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Cite this article: Suter HF, Radford AN, Houston AI. 2026 Self-control: changing our perspective on performance. *Proc. R. Soc. B* **293**: 20260488.
https://doi.org/10.1098/rspb.2026.0488

Received: 25 February 2026
Accepted: 1 June 2026

Subject Category:
Neuroscience and cognition

Subject Areas:
cognition, theoretical biology, behaviour

Keywords:
self-control, comparative cognition, cognitive evolution, cognitive performance, optimal foraging theory, rate maximization

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Self-control: changing our perspective on performance

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To measure self-control in non-human animals, subjects are typically tested on how long they will wait for a larger–later food reward instead of taking a smaller–sooner food reward. Animals that wait longer are deemed to have exhibited better self-control. We develop an optimal foraging model to show that waiting for longer for a larger–later food reward does not always increase fitness whereas minimizing the difference between predicted and observed wait times does—a measure we propose as a novel performance metric. We use our model to generate qualitative predictions that capture trends in wait times observed in empirical studies across species. Moreover, we show that, all else being equal, waiting time increases with basal metabolic rate. Together, our results suggest that variation in wait times may be better understood in the context of animals attempting to meet their individual metabolic demands rather than an inability to wait. Our work raises questions about a large body of empirical support for key hypotheses in cognitive evolution, while our novel performance metric provides a framework for future empirical work to compare self-control appropriately between species.

1. Introduction

To measure self-control in non-human animals, subjects are typically tested on how long they will wait for a larger–later food reward at the expense of a smaller–sooner food reward [1], with wait times commonly used as the basis to compare cognition between species (e.g. [1–6]). Self-control is thought to require the use of two cognitively demanding abilities in tandem: future planning is required for an animal to decide if it is better to wait for the larger–later reward, while inhibitory control is required to resist the immediacy of the smaller–sooner reward [7–9]. Thus, waiting for longer is believed to be more cognitively demanding because it requires an animal to plan further into the future and resist the currently available reward for longer (e.g. [2–4,6,10,11]). It is also thought to be a pivotal cognitive mechanism in the evolution of complex social systems and foraging behaviours. For example, the ability to wait for longer may be essential in generating cooperative outcomes with conspecifics, thus allowing the formation of stable and consistent relationships [12,13]. In the context of foraging, waiting for longer is probably an important basis for the evolution of behaviours that require an initial investment of time before any energy is gained, such as extractive foraging [1,2], innovation [8,14] and tool use [15,16]. Finally, the ability to wait for longer has been shown to correlate with general intelligence and reversal learning, suggesting that it may be a hallmark of advanced cognition [10,11]. Hence, there has been considerable use of food-based self-control tasks to compare cognition across a wide range of taxonomic groups from ants to humans [2,8,17].

To establish how long animals are willing to wait for a larger–later food reward, they are typically given Mazur's [18] classic delay-choice procedure

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or the delay-maintenance procedure [19]. In both procedures, animals are initially offered a simultaneous choice between a small and a large food reward with no delay. Assuming the animal consistently chooses the larger reward, the delay to its awarding is increased over multiple trials until the subject consistently chooses the smaller–sooner reward. The delay to the larger–later reward is then decreased and increased in a titration-style procedure until the subject chooses both rewards with equal probability. The delay to the larger–later reward at which both rewards are chosen with equal probability is known as the 'indifference point' or the 'wait time' (the term we use hereafter). The two procedures mainly differ in when animals can choose the smaller–sooner reward. In the delay-choice procedure, the smaller–sooner reward is not an option after the animal has made their initial decision [18]. By contrast, in the delay-maintenance procedure, subjects have the option to choose the smaller–sooner reward for the entirety of the delay experienced until receiving the larger–later reward [19]. The larger–later reward may also accumulate during the delay until its receipt in the delay-maintenance procedure, to control against animals biassing their decisions towards the larger size of the larger–later reward [20]. The delay-maintenance procedure may therefore be more ecologically relevant because it represents a scenario in which an animal has the choice of leaving a foraging patch that is currently available. To standardize testing across species, animals are typically given the same reward ratio between the larger and smaller rewards (often 3v1). The magnitude of the rewards themselves can vary (e.g. 3v1 and 6v2) because wait times in non-human animals have previously been shown to be unaffected by differences in reward magnitudes for the same reward magnitude ratio [21]. Both the delay-choice and delay-maintenance procedures have now been successfully adapted to different taxonomic groups, thereby generating wait time data across a wide range of species.

