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SHORT COMMUNICATION

How to fail in advertising: The potential of marketing theory to predict the community-level selection of defended prey

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Abstract

Economics and ecology both present us with a key challenge: scaling up from individual behaviour to community-level effects. As a result, biologists have frequently utilized theories and frameworks from economics in their attempt to better understand animal behaviour. In the study of predator–prey interactions, we face a particularly difficult task—understanding how predator choices and strategies will impact the ecology and evolution not just of individual prey species, but whole communities. However, a similar challenge has been encountered, and largely solved, in Marketing, which has created frameworks that successfully predict human consumer behaviour at the community level. We argue that by applying these frameworks to non-human consumers, we can leverage this predictive power to understand the behaviour of these key ecological actors in shaping the communities they act upon. We here use predator–prey interactions, as a case study, to demonstrate and discuss the potential of marketing and human-consumer theory in helping us bridge the gap from laboratory experiments to complex community dynamics.

KEYWORDS
natural selection, predator-prey interactions, theory

1 | INTRODUCTION

There is a long history of productive cross-talk between behavioural biology and other fields. The incorporation of principles from economics, such as economically rational decision making, have been applied to predict optimal foraging strategies (Monteiro et al., 2013) and to plant–pollinator interactions (Francis et al., 2019; Muth et al., 2016; Waddington & Holden, 1979). These ideas provided not only concepts, but clear testable hypotheses, predicting how organisms should make decisions in order to maximize their fitness, and then testing if they follow these predictions. However, they often focus on trading—be it of goods, gametes or genes—and thus on the cooperative relationships between partners (Hammerstein & Noë, 2016; Noë & Hammerstein, 1994). Here, the clear parallels are to the relationship between trading partners in human markets, or businesses and their customers.

Yet despite this, the interactions between species that do not appear to be trading can still be likened to that of brands within a market because they are in competition with each other—mediated through the behaviour and choices of other species within their community. This is true even when no real trade is happening between the different parties, and their relationship does not immediately fall under intraspecific cooperation.

Nowhere is this truer than in the study of predator–prey interactions. Predator–prey (Hanifin et al., 2008; Menge &

Sutherland, 1976; Rönkä et al., 2020) interactions are one of the most influential interactions shaping community assemblages (Birskis-Barros et al., 2021). Prey species have evolved a huge variety of defences to deter potential predators, whilst predators rely on finding and consuming suitable prey for survival. Prey compete for enemy-free space (Jeffries & Lawton, 1984), however, their competition is mediated by the predators they interact with (Chaneton & Bonsall, 2000; Holt, 1977). How, then, can we understand the impacts of such "apparent" competition, acting as it does through multiple species on both sides of the interactions? One type of anti-predator adaptation, the use of chemical defences coupled with conspicuous warning signals (i.e. aposematism; Rojas et al., 2015; Ruxton et al., 2019), has been an important focus of research as it provides a classic story of predator–prey coevolution. Nevertheless, we still struggle to explain why aposematic species make up a relatively small proportion of prey communities (Kikuchi et al., 2021). This highlights the disconnect between studies of the behavioural ecology of one or a few species in close detail and the broader ecological context of species within communities. How can we challenge that disconnect?

One approach is to use insights from an area where we already have a well-developed understanding of how multiple predators and prey interact: marketing. Of course, in marketing "predators" are consumers and "prey" are products. Crucially, marketing theory aims not only to describe the behaviour of human consumers, but to predict the optimal strategies for brands to market themselves to consumers. As with natural selection, only successful brands can survive. Although brands in a market compete to be most appealing to potential consumers, the same principles could also be used to predict how to become undesirable, the strategy of aposematically signalling prey, who wish to convince would-be predators that they are the worst option amongst an array of potential prey. Therefore our aim in this paper is to expand the range of scenarios where, at least some of, the principles of biological markets can be applied—and emphasize their use for understanding intraspecific competition as well as cooperation.

