Understanding human decision-making with models of animal foraging

Kathryn Coburn O'Nell
New College
MscRes in Experimental Psychology

Table of contents

Abstract

Classic research in human decision-making has typically required participants to make choices between two options associated with different reward values. However, models of animal foraging suggest that there is another important class of problems that animals have to solve frequently – patch-leaving decisions. In patch-leaving decisions, the important variable is not which option an agent picks at a standardised timepoint, but rather, when an agent leaves a current location to travel and find rewards elsewhere. In this thesis, I'll be discussing how we can use models of animal foraging to better explain human decision-making. Across two studies I will examine whether humans conform to the principles identified in studies of animal foraging, when making patch-leaving decisions. The first experiment I'll be discussing explores a range of factors that can affect economic decision-making under a patch-foraging paradigm, including the value of the environment in which an individual patch is situated, the time and effort costs of leaving a particular patch, and the value of the patch itself. The second set of experiments I'll be discussing explores how we can use this same patch-leaving paradigm to better understand human social decision-making. These studies both support the notion that humans make decisions about when to leave locations in a manner that conforms to the principles of theories of how animals solve patch-leaving problems. Across the thesis, I will review animal foraging research, as well as relevant human research, and discuss the strengths of this approach and highlight the work's limitations. Overall, I conclude that behavioural ecology approaches to animal behaviour may be fruitful for understanding human decision-making.

Chapter 1. Introduction

In this thesis, I'll be discussing how we can use models of animal foraging to better explain human decision-making. The first experiment I'll be discussing explores a range of factors that can affect economic decision-making under a patch-foraging paradigm, including the value of the environment in which an individual patch is situated, the time and effort costs of leaving a particular patch, and the value of the patch itself. The second set of experiments I'll be discussing explores how we can use this same patch-leaving paradigm to better understand how these models of animal foraging apply to human social decision-making.

In order to motivate the use of this foraging paradigm, I will review mathematical underpinning of Optimal Foraging Theory and demonstrate how foraging frameworks provide a mechanistic account of many leaving decisions in human life. Choosing when to disengage from a depleting resource is a widely-transferable skill, and has strong roots in human evolutionary history.

Next, to motivate the second set of experiments, I'll provide some theoretical framing for how social interactions can be cast in terms of patch foraging. Specifically, I will explain how leaving a dyadic interaction is a special case of 'Exit' as proposed in Albert O. Hirshman's 'Exit, Voice, and Loyalty' and how Exit interacts with the other two prongs of the theory.

As participants in our second set of experiments forage for fairness, I'll spend the next section of this introduction defining fairness and reviewing the literature on economic games related to fair splitting of resources. In the process, I'll discuss the limitations of traditional economic games with one-off decisions for studying fairness perception and why the foraging paradigm allows us to better understand more naturalistic continuous valuation processes.

Why Foraging Theory?

Within classic decision-making literature, researchers often ask humans, non-human primates, or rodents to make discrete choices between two options. These two options are generally associated with different magnitudes or probabilities of rewards, and are sometimes coupled with complementary risks (Mobbs et al., 2018). For example, in reinforcement learning (RL) experiments, human participants learn the reward probability structure of a set of hierarchical options (Pessiglione et al., 2006; Behrens et al., 2007) and in effort-based decision-making experiments, human participants choose between options which differ in how much effort is required to obtain rewards of different values (Chong et al., 2017; Klein-Flugge et al., 2015). Even in decision-making experiments that account for temporal dynamics, these decisions are still largely one-off binary choices. In temporal discounting experiments, for example, participants choose between an immediately-accessible reward and a larger-reward that can only be redeemed in the future (Kable & Glimcher 2007). This class of experiments has been helpful for understanding many aspects of human decision-making. However, these binarized decisions made at single timepoints are not necessarily the kinds of problems that the human (or non-human primate or rodent) brain evolved to respond to. Evolution is necessarily guided by properties of the natural environment, so in studying human decision-making, we must also consider the kinds of problems that are and were central to survival in the natural world (Mobbs et al., 2018).

In contrast to much of the human decision-making neuroscience literature, behavioural ecology and ethology have long studied how animal decision-making is shaped by properties of the environment. One major category of problem that animals face in their native ecosystems is that rewards like food and water are not uniformly distributed across their environments -- consider fruits clustered in trees, prey animals moving in herds, and water sources constrained to lakes and ponds. This uneven spread of rewards creates an optimization problem called the patch-leaving problem. In order to maximise rewards, animals must decide how long to spend exploiting a patch (e.g. eating apples from a tree) based on the quality of other patches (e.g. whether other trees have more or less apples available) and how long it will take to travel between patches. The analytic solution to this optimization problem will be discussed in the next section (Charnov 1976). While this problem is central to the behavioural ecology literature, little experimental research had examined how such decisions were made by humans until recently (Hayden, Pearson & Platt, 2011; Kolling et al., 2012; Gabay & Apps, 2020).

In this thesis, I propose that humans may often make decisions that are functionally isomorphic to the patch-leaving problem. In service of this argument, I will test the efficacy of theories of animal patch-foraging for explaining how humans make decisions regarding economic rewards. Further, I will test how well these same models can be applied to decision-making in the social world, i.e. how people make decisions about when to leave social interactions.

Optimal Foraging Theory

Optimal Foraging Theory has been proposed as an overarching framework to explain animal foraging decisions. It offers an optimal mathematical account, classically in terms of energy intake, for how an animal should solve the patch-leaving problem. In particular, it determines how long an agent should spend collecting rewards in a patch, given the properties of the environment, before travelling to the next patch. In this section, I will go through the mathematical underpinnings of optimal foraging theory (OFT).

The main prediction of OFT is that animals in patchy environments should pursue resources in a way that maximises intake and minimises energy expenditure. This prediction hinges on a few key assumptions. The first assumption is that animals forage in ‘patchy’ environments: those in which resources are clustered together in patches which are separated from each other by stretches of non-resource containing land. As an example, an apple orchard or field with berry bushes would be considered patchy. The second assumption is that food consumption is the only variable on which animals are optimising while foraging. As we will discuss later, this can be complicated by factors like presence of predators or a desire to maintain an ecosystem. However, even under these constraints, food consumption is such an important factor in survival that it accounts for a large degree of variance in behaviour (Newman, 1991; Sebastián-González et al. 2019) but food still often holds true. The third assumption is that animals have good knowledge of the values of food patches in their environment. At first, this assumption may seem to be the hardest to meet given that animals can’t necessarily see or smell far-away patches. However, most species inhabit a specific niche within their larger environment and build a robust model of this niche during early development, providing sufficient knowledge of niche-wide patch quality. Lastly, MVT assumes that resources are not rapidly replenished, meaning that the value of staying in a patch declines over time. Once all the apples are collected from a tree, it will take a long time for new apples to appear. While these assumptions don’t always hold true for animals within their environments, there are many circumstances in which they are met closely enough for OFT to provide informative predictions of animal foraging behaviour.

The main mathematical construct of Optimal Foraging Theory is the Marginal

Value Theorem (MVT) which defines the optimal leaving time for a given patch based on the qualities of the patch and environment at large: the quality of the patch (how much resource it has upon encountering it and how quickly that resource will deplete), the likelihood of encountering a patch of that quality, and the time/effort needed to travel between patches. Broadly speaking, the best time to leave a patch is when the rate of return of reward from that patch (e.g. a single apple tree) is equal to the average rate of return from all the patches in the environment as a whole (e.g. an orchard), with extra terms added to account for the cost of travelling between patches (Charnov, 1976).

$$(1)\quad E_n = \frac{\sum_{i=0}^{n} P_i g_i(T_i)}{t + \sum_{i=0}^{n} P_i T_i} = \frac{\text{average reward collected per patch}}{\text{average time spent per patch visited}}$$

$$(2)\quad \frac{\partial}{\partial i} E_n = 0 \text{ for each patch type, } i\text{, is solvable for } T_i$$

(3)

E_n	average reward collection rate in a given environment
$\sum_{i=0}^{n}$	summing over all patch types (e.g. sparse or dense)
P_i	probability of encountering patch type i
$g_i(x)$	total amount of reward accumulated in a patch by time x
T_i	time point when agent exits a patch
t	time needed to travel between patches

Fig 1. MVT equations (1) formula for the average reward rate of an environment (2) given that $g_i(x)$ is strictly decreasing, setting the partial derivatives of E_n for each patch type to 0 will maximize the average reward rate of the environment (3) defining variables used in equations (1) and (2)

Equation 1 defines an animal's average reward collection rate in a particular environment, as defined by the composition of its patch types, according to MVT. In the numerator, we define the average reward collected per patch, which is equivalent to the sum over all patches of the probability of encountering a particular type of patch (e.g. a particularly full apple tree vs a tree with very few apples) multiplied by the total amount of reward collected in that patch by the time the animal decides to leave. In the denominator, we define the average amount of time spent on a particular patch, which is equivalent to the average time the animal spends travelling between patches plus the average time spent in a particular patch (i.e. probability of encountering the patch type multiplied by the total amount of time spent in that patch).

Under the assumptions of OFT, animals have full access to information about the probability of encountering different patch types in their environment, reward accumulation functions, and travel time between patches. This means that, for each patch type, we can take the derivative of the average reward rate as a function of leaving time, then find where the derivative equals zero to find the optimal leaving time for that particular patch type. More specifically, we determine the point where the line tangent to an environment's average reward accumulation curve crosses the x-axis at (-t,0), where t is the time needed to travel between patches. Then, we use the slope of that line to find tangent lines to specific patch types.

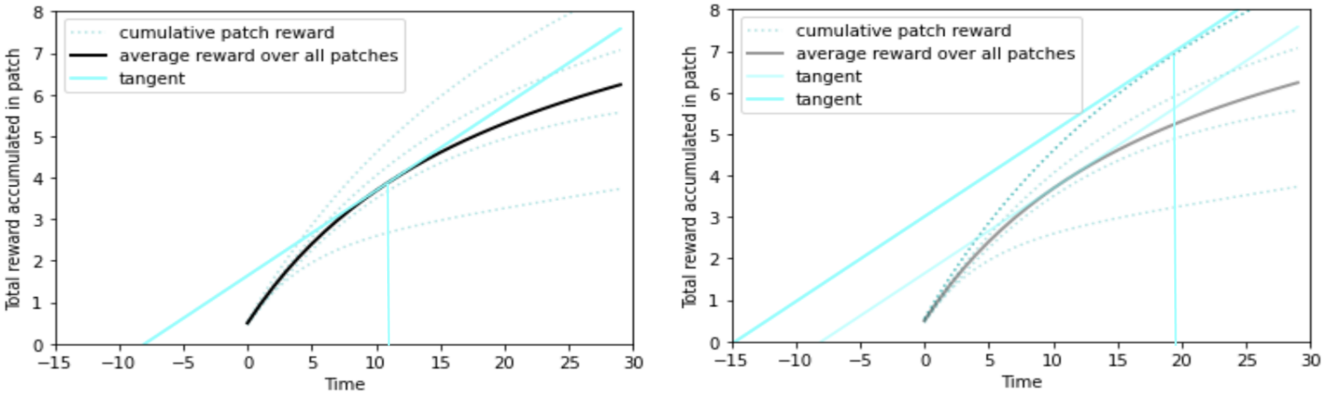


Fig 2. Finding optimal leaving times. (A) Depiction of a foraging environment with 4 patches, each with different reward accumulation patterns, and an 8-second travel cost. The average reward accumulation pattern is in solid dark blue, and is touched by its leaving-time-determining tangent line at ~11 seconds. (B) This tangent line is then used to determine leaving times in each of the patches —the optimal leaving time for each patch is defined by the point where the parallel tangent line touches that patch's reward accumulation function.

Different variables in the MVT equations affect leaving time in conjunction with each other. For the sake of building intuition as to how each one works, let's see how changing different variables changes the optimal leaving times in a model system.
For example, consider an orchard that consists of an equal mixture of healthy and unhealthy apple trees, which are distributed randomly. The healthy trees have many apples on the bottom branch, so the rate at which an agent can collect apples decays relatively slowly. The unhealthy trees, on the other hand, have few apples on the bottom

branches, so the reward collection rate decays more quickly. We can travel between trees, but the walk between each tree takes 8 minutes.

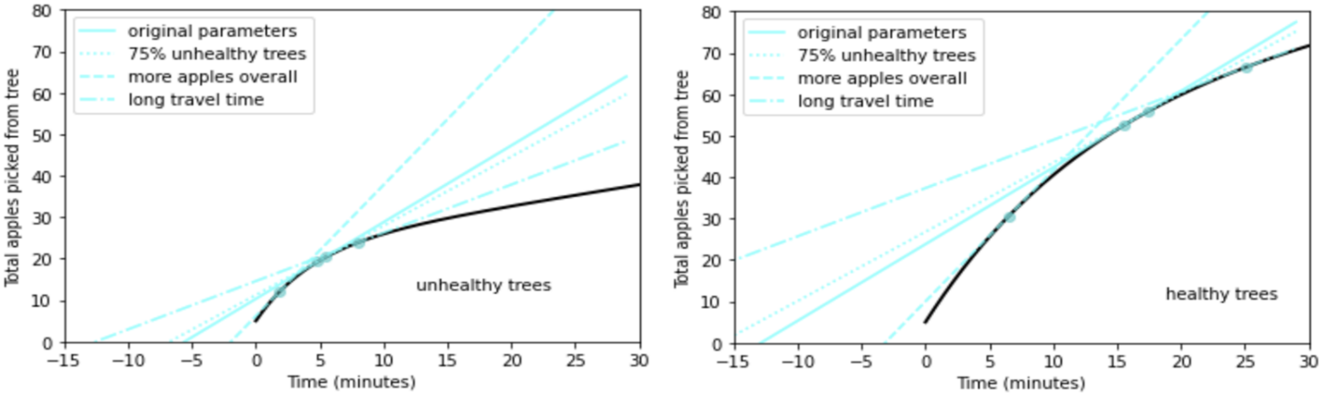


Fig 3. Changing MVT parameters Here we use Marginal Value Theorem to predict the optimal leaving time for an agent picking trees from unhealthy and healthy trees in different types of orchards. In the original parameters, the environment is 50% healthy and 50% unhealthy trees, an 8 minute travel cost between trees, and a standard number of apples accessible on the tree. Each plot shows how the ideal leaving time is calculated in three different conditions: 75% unhealthy trees, a larger number of accessible apples, and a longer leaving time. The left plot shows the effect of these changes when an agent is interacting with an unhealthy tree, the right shows the same for a healthy tree.

With the starting conditions (Fig.1; Fig.2 Fig.3) of 50% healthy/unhealthy patches and travel time of 8 minutes, the optimal leaving time would be to leave the healthy trees after 15.586 minutes and the unhealthy trees at 4.864 minutes. However, if the probability of encountering healthy and unhealthy trees changes, for instance if only 25% of the trees in the orchard are healthy and the other 75% are unhealthy, the agent should leave healthy trees after 17.5 minutes and unhealthy trees at 5.5 minutes. Note that the agent stays longer in both patch types when the quality of the overall environment decreases.

If, instead of changing the proportion of healthy and unhealthy trees, we increase the amount of apples available in each tree -- equivalent to changing g(i,x) in Fig.1 -- this increases the amount of reward that can be accumulated in total. Because the rate at which apples can be obtained over time declines (the more apples collected, the less available in the tree, and the slower each apple is collected), if the total apples in the tree increases, an agent should stay for a shorter period of time — 6.5 minutes with each healthy tree and 1.8 minutes with each unhealthy tree.

Finally, if the time needed to travel between trees (denoted as t in Fig. 1) increases, it changes optimal leaving times because no reward can be obtained while a forager is in transit. Thus, if travel time between trees rises from 8 minutes to 20 minutes, optimal leaving times for healthy trees would be 25.0 minutes and unhealthy trees would be 8.0 minutes. Thus, increasing the leaving time increases how long an agent should spend with both the healthy and unhealthy trees.

In sum, a better quality patch, a reduced time to get to the next patch, and increased likelihood of the next patch being good quality all reduce the amount of time one should spend in a patch in order to maximise reward intake.

Do animals forage for rewards in line with OFT?

Here, I will discuss the theoretical principles that underpin Optimal Foraging Theory. To show that MVT is a useful framework for describing animal foraging it needs to be demonstrated that: (1) that the assumptions of MVT hold sufficiently true in naturalistic food foraging environments and (2) that we can predict leaving times in patch foraging tasks with MVT.

MVT assumes several things about animal agents and the environments in which they forage (Charnov, 1976). With regard to the environment, we assume that the foraging space consists of distinct, randomly distributed patches and that the rate of food return in each patch decreases monotonically. In the example of an orchard, these two assumptions would indicate that the number of apples that can be picked from distinct trees in a given time period decreases with the amount of time spent at that tree. We also assume that the time it takes to travel between patches does not depend on how long a forager stays in a given patch. These assumptions are not always true in cases like hunting—for example, MVT does not make predictions about predator behaviour when nearby prey scatter on first contact, then slowly return—so this framework is limited to a narrower definition of foraging where food patches are static in location and regenerate on a timescale orders of magnitude larger than a single foraging session. With regard to animal behaviour, MVT assumes that agents have access to perfect information about patch types (e.g. the rate of food return from healthy and unhealthy trees), the time it takes to travel between patches, and energy costs. The forager also has full control over when it will leave a given patch in search of another and does so without backtracking or revisiting patches it has already exploited for rewards (Charnov, 1976).

With regard to the real-world implications of patchiness, evidence suggests that environments in the real world often are patchy, that patch distribution affects forager fitness, and that the ubiquity of patchy environments and the positive effects of food source spatial heterogeneity have shaped the evolution of food foraging strategies adherent to the predictions of MVT.

Previous observational research highlights that a large number of foraging environments exploited by different animals across the world are actually characterised by randomly-distributed patches of different quality. For example, meerkats in semi-arid southern Africa (Thornton and Hodge, 2008), flamingos in the Yucatan (Arengo and Baldassarre, 2002), and midday gerbils in the Gobi Desert (Shuai et al., 2016) all navigate patchy environments when collecting food.

The patchy nature of many real-world food foraging environments isn’t merely an artefact that happens to allow for patch-foraging behaviour, it also affects the fitness of the animal populations that they support. Specifically, the spatial heterogeneity of patchy environments contributes positively to population survival by distributing the risk of local extinction events (like fires and floods) across patches (Roff, 1973). For example, the egg-laying patterns of cabbage white butterflies: adult cabbage whites lay their eggs in multiple cabbage patches within their home biome. This way, the local species group isn’t wiped out if some individual patches are destroyed. When those cabbage patches recover, butterflies from other patches can recolonize the regrowth, thus maintaining the population size over multiple seasons (Fahrig and Paloheimo, 1988). Pale field rats also appear to follow similar patterns of recolonization after local habitat destruction — after fires in Australian northern savannas, surviving pale field rats in unburnt patches of vegetation fully recolonized new growth patches within the first year post-fire (Shaw et al., 2021). Experiments modelling population dynamics under different patch distribution regimes demonstrate that the positive effects of habitat heterogeneity decrease when patches are far away from each other, which is consistent with the account of recolonization as a driving mechanism behind environment patchiness promoting survival (Zollner and Lima, 1999). So not only are patchy environments common in the natural world, but it is also evolutionarily adaptive for animal species to forage in patchy, rather than uniform, environments.