The species tested thus far using these procedures have all shown an ability to wait for at least some time for the larger–later reward, but how long they are willing to wait ranges from a few seconds to a few minutes (table 1). Given the convenience of measuring wait times, they have formed the basis of investigations into some of the most important topics in cognitive evolution. For example, interspecific variation in wait times has been used to provide support for the two leading hypotheses of cognitive evolution: the 'social intelligence hypothesis'—the idea that increasing complexity in social environment drives cognitive evolution [26,27]; and the 'ecological intelligence hypothesis'—the idea that ecological factors such as foraging ecology drive cognitive evolution [28]. Comparisons of wait times have also been used to demonstrate a positive association between absolute brain size and cognitive ability in primates [4]. Finally, changes in wait times in individual animals have been used to investigate the evolution of behaviours that may help to increase wait times, such as 'self-distraction' [29]. However, these comparisons rely on the assumption that species that wait for longer have exhibited greater self-control, an assumption with which we do *not* agree.

One way to investigate waiting times is to estimate the discount function: that is, the function that describes how the value of a reward decreases with the time the organism has to wait before obtaining it (e.g. [18,30]). An alternative is to link behaviour to evolutionary success [31–33]. We follow the latter approach. Longer wait times will only be selected for if they increase fitness under natural foraging conditions. When choosing between foraging options—between the larger–later and smaller–sooner rewards in food-based self-control tasks—a plausible starting point is to identify optimal behaviour with the choice that maximizes the net rate of energy intake [34]. This fundamental trade-off between energy gained and energy spent to obtain each reward over time, which drives the evolution of foraging behaviour [34], is rarely acknowledged or discussed in the self-control literature (e.g. [1,2,22]; for an exception, see [32]). Instead, previous work has compared observed wait times with predicted wait times using models of gross rate (e.g. [1,22,35]). These attempts have failed to predict observed wait times consistently. Given that the energy gained from both rewards, the delay to the smaller reward and the cost of choosing the smaller–sooner reward remain the same in self-control tasks, while the delay to the larger–later reward and therefore the energetic cost to obtain it increases, it is inevitable that both the gross and net rates of energy intake associated with the larger–later reward would be less than for the smaller–sooner reward after a sufficient delay [1,32,36]. At this point, fitness will be increased by selecting the smaller–sooner reward; a longer wait time should *not* be selected for indefinitely.

To explore the effect of energetic costs, we model the net rate of energy intake gained from each food reward with increasing delay to the larger–later food reward, calculating the fitness consequences of choosing each reward. That is, we simulate a generic version of food-based self-control tasks that can represent any larger–later reward paradigm including the delay-choice and delay-maintenance procedures. In keeping with previous work, we find a 'critical delay' beyond which subjects increase their net rate of gain by choosing the smaller–sooner reward. However, we show that minimizing the difference between observed and predicted wait times, rather than continuing to wait for longer, always increases the net rate of gain. Next, we compare predictions from our model with existing data and show that animals change their wait times as if to minimize this difference. In doing so, we question a cornerstone finding in the field by showing that longer wait times in larger-brained species could be a result of higher metabolic rates, not enhanced cognition and complex socioecology. Finally, we lay out a framework for future empirical work to use models like ours that assess the difference between predicted and observed wait times to compare performance appropriately in self-control tasks.

