitness when they perceived plant food items within longer distances (high RD_{plant}; Figure 1e) compared to animals that fed equally on prey and plant foods ($p^* = 0.5$; Figure 1c) and to primarily prey-feeders ($p^* = 0.2$; Figure 1a). Reciprocally, the optimal distance for perceiving prey (optimal RD_{prey}) was highest for primarily prey-feeders ($p^* = 0.2$; Figure 1b) compared to animals that fed equally on prey and plant foods ($p^* = 0.5$; Figure 1d) or primarily plant-feeders ($p^* = 0.8$; Figure 1f). The absolute and relative abundance of prey and plant foods had a clear influence on RD_{prey} and RD_{plant}. Not only did the optimal RD_{prey} depend on the abundance of prey, but also on the abundance of plant food items, and reciprocally. Higher abundance of a certain food type resulted in lower optimal distance from which that food should be perceived, but also in higher optimal distance from which the complementary food should be perceived (Figure 1). However, the influence of prey abundance on optimal RD_{plant} was lost at low plant abundance for primarily plant-feeders ($p^* = 0.8$; Figure 1e) and at high plant abundances for primarily prey-feeders ($p^* = 0.2$; Figure 1a). Likewise, the influence of plant abundance on RD_{prey} was lost at low and high abundances of prey, for primarily prey- and plant-feeders, respectively (Figure 1b and 1f, respectively).

Only the relative, but not absolute abundance of prey and plant foods influenced the optimal level of choosiness (c). The optimal level of choosiness was minimal when the proportion of plant food in the environment was equal to the proportion of plant food that the animal must optimally consume, regardless of the absolute abundance of each food type (Figure 2a, c, e). In contrast to RD_{prey}, RD_{plant} and c, prey and plant abundance had no clear influence on the optimal time an animal should spend processing consumed food (t; Figure 2b, d, f).