As patchy environments tend to support local species fitness better than those with uniformly or randomly distributed food resources, it follows that many species have developed foraging strategies that optimise food consumption in these kinds of environments. This relationship between increased fitness in patchy environments and patch-friendly foraging strategies is not, however, unidirectional. Notably, the same foraging strategies that optimise animals' caloric intake locally also ensure genetic diversity across different patches (Lomnicki et al., 1980). In this way, the properties of patchy foraging environments and the strategies predicted by optimal foraging theory interact with each other to promote long-term survival of a species.

Foraging agents experience the fitness benefits of patchy environments even when they don't have perfect knowledge of the environment, though that knowledge is an assumption of Marginal Value Theorem. This is likely because animals frequently forage in environments with similar properties and build strong priors regarding average reward rate which are robust to temporally-localised changes to the habitat, like weather events. For example, chacma baboons foraging from trees and bushes in Namibian woodlands left individual food patches at times predicted by Marginal Value Theorem (as opposed to a more general Bayseian updating rule), even when the quality of individual patches varied dramatically day-to-day. Further, single recent foraging experiences generally had weak effects on patch leaving times in both natural and experimentally-manipulated foraging excursions, which indicates that aggregated foraging experiences over animals' lifetimes build strong priors (Marshall et al., 2013). This is not to say that information about environmental quality is irrelevant to foraging success — in competitive foraging settings, agents with fewer perceptual constraints on information gathering typically collect more reward (Koops and Abrahams et al., 2003) — rather a lifetime of experience with foraging can allow foraging success commensurate with perfect information even under limited information.

Another key assumption of Marginal Value Theorem is that animals rarely backtrack to previously-visited patches. While relatively few studies address this phenomenon specifically, it appears that this assumption holds true in scenarios where other MVT assumptions are also met. For example, when brushtail possums in Ku-ring-gai Chase National Park visited experimenter-placed feeding stations, possums' first visits to individual stations accounted for over half of their overall time spent at that station and almost all of their food consumption at that feeder (Mella et al., 2018).

In cases where revisiting is common, there is generally a violation of another major MVT assumption that makes revisiting a more productive option, like when individual patches' reward rates don't decrease over time. This is true of patches like bird feeders, where birdseed is dispensed at a steady rate. As the quality of a bird feeder is unchanged by previous visits, it makes sense that many species of birds have been recorded revisiting bird feeder patches up to 10 times per hour (Bonter et al., 2013). In the case where an agent is navigating an environment where the patches and/or overall environment are small enough that the agent can fully deplete the available resources, the agent may reach a point where it is optimal to revisit earlier patches, as there are no better options (Kilpatrick et al., 2020). Although this somewhat violates the assumptions of MVT, it is important to note that this pattern of behaviour does not differ from those predicted by MVT. Instead, it indicates that the agent has updated their estimate of the environment's average rate of return.

In sum, while not all decision-making environments conform to MVT, many environments do indeed conform to its assumptions and behaviours of different species can be characterised as conforming to its principles. Even when animal foragers deviate from optimality by over- or under-staying, they still adhere to the general patterns of leaving time behaviour predicted by MVT: they stay longer under long travel times (Elliffe et al., 1999; Doniol-Valcroae et al., 2011) and leave sooner when the environment is rich (Roberts 2013; Sheng et al 2014; Thiel & Hoffmeister 2004; Marshall 2013).

Humans as reward foragers

Can MVT be used to explain human food foraging in naturalistic environments? As the agricultural and industrial revolutions have dramatically changed the way that many human societies structure food production and cultivation, the best way to answer this question is by looking at movement between gathering patches in hunter-gatherer societies. This way, we can see how humans forage for food in environments that meet as many of the assumptions of MVT as possible — especially those regarding monotonic decreases in patch reward rate and patchy environment structure. As it turns out, in several contemporary hunter-gatherer societies across different continents, the predictions of MVT explain leaving-time decisions during food foraging on a variety of different spatial and temporal scales. On the timescale of hours — the timescale for which Charnovian foraging models were developed — Nahua mushroom gatherers in La Malinche National Park typically adhere closely to MVT predictions of when to leave a given mushroom patch (Pacheco-Cobos et al., 2019). Optimality in human food foraging, however, is not limited to this time scale. For Batek nomads in Peninsular Malaysia, group decisions on when to move camp sites every few days also occur at or near the timepoint at which the collective foraging rate of meat, tubers, and rattan drops below that of the environmental average (Venkataraman et al., 2017). Alyawara foragers in Australia choosing between seven major habitat types optimise energy return rates by staying in different patches for different lengths of time depending on their seasonal reward rates. For example, foraging trips to sandplain patches are typically much longer and more frequent in the spring when large unripe seeds, which have high caloric value and low processing costs, are available (O'Connell and Hawkes, 1984).

So, despite being a model designed to explain animal foraging behaviour, MVT is predictive of patterns of behaviour that can be observed in humans. As such, MVT may be able to explain how humans make a variety of decisions.

Foraging frameworks can explain more than traditional hunter-gatherer food foraging decisions — in fact, many decisions in contemporary life can be cast as foraging problems. In coastal Florida, sea-level changes brought on by global climate change are rapidly decreasing the viability of certain industrial fishing locations, and fishers must decide when and where to relocate inland (Stoltz et al., 2021). Car thieves in Los Angeles must consider the likelihood of encountering higher and lower value cars in their local environment while also determining the effort needed to resell different car types — and in fact often navigate these decisions with patterns of behaviour predictable by Charnovian prey selection models (Brantingham, 2013). For those of us who neither fish nor steal cars, even simple decisions around the home and workplace, like whether or not to replace a broken appliance or apply for a new job, can be understood with the vocabulary of optimal foraging: the decreasing value of a salary with no cost-of-living adjustments, or the opportunity cost of buying a new washing machine out of one's holiday savings.

Animals and humans conform to the MVT principles, albeit not optimally, in patch-leaving tasks

While MVT was originally formulated to explain how animals forage for rewards in the wild, more recent experimental research has increasingly begun to test how non-human primates and humans make patch-leaving decisions. Strikingly, even in enclosed experimental paradigms, participants' decisions conform to MVT principles across species. For example, macaque monkeys presented with patches that provided decreasing quantities of juice reward stayed longer with patches where the initial rate of reward was higher (Hayden, Pearson, Platt 2011, Nature Neuroscience).

Evidence in favour of human decision-makers' adherence to MVT comes from both experiments directly testing patch-foraging strategies and experiments in which participants must more generally attend to opportunity costs to optimise their decisions. When humans performed a task in which environments of different qualities were populated by patches from which rewards depleted from on different initial reward values -- a task mimicking Charnovian conceptions of patch-foraging -- participants stayed longer in (a) high quality patches and (b) low quality environments. Importantly, there were no interaction effects between patch and environment quality, which comports with MVT principles (Le Heron et al., 2020, Journal of neuroscience). Along similar lines, human participants in a different patch-leaving task stayed less long in a patch directly following a high-yield patch, indicating an updated model of the average environmental reward rate (Hutchinson JM, Wilke A, Todd PM 2008). Another human patch-leaving task compared two decision-making strategy learning rules -- one consisted of averaging previous rewards in an environment to estimate an opportunity cost, which is consistent with MVT, and the other ignored the structural features of foraging in favour of a model-free reinforcement learning strategy à la temporal difference learning. Of the two, the MVT-informed model better predicted participant performance (Constantino & Daw, 2015, Cognitive, affective behavioural neuro).

Even outside of strict patch-leaving experiments, human participants demonstrate sensitivity to opportunity costs when making economic decisions. When presented with a single known reward and an array of multiple possible rewards, participants chose to receive one of the alternate possible rewards when the average alternate reward was of greater value than the single known reward (Kolling et al., 2012, Science). In a similar engage/forgo task, participants reliably updated their beliefs -- and consequent preferences -- about the task environment based on the average background rate of reward (Garrett & Daw (2020; Nature comms).

Thus, many studies support the idea that species, including humans, can conform to MVT principles while in controlled experimental paradigms in tasks that mimic patch-leaving problems and related cognitive constructs. People are sensitive to how much reward there is in each patch, and to the average rate rewards can be accrued in the environment, Further, they adapt their behaviour accordingly. However, although MVT is able to explain a large amount of variance in animal leaving behaviour in patch foraging, people and primates were not optimal in the experiments outlined above. In particular, leaving times predicted by MVT are consistently shorter than people's behaviour. In other words, animals typically stay longer in individual patches than we might expect (Nonacs, 2001).

Multiple explanations have been put forward for this pattern of overstaying: a response to threats from predation and starvation (Newman, 1991), a need to allocate food to offspring (Kacelnik, 1984), or a response to self-assessment of behavioural variability (Cash-Padgett and Hayden, 2020). All of these interpretations share a key feature: they introduce an additional opportunity cost to leaving a given food patch not considered in MVT, be it exposure to predators or starvation of offspring. Opportunity-costs – or the value of a behaviour one is currently engaged in relative to the value of alternatives – powerfully influence decisions (Kurzban et al., 2013 Behavioural brain science; Niv et al., 2006 Psychopharmacology). Opportunity-costs influence people's motivation levels, the speed of their movement, and, as highlighted by the studies above, they influence human patch-leaving decisions.

At its core, MVT provides a mechanism for explaining patch-leaving in terms of opportunity cost. Early on in a patch, the rate of reward is greater than the environmental average, so there's no reason to look elsewhere for higher rewards. When that rate reaches the average, however, the agent starts losing out on potential rewards from other patches by staying where they are. What the pattern of overstaying that we see in some animal foraging behaviour tells us is that the t term of MVT needs to be expanded. Instead of just travel time between patches, animals consider travel cost in terms of effort, danger, and predictability (See Figure 2 for an illustration of how travel cost affects leaving times). This framework of opportunity cost explains important aspects of hunter-gatherer foraging strategies, like site choice. For example, Aboriginal populations in the Western Desert of Australia spent decades foraging in the same sites with easy access to water and trading sites (Bird et al., 2020). This way, time spent foraging for food did not impose an undue cost on other needs.

Human and animal mechanisms of determining opportunity cost are not always consistent across timescales. Specifically, imminent rewards are often valued much more highly than future rewards, and these delayed rewards are discounted along a pseudo-hyperbolic function (Green and Myerson, 1996). This can lead foragers to underestimate an environment's average rate of return, contributing to the consistent pattern of overstaying observed in many species' food foraging behaviour. Rats, for example, consistently choose immediate rewards over delayed rewards, and their overstaying patterns in food patches can be accounted for by a hyperbolic temporal discounting model (Kane et al., 2019).

It is important to note that "overstaying" refers specifically to a pattern of behaviour whereby an animal chooses to leave a reward patch later than Marginal Value Theorem would predict. It does not mean that the animal is staying longer than is actually optimal. In fact, the portion of overstaying attributable to temporal discounting may well allow animals to survive in variable environments: if future reward isn't guaranteed, exploiting a smaller reward at the expense of a larger future reward that might never appear is an effective strategy to forestall starvation. For chicks trained on competitive and non-competitive foraging tasks with stable and variable food rewards, the presence of competition and variability in food availability significantly increased the probability that a given chick would select a small, immediate reward over a larger, delayed reward

(Mizuyama et al., 2016). Given that chicks in the non-competitive task with stable food rewards chose the larger reward with longer delay nearly every single time, this indicates that the temporal discounting in these chicks' decision-making is caused by environmental insecurity. This causal link is reflected in findings from young human children: children who interact with an experimenter who provides reliable information prior to a standard marshmallow test wait significantly longer than those who interact with unreliable experimenters (Kidd et al., 2013).

This collective evidence suggests that Marginal Value Theorem, while successfully explaining much variance in human and animal food foraging behaviour, needs a more expansive definition of travel time that encompasses the many complicated aspects of opportunity costs involved in leaving a patch. In this thesis, I will directly aim to extend MVT, to outline how the effort of travelling, and the time it takes for travelling, need to be included to understand human, experimental, patch-leaving behaviours.

Contemporary models of human decision-making

Now that we've established that human food foraging can be successfully modelled using Optimal Foraging Theory and the Marginal Value Theorem, we can start to take a look at the domain-general mechanisms behind patch-leaving decisions. How to decide when to disengage with a depleting resource is a challenge that humans and other animals face in a wide array of domains. Some examples are intuitively obvious in their connections to foraging frameworks, like deciding when to leave a romantic relationship or place of employment. Others are more subtle, like how human participants visit patchily-distributed semantic spaces during memory retrieval tasks (Hornsby and Love, 2021). Patch-leaving is also a problem structure that is importantly different from many other decision-making tasks in the literature, as patch-leaving decisions are made on a continuous time scale rather than at discrete, predetermined evaluation points. From an evolutionary perspective, solutions to broad problem frameworks should be preserved (like the concept of memoization in computer science) and generalised, indicating that similar mechanisms might underlie social and nonsocial versions of resource disengagement decisions. If we conceptualise this in terms of Marr's three levels of analysis (alternately, Pylyshyn's three levels), we can understand foraging decisions as follows:

- Computational/Semantic: patch-leaving behaviour
- Algorithmic/Symbolic: neural drift-diffusion models
- Implementational/Biological: integrate-to-fire strategies in neural populations

Casting foraging problems in terms of neural drift diffusion models helps us understand how individual and environmental factors affect leaving times in concert. In a traditional drift diffusion model, agents make a decision between two options by collecting evidence in favour of each. In addition, the evidence accumulation process has additional noise from a random walk added to each step. When sufficient evidence has been gathered in favour of one option over the other (i.e. the threshold has been hit), the agent makes a decision. When applying this model to foraging behaviour, we make a few key substitutions. First, there is only one decision an agent can make: to leave a patch. This means that, while evidence can accumulate in the negative direction depending on an agent's priors about the quality of a patch, there is no lower threshold. Second, instead of evidence in favour of a decision, the agent is collecting food (or monetary, or social, or a combination of various types of) resources, which serve as evidence that a patch has decreased in value enough that it is worth travelling to reach another, more abundant patch (Adams et al., 2012). This formulation of foraging concepts in the terms of drift diffusion models can help us understand the system in new ways. For example, when agents' average staying time in a patch increases, the variability in their leaving times also expands. The drift term (i.e. noise introduced by randomness in the environment and neural coding processes) provides a mechanistic explanation for this trend: when the distance between the starting point and threshold increases, the room in which the drift term adds noise to the evidence accumulation process increases.

Foraging frameworks for human social decision-making

In the previous sections it has been established that MVT can account for important features of human decision-making, albeit not perfectly. But what about broader aspects of human decision-making? Strict exit-type decisions are becoming more and more common in everyday life — swiping through dating apps, attending a few MOOC lectures, scrolling through a movie streaming platform. In fact, exit is often the easiest option in increasingly-popular online communities (Frey and Schneider, 2020), and contemporary corporate employers are increasingly low-loyalty, high-exit arenas of interaction (Barlow, 2001). The increasing importance of these kinds of disengagement behaviours motivates a desire to use foraging frameworks to explain wider social decisions.

There are a variety of animal and human social decision-making problems that can be cast in terms of foraging and the Marginal Value Theorem. These tasks are importantly different from most descriptions of social foraging in the existing literature, which refer to cooperative and/or competitive foraging for food resources. In this thesis, I use social foraging to refer to distinctly social problems — like deciding when to leave a party or date — that can be explained with the vocabulary of optimal foraging.

For male macaque monkeys, gathering information about others' social status and emotional states is key to survival. Not only is this task facially isomorphic to food foraging, macaque monkeys' leaving times in a social information-gathering experiment were well-predicted by Marginal Value Theorem (Turrin et al., 2017). This raises questions about how tightly human social information gathering strategies map to food foraging strategies and whether humans and other animals forage for more abstract social qualities, like fairness.

Beyond information-gathering, many other patterns of social interaction within animal communities can also be viewed through the lens of Optimal Foraging Theory. For male insects, the task of finding a female mate has direct parallels to food foraging tasks: male insects seek both to consume as many calories and to mate with the largest number of female insects possible per unit time, different food quality and the proportion of female insects in different stages of reproductive life cycle in a given patch affect leaving times, and the amount of food that can be collected and number of female insects that can mated with strictly decreases over time in a patch (Louapre et al., 2015).

With regard to human social decision-making, a recent line of research has focused on leaving times in dyadic conversations. In many scenarios, potential conversational partners are distributed patchily with imposed travel costs between them. For example, a party-goer might stay in a boring conversation for longer than they otherwise would if leaving meant sacrificing their place in a long line for food. The composition of the environment of potential conversational partners could also affect one's willingness to stay in a conversation — if the alternatives were all close friends visiting from out of town, the party-goer would likely break off an unsatisfying conversation more quickly. In reality, however, we rarely leave conversations when we'd most like to — rather, we tend to overstay. A study of over 900 dyadic conversations, only 2% of conversations end when both participants wanted. (Mastroianni et al., 2021).

The evidence in favour of strong parallels between food foraging and social interaction are not solely behavioural. In addition to sharing an integrate-to-threshold structure, the motivations behind seeking out both food and social engagement seem to share some neural representations. In a recent cross-species study, social isolation and the resultant behaviour of seeking out social interaction was linked to neural activity in dopaminergic neurons substantia niagra and VTA in mice, as were patterns predictive of hunger craving. In healthy adult humans deprived of food or social interaction for 10 hours, fMRI-recorded activity in the same regions found was predictive of self-reported craving of whichever deprivation condition the participant was in (Tomova et al., 2020). In addition, increased ventral striatum response patterns to exposure to close friends or partners in lonely participants were found to be similar to those elicited by hunger (Inagaki et al., 2016).

These links between hunger-induced and loneliness-induced craving signals in shared neural architecture can speak to a larger debate in contemporary cognitive neuroscience over the existence of the social brain. Much of the conversation has centred on socially-oriented pathways in specific processing domains (Pitcher and Ungerleider, 2020), flexible reconstruction of social processing regions after brain damage (Kliemann et al., 2021), or reconsidering where sociality can arise in neural systems (Lockwood et al., 2020). In this case, the linkages between hunger and social craving contribute to conversations about how many social behavioural phenomena can be explained in terms of evolutionarily-older, non-social neural mechanisms.

