Are Adolescents More Optimal Decision-Makers in Novel Environments? Examining the Benefits of Heightened Exploration in a Patch Foraging Paradigm

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Conflict of Interest

The authors report no conflict of interest.

Data Availability

Computational modelling and simulation code can be found at: https://osf.io/nu627/.

Research Highlights

- Adolescents explored more than adults in a patch foraging paradigm.

- This heightened exploration in adolescents is more optimal.

- Heightened exploration in adolescence can confer benefits in the explore/exploit trade-off.

Abstract

Adolescence is a period of heightened exploration relative to adulthood and childhood. This predisposition has been linked with negative behaviours related to risk-taking, including dangerous driving, substance misuse and risky sexual practices. However, recent models have argued that adolescents' heightened exploration serves a functional purpose within the lifespan, allowing adolescents to develop experiential knowledge of their surroundings. Yet, there is limited evidence that heightened exploration in adolescence is associated with positive outcomes. To address this, the present pre-registered study utilised a foraging paradigm with a sample of adolescents aged 16-17 (N=68) and of adults aged 21 and above (N=69). Participants completed a patch foraging task, which required them to choose between exploiting a known resource which gradually yields fewer rewards, and exploring a novel, unknown resource with a fresh distribution of rewards. Findings demonstrated that adolescents explored more than adults, which – in the context of the current task – represented more optimal patch foraging behaviour. These findings indicate that adolescents' heightened exploration can be beneficial, as they were able to effectively navigate unknown environments and accrue rewards more successfully than adults. This provides evidence that heightened exploration in adolescence, relative to adulthood, can lead to positive outcomes and contributes to our understanding of the role increased novelty-seeking plays at this point in the lifespan.

Keywords: *Adolescence, exploration, development, decision-making, patch foraging*

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Introduction

Adolescence is a period of heightened exploration of novel scenarios compared to childhood and adulthood (Spear, 2000; Steinberg, 2008). Adolescents' predisposition for novelty-seeking has typically been associated with negative outcomes in this population, such as increased rates of substance misuse, delinquency and injury (e.g. Arnett, 2002; Eaton et al., 2012; Moffitt, 2018). However, exploring novel opportunities is not exclusively associated with negative outcomes. For example, by trying out a new restaurant one can discover a new favourite meal, but this also involves exploring a possibility with unknown outcomes. Recent models have proposed that heightened exploration in adolescence, relative to adulthood and childhood, plays a functional role in development and is beneficial at this point in the lifespan (Romer, Reyna & Satterthwaite, 2017). The present study will examine whether adolescents' novelty-seeking can in fact produce more optimal navigation of novel environments.

While much of the literature has focussed on negative outcomes resulting from adolescents' decision-making, more recent research has considered positive outcomes that arise from novelty-seeking. Indeed, a proposed 'imbalance' between sensation-seeking and inhibitory control that occurs during adolescence (Casey, Getz & Galvan, 2008; Shulman et al., 2016; Steinberg, 2008) has been linked to 'positive' forms of risk taking, or forms that promote socially valued goals (Duell & Steinberg, 2019). For example, defending a peer who is being victimized can put an adolescent at risk of negative outcomes, but is also a positive, prosocial behaviour. Such acts of 'prosocial risk taking' recruit similar reward networks to those implicated in non-social forms of risk taking and demonstrate how neurobiological developments during this period can lead to positive behavioural outcomes (Do et al., 2017).

Consistent with this, a recent study found that higher levels of sensation-seeking in adolescence predicted both positive and negative forms of risk taking equally (Patterson et al., 2019), suggesting that features of adolescent decision-making are not exclusively unfavourable.

The Lifespan Wisdom Model (Romer et al., 2017) builds on this by suggesting that adolescents' heightened novelty-seeking serves a functional role in development. As adolescence is a period marked by achieving autonomy from caregivers (Ellis et al., 2012), the Lifespan Wisdom Model proposes that adolescents' heightened predisposition for novelty-seeking, relative to other age groups, provides them with opportunities to gain experiential knowledge of their surroundings (Murty, Calabro & Luna, 2016). However, it is argued that a subset of adolescents do not adequately integrate their experience to inform future decisions and – as a result – persistently engage in risky behaviour. These adolescents are characterised by high levels of impulsivity, which drives them to seek immediate reward despite experience with negative outcomes associated with an action (e.g. persistent substance misuse; Khurana et al., 2015). Risk taking driven by impulsivity therefore does not support adolescents to gain experiential knowledge of their surroundings but is driven by a desire for short term rewards. For the majority of adolescents, however, exploration and novelty-seeking arguably support the transition from childhood dependence to adult independence.

Exploration is an effortful process requiring cognitive control (Daw, O'Doherty, Dayan, Seymour & Dolan, 2006; Otto, Skatova, Madlon-Kay & Daw, 2014). Recently, it has been suggested that adolescents are more motivated than other age groups to employ cognitive control to explore novel scenarios in order to acquire information about their surroundings (Do, Sharp & Telzer, 2019). Consistent with this, compared to adults, adolescents explore uncertain outcomes in conditions of ambiguity where probabilistic information is unknown, but not in conditions of risk where this information is explicit (Tymula et al., 2012; van den Bos & Hertwig, 2017). According to the Lifespan Wisdom Model, adolescents' ambiguity tolerance

is due to the information that can be learned through sampling the unknown probabilities in these options (Romer et al., 2017). However, previous studies that have investigated ambiguity tolerance in adolescence have predominantly employed economic choice tasks (van den Bos & Hertwig, 2017), which are restricted in their ability to measure exploration, as feedback does not have utility for later trials (Garrett & Daw, 2020). Furthermore, parameters measuring ambiguity tolerance are currently unable to distinguish whether this tolerance is driven by optimism that the lottery will yield a reward or by a motivation to learn the probability structure underlying the ambiguous option (Tymula et al., 2012). Therefore, there is limited evidence that adolescents' heightened ambiguity tolerance reflects an information gathering exercise.

The emphasis on exploration in the Lifespan Wisdom Model is noteworthy as exploration is utilised across species to maximise adaptive outcomes, such as those that support the health, development and safety of an organism (Ellis et al., 2012). For example, a number of animal species, including humans, utilise exploration to forage for resources such as food and mates (Cohen & Todd, 2018; Marques, Li, Schaak, Robson & Li, 2019). Indeed, human beings have spent the bulk of their evolutionary history in patch foraging economies (Smith, 1983; Venkataraman, Kraft, Dominy & Endicott, 2017). Patch foraging therefore exemplifies the significance of exploration in human decision-making. Deciding when to engage in exploration requires evaluating the trade-off between exploiting a known patch of land with gradually diminishing returns, and exploring a novel patch with a fresh distribution of supplies (i.e. the explore/exploit trade off; Stephen & Krebs, 1986). In order to maximise rewards and minimise energy costs, the decision-maker must learn when the opportunity cost of exploiting rewards from the current resource exceeds the opportunity cost of exploring a novel resource – at which point exploration is rational (Charnov, 1976).