2 | APPLYING MARKETING THEORY TO PREDATOR–PREY INTERACTIONS: APOSEMATIC PREY AS FAILED PRODUCTS

2.1 | The four Ps

One of the most fundamental theories of marketing is the four Ps: Product, Place, Price and Promotion. In order for a company to succeed, these four variables must be successfully combined to create a consistent and competitive marketing strategy. Each element has been researched in-depth independently from the others, but ultimately, it is the holistic combination of all elements together that determines success. The 4P Marketing Mix is widely considered the dominant marketing management paradigm and the archetype of marketing planning and has widespread use across the field (Constantinides, 2006; Grönroos, 1994a, 1994b). Each element has clear parallels with predation (Table 1). In predator–prey systems, the nutritional value of the prey is the product (from the predator's perspective). The price is the defence of the prey, be they behavioural, morphological, chemical or otherwise (Páez et al., 2021). Promotion is the signals used by prey to signal their defences (such as aposematic warning signals; Ruxton et al., 2019), whilst the place is the community in which the prey exists. Promotion is a key concept in marketing, and is perhaps the best-studied aspect of predation, in the form of both warning colouration and its subsequent mimicry systems. In contrast, price (aka defence) and product (nutritional value) have only recently received more attention with the role of predator state, and the nutritional value of prey is increasingly recognized in determining predator behaviour (Aubier & Sherratt, 2020; Barnett et al., 2007; Halpin et al., 2017).

2.2 | Product differentiation and positioning maps

When introducing a new product, companies must consider how it will differ from those already on the market, in terms of how both product

TABLE 1 The four Ps of marketing.

Marketing term	Biological parallel	Existing level of knowledge in this area
Product	Nutritional value of prey	Has recently received increased attention, particularly in the context of the effect of predator state (Barnett et al., 2007; Halpin et al., 2014)
Place	Community	Best studied in context of mimicry (Birskis-Barros et al., 2021; Prudic et al., 2019) (aka promotional strategies), and aggregation (Lindström et al., 2001; Riipi et al., 2001)
Price	Prey defences takes many forms (Bourdeau & Johansson, 2012; Páez et al., 2021; Rojas et al., 2017), but chemical defences in particular are widespread	Received less focus than warning signals. Improved chemical analysis has led to an increase in studies comparing chemical defence types and levels (Rojas et al., 2017; Rothschild et al., 1970, 1979). Still limited knowledge of how these chemical measurements translate to predator avoidance (Skelhorn & Rowe, 2006)
Promotion	Warning signals, anti-predator colouration	The most heavily studied component of anti-predator defence (Ruxton et al., 2019), particularly warning colouration (Briolat et al., 2019; Lindstedt et al., 2011; Mallet & Barton, 1989)

(Luchs et al., 2012; Nwabueze & Law, 2001) and price (Alinezhad Sarokolaee & Ebrati, 2012; Arora, 2011; Cockrill & Goode, 2010; Codini et al., 2012; Mathe-Soulek et al., 2016; Weisstein et al., 2013) compare. For human consumers, brands must offer either more products (in terms of quality or quantity) or lower prices—in other words, more for less. In contrast, prey seeking to avoid being chosen by a predator must do the opposite, either offer less (in terms of nutrition) to potential predators or come at a higher cost—less for more. This is reflected in studies that suggest that startle colouration is more common in larger-bodied moths (Kang et al., 2017) and that predators prefer larger-bodied prey even if distasteful (Smith et al., 2014). Indeed some lepidopteran larvae switch between crypsis and aposematism, where they invest in both chemical and physical defences, and advertise this fact with conspicuous colouration, as they grow (Medina et al., 2020; Remmel & Tammaru, 2011; Sandre et al., 2007). In marketing practice companies develop positioning maps in order to situate their product against their competitors in a given market context, based on variables deemed important to their target consumers (Moore & Pareek, 2009; Solomon et al., 2009; Figure 1). Clearly, successful strategies are dependent on those of other species in the community, creating local fitness optima that may differ depending on the evolutionary history of the community, and the environmental conditions that shape the costs of prey defences.

3 | POSITION MAPS AS FITNESS LANDSCAPES

There are clear parallels between positioning maps and fitness landscapes. The position of brands in position maps suggests that only a certain part of the space is profitable. Consumers will pay higher prices for products they perceive to be higher quality whilst producing high-quality products to sell at a low price is a waste of resources for manufacturers. Similarly, as several studies have established costs associated with the acquisition or production of chemical defences (Agrawal et al., 2021; Burdfield-Steel et al., 2019), thus, whilst there may be cases when there is variation in levels of defensive chemicals without any apparent variation in predator response (Chouteau et al., 2019), in general organisms should be selected to possess sufficient levels of defence to make them unprofitable to predators, but not to increase defence indefinitely (Speed & Ruxton, 2014; Figure 1).