Exit decisions with social goods of decreasing value

As articulated in Albert O. Hirshman's classic monograph, Exit, Voice, and Loyalty, agents faced with social goods of decreasing value can choose to disengage with an organisation (exit) or voice their dissatisfaction in order to demand change (voice) -- a non-exclusive choice modulated by the qualities of the agent, the social partner/organisation, and the dynamics of power and loyalty between the two. There are certain types of organisations and interactions in which exit and voice are more and less common (and effective) as responses to declining quality (Hirschman, 1970). Exit is a far more common strategy than voice for customers in competitive business environments, while voice is more common in more personal organisations like families and churches. For example, while parishioner attendance to Catholic church services dropped after the publication of the controversial *Humanae Vitae* encyclical, this exit response did not quickly change church policy. When lay Catholics began to speak out against sexual abuse by priests, however, many clergy boards changed the way diocesan financial counsels conducted staffing decision-making — voice at work (Bane, 2002). In some cases, like those Hirschman describes as “voluntary relations,” both exit and voice are equally viable options. For monogamous romantic relationships, continuing satisfaction with and investment in the relationship encourages voice responses to conflict, while a more appealing environment of alternative partners promotes exit decisions (Rusbult et al., 1982).

If we use the exit, voice, and loyalty interpretation in mind as we read the literature on leaving decisions in social interactions, it becomes clear that the grand majority of papers focus on exit as voice rather than pure exit.

For instance, decades of research has used economic games in humans. In these experiments participants choose between two alternative behaviours during a social interaction. Both choices have financial consequences for the participant and other players. For instance in the ultimatum game, player A offers a split of money to player B, if player B is happy with the split then both players can walk away with that amount. If player B is unhappy with that split, because they deem it unfair, they can reject the offer, in which case neither player gets any money (Güth, Schmittberger, & Schwarze, 1982). Such tasks have been hugely fruitful for understanding the boundaries of human social behaviour, how sensitive people are to unfairness, how they trust others and how they behave during iterative social interactions (Ernst Fehr and Klaus M. Schmidt, 1999;

Kahneman, D., Knetsch, J. L., & Thaler, R. 1986; Forsythe, R., Horowitz, J. L., Savin, N. E., & Sefton, M. 1994). Such tasks have also been used extensively to understand the neural mechanisms of social cognition and behaviour (Sanfey et al., 2003; Krueger et al. 2008). But, crucially, they can all be deemed as considering the "voice". In none of these cases are participants simply indicated that they can make the decision to leave the social interaction. In chapter of this thesis I will suggest that we can use MVT to explain how humans make decisions to leave social interactions.

Thesis Aims

In this thesis I aim to demonstrate that MVT can provide a framework for how humans make decisions, even though it was originally intended to explain animal foraging behaviour. To do this, I analysed data from two sets of experiments that were designed with MVT principles in mind. In each, participants were required to make patch-leaving decisions: first to try and maximise rewards in the face of travel-related effort costs, secondly when considering whether to stay in a social interaction where fairness was declining. Across the two experimental chapters I will therefore test specific hypotheses:

1. That humans are sensitive to the effort of travelling between patches and that this influences the opportunity costs of remaining in a patch
2. That humans leave social interactions of declining fairness under the principles of MVT, moving on sooner when the average fairness in the environment is higher.

Chapter 2. Travel costs in human foraging

2.1 Introduction

Research across neuroeconomics, psychology and neuroscience has studied the cognitive and neural mechanisms underlying how humans make decisions. This work typically uses paradigms in which people are presented with choices between two stimuli that differ in “value” in terms of the costs (e.g. delay before receipt or effort required) and benefits (e.g reward magnitude) associated with them. This work has been highly fruitful in identifying biases in decisions, as well as key neural and cognitive mechanisms that underlie people’s choices. But such decision problems are, to a certain degree, artificial. In the real world, animals have to solve decision-making problems that are shaped by the environments they inhabit. Recently, it has been suggested that decision-making may therefore be better understood using problems that many species brain’s evolved to solve.

One such problem is patch-leaving: when navigating a patchy environment characterised by unevenly-distributed reward-yielding regions, animals must decide when to stop exploiting a patch and travel to the next. Animals’ patch-leaving decisions are influenced by a variety of factors: the yield rates of an individual patch, the average yield rates of the environment as a whole, and the time required to travel between patches. Given these factors, one can derive an optimal leaving time for a given patch using Marginal Value Theorem (MVT). Notably, many animals conform to the predictions of MVT both under observation in their natural habitats and under experimental conditions. Given their grounding in an evolutionarily-salient optimization task, patch-leaving paradigms provide a more naturalistic alternative to two-alternative forced choice tasks and can help us better understand human economic decision-making as it occurs outside of the laboratory.

A number of recent empirical studies have begun to examine patch-leaving decision-making in humans. Constantino & Daw, (2015) required participants to collect virtual apples from gradually-depleting trees, measuring when participants decided to leave these patches to travel to the next. The authors found that participants optimised their leaving behaviour based on previously-accumulated knowledge about the average value of the environment -- otherwise put, human participants considered opportunity costs when leaving, which is consistent with the predictions of MVT. Another human patch foraging experiment, in which participants were tasked with collecting as much milk as possible from a series of farms with different continuously depleting resources, found that participants stayed longer in high-yield farms than low-yield farms and also stayed longer when the set of farms they interacted with had lower average reward rates (i.e. decreased potential gain in value from leaving a patch) (Le Heron et al, 2020). These studies broadly support the notion that humans can and do solve the patch-leaving problem in line with MVT principles. However, while systematic differences in humans' leaving times between different kinds of patches and environments are well-explained by MVT, leaving-times in general are not. More specifically, humans and other animals tend to stay longer than is optimal in each patch.

We know from existing literature that humans appear to behave similarly to non-human animals in food foraging contexts — we generally stay longer in patches of high value, environments with lower average value, and environments with lower travel times between patches. One factor that has been understudied, however, is the effect of travel costs beyond travel time — particularly travel effort. While Charnov's original formulation of MVT does not differentiate between a 15-minute walk through a flat forest clearing and a 15-minute climb up a slick mountain face, updated optimal foraging theories have gradually begun to consider the energetic costs of travelling (Kacelnik et al., 1984; Schmid-Hempel et al., 1985).

Intuitively, one could reasonably predict that an animal forager might overstay in a mountain patch to delay making the difficult and dangerous climb. In fact, blue whale diving behaviour depends not just on the time required to reach a food source, but how much effort the energetic cost transporting its body mass back to the surface (Doniol-Valcroze et al., 2011). Experimental studies in hooded rats showed hardship-mediated adherence to optimal foraging principles in the context of travel effort. In a series of studies without travel costs, animals did not approximate optimal foraging when rewards were abundant, however, when rewards were scarce, foraging became more optimal (Mitchell and Brener, 1997). Similarly, when preferred locations were raised 3 feet further off the ground, accessible by climbing a nail ladder, rats increased the optimality of their foraging behaviour (Mellgren et al., 1984). Human participants in patch-leaving tasks also demonstrate a preference for overstaying (Kilpatrick et al., 2021) -- especially when movement between patches required even minimal physical effort. In a series of patch-foraging tasks, Evan Carter and colleagues (2015) found that human participants' sub-optimal preference for staying in individual patches increased when patches were physically separated from each other, requiring participants to walk between them. Thus, both theory and empirical evidence suggest that increased effort of travel costs modulates foraging in animals, making individuals stay longer when energy must be expended to move to a new patch. But what remains unknown is how the effort of travelling between patches influences human patch-leaving decisions when other foraging properties also vary.

Previous research in humans has extensively examined how people make effort-based decisions. Participants are presented with choices between more physically or cognitively demanding levels of a task (e.g percentages of maximum grip strength or harder levels of an n-back task) for high financial rewards or less effortful but less financially rewarding. (Chong et al., 2017; Wesbrook & Braver, 2015) Overwhelmingly studies show that people are averse to the effort, and will choose less demanding tasks, unless associated with significantly higher rewards (Hull, 1956; Kool & Botvnick, 2018). However, such experiments differ considerably from patch-leaving tasks. Choices to exert effort are one-shot, and with the aim of explicitly obtaining a known magnitude of reward. They therefore measure the willingness to exert effort for reward, and not whether the effort of travelling influences how long people spend in locations, as measured in patch-leaving experiments.

Although recently a number of studies have used patch-leaving tasks in humans (Kolling et al., 2012; Constantino and Daw, 2015; Kolling and Akam, 2017; Mobbs et al., 2018; Le Heron et al., 2019; Gabay & Apps, 2021), most either do not examine effort-costs. When effort has been studied in the context of human foraging, the focus has been primarily on within-patch effort, i.e. the difficulty of extracting food from its source. Observational research of shellfish gathering behaviour in Kiribati have demonstrated foragers differentiate between strongly- and weakly-attached ark clams, preferentially harvesting the latter (Thomas, 2007). This suggests that humans do consider effort costs while travelling, but experimental examinations have not been forthcoming.

How would effortful travel influence patch-leaving behaviours within the constraints of marginal value theorem? If travel effort is treated as a cost, in a similar way to the delay cost, then people will stay longer. Thus, I hypothesise that patch residency will be longer when it takes more effort to reach the next patch. However, beyond this hypothesis, one can also determine how the effort cost influences the hypothesised travel effort induced increase in residency time. First, perceived effort could be interpreted as simply longer travel times. That is, mathematically, the effort and delay incurred while travelling is represented as a unified travel cost. Alternatively, the effort could be conceptualised as a constant term value subtracted at the end of reward collection in each patch in order to represent the energetic cost of travel.

Here, I analysed data from a human computer-based patch-leaving experiment with travel costs. Participants performed a patch-leaving task in which they were asked to collect milk from a series of farms. These farms varied in the kinds of cows they contained: some cows produced more milk than others, and some cows' milk supply diminished more rapidly than others'. Collections of farms constituted environments, and the environments varied in terms of the distribution of different farm types, how long it took to travel between farms, and how much physical effort participants had to expend to travel between farms. Using this design I could examine human patch-leaving decisions and test how travel effort influenced human patch-leaving decisions when both patch and environmental properties varied.

In this chapter, we seek to confirm that human foragers follow the predictions of Optimal Foraging Theory, determine what effect, if any, variation in achievable effort costs has on leaving time, and establish whether effort is conceptualised in the units of time or reward. In service of these goals, we ran a computerised foraging task with varying levels of effort required to move between patches.

2.2 Methods

Participants

Thirty-eight healthy adult participants were recruited to take part in this study. After excluding the participants who did not correctly answer debrief questions about the rules of the task (2), fell asleep (1), could not complete the task (1) or were tested with faulty equipment (1), we were left with data from 33 subjects. Of these 33, 17 were female and the average age was 25 (range 18-37).

Experimental Setup

Participants engaged with a computer-based patch foraging task in which they sought to maximise the amount of milk they collected from cows on farms. In each farm, participants moved from field to field, hitting a button on a hand-held box to leave as the marginal rate of return from the cows in the current field decreased exponentially (see Table N for an explanation of how experimental features map onto foraging concepts).

Foraging concept	**Experimental operationalization**
Environment	A large farm consisting of multiple fields with fences between them
Patch	A field in which cows graze
Reward rate	The rate at which the agent can collect milk from a given field at any given timepoint
Travel time	The time it takes to walk between fields
Travel cost (not included in MVT)	How difficult it is to climb the fence between fields

Table 1. Description of task features in terms of foraging variables

Each participant visited 8 different farms for 7 minutes each in counterbalanced order, each with a different combination of travel time between patches, effort cost of traveling between patches, and environmental quality (see Figure 6 for an illustrated example of a farm environment).

Travel time: In half of the farms, participants had to spend 8 seconds traveling between patches (fast travel time), while in the other half they had to spend 12 seconds to reach the next field (slow travel time).

Effort cost: In half of the farms, participants had to exert a high degree of effort to travel between patches — described in the experiment as the effort required to climb the fence between fields — while in the other half they exerted minimal effort. This was measured with a hand-held dynamometer (SS25LA, BIOPAC Systems, held in dominant hand). Before starting the task, participants squeezed the dynamometer three times at maximum strength, and the highest of those three values was used to define the effort needed to travel between patches. In high-effort farms, participants had to squeeze the dynamometer at 60% of maximum force, while in the low-effort farms, they had to squeeze the dynamometer at 10% of maximum force.

Environmental quality: Each farm environment consisted of four different field types sampled with different frequencies. Fields were generated based on two variables, initial value (A_0) and reward decay rate (λ), and the amount of milk collected per unit time decreased exponentially as defined by Equation 4. This is consistent with real-world milk production rates in dairy cows, which decrease at an approximately exponential rate (Soder et al., 2006).

$$\text{Equation 4. } A(t) = A_0 e^{-\lambda t}$$

The four field/patch types had initial values of 40 and 60 mL of milk and reward decay rates of 0.10 (fast) and 0.075 (slow). In fields with higher initial values and slower decay rates, cows were healthier and could provide more milk. Decay rates were evenly distributed across all environments, but initial values were used to define environmental quality. In rich farms, 80% of fields had an initial value of 60 mL, while in poor farms 80% of fields had an initial value of 40 mL.

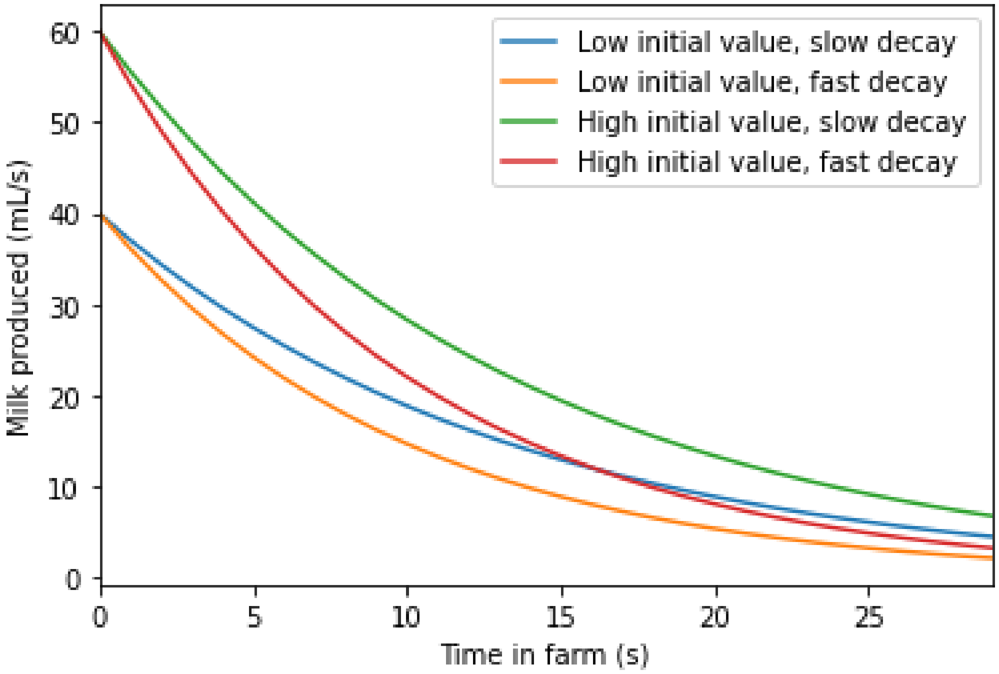


Figure 5. Experimental Design. During the experiment, participants visited four different types of field (patch), in which the properties varied. They varied in both the yield, or the initial rate of reward that would be obtained, and the decay rate (how rapidly the rate decayed). The graph shows the rate of reward (milk obtained – y-axis) that would be obtained over time (seconds – x-axis)

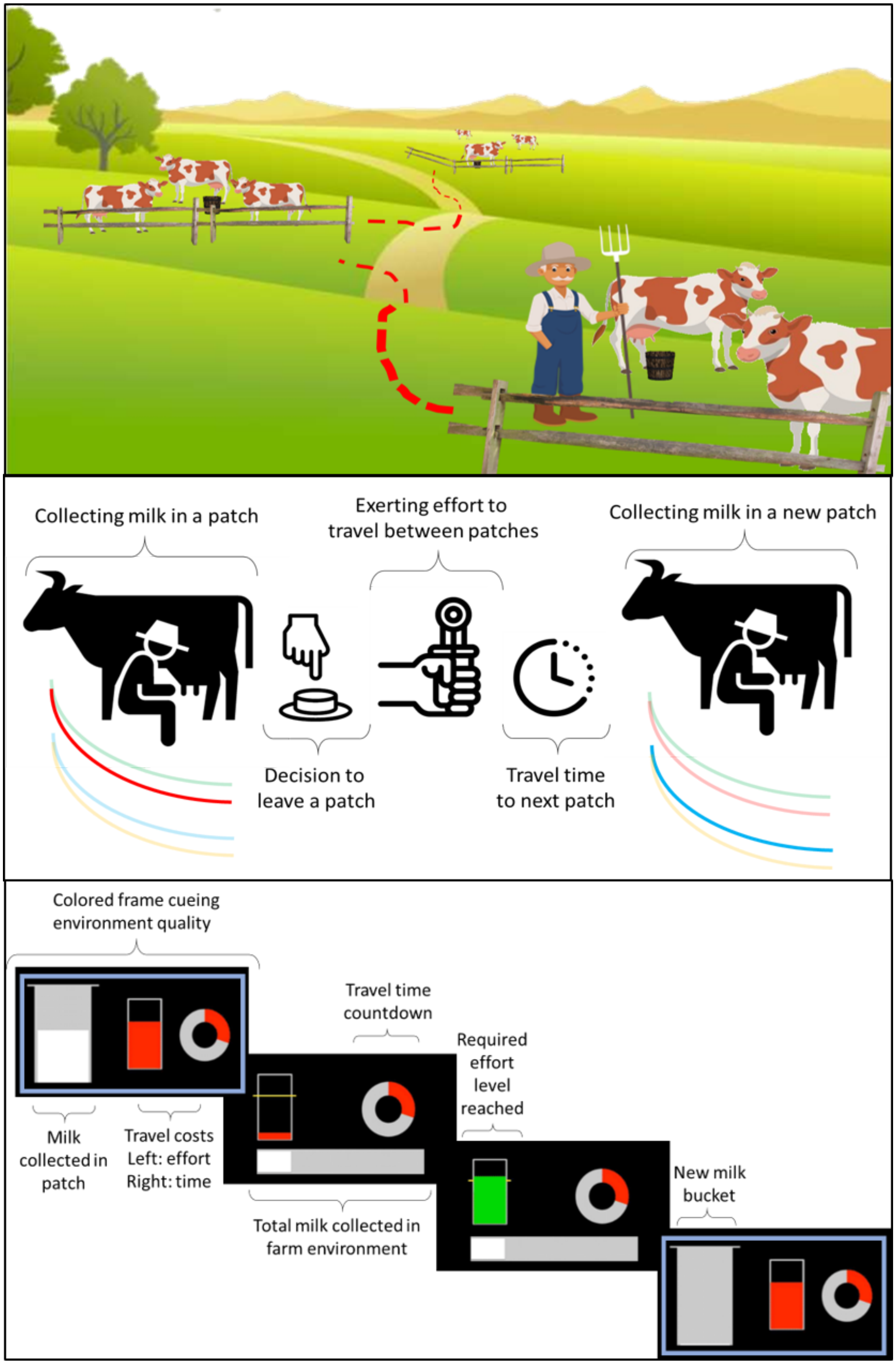


Figure 6. Schematic of the experimental design.