Yet, recent lab-based studies have found that human adults are not optimal patch foragers (Constantino & Daw, 2015; Lenow et al., 2017; Le Heron et al., 2020). Constantino

and Daw (2015) developed an apple picking patch foraging paradigm, requiring adults to maximise the number of apples collected from trees. Their paradigm had four 'environments' containing patches of different qualities. The authors predicted that participants would adjust their foraging behaviour according to the richness of the respective environments to maximise rewards. Consistent with this, Constantino and Daw (2015) found that participants altered their leaving threshold according to the quality of the environments. However, throughout their task Constantino and Daw (2015) observed that participants consistently overexploited, staying with individual patches for longer than the optimal foraging strategy would dictate. Using a computational modelling approach, the authors demonstrated that overexploiting was explained by a parameter capturing participants' risk sensitivity, resulting in too much value being placed on the immediate rewards that could be exploited. Thus, despite the adaptive pressures to maximise reward while foraging, human adults do not explore optimally in patch foraging paradigms.

Two prominent theories have been developed to explain human exploration strategies. The first of these suggests that exploration is a stochastic process, driven by introducing randomness into decision-making that leads the agent to divert from the most rewarding option known to them (Daw et al., 2006). In an environment with changing reward contingencies, this strategy can accelerate the rate at which the decision-maker learns of changes in the structure of the environment (Gershman, 2018). The second, directed exploration, proposes that the decision-maker selects options to gain information about the underlying reward distribution of the environment, which increases the subjective value of the uncertain option in an 'information bonus' (Gershman, 2018; Wilson et al., 2014). The use of directed exploration emerges in adolescence, but is only utilised when exploration is consistent with the more rewarding option (Somerville et al., 2017). In cases where there is conflict between an option that has a higher reward value and another that has a higher information value, adolescents

preferred the high reward option, whereas adults preferred the high information option (Somerville et al., 2017). This finding is consistent with evidence that, compared to other age groups, adolescents prefer immediate rewards in favour of delayed ones (van den Bos et al., 2015). However, Somerville and colleagues (2017) also found that the use of random exploration did not change with development and overall, there were no developmental differences in task performance as measured by the number of points earned in the task. These findings are consistent with an emerging body of research has demonstrated that increasingly complex model-based exploration strategies develop in late adolescence (Dubois et al., 2020; Jepma et al., 2020; Xia et al., 2020), though these may be tempered by adolescents' preference for immediate reward relative to adults (Somerville et al., 2017).

To date, research has demonstrated that adolescents explore options with unknown information more than adults and children do. However, there is limited evidence that heightened exploration of novel scenarios in adolescence is associated with more optimal outcomes compared to other age groups. Here, we investigate exploration/exploitation trade-offs in adolescents and adults in an ecologically valid paradigm, patch foraging. Unlike other paradigms, patch foraging performance has been computationally defined across humans and other animal species such that performance can be compared to an objective behavioural optimum. While research has demonstrated that adolescents prefer to exploit the option that yields an immediate reward in an explore/exploit paradigm (Somerville et al., 2017), an alternative body of work has suggested that adolescents are motivated to explore novel scenarios more than adults (Do et al., 2019; Romer et al., 2017; Steinberg, 2008). As such, we predicted that 1) there will be a difference in foraging behaviour between adolescents and adults, measured by the point at which they leave patches to explore new ones.

To examine individual differences that contribute to foraging strategies, we also measured impulsivity and risk sensitivity. Impulsive traits are associated with a preference for

immediate rather than delayed rewards (Khurana et al., 2015) and the prevalence of these traits varies across adult and adolescent populations (Chamorro et al., 2012; Romer, 2010). In a patch foraging context, we predict that heightened impulsivity will be associated with a greater tendency to select the option that yields an immediate reward, which is to exploit the current patch. As such, we predicted that 2) higher levels of impulsivity will predict greater exploitation of patches. Finally, as overexploiting has been explained by a parameter capturing risk sensitivity, we predicted that 3) participants with higher levels of risk sensitivity will exploit individual patches to a greater degree.

Methods

Design

The present study utilised a 2x2x2 mixed factorial design: Age (between-subject: adolescents, adults) x Depletion rate (within-subject: fast vs. slow patch depletion rate) x Travel time (within-subject: short vs. long travel time). Depletion rate and travel time variables are explained in greater detail in the Patch Foraging section below.

Participants

Pilot: Seven participants were recruited for an initial pilot study: three adolescents aged between 16-18 ($M = 17$, $SD = 1$) and four adults aged between 24-26 ($M = 24.66$, $SD = 1.15$). Participants were recruited from a convenience sample who had previously expressed interest in research participation.

Main study: A total of 138 participants were recruited in the main study based on an a priori power calculation (alpha = 0.05, power = 0.8, Cohen's f effect size = 0.25) using G*Power 3.1 (Faul, Erdfelder, Lang & Buchner, 2007). Adolescent participants were aged 16-17, to capture the period in which novelty-seeking peaks (Romer, 2010). Sixty-eight adolescents were recruited in total, with a mean age of 16.57 ($SD = 0.53$, 77% female). The

adult sample consisted of individuals aged 21 and above, as this is the period by which cognitive control is thought to have plateaued (Andrews-Hanna et al., 2011). During analysis, it emerged that one participant was not in this age bracket, so this person was subsequently excluded. As such, the final adult sample was comprised of 69 participants aged between 21-50 with a mean age of 30.77 ($SD = 7.96$, 46% female). The study was approved by the Ethics Committee at the authors' institution.

Task

Patch Foraging: The patch foraging task was adapted from a similar paradigm used in previous lab-based studies (Constantino & Daw, 2015; Lenow et al., 2017). The goal for participants was to collect as many apples as possible over the duration of the study. Patches that were available to forage were represented as single trees; on each trial participants could choose to stay and exploit a given patch (tree), or could leave to explore a new patch with a fresh distribution of apples. Exploiting a single patch would yield gradually diminishing rewards over time, such that the longer participants stayed with each patch, the fewer rewards they received from each exploit decision. When participants chose to exploit, they were presented with the number of apples they had collected on that harvest, alongside their cumulative score. Exploit decisions were scripted such that these would take three seconds including the decision phase and reward phase (i.e. when participants received the apples from harvesting). To ensure that faster reaction times did not permit participants to collect more apples within the time limit, the presentation of the reward phase was determined based on how quickly participants responded. For example, a participant who responded in 1.3 seconds would be presented with their score for 1.7 seconds. Participants were given up to two seconds to decide, after which they received a timeout message. Timeout trials were subsequently excluded from further analysis. If participants chose to explore, they would wait for a block-

specific interval to elapse before arriving at a new patch, which had a fresh distribution of rewards available (see Figure 1).
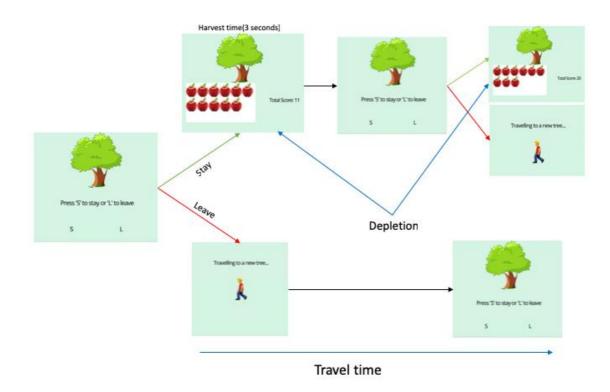