4 | WARPING THE FITNESS LANDSCAPE

Once we view anti-predator defence in this light the implications for community-level selection become obvious—as communities will form locally-adapted optima for the trade-off between nutrition and defence. That is to say, the success of a chemically defended, aposematic, species is highly dependent on the alternative prey community in its environment (Kikuchi et al., 2021; Kokko et al., 2003; Mappes et al., 2005). These could be easily disrupted by changes in species abundance and the arrival of new species that may shift the local optimum. Thus the impacts of a non-native species moving into a community may spread, even to species it does not directly interact with, as it reshapes the fitness landscape.

Furthermore, whilst both nutritional content and distastefulness can be considered absolute measures, in the context of predator choice they may be relative. Within marketing, the importance

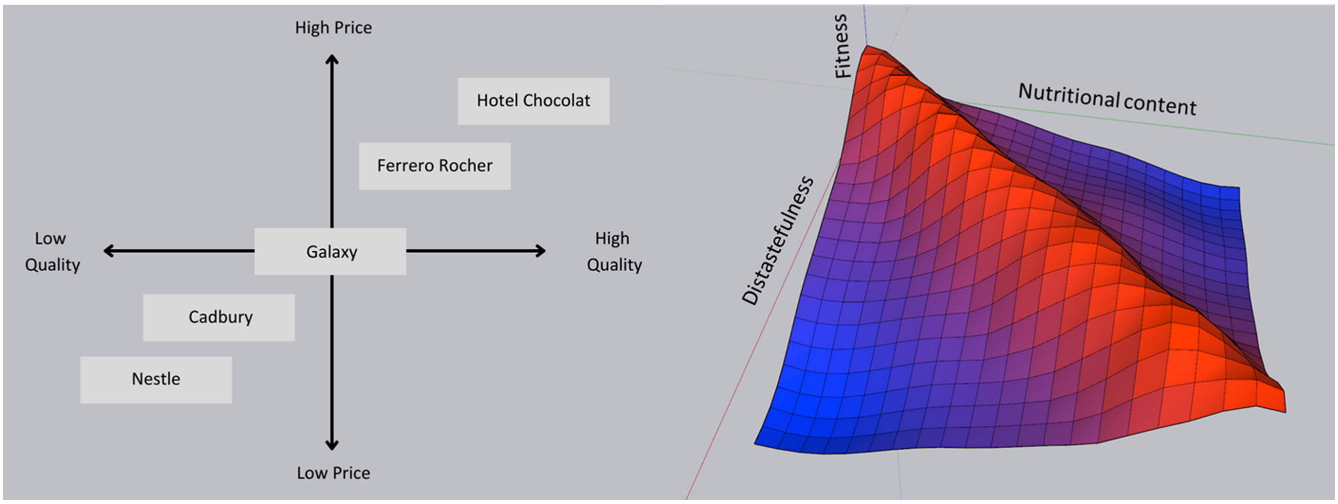

FIGURE 1 Left—Example of a positioning map showing chocolate brands mapped onto two variables, price and (perceived) quality. Right—A predicted fitness landscape for chemically defended, distasteful, prey under the assumption that predators forage optimally to maximize the nutrition-to-defence ratio (Altmann & Wagner, 1978) (thus predator preference for a specific prey type = Defence of focal prey/Nutritional value of focal prey—Average Defence of alternative prey/Average Nutritional value of alternative prey), and distastefulness comes at a cost to reproduction, whilst nutritional content is beneficial (Reproduction = Benefit of nutritional value—Cost of defence). Fitness is therefore highest along the line where distastefulness is just sufficient to make prey appear equally undesirable to predators, an amount that will increase with the nutritional value of the prey.

of positioning arises in part from comparative decision making. A key marketing concept is the Consumer Decision-Making Process, a model which maps the steps involved in making purchase decisions (Ashman et al., 2015; Engel et al., 1990; Gardner, 1985; Peter & Olson, 1990; Figure 2). This has clear parallels with existing frameworks in ecology—such as optimal diet and optimal foraging theory which posits that an individual foraging for food should maximize the rate of caloric intake relative to foraging time (Altmann & Wagner, 1978; Sih & Christensen, 2001). However, given what we now know about the willingness of predators to tolerate levels of chemical defence in order to acquire sufficient calories and/or nutrition, it is clear that such theory can easily be applied to multiple forms of costs, all of which need to be evaluated by a foraging consumer. Positioning plays a key role within alternatives evaluation (step three of the process), where different suitable products are evaluated by the consumer and choices are eliminated until a final decision is made.