The top panel represents a real-world foraging task: a farmer is tasked with collecting milk from cows in different patches of grass. These patches of grass have different properties: some allow for more overall milk production, so the cows in those fields produce more millilitres of milk per second at the beginning of a milking session than those in lower-value patches. Patches of grass also differ in how quickly cows' milk supply decreases over time. In some patches, cows' milk production declines quickly over the course of a milking session, while others maintain a more steady supply. The farmer must use this information, in addition to his knowledge of the time and effort costs of moving between grass patches, to decide when to move from one patch to the next. The middle panel represents the computerised model of the real-world task for a single farm environment. In-lab participants collected milk from patches, pressed a button when they wished to move between patches, squeezed a dynamometer with a prescribed degree of effort, then waited for the inter-patch travel time to elapse before starting over collecting milk in a new patch. The bottom panel shows annotated screen captures of what a participant would see as they completed the task. While in a patch, participants see a graphical representation of their increasing milk reward and the travel and time costs associated with leaving that patch. They also see a colored border that cues the overall quality of the environment (i.e. whether the farm consisted of 80% or 20% high-initial-production-rate cows). When they decide to leave the patch, the participant sees a graphical representation of their current and required grip force and a countdown to the next patch. When the next patch is reached, the participant sees a new, empty milk bucket and the same time and effort costs.

Before entering the first farm, participants were given an explanation of the task and practised in an example farm. After the practice period, participants were tested on their comprehension of the task. Importantly, in neither the explanation of the task nor comprehension check were participants explicitly told that there was an optimal policy for making their leaving decisions.

Because the predictions of Marginal Value Theorem depend on an assumption of perfect knowledge, participants had constant visual cues on the screen reminding them of what environment type (predominantly high or low initial value), travel time (8 or 12 seconds), and travel cost (10% or 60% of maximum squeeze effort) they were engaging with. This was especially important considering that real-life examples of foragers successfully optimising their patch-leaving behaviour without perfect knowledge of an environment have depended on extensive prior experience in a naturalistic environment.

Participants were also provided information on the success of their effort exertion when moving between patches. As they squeezed the dynamometer, a rectangle on screen increased in height, then turned green when the required force was hit. If a particular attempt was unsuccessful, the message “sorry, fence not climbed, please try again” was displayed and the participant was cued to make a second attempt with a time penalty of 5 seconds. If the second attempt was unsuccessful, another 5-second time penalty was applied before the participant would be moved to the next field.

Analysis Plan

With this experiment, I sought to better understand (a) how well Optimal Foraging Theory frameworks predict human foragers’ leaving times in patch foraging tasks and (b) how increased travel effort costs affect those same leaving times. In order to test the first question, I calculated how much milk an optimal forager would collect from the experiment, then compared the participants’ performance to that standard. I also used a mixed linear effects model to test how each experimental variable (reward scale, reward decay rate, transit time, transit effort, and environment type) affected leaving times. In order to better understand how travel effort costs fit into the original formulation of Marginal Value Theorem, I considered two potential roles. First, foragers could be conceptualising travel effort as a value that subtracts from their accumulated reward at the end of each patch interaction. Alternately, foragers could combine different forms of travel, consider travelling effort as a form of additional travel time. In order to distinguish between these two possibilities, I fit separate additive constants to the accumulated rewards and travel times at different effort levels and tested which model best explained the delay in leaving times at higher effort levels.

2.3 Results

Human foragers' leaving times are well-predicted by Marginal Value Theorem

The first thing we sought to demonstrate with this study was that human foragers' patch leaving times are well-predicted by Marginal Value Theorem. The first piece of evidence towards this claim is how close participants came to optimal performance on the task. If the participants followed leaving times as predicted by MVT perfectly, they would have earned 9490 points in a rich environment with 8 second transit times, 8260 points in a rich environment with 12 second transit times, 7470 points in a poor environment with 8 second transit times, and 6473 points in a poor environment with 12 second transit times. For each patch visited, we divided the number of points actually collected by these optimal reward values to determine participants' performance in the task. On average, participants collected 86% of the possible reward (Figure 7), with slightly better performance on patches that required less effort to travel between (low effort: 87.3% of max reward w/ std. 6.0% vs. high effort: 84.8% of max reward w/ std. 6.7%; two-sided t-test: statistic=-3.338, $p<0.001$).

In addition, participants' performance on the task was not explained by simple decision-making heuristics. We first tested the possibility that participants could have been choosing leaving times at random from an individually-defined distribution. When within-individual leaving times were scrambled, performance declined to ~82.5% of maximum reward collected. Next we considered that participants could have relied on a single go-to leaving time across all conditions. As individual leaving times varied significantly across conditions of reward rate, environment type, travel effort cost, and transit time, this possibility was ruled out. In addition to simple leaving time heuristics, we also considered reward-based rules. However, both the instantaneous value of reward (e.g. 20 units of milk per second) and total accumulated reward (e.g. 7000 units of milk collected) at the time individuals left patches varied across conditions.

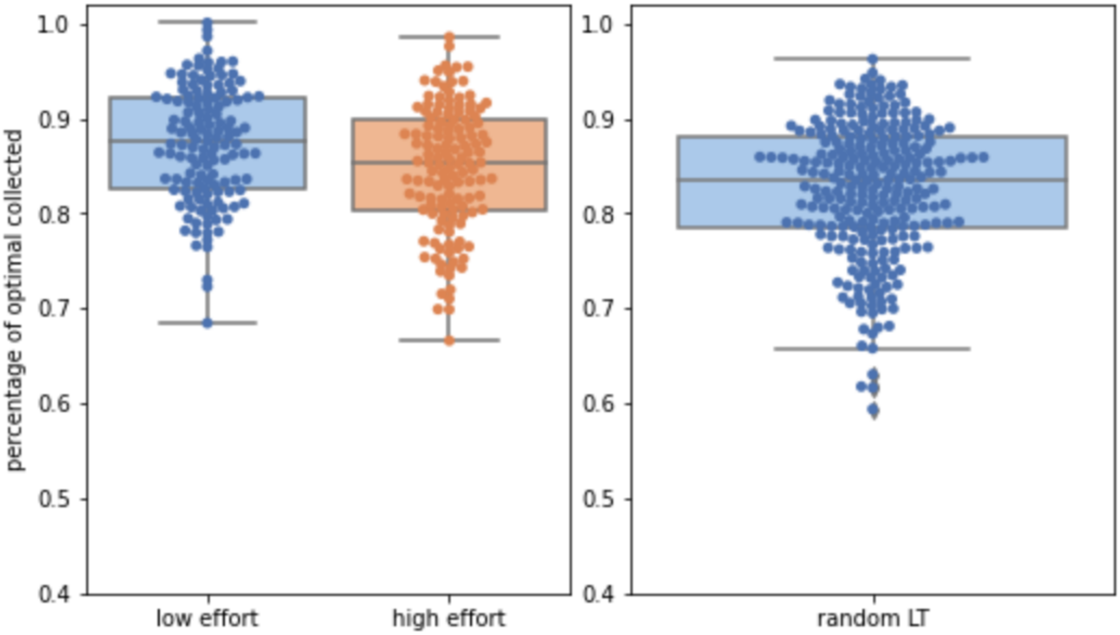


Figure 7. Percentage of potential reward collected by participants in high and low effort conditions vs when leaving times were randomised

In addition to ruling out heuristics, we also wanted to demonstrate that the fundamental variables of MVT — reward rate, transit time, effort, and environment type — all affected participants' leaving times as this is central to our claim that human decision-making in patch-foraging tasks can be better understood with foraging principles. Consistent with previous patch-foraging studies, foreground reward scale and trajectory — the most salient features — were the largest factor in determining patch-leaving time ($p < 2.2e-16$). Transit time and effort also had large effects on leaving times, with extra time and effort combining to keep foragers in individual patches for longer periods of time ($p < 8.69e-16$ and $p< 1.43e-13$ respectively). Finally, block type (or, environment type) has a significant effect on leaving time. As predicted by Marginal Value Theorem, participants stayed longer in individual patches when the overall environmental quality was poorer ($p < 1.83e-11$; for full analysis of variance of main variables and interactions, see Figure 9).

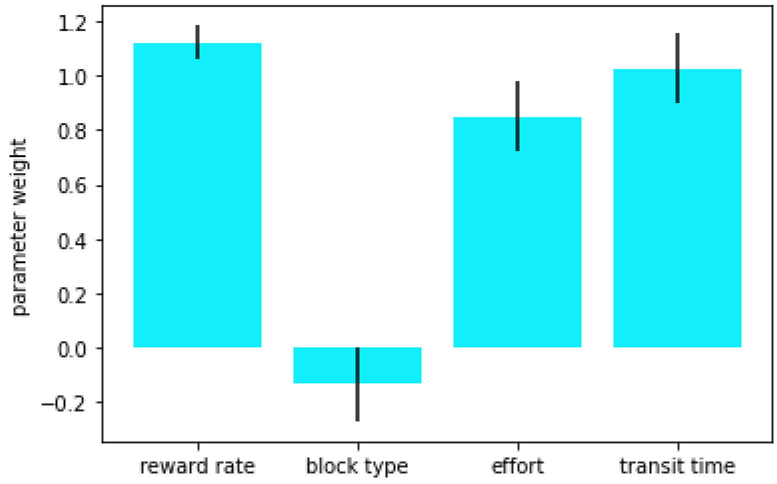
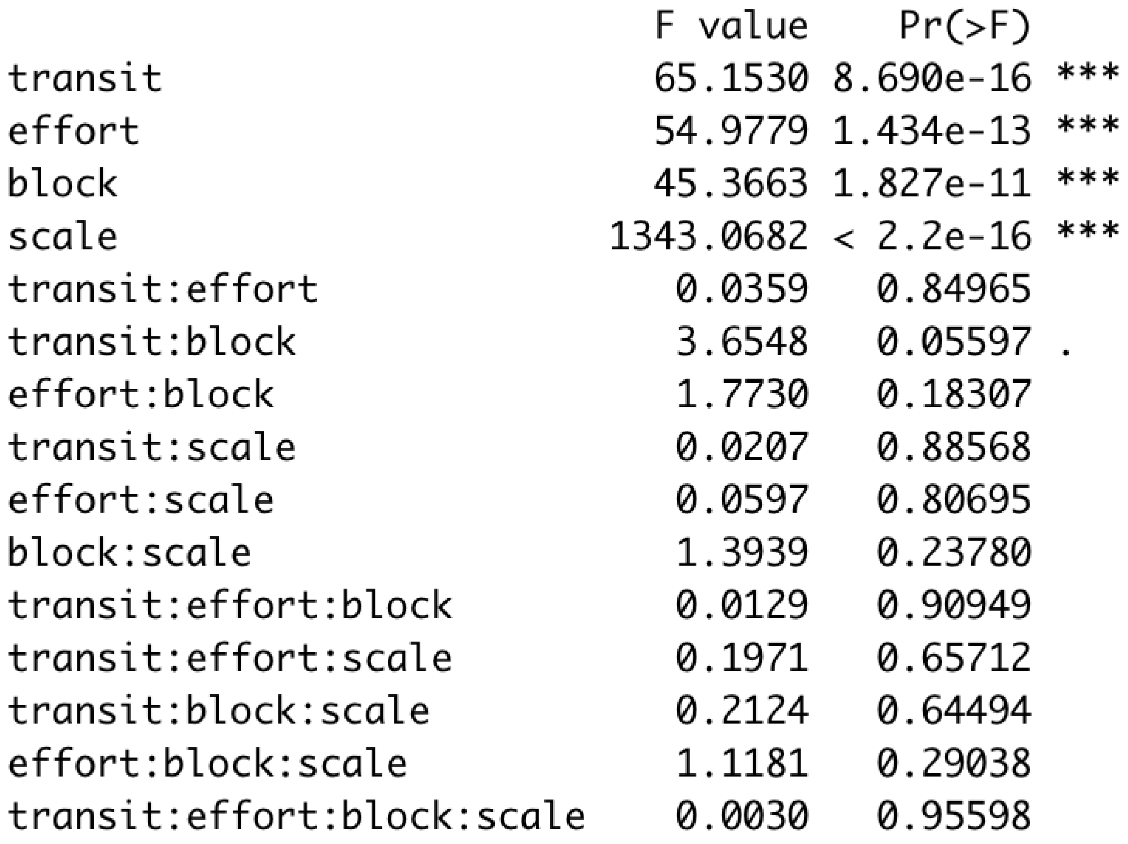


Figure 8. Fixed ANOVA parameter weights demonstrating the effect sizes of the four main experimental variables on leaving times. Higher reward rate, effort, and transit time all induced longer staying times, whereas richer environments induced shorter leaving times. Parameter weights taken from an ANOVA of the four features on leaving time.



```
                             F value    Pr(>F)    
transit                      65.1530 8.690e-16 ***
effort                       54.9779 1.434e-13 ***
block                        45.3663 1.827e-11 ***
scale                      1343.0682 < 2.2e-16 ***
transit:effort                0.0359   0.84965    
transit:block                 3.6548   0.05597 .  
effort:block                  1.7730   0.18307    
transit:scale                 0.0207   0.88568    
effort:scale                  0.0597   0.80695    
block:scale                   1.3939   0.23780    
transit:effort:block          0.0129   0.90949    
transit:effort:scale          0.1971   0.65712    
transit:block:scale           0.2124   0.64494    
effort:block:scale            1.1181   0.29038    
transit:effort:block:scale    0.0030   0.95598    
```

Figure 9. Type III Analysis of Variance Table with Satterthwaite's method Applied to a linear model of shape: leavingTime ~ transit*effort*block*scale + (1|participant) demonstrating

significant main effects and no interaction effects, as predicted by Marginal Value Theorem.

Travel effort costs delay leaving times similarly to additional reward cost

In line with my hypothesis, people stayed longer in patches if it was more effort to move onto the next patch. But how do travel costs influence people's leaving times? As additional travel effort, or as a subtracted reward value? On a first approach, these two conceptualizations of travel effort are mathematically inseparable, as each hypothetical constant added to travel time or subtracted from patch reward can be represented in terms of the other (Equation 3).

$$\frac{R - X_R}{T} = reward\ collected = \frac{R}{T + X_T} \tag{3}$$

$$TX_R = RX_T$$

Equation 3. Relationship between reward-based and time-based constants with which to describe travel cost Where R is the total reward collected in a a patch, T is the total time dedicated to a patch (foraging time + travel time), X_R is a hypothetical constant amount of reward subtracted from each patch to represent travel effort, and X_T is a hypothetical constant amount of time added to travel time to represent travel effort.

Indeed, if human foragers were perfectly optimal in their patch-leaving behaviour, these two formulations would be impossible to distinguish. However, if we assume that human foragers select either X_R or X_T values approximately normally distributed around a single value, depending on which one is the most immediate mental representation of travel cost, we can determine which of these is the most likely representation (Figure 10).

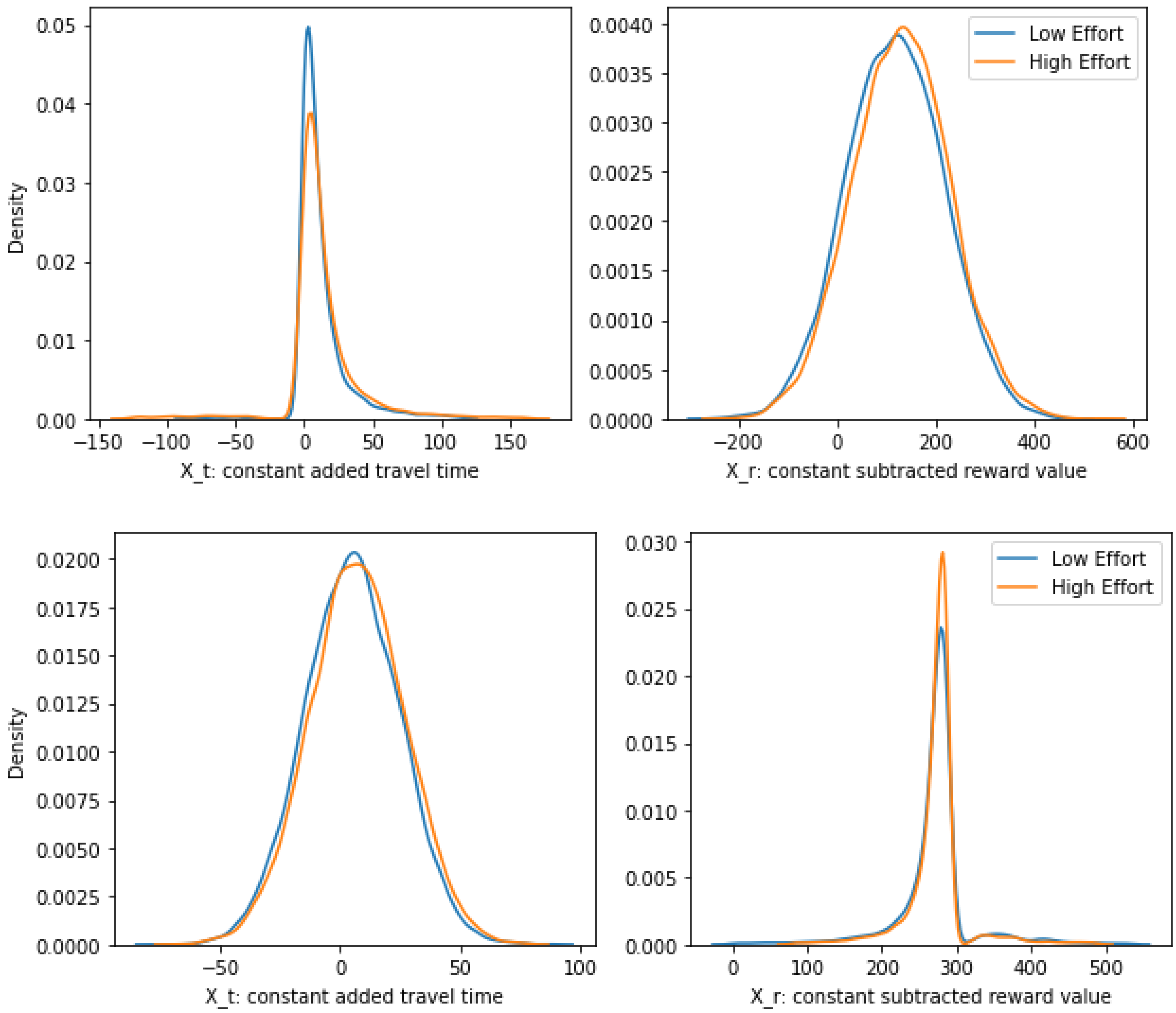


Figure 10. Theoretical distributions of X_T and X_R These values represent theoretical distributions of X_T (added time cost) and X_R (subtracted reward constant) under the condition that human foragers conceptualize travel cost in terms of a constant reward value subtracted at the end of each patch (top) or as a constant time added to the travel cost (bottom).