Figure 1: Schematic outline of the patch foraging paradigm

There were four unique environments in the present study, corresponding to four blocks. Participants completed the environments in counterbalanced order, to control for order effects. Parameters of the environments were manipulated to create environments that were either richer, yielding a higher average number of rewards over time, or poorer, yielding a lower average of rewards. Notably, participants did not know the features of each environment prior to encountering that block, requiring them to learn the state of each environment to maximise their average reward intake.

The two parameters that were manipulated in the present study were the rate at which rewards depleted in a single patch and the length of time it took to travel to a new patch. Depletion rate was manipulated such that the rate at which the apples diminished on each successive harvest was either fast or slow. As in Constantino and Daw (2015), the depletion

rate applied after each exploit decision was randomly drawn from a Gaussian distribution. In environments with a fast depletion rate, the rewards from the previous harvest were multiplied by a figure drawn from a distribution with a mean of 0.88 ($SD = 0.07$). In environments with a slow depletion rate, the mean of the distribution was 0.94 ($SD = 0.07$). To ensure that applying the depletion rate in this way did not lead to an increase in apples, the depletion rate was set to a maximum of 1, meaning the distribution of the depletion rate was negatively skewed. In environments where the depletion rate was slow, participants experienced a greater number of harvests with rich yields. As such, participants could accumulate a greater average number of rewards per unit of time compared to environments with a fast depletion rate.

The second parameter that was manipulated was the time it took to travel to a new patch if participants chose to explore. In environments with shorter travel times between patches, there is less cost in time (and thus resources) for the forager, meaning they can afford to explore more often to maximise average reward intake. However, in patches with longer travel times, there is a greater expenditure of time and resources. As such, given long travel times the forager should spend longer with each individual patch before they explore a new one.

Two dependent variables were calculated from the patch foraging task. The first was leaving threshold, i.e. the smallest reward (number of apples) that signalled to the participant the current patch had less value than exploring a novel patch (thus a high leaving threshold meant the participant left the patch earlier). The leaving threshold was operationalised as the average of the previous two rewards participants had observed in that patch prior to leaving, to provide an upper and lower bound estimate of participants' leaving threshold. We also included a second dependent variable, which was deviation from the optimal leaving policy. This was calculated through subtracting participants' actual leaving thresholds from the previously determined optimal leaving threshold in that environment (see Marginal Value Theorem below). As such, positive figures indicate participants overexploited the patch, whereas

negative figures indicate participants underexploited that patch. This provided a measure of the degree to which participants deviated from the optimal foraging strategy.

Marginal Value Theorem: Optimal patch foraging behaviour is explained by an equation called Marginal Value Theorem (MVT), developed by Charnov (1976). This rule states that the forager should leave their current patch when the reward expected from the next exploit decision falls below the average reward experienced in that environment. To predict the value of exploiting the current patch, the forager should multiply the last known state of the tree (s_i) by the block-specific depletion rate (κ). This value is compared against the average reward rate per second (p), which is multiplied by the time taken to harvest the patch in seconds (h). If the expected value of exploiting the current patch ($\kappa * s_i$) falls below the value of *ph*, the forager should explore the next patch. As our paradigm utilised discrete, rather than continuous trials, we utilised the MVT equation developed by Constantino and Daw (2015) to model foraging behaviour. Simplified, the equation states that the decision-maker should leave their current patch when the following inequality is satisfied:

$$ks_i < ph \tag{1}$$

The MVT equation demonstrates that the optimal foraging strategy follows a leaving threshold rule (see Constantino & Daw, 2015, for a full proof of the MVT equation as it relates to this task). In order to estimate the optimum threshold for the parameters in each environment used in the current study, a simulation of the task was built in R (R Core Team, 2018). For each environment, the simulation was set to run with a leaving threshold from 1-10 in increments of 0.001. This produced 9001 simulations per environment and a total of 36,004 simulations for all four environments. The total score accrued using each of these leaving thresholds was then calculated, which was subsequently divided by the units of time to empirically demonstrate that the optimum leaving threshold for each environment followed the predictions of MVT (see

Supplementary Material). For each environment, we ran each simulation ten times and averaged the optimum leaving threshold across these simulations to account for stochasticity in the rewards accumulated due to the probabilistic nature of the depletion rate and initial richness of patches. For a list of features of each environment, see Table 1.

Table 1: Parameters and optimal leaving thresholds of the four environments in the patch foraging task

	Environment 1: fast depletion, short travel	Environment 2: slow depletion, short travel	Environment 3: fast depletion, long travel	Environment 4: slow depletion, long travel
Depletion rate (*M, SD*)	0.88, 0.07	0.94, 0.07	0.88, 0.07	0.94, 0.07
Travel time (s)	6	6	12	12
Optimal leaving threshold – i.e. leave when the expected number of apples is lower than this	6.46	7.04	5.07	5.90

MVT also provides an explanation for changes to the optimum leaving threshold between environments that are richer or poorer quality. Environments with greater richness raise the value that must be expected from exploiting the current patch to make it more time-valuable than exploring a new resource-rich patch. For example, environments that have slower depleting patches will take longer to reach the environmental average compared to fast depleting patches (Gabay & Apps, 2020). Consequently, in patches with a slower depletion

rate, participants receive a higher yield of rewards for the time they invest in individual patches. This raises the average reward rate (p), which, when entered into the MVT equation (1), signals a high leaving threshold. In fast depleting patches, participants receive a lower yield of rewards for the same time investment in patches, decreasing the average reward rate and signalling a lower leaving threshold. Following this rule, participants should remain for longer in environments with a slow depletion rate and should also have a higher leaving threshold compared to environments with a fast depletion rate (Gabay & Apps, 2020).