Before we can reach the decision making stage, however, we must consider the information available to our predator/consumer. Whilst many optimal foraging, and indeed marketing, models assume individuals have access to all the relevant information on their options prior to this stage, in reality, that is unlikely to be the case. Under the Consumer Decision-Making Model acquiring information occurs during step 2, whilst in Foxall's Behavioural Perspective Model, it falls under consumer learning history. Whilst in many systems acquiring information may be costly in terms of time, for predators preying on potentially defended prey this cost can be even more direct, as sampling defended prey can expose the predator to toxins (Skelhorn et al., 2016). Such sampling is of course also damaging to the prey, and indeed aposematism has evolved to improve predator association learning, thereby reducing the time and costs of predator information acquisition for both predator and prey (Gittleman & Harvey, 1980). Ultimately it cannot be assumed that the information that predators and consumers have is perfect, or that acquiring information is free. The time and cognition costs of both acquiring information and decision making mean that in many cases simplified heuristics, or "rules of thumb" are used to speed up this process. In human consumers heuristics, loyalty, buying situations,

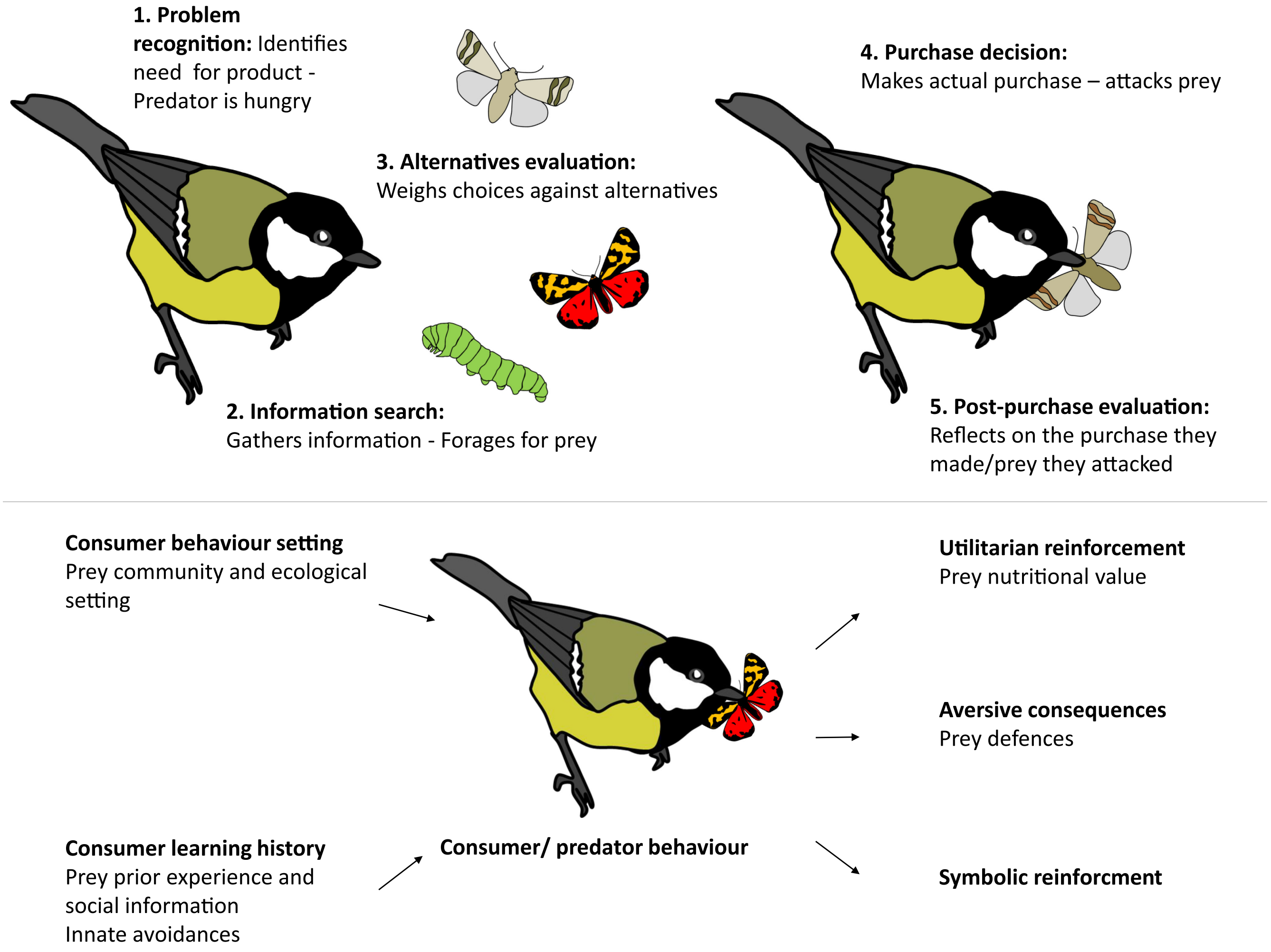

FIGURE 2 Schematics showing broad parallels between the Consumer Decision Making Model (Engel et al., 1990) (top) and Foxall's Behavioural Perspective Model (Foxall, 2002) (bottom) and interactions between predators and chemically defended prey. Comparative decisions may be made even when prey are encountered sequentially, rather than simultaneously—although this could carry more costs.

and situational or social influences all impact the decision making process. These influences can impact consumer behaviour to such a degree that consumers make illogical and irrational choices (Josiam & Hobson, 1995).

In contrast to rational decisions, where options are evaluated on a number of criteria, such as their costs and benefits, and the preferred option is consistently chosen regardless of the other options presented, in irrational decisions the preferred option is dependent on the other options presented. For example, under optimal foraging predators should, if making decisions rationally, maximize nutrition and minimize the level of defence encountered (Barnett et al., 2007; Halpin et al., 2017), and choose their prey accordingly (Hurley & Nudds, 2006; Monteiro et al., 2013). However, if they make irrational decisions their preferences may be altered by factors such as the other options available (even when those options are inferior, i.e. the decoy effect), conformity bias and framing effects.