After modeling participant results from the two effort conditions under these different assumptions, we extracted a series of time and reward constants and compared their distributions to Gaussians. In addition to being more visually similar to the distribution of X_R values predicted by the model travel-effort-as-reward, the empirical X_R values fail to reject a null hypothesis of normality under the Shapiro-Wilk test ($p < 0.075$), while the empirical X_T values allow for a significant rejection of the null hypothesis of normality (p < 1.05e-5).

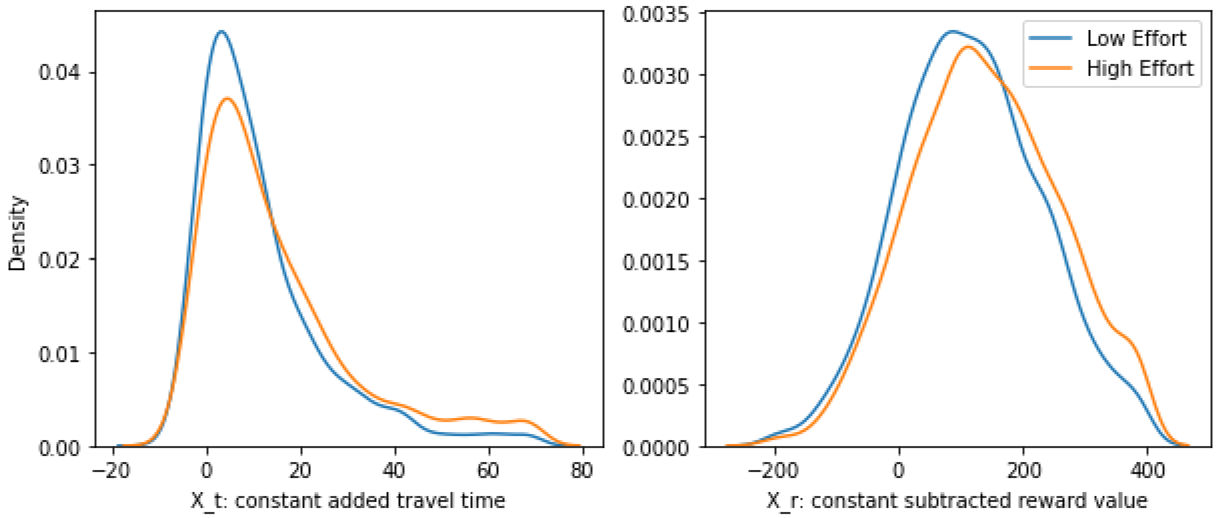


Fig 11. Distribution of travel time and reward value constants added to or subtracted from original MVT values in order to predict differences in leaving time under different effort conditions

These data suggest that human foragers in this experiment were conceptualizing travel effort in the units of accumulated reward and subtracting a constant value from the sum of each patch reward.

2.4 Discussion

In this chapter, I used animal models of patch-foraging to better understand human decision-making in the economic realm. Participants completed a computer-based patch-leaving task, framed as a farming game, where they had to decide when to leave patches in different environments. Participants moved between farms with two reward rates in the context of two kinds of larger environments of different quality. The time and effort it took to travel between farms was also varied binarily, creating 8 counterbalanced conditions. My results showed that people can make foraging decisions that allow them to collect a large proportion of reward and that they were sensitive to foreground reward rate, travel delay, travel effort and average environment reward rate. These results suggest that MVT is an appropriate framework for interpreting patch-foraging behaviour for contemporary human decision-makers and that participants adjusted their leaving decisions based on patch reward rates and environmental quality. In addition, these results support the notion that people stay longer in patches when there is a higher effort to travel. Overall my results suggest that this is because humans conceptualise additional travel effort as a constant energetic cost that is subtracted from the reward being accumulated in each patch.

Notably, this work goes significantly beyond research examining effort-based decision-making. The vast majority of effort-based decision-making studies use paradigms in which decisions are made between a less effortful, less rewarding option, and an option that is higher in effort, but offers more reward. People typically discount rewards by effort in such experiments, regardless of whether the effort is grip force, switches of attention, levels of difficulty of an n-back task or mathematical operations (Vassena et al., 2014; Apps et al., 2015; Westbrook & Braver, 2015; Chong et al., 2017). This work supports the notion that effort influences human decision-making behaviour. However, the decision being made was very different. People were deciding to stay or leave patches, to maximise rewards. People stayed longer in patches when travelling was more effort. Although effort typically is treated as a cost, it was unclear whether this would have been the case here. However, I show, consistent with effort-based decision-making work, that effort influences patch-leaving behaviour.

Notably, this work extends existing studies of patch-leaving decisions in humans. Firstly, the results replicate previous findings that patch-yield and the rate of decay of a patch can influence people's decisions (Le Heron et al., 2020). We showed that people stayed longer when the patch yield was higher, as would be predicted by MVT. Such results support the idea that people can understand and solve the patch-leaving problem and detect changes in decaying reward rates and adapt to them. Such results support the decades of research showing that humans are very adept at making economic decisions

Secondly, the results showed that changing the properties of the environment, in terms of the average rate of reward from patches, also influenced people's choices. This replicates the findings of Le Heron et al., (2020), who showed that people stay longer in poor environments, as would be predicted by MVT. Such findings support the notion that people consider opportunity-costs when making decisions. That is, extensive research has shown that people consider efforts and rewards in a relative manner. We compare the value of a reward to the alternative reward we could obtain – opportunity costs. However, the MVT framework nicely frames this in a way for how people might allocate time to different activities and quantifies the opportunity-cost effects, rather than simply a direct comparison between them (Otto and Daw, 2019; Guitart-Masip et al., 2011; Nishiyama 2014; Beierholm et al., 2013). Specifically MVT quantifies the opportunity-cost in terms of the average rate of reward in an environment as reward rates continuously change. In doing so they make decision-making research take a step towards ecological validity with people considering how much time to spend in one activity versus others within an environment, rather than choosing only between two options.

Thirdly, while previous studies have examined patch-leaving decisions in humans, they have not examined travel effort (Pacheco-Cobos et al., 2019; Venkataraman et al., 2017; O’Connell and Hawkes, 1984; Zhang et al., 2015; Bettinger and Grote, 2016). Here, we show that travel effort influences human patch-leaving decisions, when greater force was required people stayed longer in patches. Notably this treatment of effort caused sub-optimal foraging behaviour, and reduced the overall reward collected by a participant. As such, even though the MVT framework may be fruitful it needs to be adapted. These results therefore suggest an extension to the classical formulation of MVT by Charnov. As such,

$$E_n = \frac{\left(\sum_{i=0}^{n} P_i g_i(T_i)\right) - X_R}{t + \sum_{i=0}^{n} P_i T_i} .$$

In addition, our findings both replicate and complicate findings in rodent studies that indicate that travel effort modulates foragers’ adherence to the predictions of Optimal Foraging Theory. While rats foraging for food generally conducted their searches more optimally when in environments with greater travel costs, our human participants adhered most closely to optimality when in low travel effort environments (Mellgren et al., 1984). The difference in direction of effects between these two studies are not surprising — the relationship between task difficulty and performance has long been articulated as a U-shaped curve (Yerkes and Dodson, 1908). These results do, however, indicate an important role for effort costs in understanding human foraging behaviour, and set the stage for future work further exploring the travel-effort continuum.

In conclusion, humans make patch-leaving decisions that are broadly in line with the principles of marginal value theorem. However, effort makes people behave less optimally. They stay longer in patches when it will be effortful to travel, the result is a reduction in how much reward people obtain, with an extension of MVT being the treatment of effort as a continuous cost subtracted from the value of every patch in an environment. Such results may explain why humans find multiple ways to minimise the effort costs of travelling to obtain rewards.

Chapter 3. Foraging for fair social partners

3.1 Introduction

This chapter centers on extending the use of foraging frameworks to explain human behaviour in the social domain. These foraging frameworks — MVT specifically — seek to explain and predict when agents leave particular patches based on patch and environmental constraints. While leaving-time may seem like an odd measurement in terms of social interaction — what about conversation dynamics or body language? — studying leaving time behaviour can help us connect social processes to evolutionarily-older integrate-to-fire mechanisms. Recent work on leaving decisions in dyadic conversations demonstrating that only 2% of conversations between social partners end at a mutually agreeable time (despite the fact that 17% of partners reported the same desired leaving times) has sparked larger interest in the social psychology community about exit decisions (Mastroianni et al., 2021). However much of the previous work has focused on describing phenomena rather than understanding mechanisms. Using optimal foraging theory, we seek to establish opportunity cost as a driving mechanism for making social exit decisions.

In order to further motivate leaving-time as a useful measured outcome in social decision-making, let’s return to the Exit, Voice, and Loyalty framework laid out in the introductory chapter. Exit is one of the two presented responses to declining social value, and the option most readily accessible in the context of casual (i.e. low-loyalty) dyadic interactions, like conversations at cocktail parties. In individual relationships, exit and voice are often both viable responses to diminishing values, and they interact with each other in distinct ways. First, the availability of exit as an option can make voice more effective. In the context of voluntary associations like friendships, romantic partnerships, and -- to a lesser degree -- employment, each party’s ability to end the relationship grants negotiating power. Exit, or lack thereof, can also become its own form of voice. In response to diminishing quality of goods and/or treatment from a large-scale organization, exit-as-voice can be operationalized as collective action like strikes and boycotts.

The existing literature on exit decisions in social psychology centers largely on individuals' decisions to reject profitable, but unfair, offers from a social partner. In the majority of these experiments, however, exit actually functions as a form of voice -- rejecting an offer sends a message to the offerer and observers that the participant values fairness more than monetary reward. In this chapter, I sought to isolate exit decisions from their communicative role, which required creating a social interaction in which participants' choices were neither visible nor impactful to their social partners. In this type of scenario, participants' choices change from exit and voice to exit and silence. This way, we can study parallels between social and non-social exit decisions without interference from communicative intent.

Much like food resources in a natural patch, the percentage of reward that healthy adult human participants shared with their partners decreased steadily over time (Brosig-Koch et al., 2017). This parallel allows for a realistic modification of traditional patch-foraging tasks to operationalize fairness (or evenness of split) as the value foragers could optimize for. Under the *homo oeconomicus* model of purely rational economic decision-making, foragers should focus strictly on economic reward. If participants attend to and make decisions based on fairness, however, we should be able to predict people's leaving times from social scenarios based on the qualities of different partners and environments.

3.2 Methods

Participants

We ran two studies to assess whether healthy adult participants would engage with partner fairness under the frameworks of Optimal Foraging Theory. In the first — the numerical version — we collected data from 25 participants. In the second — the visual block version — we planned to recruit 35 participants, but only collected data from 15 participants before in-person testing paused due to the ongoing coronavirus pandemic. Participants were Oxford students and staff with no formal background in psychology.

Experimental Setup

The two versions of the fairness studies were functionally identical, aside from how stimuli were displayed. In the numerical version, reward values were displayed as numbers on the screen (e.g. 400 credits offered of 2000 credit pot), while in the visual block version, reward values were displayed in the form of a subdivided rectangle.

Overview: For each participant, the experiment proceeded as follows. After answering demographic questions, they watched a standardized training video explaining their objectives, how to control the environment, and the meanings of visual cues in the experiment. After watching this video, they answer multiple choice questions to test their understanding of the task. If any question was answered incorrectly, the participant was prompted to answer again. Participants were then allowed to ask the experimenter present any remaining questions they had about the task structure. After this, the participants practiced exploring fair and unfair environments (explained in more detail below) for two minutes each. After the experimenter confirmed that the participants fully understood the task, the participants completed the main task (foraging in 10 different fairness environments) with a self-timed break halfway through. After completing the task, the participants answered debrief questions and were compensated for their time with a standard £3 bonus. While participants were told that this bonus was based on their performance on the task, it was actually the same for all participants.

Technical details: All experiments were conducted using PsychoPy version 3.1.0 on a laptop running Windows 10.

Task structure: Within the body of the experiment, participants engaged with 10 environment blocks for 5 minutes each. Within each environment block, participants interacted with up to 30 different social partners.

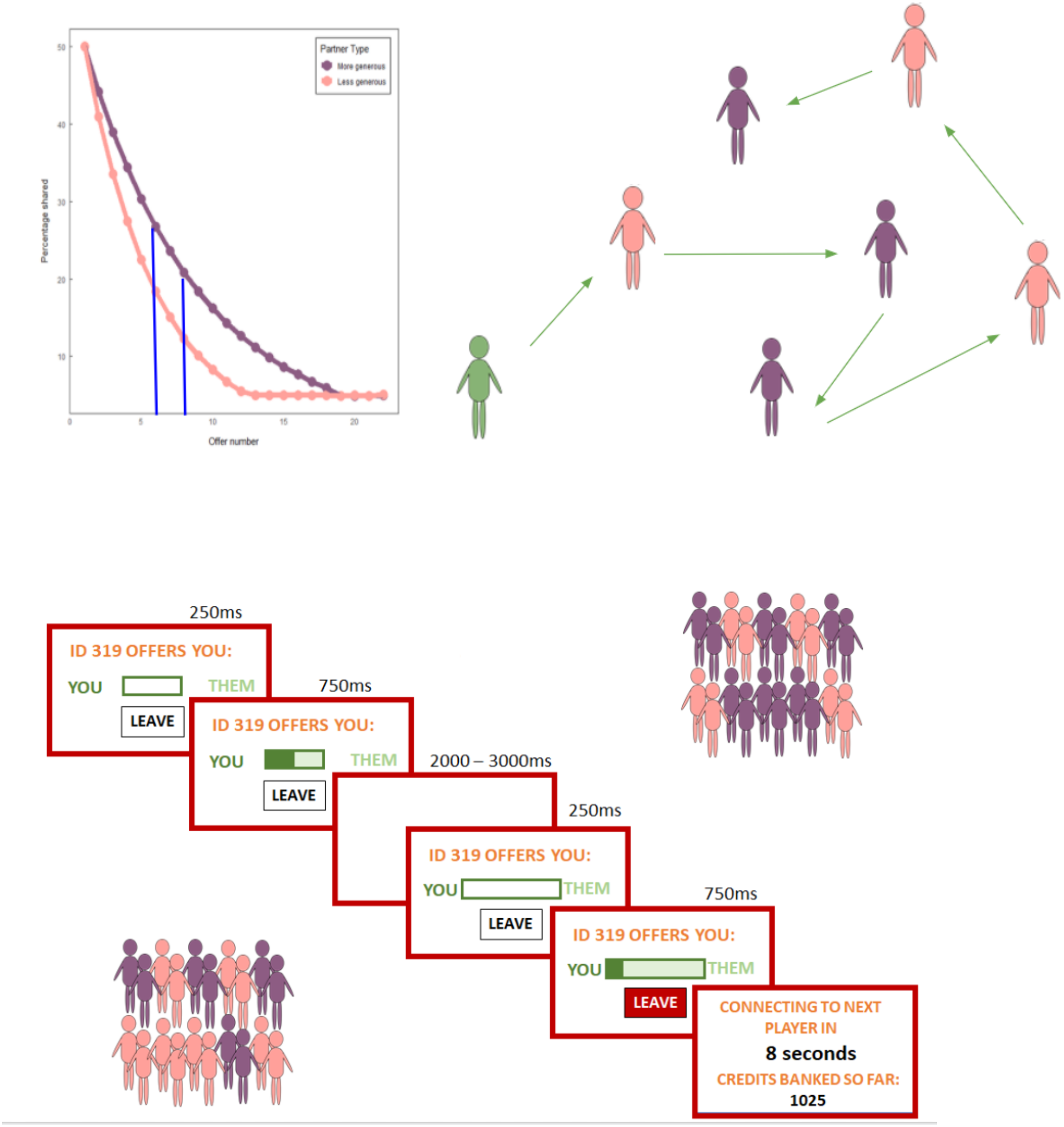


Fig 12. Experimental setup for visual block study Top left: differing decay trajectories of fairness for more and less generous partners; Top right: schematic of a participant visiting multiple different social partners in an environment; Bottom: example display for a single partner interaction, flanked by illustrations of an unfair and fair environment.

Interaction with an individual social partner: Each interaction with a social partner centers on fair division of a pot of monetary credits. Over the course of an interaction, the social partner is given a new pot of money approximately once every 2 seconds. They start out by offering between 47% and 53% of this pot to the participant, decreasing the proportion with each offer. A small amount of Gaussian noise (mean of 0% and std of 0.015%) is added to each fairness value in an individual partner's trajectory. Importantly, the size of the overall pot increases over time so that the absolute value of shared reward does not change (except for the small amount of noise). When the participant no longer wishes to receive money from a given social partner, they press the spacebar to leave for another partner. Participants are aware that there are two types of social partners: fair and unfair, defined by how quickly the proportion of credits shared decreases over time. Fair partners have exponential decay rates uniformly distributed between -0.115 and -0.075, while unfair partners have exponential decay rates uniformly distributed between -0.175 and -0.135. When a participant decides that they no longer wish to collect reward from a particular social partner, they press the spacebar to disconnect and reconnect with another social partner from the same environment. The disconnect/reconnect time totals 8 seconds per switch.

Interactions within an environment block: There are two types of environment blocks, fair and unfair. Participants are aware of which environment type they are in from the first encounter, cued by the color of the rectangle surrounding the interaction window. Each environment contains 40 social partners that a participant can interact with. In a fair environment, 3 out of every 4 consecutive social partners a participant encounters are fair, while in an unfair environment the ratio is inverted.

Analysis Plan

With this experiment, I sought to test whether social partner choice could be explained within optimal foraging frameworks. Specifically, I tested how well Marginal Value Theorem could predict participants' leaving times from fair and unfair social partners in fair and unfair social environments. In order to do this, I fit a linear mixed model to the leaving time data to see how environment type and partner type affected leaving times. Critically, if participants were optimizing purely on economic value, neither of these variables should be predictive of leaving times.