2. Modelling and results

(a) Modelling net rate of energy intake in food-based self-control tasks

We follow Kacelnik [32] in modelling choice in experiments on the basis of maximizing the net rate of gain but extend the analysis to include, explicitly, energy expenditure over the whole cycle of choice. To obtain a reward in food-based self-control tasks, an animal is required to wait for the reward option that it chooses and then handle the chosen food reward to consume it. Thus, to model net rate of energy intake, we need to account for the time and energy spent in waiting for and handling each

Table 1. Mean wait times (s) for a larger–later reward at the expense of a smaller–sooner reward in different species generated using Mazur's [18] delay-choice procedure. The reward ratio between the larger–later and smaller–sooner rewards used for each species is included. Data have been reformatted from the electronic supplementary material in Steven & Mühlhoff [22].

species	wait time (s)	sample size	reward ratio	body mass (g)	reference
white Carneau pigeon (*Columba livia*)	4.93	7	30v5	273	Green *et al.* [23]
cotton-top tamarin (*Saguinus oedipus*)	7.88	6	6v2	431	Stevens *et al.* [1]
wistar rat (*Rattus norvegicus*)	10.26	21	3v1	390	Perry *et al.* [24]
common marmoset (*Callithrix jacchus*)	14.36	5	6v2	320	Stevens *et al.* [1]
black lemur (*Eulemur macaco*)	14.80	1	6v2	2390	Stevens & Mühlhoff [22]
red-ruffed lemur (*Varecia rubra*)	16.60	1	6v2	3470	Stevens & Mühlhoff [22]
black-and-white-ruffed lemur (*Varecia variegata*)	17.87	3	6v2	3575	Stevens & Mühlhoff [22]
brown capuchin (*Cebus apella*)	21.67	12	3v1	2936	Amici *et al.* [3]
long-tailed macaque (*Macaca fascicularis*)	24.33	12	3v1	4251	Amici *et al.* [3]
long-tailed macaque (*Macaca fascicularis*)	38.80	2	6v2	4251	Tobin *et al.* [25]
lowland gorilla (*Gorilla gorilla*)	44.00	4	3v1	120 950	Amici *et al.* [3]
orangutan (*Pongo pygmaeus*)	49.63	8	3v1	58 542	Amici *et al.* [3]
bonobo (*Pan paniscus*)	74.40	5	6v2	39 100	Rosati *et al.* [2]
black-handed spider monkey (*Ateles geoffroyi*)	76.00	12	3v1	7535	Amici *et al.* [3]
brown capuchin (*Cebus apella*)	81.13	16	6v2	2936	Addessi *et al.* [16]
chimpanzee (*Pan troglodytes*)	122.60	5	6v2	44 967	Rosati *et al.* [2]

reward option, as well as the energy gained from each reward option. We do not include the time and energy costs associated with time between the end of one trial and the start of the next (the inter-trial interval) as many animals have been shown to ignore these intervals when choosing between reward options in self-control tasks ([32,37]; although [38] show some effect). By waiting, a foraging animal may gain information (e.g. [39]) but might also fail to obtain food because foraging is interrupted (e.g. [40]). We ignore these issues. We emphasize that we do not need to assume that animals explicitly calculate net rate in the experimental procedure; they may follow rules that approximate the optimal behaviour (see [33,41–45]).

Let option 1 represent the larger–later reward and option 2 the smaller–sooner reward. For each option, the gross energy gained is given by A_i, the delay is given by D_i and the time required to handle the reward is given by h_i. The larger–later reward is always larger and more delayed than the smaller–sooner reward, so we assume that $A_1 > A_2$, $D_1 > D_2$ and $h_1 > h_2$. The gross rate of energy gain, g_i, is therefore given by

$$g_i = \frac{A_i}{D_i + h_i}, \tag{2.1}$$

where $D_i + h_i$ is the total delay experienced to obtain a reward option. The net rate of energy intake, γ_i, is found by subtracting the rate of energy expenditure, e_i, from the gross rate of energy intake

$$\gamma_i = g_i - e_i. \tag{2.2}$$

The rate of energy expenditure is given by

$$e_i = \frac{m_i D_i + k_i m_i h_i}{D_i + h_i}, \tag{2.3}$$

where m_i is the subject's metabolic rate while waiting for a reward option and km_i is the subject's metabolic rate while handling a reward option. k is a multiplication factor that accounts for the change in metabolic rate when an animal switches from waiting to handling. k is expected to be greater than 1 as animals probably have a higher rate of energy expenditure while handling than waiting owing to the increase in movement required. We also expect the rate of energy expenditure while waiting and handling to be the same, whether exploiting the larger–later reward or the smaller–sooner reward; we therefore assume that $m_1 = m_2 = m$ and $k_1 = k_2 = k$. We substitute equations (2.1) and (2.3) into equation (2.2) to give a fully descriptive model of net rate of energy intake when choosing a reward option in self-control tasks