Interestingly, across most of the parameter space, there was a negative association between the optimal values of RD_{prey} and RD_{plant} (Figure 3). The average correlation coefficient across all 75 combinations of p^*, prey abundance and plant abundance was -0.22 (± 0.02 SE). In comparison, no such association was observed between optimal RD_{prey} or RD_{plant} and optimal choosiness (c), the only other parameter which varied across the parameter space (mean $\pm$ SE -0.03 ± 0.02 and -0.01 ± 0.02, respectively).
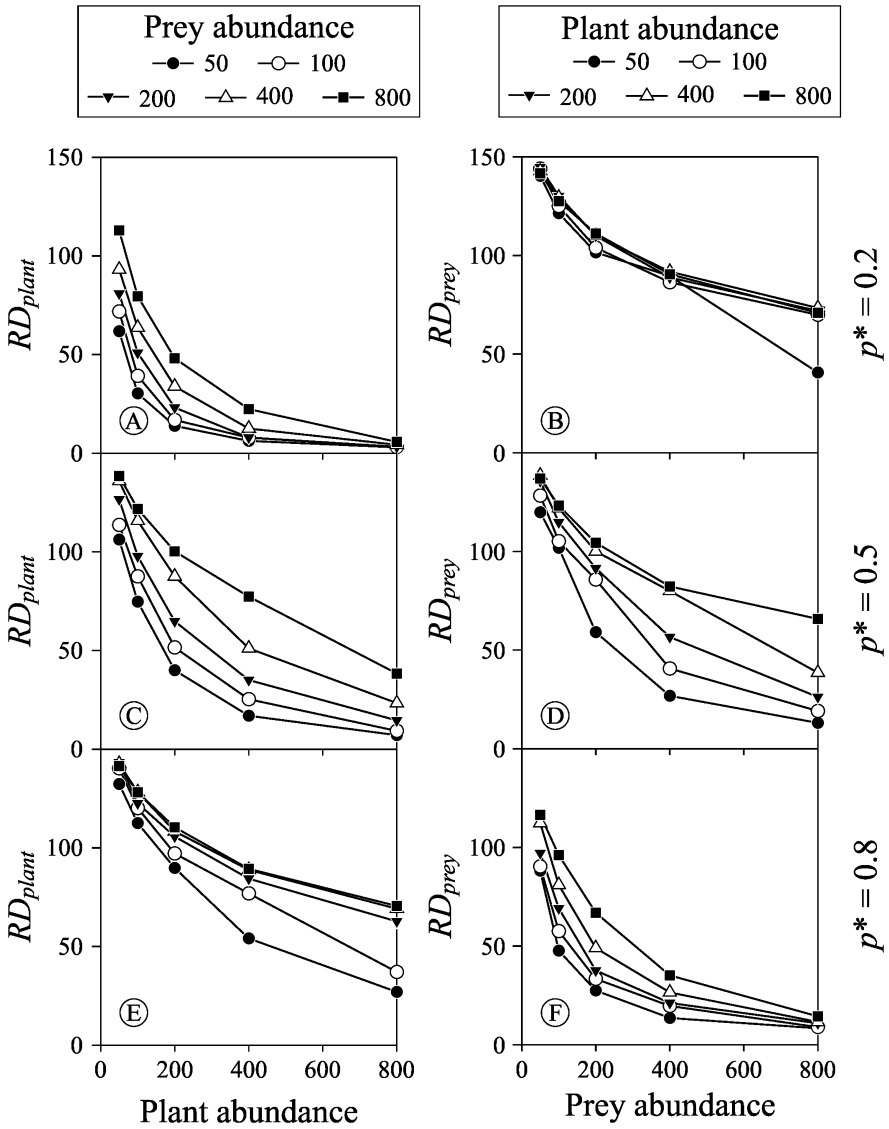
Figure 1. Influence of plant and prey food abundances on the optimal distance from which plant (RD_{plant} (a, c, e)) and prey (RD_{prey} (b, d, f)) foods should be perceived to maximize the forager's fitness. Data are presented separately for primarily prey-feeders ($p^* = 0.2$ in a and b), animals that feed equally on prey and plant foods ($p^* = 0.5$ in c and d) and primarily plant-feeders ($p^* = 0.8$ in e and f). Each point is the average of 100 simulations. Results for primarily prey-feeders and primarily plant-feeders do not mirror each other perfectly, as expected, due to stochastic differences among simulations.
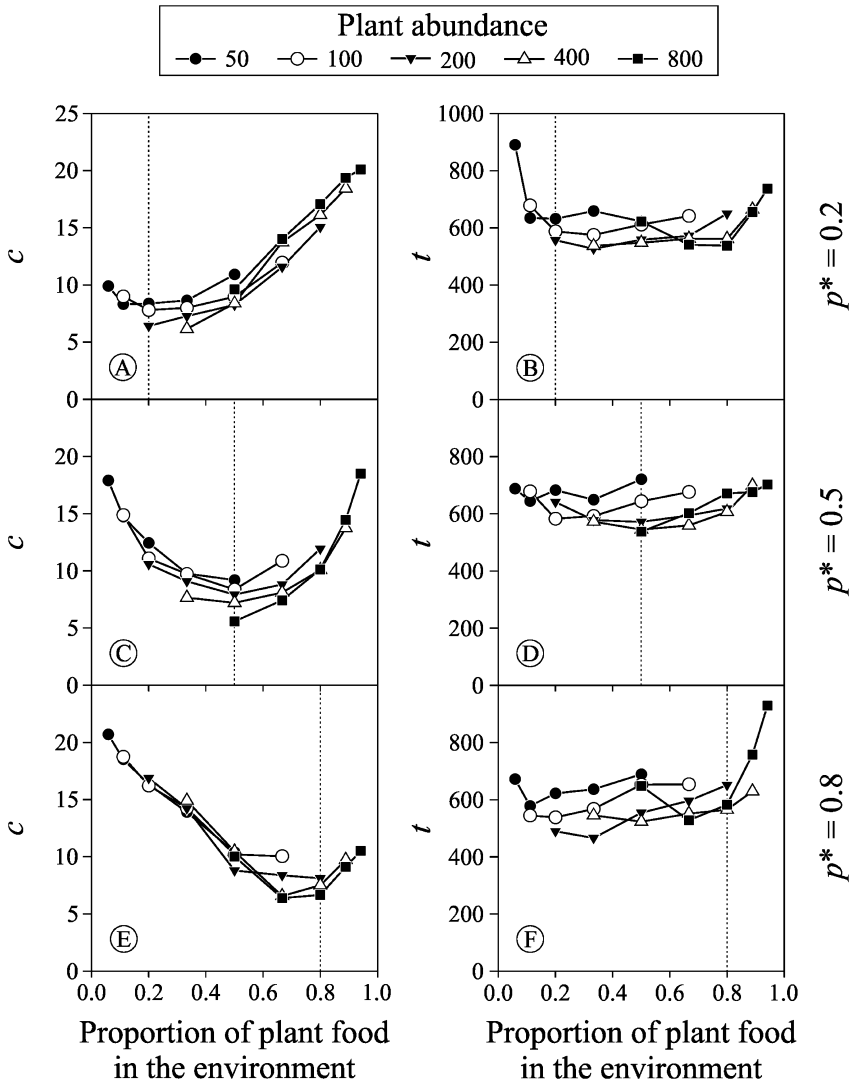