Based on the distribution of leaving times from the experiments of the last chapter, we were concerned about how to interpret possible overstaying. In the context of this experiment, overstaying could be interpreted in multiple different ways. First, it could represent the degree to which participants discounted fairness-based processing in order to optimize for financial reward. Because financial reward did not decay with fairness, any overstaying (as predicted by applying MVT to fairness values) would result in increased cumulative financial reward. On the other hand, overstaying can also be a rational strategy for agents aware of their own behavioural variability. In a study of three macaques in a patch-foraging task, agents deviated significantly from optimal foraging behaviour. Specifically, they overstayed in most patches. In previous literature, overstaying behaviour has been described as a failure in agents' judgment accuracy: their estimates of correct leaving thresholds are biased towards longer stays. However, this same overstaying behaviour could also be described in terms of precision errors — these macaques could have highly accurate threshold estimates but apply them variably. When the participants' variability in leaving time was included in models of the experimental structure, predicted optimal leaving times shifted later in each patch (Cash-Padget and Hayden, 2020). With this in mind, human participants could have highly accurate fairness thresholds while also accounting for variability in their applications — inducing leaving times without involving monetary reward. In order to determine whether this was the case, I simulated noisy agent behaviour in the experimental task and re-evaluated optimal leaving times for different noise levels.

3.3 Results

Environment and partner fairness affect participant leaving times as predicted by MVT

As would be predicted under Marginal Value Theorem if participants attend to fairness as a value to maximise, participants stayed significantly longer with fair partners than unfair partners and longer in unfair environments than fair environments. In the numerical version of the task, there was a strong effect of both partner type (fair or unfair) on leaving time ($p < 0.00075$) and environment ($p < 0.00087$) on participants' leaving times. There were no interaction effects between the two variables. In the visual block version, both partner type ($p < 2.84e-12$) and environment quality ($p < 1.22e-5$) were strong predictors of leaving time. The stronger environment effects in the visual block version of the study could have been due to be for any number of reasons, including that the visual presentation of offers as rectangle proportions rather than numerical fractions might have made estimating the value of an environment easier. When the data were combined across block and numerical conditions, partner ($p < 2.28e-12$) and environment quality ($p < 1.22e-5$) were still both significantly predictive of leaving times, and did not demonstrate interaction effects, as predicted by MVT (Fig 13; Fig 14; Fig 15).

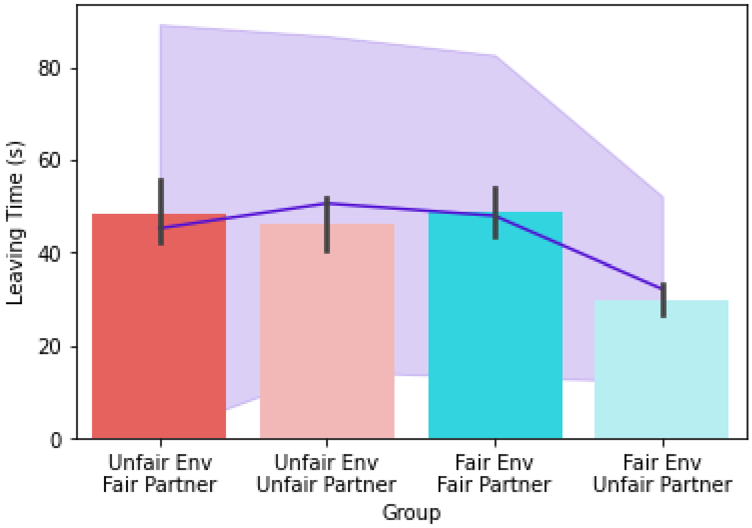


Fig 13. Linear mixed model predictions for participant leaving times in individual patches separated be environment and partner quality in the numerical version of the experiment

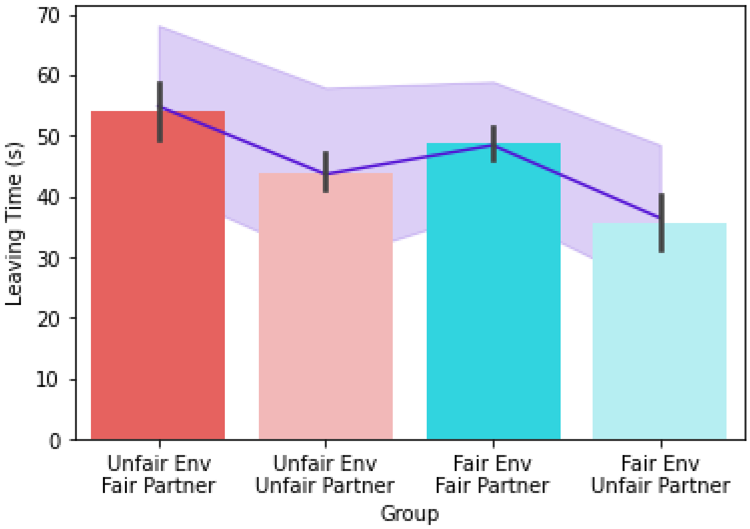
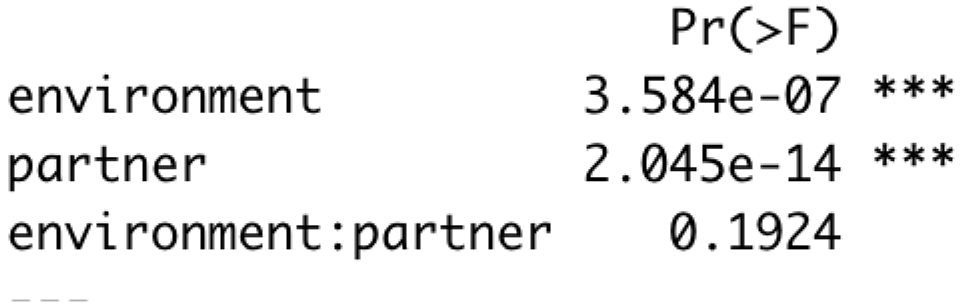


Fig 14. Linear mixed model predictions for participant leaving times in individual patches separated by environment and partner quality in the visual block version of the experiment



```
                         Pr(>F)    
environment            3.584e-07 ***
partner                2.045e-14 ***
environment:partner       0.1924    
---
```

Figure 15. Type III Analysis of Variance Table with Satterthwaite's method to show main effects of environment quality and partner quality when the results of the numerical and visual block design were combined for a total n of 40 participants. The linear model was defined as linear model defined as: leavingTime ~ environment*partner + (1|participant), and the analysis showed no significant interaction effects.

Behavioral variability can explain much of participants' collective overstaying behaviour

Before running the simulation analysis, we checked whether overstaying was associated with variance in leaving time. For the 15 participants in the visual block-based study, there was a strong linear relationship between the standard deviation of one's leaving times across the experiment, and the average amount of time one spent overstaying in individual patches (R2 value: 0.868). We then simulated the performance of 3 artificial agents with different levels of behavioural variability on the experimental task. As the standard deviation of noise added to leaving-time decisions increased, so too did the amount of overstaying that predicted maximal reward collection. A fourth artificial agent was instantiated with a noise level equivalent to the average variability in the visual block study participants — standard deviation of 24.1 seconds — which performed optimally with an overstaying time of 15.5 seconds, compared to the participants' actual average overstaying time of 14.1 seconds. While these variability-matched artificial agents did not successfully predict individual overstaying patterns, they can provide insight into overstaying as a mechanism for optimizing reward intake under the constraints of group-level behavioural variation.

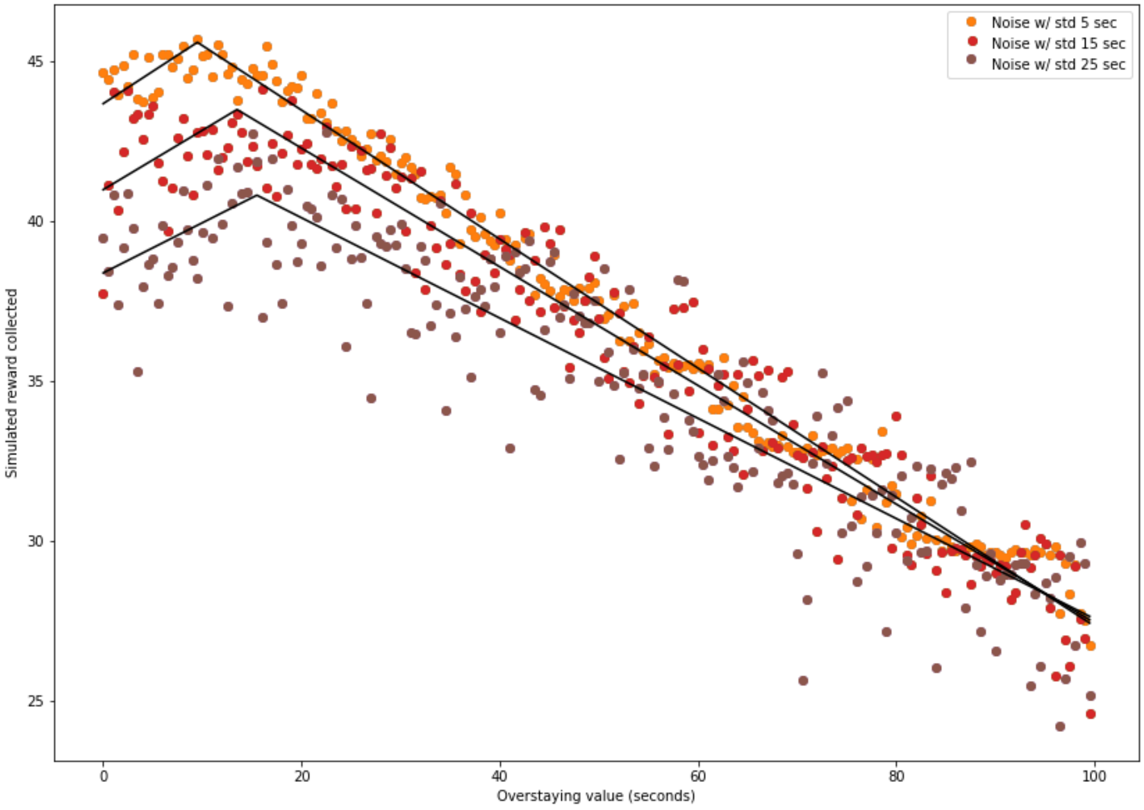


Fig 16. Simulated reward values for three artificial agents affected by increasing degrees of behavioural variability, and their associated absolute value function fits with peaks at optimal overstaying values. Note that the peaks of these three noise functions occur at monotonically increasing overstaying values -- the higher the degree of noise, the longer an agent should

overstay to maximise reward in the social reward patch-leaving task.

3.4 Discussion

The experiments in this chapter demonstrate that we can use frameworks for understanding evolutionarily-old behaviours like food foraging. This provides useful openings for future research on the mechanisms of disengagement from the social world in both pure research and clinical applications. For example, these foraging frameworks could be used to better understand why and how older adults disengage from certain elements of social life after the death of a spouse (Utz et al., 2002). This work also contributes to a large body of research demonstrating that humans often attend to and make decisions based on perceived fairness, even when those decisions are economically suboptimal.

In future work, we could study how different operationalizations of fairness affect adherence to the predictions of optimal foraging theory with regard to leaving dyadic money-splitting interactions. Relating MVT adherence to individual differences in just-world beliefs and conceptions of how wealth redistribution should work (motivated by Alesina and Angeletos, 2005), varying the social acceptability of the source of the monetary pot, introducing the possible of charitable donations, allowing for longer-term relationships and reputation-development, introducing third-party punishment, removing the option of sending nothing, and many other traditional modifications on ultimatum/dictator type games could all provide interesting avenues for understanding how social forces interact with low-level mechanisms of decision-making.

Chapter 4. Conclusions

In this thesis, I have discussed foraging frameworks in terms of both mathematical underpinnings and broader conceptual promiscuity, developed a more robust understanding of the cost of travelling between patches for human food foragers, and extended foraging frameworks to the social domain to explain elements of social partner choice. In this conclusion, I will briefly recapitulate the key theoretical underpinnings of this work, summarise my experimental findings, highlight their overarching implications for our understanding of social behaviour, and suggest avenues for future follow-up work.

Theoretical underpinnings

Optimal Foraging Theory (OFT) provides the basis for my two thesis experiments. Under OFT, animals attempt to collect food as efficiently as possible within a patchy environment. A patchy environment is one that consists of disconnected regions in which food can be collected at a continuously decreasing rate until an animal decides to travel to another region. Within a patchy environment, it is possible to model the optimal time at which an animal should leave each patch and move to the next. More specifically, an animal should leave a patch when the rate of reward collection dips below the average reward collection rate for the environment as a whole -- taking the time it takes to travel between patches into consideration. This formulation leads us to some intuitive predictions about how animals should take opportunity costs into account in their patch-leaving behaviour: the faster the reward collection rate decreases, the faster an animal should leave a patch; and the longer it takes to travel between patches, the longer an animal should stay in a given patch.

However, OFT would not be useful if it did not accurately predict animals' patch-leaving behaviour in real-world foraging. This depends on two key features: that animals' foraging environments are actually patchy, and that leaving times follow MVT predictions. Not only does the first hold true observationally -- meerkats, flamingos, gerbils, and many other animals forage in patchy environments (Thornton and Hodge, 2008; Arengo and Baldassarre, 2002; Shuai et al., 2016) -- but patchy environments actually better support evolutionary fitness than uniform environments (Roff, 1973; Fahrig and Paloheimo, 1988; Shaw et al., 2021; Zollner and Lima, 1999). Within these patchy environments, animals do exhibit MVT-adherent patch-leaving behaviour. Foragers stay longer at each patch when travel times are high (Elliffe et al., 1999; Doniol-Valcroae et al., 2011) and when the overall environmental quality is poor (Roberts 2013; Sheng et al 2014; Thiel & Hoffmeister 2004; Marshall 2013). In cases where animals do not adhere to MVT predictions -- specifically the case of chronic overstaying -- these deviations are still well-explained under an opportunity cost account (Cash-Padgett and Hayden, 2020; Harhen and Bornstein, 2023).

In addition to explaining non-human animals' foraging behaviour, OFT can also be applied to human reward foraging. The most obviously patchy environments can be found by studying contemporary hunter-gatherer societies. Across continents and timescales, contemporary gatherers leave patches according to MVT predictions (Pacheco-Cobos et al., 2019; Venkataraman et al., 2017; O'Connell and Hawkes, 1984). However, patch foraging is not limited to pre-industrial food gathering. In fact, OFT can be used to better understand modern problems like deciding when to abandon habitats threatened by climate change (Stoltz et al., 2021) or deciding if a car is worth stealing (Brantingham, 2013). While these phenomena have not been experimentally cast as foraging decisions, we can also use MVT to better understand job hunting, grocery shopping, and housing searches. This symmetry between animal and human reward-foraging behaviours allows us to use foraging as a framework for understanding our reward-optimization process of interest: social partner choice.

Experimental findings

In this thesis, I focused on two key aspects of understanding human reward foraging: the effects of effort costs in reward-foraging, and whether partner fairness can be operationalized as patch-reward during social partner choice.

Previous research on the behavioural effects of effort on human decision-making has been largely focused on two-alternative forced choice tasks, in which participants choose between high-effort high-reward and low-effort low-reward conditions

(CITATION). This line of experimentation has been used to establish that humans are sensitive to effort in reward-seeking decision-making. However, these experiments are structured quite differently from much of naturalistic reward seeking. In foraging, we make decisions about *when* to exert effort, rather than *whether* to exert effort. Thus, our patch-foraging task that modulated travel effort represented an important deviation from existing literature: participants in our patch-foraging task had control over the frequency, rather than degree, of their exertion, which could change one's sensitivity to effort. In addition to exhibiting sensitivity to typical MVT variables -- patch quality, environmental quality, travel time -- participants faced with higher degrees of travel effort did, indeed, stay longer in individual patches. This suggests the need for an updated approach to Marginal Value Theorem that takes a broader view of opportunity cost. If we acknowledge that foragers are weighing their decisions against their opportunity costs, MVT naturally expands to include the effects of travel effort, extraction effort, predation, starvation, and a host of other factors that -- while not included in classical Charnovian foraging accounts -- influence foraging behaviour. Further, different aspects of opportunity costs can be represented in different ways. Additional travel effort can be conceptualised as a value added to travel time, or a value subtracted from patch reward. While the two are mathematically identical under perfectly optimal foraging, individual variations in optimality result in two distinct distributions of effort values under these two accounts, suggesting that additional travel effort is conceptualised as a value subtracted from patch reward.

In my second experiment, I tested whether Marginal Value Theorem could be used to predict patch-leaving behaviour with a more abstract operationalization of reward -- specifically social partner fairness. Participants were told that they would be paired with another online participant who had previously chosen how much of a reward pool to share. In reality, these trajectories were defined such that participants received approximately the same magnitude of reward at each time point but that the fairness of the split decreased exponentially. This experimental design provided a key dissociation: if participants made decisions that optimised for financial reward, they would never leave any social partner because any time spent in transit would interrupt a constant flow of reward; however, if they made decisions that optimised for fairness, they would leave when fairness dipped below the environmental average. While *any* patch-leaving decisions would indicate a sensitivity to fairness, participants further demonstrated sensitivity to key MVT variables for partner fairness: patch fairness decay rate and environmental fairness. This finding has important implications for our understanding of both reward foraging and fairness as a concept. First, it demonstrates that optimal foraging is an appropriate framework for studying abstract social concepts like fairness. While fairness was our variable of choice in this experiment, further experiments could explore further isomorphisms between food foraging and other social rewards like belongingness, control, trust, affiliation, disclosure, or praise.

Second, these findings support the notion that fairness is a salient element of social decision-making under more naturalistic conditions than those induced by two-alternative forced choice tasks like dictator and ultimatum games. For decades, psychological research has used economic games to study humans' conceptions of fairness. These tasks have helped us better understand how and when people are sensitive to fairness, the influences of trust and reputation on cooperation, and even the neural underpinnings of social evaluation (Güth, Schmittberger, & Schwarze, 1982; Ernst Fehr and Klaus M. Schmidt, 1999; Kahneman, D., Knetsch, J. L., & Thaler, R. 1986; Forsythe, R., Horowitz, J. L., Savin, N. E., & Sefton, M. 1994; Sanfey et al., 2003; Krueger et al. 2008). However, these experiments all share a key feature: forced choice. When we consider the strength of task demands, particularly in unnatural laboratory tasks, this shared feature necessitates a more naturalistic confirmatory approach (Steele-Johnson et al., 2000). My experimental demonstration that fairness is a salient reward feature under a more natural patch-foraging paradigm -- particularly one that does not allow patch-leaving to serve as a communicative signal to one's social partner -- strengthens pre-existing evidence of fairness as a variable that influences human behaviour beyond rational economic choice.

Together, these two experimental approaches provide greater insight into how to use animal foraging models to understand human behaviour.

Implications for the social brain hypothesis

In previous sections of this thesis, I have discussed the implications of my experimental findings in the context of human decision-making literature. However, these findings also have important implications for a larger debate on the evolutionary origins of neocortical development. Specifically, these findings complicate the social brain hypothesis, which holds that the complexities of humans' (and other primates') social lives necessitated the development of complex cognitive tools like theory of mind, which resulted directly in the expansion of neocortex. The original formulation of this hypothesis served as a pushback to the common notion that human brain evolution was driven primarily by non-social, ecological decision-making needs (Dunbar, 1998). However, my findings in Chapter 3 demonstrate fundamental isomorphisms between a fundamental outcome of social cognition -- partner choice -- and an evolutionarily old pattern of food foraging. This suggests that the evolutionary history of social cognition may be more tightly-linked to ecological problem-solving than previously believed.