Similarly, in environments with shorter travel times between patches, the average rewards accumulated are higher, as less time is required to reach novel patches with a fresh distribution of rewards. This subsequently raises the average reward rate (p) in environments with short travel times compared to long between-patch travel times. Therefore, the leaving threshold signalling when the forager should explore is higher when travel time between patches is shorter (Marshall, Carter, Ashford Rowcliffe & Cowlishaw, 2013). The predictions of MVT across different quality environments have been mathematically and empirically evidenced across a range of human and animal studies, providing a robust account of optimal foraging behaviour (Bettinger & Grote, 2016; Charnov, 1976; Stephen & Krebs, 1986)

Questionnaire Measures

Demographic Measures: Participants were asked to report the following demographic variables: age, gender (male or female), ethnicity and socioeconomic status. Ethnicity options were based on recommendations from the UK Office for National Statistics (Office for National Statistics, 2009). Participants that did not fall into one of these categories were asked to report their ethnicity in a text-entry box. Adolescents' socioeconomic status was approximated with a measure of parental education, with options ranging from no formal

qualifications to university degree (Steinberg et al., 2018). Adults' socioeconomic status was measured by their own highest level of education, comprised of the same options.

Pubertal Development: The Pubertal Status scale (Carskadon & Acebo, 1993) is a measure of adolescents' pubertal development. As development is subject to individual differences, this measure provides information about an individual's development that is distinct from chronological age. The scale is comprised of five questions which ask whether particular developmental milestones, such as their physical growth, are underway or complete. The individuals' pubertal development is calculated as a mean of their scores on the scale. The mean scores range from 1-4 with higher values denoting more highly developed individuals.

Behavioural Inhibition and Behavioural Activation: The BIS/BAS (Carver & White, 1994) is a combination of 20 items capturing behavioural inhibition scores (BIS) and behavioural approach scores (BAS). Higher average scores on the BIS subscale (ranging from 1-4) denote higher sensitivity towards non-rewarding or unpleasant stimuli, for example: "I worry about making mistakes". The BAS is divided into three subscales measuring drive, fun seeking and reward responsiveness. Higher average scores on the BAS subscales (ranging from 1-4 per subscale) indicate participants' responsiveness to rewarding stimuli, for example: "When I get something I want, I feel excited and energized". Together, these items measure participants' responsiveness to rewarding or aversive stimuli and predict risk sensitivity across development (Urošević, Collins, Muetzel, Lim, & Luciana 2012). The reliability of the subscales ranged from acceptable to good (α = .66-.81).

Impulsivity: The Barratt-11 (Patton, Standford & Barratt, 1995) measures the degree to which the individual acts impulsively. The scale is comprised of 30 items, each presented on a Likert scale ranging from 1-4. The items capture the degree to which individuals act without thinking, or do not engage in self-regulation. The individual's impulsivity is calculated as their

mean score on the items in the scale. Mean scores range from 1-4, with higher values indicating greater impulsivity. The scale demonstrated good reliability ($\alpha = .82$).

Procedure

Participants were invited in groups to an IT suite where they were provided with either a laptop or desktop computer. Participants were briefed as to the aims of the study and provided with the opportunity to ask questions. Following this, participants were asked to complete a consent form, demographic information, and were provided with task instructions that specified participants should only focus on their own screen. Participants were informed that they would be awarded a gift card for taking part that would be loaded with a base reward of £4. They were also informed that a bonus of up to £3 could be earned, which was determined by the number of points they accumulated during the task. As such, they should aim to collect as many apples as possible throughout the task. All incentives were transparent, and no deception was used. The average amount awarded to participants was £5.62. The task was run on Gorilla.sc, an online platform for running behavioural experiments (Anwyl-Irvine, Massonnie, Flitton, Kirkham & Evershed, 2019).

Participants completed a practice task, which used different parameters to the main task. After the practice, participants completed each of the four unique patch foraging environments. Each environment was scripted to last for 7 minutes, which was determined based on previous research (Lenow et al., 2017). Once participants completed each environment, they were directed to a screen explaining that they were now in a new environment, which might have different properties to the one they had just completed. After the task ended, participants completed the BIS/BAS, the Barratt-11 and, for adolescent participants only, the Pubertal Status Scale. Participants were then provided with their final score and debriefed as to the aims of the study.

Results

Confirmatory Analyses

Analyses were conducted in R v3.5.1 and JASP v0.10.2 (JASP Team, 2019). Results of the pilot study indicated that participants' behaviour was qualitatively consistent with the predictions of MVT. Descriptive statistics indicated that participants adjusted their leaving threshold according to the different qualities of the environment, which was considered adequate support to run the main study.

Results of the main analyses demonstrated that across the different quality environments, adolescents consistently explored more compared to adults. A mixed 2 (age group: adolescents vs adults) x 2 (patch depletion rate: fast vs slow) x 2 (travel time: short vs long) ANOVA demonstrated a main effect of age on the leaving threshold $F_{(1, 122)} = 13.56$, $p < .001$, $\eta^2 = .10$, $BF_{10} = 2.117e-7$. Compared to adults, adolescents had a higher average leaving threshold, meaning the number of apples required to stay at a patch was higher and thus they explored more often. Across the four environments, adolescents' mean leaving threshold was 5.82 ($SD = 1.79$) apples, whereas adults' mean leaving threshold was 4.78 ($SD = 1.66$) apples (see Figure 2). Furthermore, results of this analysis revealed a main effect of travel time $F_{(1, 122)} = 15.57$, $p < .001$, $\eta^2 = .01$, $BF_{10} = 6.985e-7$. This suggests that participants explored more in environments where travel times between patches was short compared to environments when travelling between patches incurred a greater time cost, consistent with a rational foraging strategy. Further, there was a main effect of changes to the depletion rate between environments $F_{(1,122)} = 32.28$, $p < .001$ $\eta^2 = .01$, $BF_{10} = 2.936e-5$. In environments where the patch depletion rate was fast participants had a lower leaving threshold, whereas in environments where the patch depletion was slow, participants had a higher leaving threshold, which is consistent with optimal foraging behaviour. However, there was an interaction between age group and patch

depletion rate $F_{(1,122)} = 6.13$, $p = .015$ $\eta^2 = .002$, $BF_{10} = 0.002$. Post hoc tests using the Bonferroni correction demonstrated that there was not a significant difference between adolescents' leaving thresholds in the fast depletion conditions compared to the slow depletion conditions ($p_{bonf} = .172$). However, there was a significant difference between adults' leaving thresholds in the slow depletion conditions compared to the fast depletion conditions ($p_{bonf} < .001$). These findings indicate that adults were more responsive to changes in the depletion rate compared to adolescents and adjusted their leaving thresholds accordingly. As this was an ordinal interaction, it was still valid to interpret the main effects of this model. Results of the ANOVA revealed no interaction effect between travel time and depletion rate $F_{(1,122)} = 0.91$, $p = .343$, age group and travel time $F_{(1,122)} = 1.149e\text{-}9$, $p = .991$, nor between age group, depletion rate and travel time $F_{(1,122)} = 1.26$, $p = .264$.
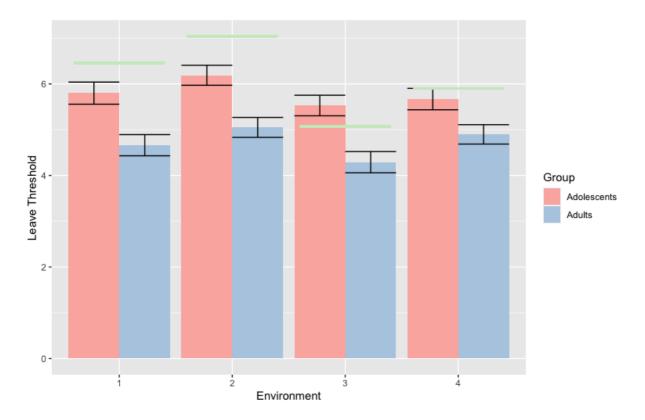