Figure 2. Influence of relative and absolute abundance of plant food in the environment on the optimal level of choosiness (c), i.e., defining the probability of consuming a food item that will distance the animal further from its optimal balanced diet (a, c, e) and on the optimized food processing time (t; b, d, f). Data is presented separately for primarily prey-feeders ($p^* = 0.2$ in a and b), animal that feed equally on prey and plant foods ($p^* = 0.5$ in c and d) and primarily plant-feeders ($p^* = 0.8$ in e and f). p^* (shown as vertical dotted lines) is defined as the optimal (=target) proportion of plant food in consumer's gut. Each point is the average of 100 simulations. Results for primarily prey-feeders and primarily plant-feeders do not mirror each other perfectly, as expected, due to stochastic differences among simulations.
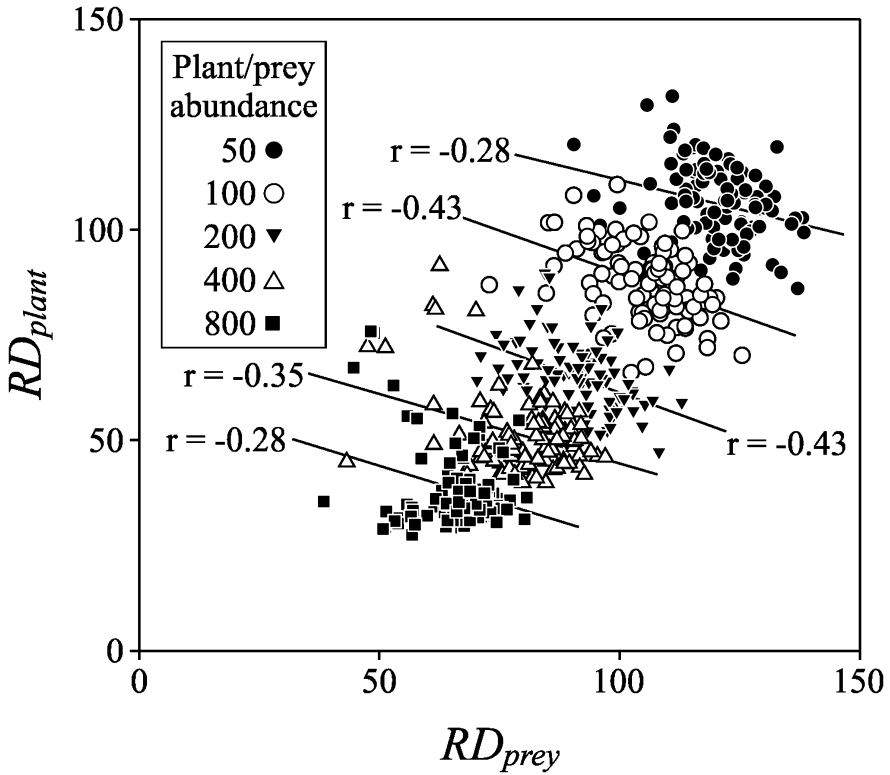
Figure 3. Negative correlations between the optimized values of RD_{prey} and RD_{plant} in each simulation. As an example, data are presented for simulations in which animals feed equally on plant and prey foods ($p^* = 0.5$) and both plant/prey are equally abundant in the environment. Qualitatively similar results were obtained in all other situations. Separate Pearson correlation coefficients and regression lines are specified for each food abundance.