$$\gamma_i = \frac{A_i - mD_i - kmh_i}{D_i + h_i}. \tag{2.4}$$

It is worth noting that, while the psychological processes associated with the procedures may differ [19], the parameters and equations above are identical for both the delay-choice and delay-maintenance procedures. This is because the only procedural difference between them is the accessibility of the smaller–sooner reward during the delay to the larger–later reward. That does not affect the energy gained or spent, nor the delay experienced for either option (under the assumption that any potential

added cognitive effort in maintaining the decision in the delay-maintenance procedure does not result in a significant increase in metabolic rate while waiting).

(i) Simulating self-control tasks with our model

To simulate food-based self-control tasks and demonstrate how net rate of energy intake for both reward options changes as the delay to the larger–later reward increases, we plot net rate of energy intake for both reward options while increasing the delay to the larger–later reward and fixing all other parameters (figure 1a).

Figure 1a demonstrates that there is a specific delay to the larger–later reward at which both reward options give the same net rate of intake. We refer to this delay as the 'critical delay', D_1*, because net rate of energy intake is maximized by choosing a different reward option either side of this delay. The critical delay is found when

$$\gamma_1 = \gamma_2, \tag{2.5}$$

which is the same as

$$\frac{A_1 - mD_1 - kmh_1}{D_1 + h_1} = \frac{A_2 - mD_2 - kmh_2}{D_2 + h_2}. \tag{2.6}$$

The delay to the smaller–sooner reward in self-control tasks is negligible in the majority of experiments, so we assume that it is equal to 0 ($D_2 = 0$). It is possible to replicate the rarer experimental occurrence of a delay to both options by making $D_2 > 0$ and retaining it in equation (2.6) when rearranging to find the critical delay. When $D_2 = 0$, equation (2.6) therefore simplifies to

$$\frac{A_1 - mD_1 - kmh_1}{D_1 + h_1} = \frac{A_2 - kmh_2}{h_2}. \tag{2.7}$$

To produce an equation that predicts the critical delay, we rearrange equation (2.7) in terms of D_1 to give

$$D_1^* = \frac{Ah_2 - h_1}{1 - z}, \tag{2.8}$$

where A is the reward ratio between both reward options (we assume $A = A_1/A_2 > 1$ because the larger–later reward must always be larger than the smaller–sooner reward). z is the excess energy spent when choosing to handle the smaller–sooner reward rather than waiting for the larger–later reward (mh_2k–mh_2, which simplifies to mh_2y where $y = k - 1$) divided by the gross energy gained from the smaller–sooner reward. It is important to note that z fully encapsulates the influence of metabolic costs (as it includes m and y) and absolute reward magnitude (as it includes A_2) on the critical delay. z is given by

$$z = \frac{mh_2y}{A_2} \tag{2.9}$$

and must be smaller than 1. From equation (2.8), it can be seen that

$$\frac{\mathrm{d}D_1^*}{\mathrm{d}A} = \frac{h_2}{1 - z} \tag{2.10}$$

and

$$\frac{\mathrm{d}D_1^*}{\mathrm{d}h_1} = \frac{-1}{z}. \tag{2.11}$$

Our model of net rate of energy intake predicts the same critical delay as the model of gross rate of energy intake when handling food items does not increase an animal's metabolic rate from its value while waiting (i.e. when $y = 0$). The critical delay predicted by maximizing gross rate is given by

$$D_g^* = Ah_2 - h_1. \tag{2.12}$$

The ratio of the critical delays predicted by gross and net rate of energy intake is found by dividing one by the other, which gives

$$\frac{D_g^*}{D_1^*} = 1 - z. \tag{2.13}$$

Thus, the difference between the two critical delays is dependent on z, which is dependent on y. When $y = 0$, $z = 0$ equation (2.9) and so the critical delays are equal. We know from equations (2.8) and (2.9) that the critical wait time for net rate of energy intake increases as y increases. Using our model of net rate of intake, we therefore predict that animals will wait for longer than the wait times predicted by models of gross rate when rate of energy expenditure while handling is higher than that experienced while waiting (i.e. when $y > 0$) and shorter when $y < 0$. For the species studied by Stevens *et al.* [1] and Rosati *et al.* [35], z is small and hence D_1* is not much bigger than D_g*.