Figure 2: Plot of the mean leaving threshold for adolescents and adults for Environment 1 (fast depletion and short travel), Environment 2 (slow depletion and short travel), Environment 3 (fast depletion and long travel)

and Environment 4 (slow depletion and long travel). Green bars indicate the optimal leaving value for that environment.

Although adolescents' leaving threshold was higher than adults', this does not confirm that their behaviour was more optimal. To address this, we conducted a mixed 2x2x2 ANOVA using average deviation from the optimum leaving threshold as the dependent variable. Results demonstrated a main effect of age on deviation from the optimum $F_{(1, 122)} = 13.56$, $p < .001$ $\eta^2 = .08$, $BF_{10} = 1.324e\text{-}27$, with adolescents' behaviour closer to the optimum leaving threshold compared to adults'. There was a main effect of travel time on deviation from the optimum $F_{(1,122)} = 135.43$, $p < .001$, $\eta^2 = .06$, $BF_{10} = 2.472e\text{-}4$, with participants being closer to the optimum leaving threshold in the long travel time environments. In addition, there was a main effect of depletion rate on deviation from the optimum $F_{(1,122)} = 23.76$, $p < .001$, $\eta^2 = .01$, $BF_{10} = 6.426e\text{-}28$. Participants were closer to the optimum leaving threshold in environments with a fast depletion rate compared to environments with a slow depletion rate. There was also a significant interaction effect between depletion and age group $F_{(1,122)} = 6.13$, $p = .015$, $\eta^2 = .002$, $BF_{10} = 4.393e\text{-}26$. Post hoc tests using the Bonferroni correction demonstrated that adults' deviation from the optimum did not change significantly between fast and slow depleting environments ($p_{bonf} = .508$), whereas adolescents were significantly less optimal in slow depleting environments compared to fast depleting environments ($p_{bonf} < 001$). As adolescents did not adjust their leaving threshold to the same extent as adults in response to changes to the depletion rate, they exhibited greater suboptimality in the slow depletion environments compared to the fast depletion environments. However, there were no interactions between travel time and depletion rate $F_{(1,122)} = 0.36$, $p = .552$, travel time and age group $F_{(1,122)} = 1.149e\text{-}4$, $p = .991$, nor travel time, depletion rate and age group $F_{(1,122)} = 1.26$, $p = .264$ (see Table 2).

Consistent with these findings, adolescents accumulated a higher average number of apples in each environment ($M = 650.82$, $SD = 99.50$) compared to adults ($M = 626.71$, $SD = 95.05$). However, this difference was not statistically significant as demonstrated by a mixed ANOVA $F_{(1, 130)} = 1.04$, $p = .310$, though the Bayes factor demonstrated extreme evidence for the alternative hypothesis (i.e. that adolescents accumulated a higher average number of rewards compared to adults) $BF_{10} = 4.342e\text{-}86$. This inconsistency could be attributed to the probabilistic nature of the reward schedule. Consistent with MVT, there was a main effect of depletion rate $F_{(1,130)} = 216.27$, $p < .001$, $BF_{10} = 2.280e\text{-}67$ and travel time $F_{(1,130)} = 443.62$, $p < .001$, $BF_{10} = 9.617e\text{-}39$, with participants accumulating a higher number of rewards in richer environments compared to poorer environments (see Table 2). In addition, there was an interaction effect between travel time and depletion rate $F_{(1,130)} = 13.72$, $p < .001$, $BF_{10} = 0.027$, but no interaction between depletion rate and age group $F_{(1, 130)} = 3.26$, $p = .073$, travel time and age group $F_{(1, 130)} = 0.02$, $p = .890$, nor depletion rate, travel time and age group $F_{(1, 130)} = 0.75$, $p = .389$.

Table 2: Mean (SD) of participants' deviation from the optimum and number of apples accumulated in each environment

	Adolescent deviation from the optimum	Adult deviation from the optimum	Adolescent number of apples accumulated	Adult number of apples accumulated
Environment 1	0.66 (1.98)	1.80 (1.89)	675.01 (105.35)	652.36 (110.64)
Environment 2	0.85 (1.72)	1.99 (1.76)	724.60 (135.12)	711.77 (108.73)

Environment 3	-0.46 (1.85)	0.78 (1.95)	588.77 (91.59)	529.94 (76.45)
Environment 4	0.23 (1.82)	1.00 (1.74)	633.13 (113.16)	629.25 (105.12)
Total	0.30 (1.84	1.37 (1.84)	650.82 (99.50)	626.71 (95.05)

To examine whether patch foraging behaviour was predicted by any of the disposition measures, we conducted a linear regression. When the BAS subscales, the BIS and the Barratt-11 were all entered as predictors of participants' deviation from the optimum threshold, the model was not significant $F_{(5,132)} = 1.05$, $p = .393$, $R^2 = 0.04$, nor were any individual predictors significant ($ps > .05$). Following this, a second regression model was conducted with the addition of interaction terms to account for the interaction between age group and the disposition measures. Consistent with our previous analysis, none of the predictors were significant and we did not find evidence of an interaction effect between participants' age group and any of the disposition measures ($ps > .05$).

Exploratory Analyses

As the gender split between the adult and adolescent sample was imbalanced, we first ran our model including gender as a covariate in a mixed 2x2x2 ANCOVA. Following this, we entered gender as an additional fixed factor into a 2x2x2x2 ANOVA to examine whether foraging performance differed as a main effect of gender. These analyses suggested gender did not appreciably affect the results, as foraging behaviour differed between age groups but not genders (see Supplementary Material).

<div align="center">

Discussion

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Adolescents Exhibit Heightened Exploration During Patch Foraging

Although risk and novelty-seeking during adolescence have often been associated with negative consequences, recent theories have proposed that these tendencies can in fact be beneficial. The present study utilised a realistic decision-making problem that is almost universal across animal species: patch foraging. Adolescents had higher leaving thresholds across all four patch foraging environments, which meant this group explored more than adults. This behaviour was also closer to the optimal foraging behaviour as defined computationally using MVT. In line with previous research (Constantino & Daw, 2015; Le Heron et al., 2020; Lenow et al., 2017), our results demonstrated that adults remained with individual patches for longer than the optimal strategy would dictate. These findings indicate that heightened exploration during adolescence can be beneficial when exploration is associated with rewarding outcomes, which can support this age group to gain experiential knowledge of their surroundings.