Next steps

While this work provides a springboard for many potential directions of future research, the path I find most interesting involves expanding our understanding of social-reward foraging under an opportunity cost framework. More specifically, this entails expanding the classical Charnovian model of foraging to include individual and environmental factors that affect the opportunity cost landscape of a foraging environment: travel effort, predation, risk of starvation, daily and seasonal climate shifts, niche construction, environmental variability, age, parenthood, and more. Predation can evoke both longer and shorter leaving times depending on the relative risk of being spotted by a predator in a patch versus in transit; risk of starvation can encourage overstaying when a sub-optimal rate of food reward is preferable to starvation; preparations for hibernation can place a higher energy cost on travel time and effort, encouraging overstaying. These features also interact with each other in nonlinear ways. Animals in the wild often face constraints on their food foraging behaviour from threats of starvation and predation, making decisions based on predicted energy reserve decay rates (McNamara, 1990). These constraints affect — and are affected by — individual differences in reactivity. When presented with feeders that offered various combinations of low and high safety and caloric output, great tits with high reactivity sought out high-quality food sources when they were at highest risk of starvation — which also happened to be the time at which predation risk was highest. More proactive birds, however, sought out food sources of all qualities during low predation-risk time periods (Quinn et al., 2012). These same factors affect human decision-making in social contexts, especially when confounded with psychiatric conditions like anxiety and depression.

Together, these variables converge to shift patch-leaving times in different directions based on the relative benefits and opportunity costs of leaving a patch. Then, the effects of these features can be compared between social and non-social reward, and between different categories of social reward (e.g. fairness versus control.) These comparisons would help map out the edges of the isomorphisms between social and non-social reward foraging.

Some forms of environmentally-induced opportunity costs that are present in food foraging only have natural analogues in certain kinds of social reward. For example, parrots are notorious food-wasters, dropping large amounts of high quality fruits and seeds. This food-wasting activity turns out to benefit the ecosystem as a whole, allowing new trees to grow and older trees to allocate resources to their healthiest branches (Sebastián-González et al 2019). In the case of niche-constructive food-wasting, an analogue is readily-available for the social reward of control. Forgoing an opportunity to exert social control can encourage trust, which consequently results in greater access to social control in the future. However, this kind of symmetrical experience is harder to devise for other social rewards like fairness. Is there a situation in which rejecting a fair offer could elicit more fair offers in the future? However, this metaphor of environmental maintenance translates well to human phenomena like philanthropy and community investment, and may help us better understand these phenomena under a foraging account.

There are also cases where individual differences in sensitivity to social rewards are far more variable than their counterparts in the non-social domain. For example, individual differences in justice sensitivity affect one’s willingness to endorse and engage in costly altruistic punishment (Lotz et al., 2011). Were I to repeat the experiments in Chapter 3 with a sample of participants recruited to maximise variance along justice-sensitivity, I would likely observe trait-related differences in the impact of different MVT features on patch-leaving times. Similarly, individual differences in trait paranoia, psychopathy, locus of control, and social responsiveness, would likely affect participants' sensitivity to associated social rewards. In addition to individual differences, there are also general demographic features that seem to affect foraging behaviour. For example, older adults tend to stay longer in individual patches during foraging patches than do their younger counterparts, indicating an age-based bias towards exploitation over novelty-seeking (Mata et al., 2013; Bukvic et al., 2018; Lloyd et al., 2020). However, older adults also tend to exhibit increased prosocial behaviour ((Engel, 2001; Cutler et al., 2021). In a future line of experimentation, placing exploration-exploitation preferences and prosociality preferences at odds with each other could demonstrate how group-differences in foraging behaviour and social preferences interact.

Social information processes also have key insights to bear for understanding how foragers come to understand their reward environments. Under ideal Charnovian foraging, agents have perfect knowledge of the distribution of patches in an environment. In the real world, this is rarely the case, which affects forager success (Kilpatrick et al., 2020). In response, foragers have had to develop alternate strategies in order to extract enough food from the environment to survive. In some communities, like ant colonies, decentralisation and communication provides key benefits. While no individual ant forages optimally, the ants that overstay collect food over more uniform time distribution than their more adventurous under-staying counterparts, which are responsible for finding new patch and environment types (Kulkarni, 2018; Kitcher, 1990). Working together, group-level optimality arises from individually suboptimal decisions. In the case of social reward foraging, hierarchy and gossip likely play important roles in biassing foragers' models of their reward space.

The work I have presented in this thesis provides fertile ground for future work using an expanded optimal foraging approach to understand social reward foraging in humans. More generally, this work serves to further our knowledge of human decision-making by highlighting behavioural isomorphisms between animal food foraging and human partner choice.

Works Cited

Addicott, M., Pearson, J., Sweitzer, M., Barack, D., & Platt, M. (XXXX). *A Primer on Foraging and the Explore/Exploit Trade-Off for Psychiatry Research* (p. 9).

Alesina, A., & Angeletos, G.-M. (2005). Fairness and Redistribution. *American Economic Review*, *95*(4), 960–980. https://doi.org/10.1257/0002828054825655

Apps, M. A., Grima, L. L., Manohar, S., & Husain, M. (2015). The role of cognitive effort in subjective reward devaluation and risky decision-making. *Scientific Reports*, *5*(1), 1–11.

Arengo, F., & Baldassarre, G. A. (2002). Patch Choice and Foraging Behavior of Nonbreeding American Flamingos in Yucatán, Mexico. *The Condor*, *104*(2), 452–457. https://doi.org/10.1093/condor/104.2.452

Averbeck, B. B. (2015). Theory of Choice in Bandit, Information Sampling and Foraging Tasks. *PLOS Computational Biology*, *11*(3), 1004164. https://doi.org/10.1371/journal.pcbi.1004164

Barlow, R. (2001). Exit, voice and loyalty in a computer-mediated customer service environment [M.A., San Jose State University. In *ProQuest Dissertations and Theses*. https://www.proquest.com/docview/220055132/abstract/8ABDC6AC54B844ECPQ/1

Baumard, N., André, J.-B., & Sperber, D. (2013). A mutualistic approach to morality: The evolution of fairness by partner choice. *Behavioural and Brain Sciences*, *36*(1), 59–78. https://doi.org/10.1017/S0140525X11002202

Beierholm, U., Guitart-Masip, M., Economides, M., Chowdhury, R., Düzel, E., Dolan, R., & Dayan, P. (2013). Dopamine modulates reward-related vigour. *Neuropsychopharmacology: Official Publication of the American College of Neuropsychopharmacology*, *38*(8), 1495–1503. https://doi.org/10.1038/npp.2013.48

Benvenisti, E. (1999). Exit and Voice in the Age of Globalization. *Michigan Law*

Review, *98*(1), 167–213. https://doi.org/10.2307/1290198

Bethea, A. (2020). What Black Employee Resource Groups Need Right Now. *Harvard Business Review*. https://hbr.org/2020/06/what-black-employee-resource-groups-need-right-now

Bettinger, R. L., & Grote, M. N. (2016). Marginal value theorem, patch choice, and human foraging response in varying environments. *Journal of Anthropological Archaeology*, *42*, 79–87. https://doi.org/10.1016/j.jaa.2016.03.002

Bird, R. B., McGuire, C., Bird, D. W., Price, M. H., Zeanah, D., & Nimmo, D. G. (2020). Fire mosaics and habitat choice in nomadic foragers. *Proceedings of the National Academy of Sciences*, *117*(23), 12904–12914. https://doi.org/10.1073/pnas.1921709117

Blount, S. (1995). When Social Outcomes Aren't Fair: The Effect of Causal Attributions on Preferences. *Organisational Behaviour and Human Decision Processes*, *63*(2), 131–144. https://doi.org/10.1006/obhd.1995.1068

Bonter, D. N., Zuckerberg, B., Sedgwick, C. W., & Hochachka, W. M. (2013). Daily foraging patterns in free-living birds: Exploring the predation–starvation trade-off. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1760), 20123087. https://doi.org/10.1098/rspb.2012.3087

Brantingham, P. J. (2013). Prey selection among Los Angeles car thieves. *Crime Science*, *2*(1), 3. https://doi.org/10.1186/2193-7680-2-3

Broccardo, E., Hart, O. D., & Zingales, L. (2020). Exit vs. Voice (Working Paper No. 27710; Working Paper Series. *National Bureau of Economic Research*. https://doi.org/10.3386/w27710

Brosig-Koch, J., Riechmann, T., & Weimann, J. (2017). The dynamics of behaviour in modified dictator games. *PLOS ONE*, *12*(4), 0176199. https://doi.org/10.1371/journal.pone.0176199

Brosnan, S. F., & Waal, F. B. M. de. (2014). Evolution of responses to (un)fairness. *Science*, *346*(6207). https://doi.org/10.1126/science.1251776

Bukvic, A., Gohlke, J., Borate, A., & Suggs, J. (2018). Ageing in Flood-Prone Coastal Areas: Discerning the Health and Well-Being Risk for Older Residents. *International Journal of Environmental Research and Public Health*, *15*(12),

2900. https://doi.org/10.3390/ijerph15122900

Cash-Padgett, T., & Hayden, B. (2020). Behavioural variability contributes to over-staying in patchy foraging. *Biology Letters*, *16*(3), 20190915. https://doi.org/10.1098/rsbl.2019.0915

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, *9*(2), 129–136. https://doi.org/10.1016/0040-5809(76)90040-X

Chong, T. T.-J., Apps, M., Giehl, K., Sillence, A., Grima, L. L., & Husain, M. (2017). Neurocomputational mechanisms underlying subjective valuation of effort costs. *PLOS Biology*, *15*(2), e1002598. https://doi.org/10.1371/journal.pbio.1002598

Clinchy, M., Sheriff, M. J., & Zanette, L. Y. (2013). Predator-induced stress and the ecology of fear. *Functional Ecology*, *27*(1), 56–65. https://doi.org/10.1111/1365-2435.12007

Cresswell, W., Clark, J. A., & Macleod, R. (2009). How climate change might influence starvation–predation risk trade-off response. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1672), 3553–3560. https://doi.org/10.1098/rspb.2009.1000

Cutler, J., Nitschke, J. P., Lamm, C., & Lockwood, P. L. (2021). Older adults across the globe exhibit increased prosocial behaviour but also greater in-group preferences. *Nature Aging*, *1*(10), Article 10. https://doi.org/10.1038/s43587-021-00118-3

Dana, J., Cain, D. M., & Dawes, R. M. (2006). What you don't know won't hurt me: Costly (but quiet) exit in dictator games. *Organisational Behaviour and Human Decision Processes*, *100*(2), 193–201. https://doi.org/10.1016/j.obhdp.2005.10.001

Dana, J., Weber, R. A., & Kuang, J. X. (2007). Exploiting moral wiggle room: Experiments demonstrating an illusory preference for fairness. *Economic Theory*, *33*(1), 67–80. https://doi.org/10.1007/s00199-006-0153-z

Davidson, J. D., & Hady, A. E. (2019). Foraging as an evidence accumulation process. *PLoS Computational Biology*, *15*(7), 1007060.

https://doi.org/10.1371/journal.pcbi.1007060

Denaro, C. (2020). Voice through exit: Syrian refugees at the borders of Europe and the struggle to choose where to live. In *Displacement* (pp. 131–152). Manchester University Press. https://www.manchesterhive.com/view/9781526123473/9781526123473.00016.xml

Doniol-Valcroze, T., Lesage, V., Giard, J., & Michaud, R. (2011). Optimal foraging theory predicts diving and feeding strategies of the largest marine predator. *Behavioral Ecology*, *22*(4), 880–888. https://doi.org/10.1093/beheco/arr038

Dunbar, R. I. M. (n.d.). *The Social Brain Hypothesis*.

EBSCOhost | 150813491 | Fishing Industry Perspectives on Sea-Level Rise Risk and Adaptation. (n.d.). https://web.b.ebscohost.com/abstract?direct=true&profile=ehost&scope=site&authtype=crawler&jrnl=20734441&AN=150813491&h=%2fEFaYrZHCJkCCaiTsPaX29oLBEyCf9LLJ5jXksWRozitFu3RIYo1%2fUqo3KC09OSn0SXdJCwlAgKKSX1DdUxuTA%3d%3d&crl=c&resultNs=AdminWebAuth&resultLocal=ErrCrlNotAuth&crlhashurl=login.aspx%3fdirect%3dtrue%26profile%3dehost%26scope%3dsite%26authtype%3dcrawler%26jrnl%3d20734441%26AN%3d150813491

Engel, C. (2011). Dictator games: A meta study. *Experimental Economics*, *14*(4), 583–610. https://doi.org/10.1007/s10683-011-9283-7

Exit, voice and loyalty: Analytic and empirical developments. (n.d.). https://ezproxy-prd.bodleian.ox.ac.uk:2869/doi/epdf/10.1111/1475-6765.00522

Fahrig, L., & Paloheimo, J. (1988). Effect of Spatial Arrangement of Habitat Patches on Local Population Size. *Ecology*, *69*(2), 468–475. https://doi.org/10.2307/1940445

FeldmanHall, O., & Shenhav, A. (2019). Resolving uncertainty in a social world. *Nature Human Behaviour*, *3*(5), 426–435. https://doi.org/10.1038/s41562-019-0590-x

Food Choice and Foraging Sites among the Alyawara on JSTOR. (n.d.). https://ezproxy-prd.bodleian.ox.ac.uk:2116/stable/3629795

FOULK, T. A., PATER, I. E. D., SCHAERER, M., PLESSIS, C. D., LEE, R., & EREZ, A. (2020). It's lonely at the bottom (too): The effects of experienced powerlessness on social closeness and disengagement. *Personnel Psychology*, *73*(2), 363–394. https://doi.org/10.1111/peps.12358

Frey, S., & Schneider, N. (2021). *Effective Voice: Beyond Exit and Affect in Online Communities*. http://arxiv.org/abs/2009.12470

Gabay, A., & Apps, M. A. J. (2019). *Foraging Optimally in Social Neuroscience: Computations and Methodological considerations* (Preprint]. PsyArXiv). https://doi.org/10.31234/osf.io/fud9p

Gabay, A. S., Radua, J., Kempton, M. J., & Mehta, M. A. (2014). The Ultimatum Game and the brain: A meta-analysis of neuroimaging studies. *Neuroscience & Biobehavioral Reviews*, *47*, 549–558. https://doi.org/10.1016/j.neubiorev.2014.10.014

Gehlbach, S. (2006). A Formal Model of Exit and Voice. *Rationality and Society*, *18*(4), 395–418. https://doi.org/10.1177/1043463106070280

Gittins, J. C. (1979). Bandit Processes and Dynamic Allocation Indices. *Journal of the Royal Statistical Society: Series B (Methodological*, *41*(2), 148–164. https://doi.org/10.1111/j.2517-6161.1979.tb01068.x

Green, L., & Myerson, J. (1996). Exponential versus Hyperbolic Discounting of Delayed Outcomes: Risk and Waiting Time. *American Zoologist*, *36*(4), 496–505.

Guitart-Masip, M., Beierholm, U. R., Dolan, R., Duzel, E., & Dayan, P. (2011). Vigor in the face of fluctuating rates of reward: An experimental examination. *Journal of Cognitive Neuroscience*, *23*, 3933–3938. https://doi.org/10.1162/jocn_a_00090

Happ, G. M., & Eisner, T. (1961). *Haemorrhage in a Coccinellid Beetle and Its Repellent Effect on Ants* (Vol. 134, Issue 3475, pp. 329–331). https://doi.org/10.1126/science.134.3475.329

Haralambos, M. (1985). *Sociology: Themes and perspectives* (2nd ed.). University Tutorial Press.

Harhen, N. C., & Bornstein, A. M. (2023). Overharvesting in human patch foraging reflects rational structure learning and adaptive planning. *Proceedings of the National Academy of Sciences*, *120*(13), e2216524120. https://doi.org/10.1073/pnas.2216524120

Hayden, B. Y., Pearson, J. M., & Platt, M. L. (2011). Neuronal basis of sequential foraging decisions in a patchy environment. *Nature Neuroscience*, *14*(7), 933–939. https://doi.org/10.1038/nn.2856

Heeren, A., Lievens, L., & Philippot, P. (2011). How does attention training work in social phobia: Disengagement from threat or re-engagement to non-threat? *Journal of Anxiety Disorders*, *25*(8), 1108–1115. https://doi.org/10.1016/j.janxdis.2011.08.001

Higginson, A. D., McNamara, J. M., & Houston, A. I. (2012). The Starvation-Predation Trade-Off Predicts Trends in Body Size, Muscularity, and Adiposity between and within Taxa. *The American Naturalist*, *179*(3), 338–350. https://doi.org/10.1086/664457

Hirschman, A. O. (XXXX). Exit, voice, and loyalty: Responses to decline in firms, organisations, and states. In *Fulcrum.org*. Harvard University Press.