4. Discussion

Using a Monte Carlo model, we found that simulated foraging animals facing two types of complementary resources in their environment must optimally invest more effort in detecting the resource that is scarce, both in absolute or in relative amount, compared to the alternative one. Several experimental studies used one type of resource only or tested the effect of relative/absolute abundance and quality of two food types that can play a substitutional role (see, e.g., Bell, 1990, 1991; Forget et al., 2002; Tucker et al., 2018). For example, the presence of low-quality foods altered leaf consumption and the functional response in cattle (Drescher et al., 2006), and led to compen-

satory consumption or foraging for better quality foliage by various sawfly species (Kause et al., 1999). In the work presented here, however, the two food sources are of a complementary, not substitutional nature, as is the case, for example, for true omnivorous consumers (Coll & Guershon, 2002; Ugine et al., 2019) that need to target optimally a mix of plant and prey food offering totally different, although complementary nutrients to maximize their reproductive output. Until recently, however, the nutritional mechanisms underlying food choice by omnivores have not been explored (Coll & Guershon, 2002; but see Ugine et al., 2019; Toft et al., 2021). Generalist consumers that forage for a variety of food sources in their environment commonly exhibit preferential choice depending on the relative abundance of each resource type available (Krebs, 1973; Curio, 1976). Food types uncommon in the environment tend to be disproportionately underrepresented in the diet, whereas foods that are more abundant are consumed in excess (Bell, 1990, 1991). In our model, when one food type is frequently available in the environment, consumers should increase their effort to locate the other, complementary food type. The less preferred food that animals are not searching for can thus be somewhat 'distracting' when it becomes very abundant. Neurological or physiological processes involved in generating such selection bias likely result from preferential responses to food-related stimuli according to prior history of reward (Bond, 1983).

In some situations, however, results of the model indicate that the relative proportion of the two types of food has no influence on the optimal distance from which both food type items are perceived ('Reactive Distance'). There can be several possible mechanisms to explain such a result. If a food type that animals are searching for is extremely abundant in their environment, there will be no need to invest much effort in detecting this food type and it makes no difference how abundant the alternative resource is (Mayntz et al., 2005; Abrams, 2010; Jaworski et al., 2011; Schmidt et al., 2012). Also, in the model, as this is likely the case in real animals, reactive distance values cannot be negative, and have some upper limit since higher values would mean investing less energy in survival and would thus lead to a reduction in the overall animals' foraging time. Hence, when reactive distances approach their maximum/minimum values, changes in the abundance of the complementary resource likely make less of a difference.

Results of the model also indicate the existence of a negative relationship between the reactive distances to each of the two food types when foraging animals are maximizing their overall fitness. Such negative trade-offs

between biological or physiological functions are a common feature that has been intensively studied in life-history theory (Stearn, 1992; Roff, 2002; Segoli & Wajnberg, 2020). The idea is that any investment in one trait likely comes at the expense of another. In the model, higher values of a parameter lead to shorter survival times, which might indirectly lead to a lower value for another in order to maintain a sufficient overall foraging time. However, in the present case, this is unlikely to explain the negative relationship between the two reactive distance values, as no negative correlations were found in the other parameters of the model. The negative association we found thus seems to indicate that there is a direct optimized trade-off in the model between the two reactive distances, which is in agreement with neural constrains (Bernays, 2001). Hence, evolving high detectability for one resource (e.g., prey) must likely and optimally be associated with losing detectability for the other resource (e.g., plant). We note also that the negative correlations were found among simulations with the same relative and absolute food abundances and the same consumer feeding habits. Therefore, the negative association is not the result of different food abundances and feeding habits that select for high detectability of one resource and low detectability in the other.

The model results also showed that animals should increase their selectivity (choosiness) towards a food resource if the relative abundance of essential food types in the environment does not accurately match the ratio they should optimally consume. Several empirical studies have demonstrated that selectivity to different food types can indeed be influenced by their frequency in the environment. For example, the African topi (*Damaliscus korrigum*) is more selective (in terms of plant quality) if food abundance is high (Jarman & Sinclair, 1979). Similar results were found for females of different species when the choice is not among different food types, but among male mates of different size/quality (Bateman, 1997; Jirotkul, 1999; Passos et al., 2014). However, in some other cases, selectivity level varies with the actual quality of the available resources and not their abundance (Garrigan, 1994). Moreover, there may be a functional link between food limitation (low abundance of optimal foods) and nutrient deficiency. When food is scarce, feeding on a few available items in the habitat is likely to induce/exacerbate nutrient deficiencies (Toft et al., 2021).