The present findings extend upon the current patch foraging literature, which has previously demonstrated that human adults are suboptimal patch foragers (e.g. Le Heron et al., 2020). Whilst multiple studies have shown that human adults overexploit patches, our findings indicate that adolescents did not demonstrate this pattern of overexploiting to the same degree as adults, meaning their behaviour was closer to the optimal patch foraging strategy.

Adolescents' predisposition for exploration has been attributed to the hyperactivity of the dopaminergic reward system, motivating this age group to seek novel sensations and experiences (van Leijenhorst et al., 2010). In the current patch foraging paradigm, new patches represented novel opportunities, as each tree was only visited once. Adolescents' behaviour was therefore consistent with a pattern of heightened novelty-seeking relative to adult participants. Importantly, however, adolescents' predisposition for exploration was not indiscriminate, as they adjusted their leaving thresholds according to changes in the inter-patch travel time between the different environments. While the difference was not statistically

significant, we also found that adolescents adjusted their leaving thresholds according to changes in the depletion rate. Adolescents' suboptimality between conditions with fast and slow depletion rates was primarily driven by overexploiting in the richest quality environment (environment 2), which had the highest optimal leaving threshold. However, in environment 4, which also had a slow depletion rate, adolescents were close to the optimal leaving threshold. As such, the finding that adolescents did not adjust their behaviour to changes in the depletion rate could be due to the high leaving threshold required in the richest environment, rather than an insensitivity towards this change in the environment.

Heightened novelty-seeking in the second decade of life has also been associated with the increased rates of risk behaviour observed in adolescence relative to other age groups (Steinberg, 2008). In the context of patch foraging, previous research has demonstrated that adults' tendency to overexploit is explained by a parameter capturing risk sensitivity (Constantino & Daw, 2015). That adolescents explored more than adults could indicate that heightened levels of novelty-seeking were associated with diminished risk sensitivity in this age group, but this tolerance for risk led to more optimal outcomes compared to risk-averse adults. In contrast to recent research (Bach, Moutoussis, Bowler, Neuroscience in Psychiatry Network consortium & Dolan, 2020), we did not find gender differences in foraging behaviour in a developmental sample. The current study suggests that when exploration is associated with opportunity, adolescents' propensity for heightened exploration can be beneficial. In scenarios where exploration can lead to negative outcomes (as in some behavioural tasks e.g. the Balloon Analogue Risk Task; Lejuez et al., 2002), the same predisposition for exploration can lead to suboptimal outcomes (Peper, Braams, Blankenstein, Bos & Crone, 2018). Taken together, these findings demonstrate how adolescents' novelty-seeking can lead to both positive and negative outcomes for this age group (Patterson et al., 2019).

These findings build on evidence of developmental differences in ambiguity tolerance. Compared to other age groups, adolescents are more tolerant to variable outcomes and thus riskier choices where the probabilities involved in the decisions are unknown (van den Bos & Hertwig, 2017). In the present patch foraging paradigm, participants were not aware of the distribution of rewards in novel patches and therefore exploration required tolerance of an ambiguous outcome. Adolescents invested less time in the known option, instead choosing to explore the unknown, ambiguous opportunity. Through using a serial decision-making task, our findings contribute evidence that adolescents are more motivated than adults to explore ambiguous options and that this can lead to more optimal outcomes.

The use of complex exploration strategies develops in later adolescence and remains into adulthood, which can support individuals to effectively navigate their environment (Jepma et al., 2020; Somerville et al., 2017). In contrast to our findings, previous work has demonstrated that adolescents prefer to exploit a known option for an immediate reward rather than explore a novel one to gain information about their surroundings (Somerville et al., 2017). However, in this study, adolescents only preferred the high reward option when this was incongruent with the high information option. Further work examining the development of explore/exploit strategies has found that adolescents explore more than is optimal, leading them to accrue fewer rewards than adults (Xia et al., 2020). In the present patch foraging paradigm, relative to adults' performance, heightened levels of exploration were congruent with the high reward option, as this raised the average reward rate according to MVT.

When examining the development of strategic exploration, previous research has demonstrated that directed exploration emerges in late adolescence and stabilises in adulthood, whereas random exploration is age-invariant (Somerville et al., 2017). Random exploration involves introducing stochasticity into one's decisions, which can lead the agent to select the option perceived to have the lower reward (Gershman, 2018). While this exploration strategy

can be beneficial for uncovering information about the environment (Wilson et al., 2014), it is less precisely tuned to the structure of that environment (Somerville et al., 2017). The use of random exploration strategies in adolescence may have contributed to the finding that this age group adjusted their leaving threshold to a lesser extent in response to changes in the depletion rate, as their behaviour was influenced by a stochastic process that was less finely calibrated to the structure of the environments.

Taken in context of previous studies, our findings highlight that adolescents' reward seeking behaviour and heightened propensity for exploration can complement one another when exploration is associated with reward. This may afford adolescents opportunities that are forfeited by other age groups that are averse to uncertain outcomes (for example, trialling out for a new sports team or going to a summer camp). As such, our findings contribute to understanding when adolescents' heightened exploration can lead to positive outcomes for this age group.

The Benefits of Exploration in Adolescence

Heightened exploration during adolescence supports this age group to gain experience of novel scenarios, which can be utilised to guide future decisions (Romer et al., 2017). At the onset of puberty, there is increased activation of the dopaminergic reward network (van Leijenhorst et al., 2010), which promotes novelty-seeking behaviour (Costa, Tran, Turchi & Averbeck, 2014). Further, adolescents are motivated to employ cognitive control resources to explore unknown scenarios that can yield information about the probability structure of their environment (Do et al., 2019). Consistent with this account, adolescents in the present study were motivated to seek out novel patches, which required the deployment of cognitive resources to engage in effortful exploration rather than choosing the comparatively less taxing option of exploiting the known option (Daw et al., 2006; Do et al., 2019; Otto et al., 2011).

According to the Lifespan Wisdom Model, this decision-making strategy is employed across adolescence to aid adolescents to learn about their surrounding environment (Romer et al., 2017). The information gained through foraging is then subsequently exploited later in life (Mata, Wilke & Czienskowski, 2013). Findings from the present study support this account, as when adolescents were faced with an unknown environment, these participants were motivated to explore in order to effectively navigate this novel scenario compared to adults. Heightened exploration in adolescence may therefore be considered adaptive within the lifespan, as it supports the development of the individual's experiential knowledge in unknown scenarios (Ellis et al., 2012).