In animal behaviour, the decoy effect in particular has been demonstrated in both vertebrates and invertebrates (Bateson et al., 2002; Glaser et al., 2021; McNamara et al., 2014; Shafir et al., 2003), although not without its difficulties (Schuck-Paim et al., 2004) and may arise from heuristics, or shortcuts, to allow for decisions to be made quickly (Merlo et al., 2008), and with less investment in neural machinery or information gathering. Such a system is thought to reduce the time and cognitive costs of decision making (Merlo et al., 2008). This assumption is supported by the finding that *Nasonia* wasps make rational choices when deciding where to lay their eggs, but are irrational when foraging (which requires many choices made throughout the animal's lifespan) (Glaser et al., 2021). As predators must make many choices during foraging, there will often be the need for rapid decision making, and so these behaviours are likely to be impacted by irrational choices. However, the decoy effect is not the only form of irrationality seen in animals. Evidence has been found in great tits for conformity bias (Aplin et al., 2015, 2017), and in chimps for framing effects (Krupenye et al., 2015), to name but a few examples.

This irrationality has important implications for community co-evolution. If predators make irrational decisions, then the introduction of new species into a community may alter the fitness landscape in non-intuitive ways. Other phenomena that can alter fitness landscapes are the informational state of the predators (Sherratt, 2011) and phenomena such as social learning (Hämäläinen et al., 2021) (where there is some evidence that information on negative characteristics of prey, such as distastefulness, are more easily socially transmitted than positive characteristics; Hämäläinen et al., 2019). All of these can be viewed through existing Marketing frameworks, for example, the Consumer Decision Making Model and Foxall's Behavioural Perspective Model (Foxall, 2002; Figure 2), although it should be noted the authors are still not sure how symbolic reinforcement, aka where people choose products that reflect and communicate their identity (Luna-Cortés, 2017), would translate to non-human animals. These frameworks have clear similarities and parallels to optimal foraging theory (Altmann & Wagner, 1978; Waddington & Holden, 1979). By applying the Consumer Decision Making Model and Foxall's Behavioural Perspective Model to predators we can model how they gather the information needed to choose the most optional food under optimal foraging theory. However, just like humans, predators do not necessarily gather the wholly correct information. Heuristics and manipulation by the product/prey can interfere in the information-gathering stage, and therefore disrupt the decision making process within optimal foraging theory, causing predators to choose non-optimal choices that they (wrongly) believe to be the most optimal. Evolutionary developments such as aposematism can be seen as prey trying to invoke specific heuristics in order to manipulate the predators' evaluation, triggering them to be eliminated from consideration within the decision making process, and therefore discounted with optimal foraging theory. Thus, considering marketing frameworks alongside these existing behavioural frameworks may better allow us to conceptualize the different processes influencing predator decisions, allowing them to be more easily tested and parameterised. This in turn can help us predict how predators and their prey communities will respond if one or more factors are altered.