Hornsby, A., & Love, B. C. (2021). *Sequential consumer choice as multi-cued retrieval*. https://doi.org/10.31234/osf.io/cx9r4

Inagaki, T. K., Muscatell, K. A., Moieni, M., Dutcher, J. M., Jevtic, I., Irwin, M. R., & Eisenberger, N. I. (2016). Yearning for connection? Loneliness is associated with increased ventral striatum activity to close others. *Social Cognitive and Affective Neuroscience*, *11*(7), 1096–1101. https://doi.org/10.1093/scan/nsv076

Jaatinen, K., Møller, A. P., & Öst, M. (2019). Annual variation in predation risk is related to the direction of selection for brain size in the wild. *Scientific Reports*, *9*(1), 11847. https://doi.org/10.1038/s41598-019-48153-w

Kacelnik, A. (1984). Central Place Foraging in Starlings (Sturnus vulgaris). I. Patch Residence Time. *Journal of Animal Ecology*, *53*(1), 283–299. https://doi.org/10.2307/4357

Kane, G. A., Bornstein, A. M., Shenhav, A., Wilson, R. C., Daw, N. D., & Cohen, J. D. (2019). Rats exhibit similar biases in foraging and intertemporal choice tasks. *ELife*, *8*, 48429. https://doi.org/10.7554/eLife.48429

Kappes, A., Nussberger, A.-M., Siegel, J. Z., Rutledge, R. B., & Crockett, M. J. (2019). Social uncertainty is heterogeneous and sometimes valuable. *Nature Human Behaviour*, *3*(8), 764–764. https://doi.org/10.1038/s41562-019-0662-y

Katz, K., & Naug, D. (2015). Energetic state regulates the exploration–exploitation trade-off in honeybees. *Behavioral Ecology*, *26*(4), 1045–1050. https://doi.org/10.1093/beheco/arv045

Kidd, C., Palmeri, H., & Aslin, R. N. (2013). Rational snacking: Young children's decision-making on the marshmallow task is moderated by beliefs about environmental reliability. *Cognition*, *126*(1), 109–114. https://doi.org/10.1016/j.cognition.2012.08.004

Kilpatrick, Z. P., Davidson, J. D., & Hady, A. E. (2020). Normative theory of patch foraging decisions. *BioRxiv*. https://doi.org/10.1101/2020.04.22.055558

Kivinen, S., Nummi, P., & Kumpula, T. (2020). Beaver-induced spatiotemporal patch dynamics affect landscape-level environmental heterogeneity. *Environmental Research Letters*, *15*(9), 094065. https://doi.org/10.1088/1748-9326/ab9924

Kliemann, D., Adolphs, R., Paul, L. K., Tyszka, J. M., & Tranel, D. (2021). Reorganisation of the Social Brain in Individuals with Only One Intact Cerebral Hemisphere. *Brain Sciences*, *11*(8), 965. https://doi.org/10.3390/brainsci11080965

Kolling, N., Behrens, T. E. J., Mars, R. B., & Rushworth, M. F. S. (2012). Neural Mechanisms of Foraging. *Science*, *336*(6077), 95–98. https://doi.org/10.1126/science.1216930

Kolling, N., Wittmann, M. K., Behrens, T. E. J., Boorman, E. D., Mars, R. B., & Rushworth, M. F. S. (2016). Value, search, persistence and model updating in anterior cingulate cortex. *Nature Neuroscience*, *19*(10), 1280–1285. https://doi.org/10.1038/nn.4382

Koops, M. A., & Abrahams, M. V. (2003). Integrating the roles of information and competitive ability on the spatial distribution of social foragers. *The American Naturalist*, *161*(4), 586–600. https://doi.org/10.1086/368297

Krebs, J. R., Kacelnik, A., & Taylor, P. (1978). Test of optimal sampling by foraging great tits. *Nature*, *275*(5675), 27–31. https://doi.org/10.1038/275027a0

Kulkarni, P. A. (2019). Explore-Exploit-Explore in Ant Colony Optimization. In A. J. Kulkarni, S. C. Satapathy, T. Kang, & A. H. Kashan (Eds.), *Proceedings of the 2nd International Conference on Data Engineering and Communication Technology* (pp. 183–189). Springer. https://doi.org/10.1007/978-981-13-1610-4_19

Kumar, N., Qiu, L., & Kumar, S. (2018). Exit, Voice, and Response on Digital Platforms: An Empirical Investigation of Online Management Response Strategies. *Information Systems Research*, *29*(4), 849–870. https://doi.org/10.1287/isre.2017.0749

Lagoze, C., Edwards, P., Sandvig, C., & Plantin, J.-C. (2015). Should I Stay or Should I Go? Alternative Infrastructures in Scholarly Publishing. *International Journal of Communication*, *9*(0), 20.

Langworthy, R. H., & LeBeau, J. L. (1992). The spatial distribution of sting targets. *Journal of Criminal Justice*, *20*(6), 541–551. https://doi.org/10.1016/0047-2352(92)90063-F

Laver, M. (1976). Exit, Voice, and Loyalty' Revisited: The Strategic Production and Consumption of Public and Private Goods. *British Journal of Political Science*, *6*(4), 463–482. https://doi.org/10.1017/S0007123400000855

Lee, S. J., & Lee, Z. (2006). An experimental study of online complaint management in the online feedback forum. *Journal of Organisational Computing and Electronic Commerce*, *16*(1), 65–85. https://doi.org/10.1080/10919390609540291

Lima, S. L. (1986). Predation Risk and Unpredictable Feeding Conditions: Determinants of Body Mass in Birds. *Ecology*, *67*(2), 377–385. https://doi.org/10.2307/1938580

Lloyd, A., McKay, R., Sebastian, C., & Balsters, J. (2020). Are adolescents more optimal decision‐makers in novel environments? Examining the benefits of heightened exploration in a patch foraging paradigm. *Developmental Science*, *24*. https://doi.org/10.1111/desc.13075

Lockwood, P. L., Apps, M. A. J., & Chang, S. W. C. (2020). Is There a 'Social' Brain? Implementations and Algorithms. *Trends in Cognitive Sciences*, *24*(10), 802–813. https://doi.org/10.1016/j.tics.2020.06.011

Łomnicki, A. (1980). Regulation of Population Density Due to Individual Differences and Patchy Environment. *Oikos*, *35*(2), 185–193. https://doi.org/10.2307/3544426

Lotz, S., Baumert, A., Schlösser, T., Gresser, F., & Fetchenhauer, D. (2011). Individual differences in third‐party interventions: How justice sensitivity shapes altruistic punishment. *Negotiation and Conflict Management Research*, *4*, 297–313. https://doi.org/10.1111/j.1750-4716.2011.00084.x

Louâpre, P., Fauvergue, X., Baaren, J., & Martel, V. (2015). The male mate search: An optimal foraging issue? *Current Opinion in Insect Science*, *9*, 91–95. https://doi.org/10.1016/j.cois.2015.02.012

MacLeod, R., MacLeod, C. d, Learmonth, J. a, Jepson, P. d, Reid, R. j, Deaville, R., & Pierce, G. j. (2007). Mass-dependent predation risk and lethal dolphin–porpoise interactions. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1625), 2587–2593. https://doi.org/10.1098/rspb.2007.0786

Marshall, H. H., Carter, A. J., Ashford, A., Rowcliffe, J. M., & Cowlishaw, G. (2013). How do foragers decide when to leave a patch? A test of alternative models under natural and experimental conditions. *Journal of Animal Ecology*, *82*(4), 894–902. https://doi.org/10.1111/1365-2656.12089

Mastroianni. (2021). *Do conversations end when people want them to? | PNAS*. https://www.pnas.org/content/118/10/e2011809118

Mata, R., Wilke, A., & Czienskowski, U. (2013). Foraging across the life span: Is there a reduction in exploration with ageing? *Frontiers in Neuroscience*, *7*. https://www.frontiersin.org/articles/10.3389/fnins.2013.00053

McGuire, J. T., & Kable, J. W. (2015). Medial prefrontal cortical activity reflects dynamic re-evaluation during voluntary persistence. *Nature Neuroscience*, *18*(5), 760–766. https://doi.org/10.1038/nn.3994

McNamara, J. M. (1990). The Policy Which Maximises Long-Term Survival of an Animal Faced with the Risks of Starvation and Predation. *Advances in Applied Probability*, *22*(2), 295–308. https://doi.org/10.2307/1427537

McNamara, J. M., & Houston, A. I. (1997). Currencies for foraging based on energetic gain. *The American Naturalist*, *150*(5), 603–617. https://doi.org/10.1086/286084

Mella, V. S. A., Possell, M., Troxell-Smith, S. M., & McArthur, C. (2018). Visit, consume and quit: Patch quality affects the three stages of foraging. *Journal of Animal Ecology*, *87*(6), 1615–1626. https://doi.org/10.1111/1365-2656.12882

Mellgren, R. L. (1982). Foraging in a simulated natural environment: There's a rat loose in the lab. *Journal of the Experimental Analysis of Behavior*, *38*(1), 93–100. https://doi.org/10.1901/jeab.1982.38-93

Mellgren, R. L., Misasi, L., & Brown, S. W. (1984). Optimal foraging theory: Prey density and travel requirements in Rattus norvegicus. *Journal of Comparative Psychology*, *98*(2), 142–153. https://doi.org/10.1037/0735-7036.98.2.142

Mitchell, S. H., & Brener, J. (1997). The work costs of earning food as a determinant of patch leaving. *Journal of Experimental Psychology. Animal Behavior Processes*, *23*(2), 136–144. https://doi.org/10.1037//0097-7403.23.2.136

Mizuyama, R., Uno, L., & Matsushima, T. (2016). Food variance and temporal discounting in socially foraging chicks. *Animal Behaviour*, *120*, 143–151. https://doi.org/10.1016/j.anbehav.2016.07.032

Mobbs, D., Hassabis, D., Yu, R., Chu, C., Rushworth, M., Boorman, E., & Dalgleish, T. (2013). Foraging under Competition: The Neural Basis of Input-Matching in Humans. *Journal of Neuroscience*, *33*(23), 9866–9872. https://doi.org/10.1523/JNEUROSCI.2238-12.2013

Morey: The early evolution of the domestic dog—Google Scholar. (n.d.). https://scholar.google.com/scholar_lookup?title=The%20early%20evolution%20of%20the%20domestic%20dog&publication_year=1994&author=D.F.%20Morey

Morrison, L. W. (XXXX). *Indirect effects of phorid ȳ parasitoids on the mechanisms of interspeci®c competition among ants* (p. 10).

Newman, J. A. (1991). Patch Use under Predation Hazard: Foraging behaviour in a Simple Stochastic Environment. *Oikos*, *61*(1), 29–44. https://doi.org/10.2307/3545404

Nishiyama, R. (2014). Response effort discounts the subjective value of rewards.

Behavioural Processes, *107*, 175–177. https://doi.org/10.1016/j.beproc.2014.08.002

Nonacs, P. (2001). State dependent behaviour and the Marginal Value Theorem. *Behavioral Ecology*, *12*(1), 71–83. https://doi.org/10.1093/oxfordjournals.beheco.a000381

Normative theory of patch foraging decisions | bioRxiv. (n.d.). https://www.biorxiv.org/content/10.1101/2020.04.22.055558v1.full

Otto, A. R., & Daw, N. D. (2019). The opportunity cost of time modulates cognitive effort. *Neuropsychologia*, *123*, 92–105. https://doi.org/10.1016/j.neuropsychologia.2018.05.006

Pacheco-Cobos, L., Winterhalder, B., Cuatianquiz-Lima, C., Rosetti, M. F., Hudson, R., & Ross, C. T. (2019). Nahua mushroom gatherers use area-restricted search strategies that conform to marginal value theorem predictions. *Proceedings of the National Academy of Sciences*, *116*(21), 10339–10347. https://doi.org/10.1073/pnas.1814476116

Peng, C., Nelissen, R. M. A., & Zeelenberg, M. (2018). Reconsidering the roles of gratitude and indebtedness in social exchange. *Cognition and Emotion*, *32*(4), 760–772. https://doi.org/10.1080/02699931.2017.1353484

Pitcher, D., & Ungerleider, L. G. (2021). Evidence for a Third Visual Pathway Specialized for Social Perception. *Trends in Cognitive Sciences*, *25*(2), 100–110. https://doi.org/10.1016/j.tics.2020.11.006

Pospíšilová, T. (2019). Giving and Refusing: The Contested Reception of Transnational Philanthropy in the Case of the Prague Central European University Foundation. *Nonprofit and Voluntary Sector Quarterly*, *48*(2), 266–282. https://doi.org/10.1177/0899764018802366

Preisser, E. L., Bolnick, D. I., & Benard, M. E. (2005). Scared to Death? The Effects of Intimidation and Consumption in Predator-Prey Interactions. *Ecology*, *86*(2), 501–509.

Quinn, J. L., Cole, E. F., Bates, J., Payne, R. W., & Cresswell, W. (2012). Personality predicts individual responsiveness to the risks of starvation and predation. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1735), 1919–1926. https://doi.org/10.1098/rspb.2011.2227

Raihani, N. J., & Barclay, P. (XXXX). Exploring the trade-off between quality and fairness in human partner choice. *Royal Society Open Science*, *3*(11), 160510. https://doi.org/10.1098/rsos.160510

Roberts, W. A. (1993). Testing a stochastic foraging model in an operant simulation: Agreement with qualitative but not quantitative predictions. *Journal of the Experimental Analysis of Behavior*, *59*(2), 323–331. https://doi.org/10.1901/jeab.1993.59-323

Roff, D. A. (1974). Spatial heterogeneity and the persistence of populations. *Oecologia*, *15*(3), 245–258. https://doi.org/10.1007/BF00345181

Ruff, C. C., & Fehr, E. (2014). The neurobiology of rewards and values in social decision making. *Nature Reviews Neuroscience*, *15*(8), 549–562. https://doi.org/10.1038/nrn3776

Rusbult, C. E., Zembrodt, I. M., & Gunn, L. K. (1982). Exit, voice, loyalty, and neglect: Responses to dissatisfaction in romantic involvements. *Journal of Personality and Social Psychology*, *43*(6), 1230–1242. https://doi.org/10.1037/0022-3514.43.6.1230

Sato, S., Kushibuchi, K., & Yasuda, H. (2009). Effect of reflex bleeding of a predatory ladybird beetle, Harmonia axyridis (Pallas) (Coleoptera: Coccinellidae), as a means of avoiding intraguild predation and its cost. *Applied Entomology and Zoology*, *44*(2), 203–206. https://doi.org/10.1303/aez.2009.203

Shaw, R. E., James, A. I., Tuft, K., Legge, S., Cary, G. J., Peakall, R., & Banks, S. C. (2021). Unburnt habitat patches are critical for survival and in situ population recovery in a small mammal after fire. *Journal of Applied Ecology*, *58*(6), 1325–1335. https://doi.org/10.1111/1365-2664.13846

Sheng, S., Feng, S., Meng, L., & Li, B. (2014). Departure Mechanisms for Host Search on High-Density Patches by the Meteorus pulchricornis. *Journal of Insect Science*, *14*(1). https://doi.org/10.1093/jisesa/ieu067

Shuai, L.-Y., Song, Y.-L., Kotler, B. P., Embar, K., & Zeng, Z.-G. (2016). Foraging behaviour in East Asian desert rodents and its implications on coexistence. *Israel Journal of Ecology & Evolution*, *62*(3–4), 171–177.

https://doi.org/10.1080/15659801.2015.1045279

Soder, K. J., Sanderson, M. A., Stack, J. L., & Muller, L. D. (2006). Intake and performance of lactating cows grazing diverse forage mixtures. *Journal of Dairy Science*, *89*(6), 2158–2167. https://doi.org/10.3168/jds.S0022-0302(06)72286-X

Steele-Johnson, D., Beauregard, R. S., Hoover, P. B., & Schmidt, A. M. (2000). Goal orientation and task demand effects on motivation, affect, and performance. *The Journal of Applied Psychology*, *85*(5), 724–738. https://doi.org/10.1037/0021-9010.85.5.724

Taylor, C. T., Cross, K., & Amir, N. (2016). Attentional control moderates the relationship between social anxiety symptoms and attentional disengagement from threatening information. *Journal of Behavior Therapy and Experimental Psychiatry*, *50*, 68–76. https://doi.org/10.1016/j.jbtep.2015.05.008

Teo, H. T., O'Donohue, W., & Grimmer, M. R. (2009). Linking psychological contract type and power distance orientation to exit, voice, loyalty and neglect behaviours. *Proceedings of the 2009 British Academy of Management Conference*, *1*, 1–21. http://www.bam.ac.uk/site/cms/contentChapterView.asp?chapter=1

The Fragility of Fairness: An Experimental Investigation on the Conditional Status of Pro-Social Norms on JSTOR. (n.d.). https://ezproxy-prd.bodleian.ox.ac.uk:2116/stable/27749908

Thiel, A., & Hoffmeister, T. S. (2004). Knowing your habitat: Linking patch-encounter rate and patch exploitation in parasitoids. *Behavioral Ecology*, *15*(3), 419–425. https://doi.org/10.1093/beheco/arh030

Thomas, F. R. (2007). The Behavioral Ecology of Shellfish Gathering in Western Kiribati, Micronesia 1: Prey Choice. *Human Ecology*, *35*(2), 179–194. https://doi.org/10.1007/s10745-006-9066-5

Thornton, A., & Hodge, S. J. (2009). The development of foraging microhabitat preferences in meerkats. *Behavioral Ecology*, *20*(1), 103–110. https://doi.org/10.1093/beheco/arn120

Tomova, L., Wang, K. L., Thompson, T., Matthews, G. A., Takahashi, A., Tye, K. M., & Saxe, R. (2020). Acute social isolation evokes midbrain craving responses similar to hunger. *Nature Neuroscience*, *23*(12), 1597–1605. https://doi.org/10.1038/s41593-020-00742-z

Turrin, C., Fagan, N. A., Dal Monte, O., & Chang, S. W. C. (2017). Social resource foraging is guided by the principles of the Marginal Value Theorem. *Scientific Reports*, *7*(1), 11274. https://doi.org/10.1038/s41598-017-11763-3

Utz, R. L., Carr, D., Nesse, R., & Wortman, C. B. (2002). The Effect of Widowhood on Older Adults' Social Participation: An Evaluation of Activity, Disengagement, and Continuity Theories. *The Gerontologist*, *42*(4), 522–533. https://doi.org/10.1093/geront/42.4.522

Vassena, E., Krebs, R. M., Silvetti, M., Fias, W., & Verguts, T. (2014). Dissociating contributions of ACC and vmPFC in reward prediction, outcome, and choice. *Neuropsychologia*, *59*, 112–123. https://doi.org/10.1016/j.neuropsychologia.2014.04.019

Venkataraman, V. V., Kraft, T. S., Dominy, N. J., & Endicott, K. M. (2017). Hunter-gatherer residential mobility and the marginal value of rainforest patches. *Proceedings of the National Academy of Sciences*, *114*(12), 3097–3102. https://doi.org/10.1073/pnas.1617542114

Wagner, B., Clos, M., Sommer, T., & Peters, J. (2020). Dopaminergic Modulation of Human Intertemporal Choice: A Diffusion Model Analysis Using the D2-Receptor Antagonist Haloperidol. *Journal of Neuroscience*, *40*(41), 7936–7948. https://doi.org/10.1523/JNEUROSCI.0592-20.2020

Westbrook, A., & Braver, T. S. (2015). Cognitive effort: A neuroeconomic approach. *Cognitive, Affective & Behavioral Neuroscience*, *15*(2), 395–415. https://doi.org/10.3758/s13415-015-0334-y

Yerkes, R. M., & Dodson, J. D. (1908). The relation of strength of stimulus to rapidity of habit-formation. *Journal of Comparative Neurology and Psychology*, *18*(5), 459–482. https://doi.org/10.1002/cne.920180503

Zhang, J., Gong, X., Fougnie, D., & Wolfe, J. M. (2015). Using the past to anticipate the future in human foraging behavior. *Vision Research*, *111*, 66–74. https://doi.org/10.1016/j.visres.2015.04.003

Zimmer, C., Boos, M., Poulin, N., Gosler, A., Petit, O., & Robin, J.-P. (2011).

Evidence of the Trade-Off between Starvation and Predation Risks in Ducks. *PLOS ONE*, *6*(7), 22352. https://doi.org/10.1371/journal.pone.0022352

Zollner, P. A., & Lima, S. L. (1999). Search Strategies for Landscape-Level Interpatch Movements. *Ecology*, *80*(3), 1019–1030. https://doi.org/10.2307/177035