There are limitations to the present study that are important to consider. This study only measured exploration in relation to positive reward feedback. Previous research has demonstrated that adolescents respond differently to positive and negative feedback (McCormick & Telzer, 2017). Future studies should consider whether adolescents are able to utilise optimal decision-making strategies when exploring novel scenarios to avoid negative outcomes, as well as acquire rewards. Further, the environmental parameters utilised in the present study were more suited to strategies that required higher levels of exploration rather than exploitation. As such, adolescents' more optimal performance could be due to the structure of the environments rather than their ability to effectively navigate patches. However, we note that adolescents were more optimal in environments with fast depletion rates, where the optimal strategy is to explore less, suggesting this age group were better able to estimate the optimal leaving threshold when less exploration was required. Nevertheless, future research could consider designing environments with a wider range of environmental parameters to test whether adolescents retain their optimality in foraging scenarios that favour less exploration.

This study has implications for our understanding of the role of adolescence within the lifespan. Our findings indicate that exploration plays a key role at this developmental stage and

can support individuals to benefit from novel opportunities available to them. As such, priority should be given to facilitating adolescents' exploration and providing them with the opportunity to learn in unfamiliar scenarios. The importance of allowing developmentally-appropriate levels of exploration and learning are currently highlighted in safeguarding documents for young people (NHS England, 2015). Findings of the present study support these guidelines as adolescents require exposure to novel experiences in order to develop knowledge of their surroundings.

Overall, findings of the present study suggest that compared to adults, adolescents exhibit heightened rates of exploration in novel, unknown environments. Contributing to the patch foraging literature, we replicate findings that adults overexploit patches compared to the optimal foraging strategy. Our findings suggest that when exploration is associated with reward, adolescents' heightened propensity for exploration and reward-driven behaviour can be beneficial, leading this age group to exhibit more optimal behaviour relative to adults. This strategy of novelty-seeking behaviour can allow this age group to benefit from novel opportunities and gain experience at the developmental stage where the individual transitions from childhood dependence to adult independence.

References

Andrews-Hanna, J. R., Seghete, K. L. M., Claus, E. D., Burgess, G. C., Ruzic, L., & Banich, M. T. (2011). Cognitive control in adolescence: neural underpinnings and relation to self-report behaviors. *PloS one*, *6*(6), e21598.

Anwyl-Irvine, A. L., Massonnié, J., Flitton, A., Kirkham, N., & Evershed, J. K. (2019). Gorilla in our Midst: An online behavioral experiment builder. *Behavior Research Methods*, 1-20.

Arnett, J. J. (2002). Developmental sources of crash risk in young drivers. *Injury Prevention*, *8*, ii17-ii23.

Bach, D. R., Moutoussis, M., Bowler, A., Neuroscience in Psychiatry Network consortium, & Dolan, R. J. (2020). Predictors of risky foraging behaviour in healthy young people. *Nature Human Behaviour*, 1-12.

Behrens, T. E., Woolrich, M. W., Walton, M. E., & Rushworth, M. F. (2007). Learning the value of information in an uncertain world. *Nature Neuroscience*, *10*(9), 1214-1221.

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.

Carskadon, M. A., & Acebo, C. (1993). A self-administered rating scale for pubertal development. *Journal of Adolescent Health*, *14*(3), 190-195.

Carver, C. S., & White, T. L. (1994). Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: the BIS/BAS scales. *Journal of Personality and Social Psychology*, *67*(2), 319-333.

Casey, B. J., Getz, S., & Galvan, A. (2008). The adolescent brain. *Developmental Review*, *28*(1), 62-77.

Chamorro, J., Bernardi, S., Potenza, M. N., Grant, J. E., Marsh, R., Wang, S., & Blanco, C. (2012). Impulsivity in the general population: a national study. *Journal of Psychiatric Research*, *46*(8), 994-1001.

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, *9*(2), 129-136.

Cohen, S. E., & Todd, P. M. (2018). Relationship foraging: Does time spent searching predict relationship length? *Evolutionary Behavioral Sciences*, *12*(3), 139-151.

Constantino, S. M., & Daw, N. D. (2015). Learning the opportunity cost of time in a patch-foraging task. *Cognitive, Affective, & Behavioral Neuroscience*, *15*(4), 837-853.

Costa, V. D., Tran, V. L., Turchi, J., & Averbeck, B. B. (2014). Dopamine modulates novelty seeking behavior during decision making. *Behavioral Neuroscience*, *128*(5), 556-566.

Daw, N. D., O'Doherty, J. P., Dayan, P., Seymour, B., & Dolan, R. J. (2006). Cortical substrates for exploratory decisions in humans. *Nature*, *441*(7095), 876.

Do, K. T., Moreira, J. F. G., & Telzer, E. H. (2017). But is helping you worth the risk? Defining prosocial risk taking in adolescence. *Developmental Cognitive Neuroscience*, *25*, 260-271.

Do, K. T., Sharp, P. B., & Telzer, E. H. (2019). Modernizing Conceptions of Valuation and Cognitive-Control Deployment in Adolescent Risk Taking. *Current Directions in Psychological Science*, 0963721419887361.

Dubois, M., Aislinn, B., Moses-Payne, M. E., Habicht, J., Steinbeis, N., & Hauser, T. U. (2020). Tabula-rasa exploration decreases during youth and is linked to ADHD symptoms. *bioRxiv*.

Duell, N., & Steinberg, L. (2019). Positive risk taking in adolescence. *Child Development Perspectives*, *13*(1), 48-52.

Eaton, D. K., Kann, L., Kinchen, S., Shanklin, S., Flint, K. H., Hawkins, J., ... & Whittle, L. (2012). Youth risk behavior surveillance—United States, 2011. *Morbidity and Mortality Weekly Report: Surveillance Summaries*, *61*(4), 1-162.

Ellis, B. J., Del Giudice, M., Dishion, T. J., Figueredo, A. J., Gray, P., Griskevicius, V., ... & Wilson, D. S. (2012). The evolutionary basis of risky adolescent behavior: Implications for science, policy, and practice. *Developmental Psychology*, *48*(3), 598-623.

Faul, F., Erdfelder, E., Lang, A. G., & Buchner, A. (2007). G* Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, *39*(2), 175-191.

Gabay, A. S., & Apps, M. A. (2019). Foraging Optimally in Social Neuroscience: Computations and Methodological considerations. *Social Cognitive and Affective Neuroscience*, nsaa037.

Garrett, N., & Daw, N. D. (2020). Biased belief updating and suboptimal choice in foraging decisions. *Nature Communications*, *11*(1), 1-12.

Gershman, S. J. (2018). Deconstructing the human algorithms for exploration. *Cognition*, *173*, 34-42.

JASP Team (2019). JASP (Version 0.11.1)[Computer software].

Jepma, M., Schaaf, J. V., Visser, I., & Huizenga, H. (2020). Uncertainty-driven regulation of learning and exploration in adolescents: A computational account. *bioRxiv*.