Regarding the time in which resources are processed by the foraging animals once they have been consumed, no specific trend was found in the

simulation output, which is somewhat surprising. The optimal food processing time is expected to be balanced by a trade-off between nutrient extraction time that is positively related to consumer fitness, and the need to 'free gut space' so that other food items could be consumed in order to reach the targeted diet mix. Such a trade-off should lead to an optimized food processing time in different situations. All else being equal, if there is not enough food (preferred or not) in their environment, foraging animals are expected to extend their food digestion time in order to assimilate additional nutrients and avoid subsequent starvation. In contrast, availability of desirable foods has been shown to accelerate gut peristaltic and emptying in several herbivores (Spalinger et al., 1986; Lundberg & Palo, 1993). In this respect, Hoffmann (1989) observed that moose show long rumination and retention times in winter when food is less abundant while, in the summer, food retention times drastically decreases. It should be noted that, in our model, both food types had the same processing time. This, however, might not be a realistic situation for some animals. For example, the half-life of pollen and prey (aphid) in the gut of the ladybird *Coccinella septempunctata* is about 5 h and 3 h, respectively (Oz, 2019). The effect of different food processing time on optimal gut emptying remains to be explored.

To keep our simulation model tractable and sufficiently general, we made several simplifying assumptions compared to real consumers. In the model, the simulated animals have a fixed foraging strategy (i.e., nutritional needs) over their entire life, whereas the nutritional needs (and behaviour) of real consumers vary with changes in physiological needs (e.g., dispersal, reproduction, overwintering), age, and experience (e.g., learning/forgetting dynamics) (Mayntz et al., 2005; Raubenheimer et al., 2007; Runagall-McNaull et al., 2015; Raubenheimer & Simpson, 2018; Simpson et al., 2018; Al Shareefi & Cotter, 2019; Damien et al., 2019; Morehouse et al., 2020). Future models could include plasticity of foraging strategy (and nutritional needs) and variation in the nutritional values of the food sources, and thus different optimal balanced diets e.g., at different life stages. Another simplification of our model is that the energy invested in walking and food-hunting effort is constant, although there is some empirical evidence that this may change with consumer's age (see, e.g., Bell, 1990, 1991; Hagler et al., 2010). In this respect, we consider our model was based on the average energy the simulated consumer invests over its entire life. Additionally, more realistic future simulations could allow changes in the environment, such as resource

depletion. The incorporation of environmental changes together with learning/forgetting abilities in such models is expected to make the simulated consumers more efficient in meeting their changing nutritional needs, and thus to attain higher fitness. Another simplifying assumption of our model is the absence of food handling time. In the model, encountered food items are exploited and the consumer resumes foraging instantaneously. Although it takes real consumers time to subdue, consume and process food items, and such handling time might differ greatly between different food resources, we do not expect this assumption to have a qualitative impact on the obtained results. Taking into account resource handling times will most likely just delay the animal's response to its environment. Finally, the model does not consider competition (or any other interaction) among foraging animals, as we simulated isolated individuals. Yet such interactions often play an important role in consumer-resource dynamics (Groenteman et al., 2006; Leon-Beck & Coll, 2007; Shakya et al., 2009), for example when consumers are released as biocontrol agents to control crop pests (see below). Future theoretical work could 'release' several individuals simultaneously in the grid, and study how direct and indirect interference changes the model outcome.

Our results hold several implications for optimizing the use of predators in biological pest control programs. Providing natural predators with supplemental, plant-based foods, such as pollen and nectar, has long been acknowledged as a means of enhancing the biological pest control services provided by these consumers (van Rijn et al., 2002; Wäckers et al., 2005; Put et al., 2012). Because plant foods often complement predators' prey diets, their addition attracts, retains and supports natural enemy populations within the agricultural environment, thereby increasing their overall impact on pest populations (Wäckers et al., 2005). Our simulation results suggest that, to optimize pest suppression by omnivores, biological control programs should employ omnivorous agents with an optimal diet mixture p^* that corresponds as much as possible to the actual availability of prey and plant foods in the targeted crop habitat. Furthermore, in such cropping systems, desirable plant resources, such as pollen, should not be available when high degree of pest suppression is needed. Our model indeed predicts that pollen availability would hamper prey consumption, and thus pest control efficacy. Finally, our model indicates that biological control programs should favor natural enemies with shorter digestion time, as long as there is no trade-off with other important functions. This would suggest preferential use of sucking over

chewing natural enemies because the former, that ingest liquid foods, tend to have a shorter digestion time than the latter (e.g., Pumariño et al., 2011).

In conclusion, our results show that (1) simulated foraging animals facing two types of resource in their environment must optimally invest more effort in detecting the resource that is scarce, both in absolute or in relative amounts, compared to the alternative one; (2) there is a negative relationship between the reactive distances to each of the food types when foraging animals are maximizing their overall fitness; and (3) animals should increase their selectivity (choosiness) towards a food resource if the relative abundance of essential food types in the environment does not accurately match the ratio they should optimally consume.

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