5 | APPLICATIONS OF THE MARKETING FRAMEWORK

It has long been suggested that the number and type of alternative prey available are likely to play a large role in the success of warning signals, and thus aposematism as an antipredator strategy (Kikuchi et al., 2021). It is here that marketing frameworks have the most to offer. Aposematism functions as a so-called differentiation strategy. Product differentiation means that a product is perceived by the consumer to differ from its competition in some way (Dickson & Ginter, 1987). However, if differentiation strategies are copied or used by too many products in a single market their effectiveness is impacted (van Horen & Pieters, 2012). The same is likely to be true for aposematism. If everyone is defended, or indeed if everyone displays warning signals, then no one is. By testing the comparative ability of predators—for example starting with commonly-used model predators in predation studies, such as great tits and parameterising their preferences across contexts—aka how they compare prey that varies in more than one characteristic (such as defence and nutrition) simultaneously—we could begin to build predictive models of how predator choice impacts species coexistence.

Whilst here we have used aposematic species as our main example, the same framework can easily be applied to cryptic species. Here ease of locating the prey in the environment (aka search time required to find them) would replace defence level as the prey's cost. Optimal foraging theory can provide clear predictions as to the predator behaviour (Sih & Christensen, 2001)—but adoption of the position mapping framework can help to predict the range of "market strategies" available to prey. This approach also emphasizes the role of chance in the formation of community assemblages. As a predator's responses are expected to be shaped by the options it encounters, different starting assemblages of species may lead to very different local selection within communities—something that holds true across all the scenarios described.

Closer to the realm of aposematism—we can also apply this framework to phenomena such as Batesian, quasi-Batesian (Speed, 1999) and even automimicry (Brower et al., 1967). All of these involve prey that is similar in appearance to defended prey, but that possesses less or even no defence. The clear parallel to marketing would be copy-cat or counterfeit products, and ultimately the predicted effects will be similar—reducing consumer trust in the brand (Prathap & Sreelaksmi, 2022), and predator avoidance of the signal. In fact, what these will do is reduce the reliability of predator information and prior learning. This may select different predator sampling strategies (Kikuchi & Sherratt, 2015), which will in turn alter the fitness landscape as predicted by positioning maps of the species or populations involved. Changes to the fitness landscape will then influence the relative proportions of species, or individuals, serving as models and mimics in the mimicry system, which will in turn further alter predator behaviour (Honma et al., 2008) and the fitness landscape—creating an iterative process that may run away or perhaps lead to stable oscillations. Another interesting question this approach may prove fruitful to address is how social information can alter the fitness landscape, particularly since recent research suggests individuals, in this case, blue and great tits, pay more attention to social information on defence or distastefulness, compared with information of other aspects of a food's quality (Hämäläinen et al., 2021)—which could then impact both the rationality of their decisions or simply alter the fitness landscape, and, therefore, local species composition, depending on the availability of social information.

Finally, much like recessions alter consumer preferences and behaviour, environmental degradation and changes in prey, food and availability, can also shift animals' foraging preferences. The marketing framework could therefore be applied to understand how animal consumers will respond to reductions in the number of options available to them, and what this means for the community structure they forage in, be it prey, host plants or flowers from which to collect nectar.

6 | CONCLUSIONS

Ecological communities do not stand still. Environmental shifts and the endless forms of evolutionary change of the species that comprise them mean that ecological communities are a dynamic balance between stability and impermanence. However, human activity—changing habitats, species ranges, and natural processes at local and global scales—now presents ecological communities with an unprecedented scale and pace of change. This means that now, more than ever, we need to understand community-level ecology and how communities are shaped by species interactions, to predict how such changes will alter the stability and function of our ecosystems (Valdovinos, 2019). We believe marketing frameworks offer a highly useful way to convert complex behavioural interactions—like predator–prey interactions, into testable predictions. Whilst we do not suggest that they could supplant existing frameworks, we do think they can complement and strengthen them and continue the fruitful crosstalk between the fields of economics, animal behaviour and beyond.

AUTHOR CONTRIBUTIONS

Emily Burdfield-Steel: Conceptualization (equal); writing – original draft (lead); writing – review and editing (equal). **Claire Burdfield:** Conceptualization (equal); writing – original draft (supporting); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors confirm that they have no conflicts of interest.

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There is no new data associated with this manuscript.

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