Le Heron, C., Kolling, N., Plant, O., Kienast, A., Janska, R., Ang, Y. S., ... & Apps, M. (2020). Dopamine modulates dynamic decision-making during foraging. *Journal of Neuroscience*, *40(27),* 5273-5282.

Lejuez, C. W., Read, J. P., Kahler, C. W., Richards, J. B., Ramsey, S. E., Stuart, G. L., ... & Brown, R. A. (2002). Evaluation of a behavioral measure of risk taking: the Balloon Analogue Risk Task (BART). *Journal of Experimental Psychology: Applied*, *8*(2), 75.

Lenow, J. K., Constantino, S. M., Daw, N. D., & Phelps, E. A. (2017). Chronic and acute stress promote overexploitation in serial decision making. *Journal of Neuroscience*, *37*(23), 5681-5689.

Marques, J. C., Li, M., Schaak, D., Robson, D. N., & Li, J. M. (2019). Internal state dynamics shape brainwide activity and foraging behaviour. *Nature*, 1-5.

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.

Mata, R., Wilke, A., & Czienskowski, U. (2013). Foraging across the life span: is there a reduction in exploration with aging? *Frontiers in Neuroscience*, *7*, 1-7.

McCormick, E. M., & Telzer, E. H. (2017). Failure to retreat: Blunted sensitivity to negative feedback supports risky behavior in adolescents. *NeuroImage*, *147*, 381-389.

Moffitt, T. E. (2018). Male antisocial behaviour in adolescence and beyond. *Nature Human Behaviour*, *2*(3), 177-186.

Murty, V. P., Calabro, F., & Luna, B. (2016). The role of experience in adolescent cognitive development: Integration of executive, memory, and mesolimbic systems. *Neuroscience & Biobehavioral Reviews*, *70*, 46-58.

NHS England. (2015). *Safeguarding Policy*. Leeds: Nursing Directorate.

Office for National Statistics. (2009). Final recommended questions for the 2011 Census in England and Wales: Ethnic group.

Otto, A. R., Skatova, A., Madlon-Kay, S., & Daw, N. D. (2014). Cognitive control predicts use of model-based reinforcement learning. *Journal of Cognitive Neuroscience*, *27*(2), 319-333.

Patterson, M. W., Pivnick, L., Mann, F. D., Grotzinger, A. D., Monahan, K. C., Steinberg, L. D., ... & Harden, K. P. (2019). Positive risk-taking: Mixed-methods validation of a self-report scale and evidence for genetic links to personality and negative risk-taking. *PsyArXiv,* 1-45.

Patton, J. H., Stanford, M. S., & Barratt, E. S. (1995). Factor structure of the Barratt impulsiveness scale. *Journal of Clinical Psychology*, *51*(6), 768-774.

Peper, J. S., Braams, B. R., Blankenstein, N. E., Bos, M. G., & Crone, E. A. (2018). Development of multifaceted risk taking and the relations to sex steroid hormones: A longitudinal study. *Child Development*, *89*(5), 1887-1907.

R Core Team (2018). R: A language and environment for statistical computing. *R Foundation for Statistical Computing*, Vienna, Austria. URL http://www.R-project.org/

Romer, D. (2010). Adolescent risk taking, impulsivity, and brain development: Implications for prevention. *Developmental Psychobiology: The Journal of the International Society for Developmental Psychobiology*, *52*(3), 263-276.

Romer, D., Reyna, V. F., & Satterthwaite, T. D. (2017). Beyond stereotypes of adolescent risk taking: Placing the adolescent brain in developmental context. *Developmental Cognitive Neuroscience*, *27*, 19-34.

Shulman, E. P., Smith, A. R., Silva, K., Icenogle, G., Duell, N., Chein, J., & Steinberg, L. (2016). The dual systems model: Review, reappraisal, and reaffirmation. *Developmental Cognitive Neuroscience*, *17*, 103-117.

Smith, E. A. (1983). Anthropological applications of optimal foraging theory: A critical review. *Current Anthropology*, *24*(5), 625-651.

Somerville, L. H., Sasse, S. F., Garrad, M. C., Drysdale, A. T., Abi Akar, N., Insel, C., & Wilson, R. C. (2017). Charting the expansion of strategic exploratory behavior during adolescence. *Journal of Experimental Psychology: General*, *146*(2), 155-164.

Spear, L. P. (2000). The adolescent brain and age-related behavioral manifestations. *Neuroscience & Biobehavioral Reviews*, *24*(4), 417-463.

Steinberg, L. (2008). A social neuroscience perspective on adolescent risk-taking. *Developmental Review*, *28*(1), 78-106.

Steinberg, L., Icenogle, G., Shulman, E. P., Breiner, K., Chein, J., Bacchini, D., ... & Fanti, K. A. (2018). Around the world, adolescence is a time of heightened sensation seeking and immature self-regulation. *Developmental Science*, *21*(2), e12532.

Stephens, D. W., & Krebs, J. R. (1986). *Foraging Theory*. Princeton University Press: Princeton, NJ

Tymula, A., Belmaker, L. A. R., Roy, A. K., Ruderman, L., Manson, K., Glimcher, P. W., & Levy, I. (2012). Adolescents' risk-taking behavior is driven by tolerance to ambiguity. *Proceedings of the National Academy of Sciences*, *109*(42), 17135-17140.

Urošević, S., Collins, P., Muetzel, R., Lim, K., & Luciana, M. (2012). Longitudinal changes in behavioral approach system sensitivity and brain structures involved in reward processing during adolescence. *Developmental Psychology*, *48*(5), 1488.

Van Den Bos, W., & Hertwig, R. (2017). Adolescents display distinctive tolerance to ambiguity and to uncertainty during risky decision making. *Scientific Reports*, *7*, 40962, 1-11.

Van Den Bos, W., Rodriguez, C. A., Schweitzer, J. B., & McClure, S. M. (2015). Adolescent impatience decreases with increased frontostriatal connectivity. *Proceedings of the National Academy of Sciences*, *112*(29), E3765-E3774.

Van Leijenhorst, L., Moor, B. G., de Macks, Z. A. O., Rombouts, S. A., Westenberg, P. M., & Crone, E. A. (2010). Adolescent risky decision-making: neurocognitive development of reward and control regions. *Neuroimage*, *51*(1), 345-355.

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.

Wilson, R. C., Geana, A., White, J. M., Ludvig, E. A., & Cohen, J. D. (2014). Humans use directed and random exploration to solve the explore–exploit dilemma. *Journal of Experimental Psychology: General*, *143*(6), 2074.

Xia, L., Master, S., Eckstein, M., Wilbrecht, L., & Collins, A. G. (2020, July). Learning under uncertainty changes during adolescence. *Proceedings of the Cognitive Science Society*.