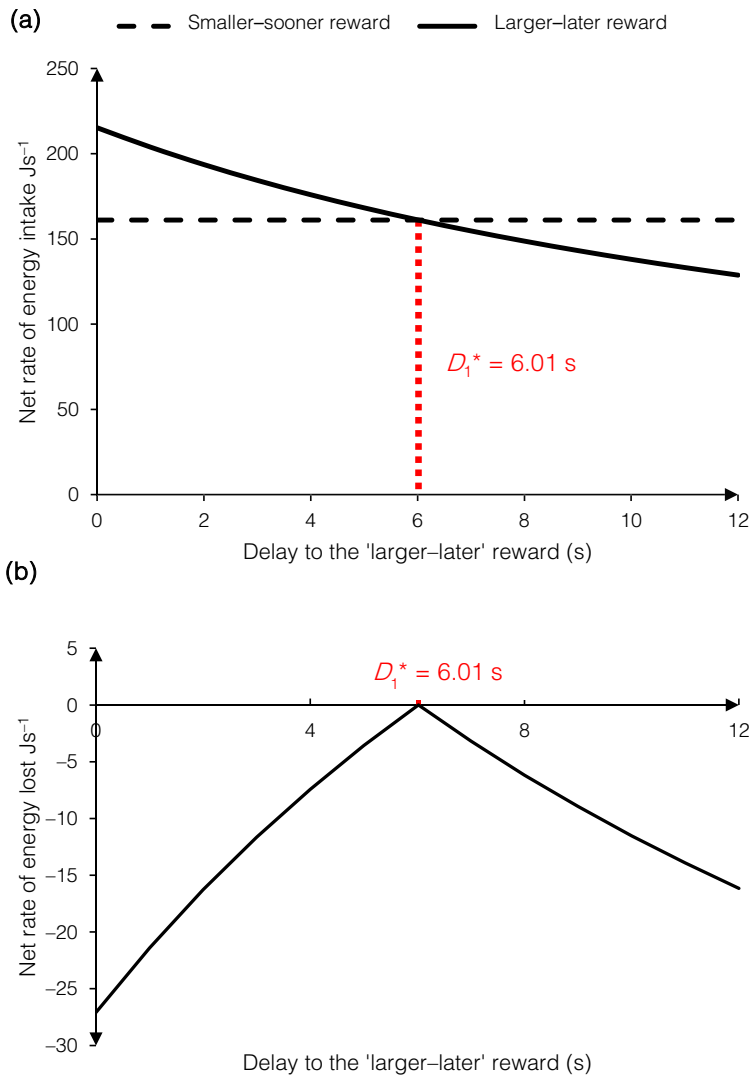

Figure 1. (a) Net rate of energy intake with increasing delay to the larger–later reward in food-based self-control tasks. The black solid line represents the net rate of energy intake obtained from the larger–later reward and the black dashed line represents that obtained from choosing the smaller–sooner reward. The red dotted line represents the delay at which the net rate of energy intake of both reward options is equal, which we refer to as the 'critical delay', D_1*. (b) Net rate of energy intake lost when choosing both rewards with equal probability in food-based self-control tasks over the optimal strategy with increasing delay to the larger–later reward. Before the critical delay, the optimal strategy is always to choose the larger–later reward as it yields the highest net rate of intake. After the critical delay, always choosing the smaller–sooner reward is the optimal strategy for the same reason. The indicated value of D_1* is for $A_1 = 3900$ J, $A_2 = 1300$ J, $h_1 = 18$ s, $h_2 = 8$ s, $m = 0.95$ J s^{-1}, $k = 1.5$ (below we work with $y = k - 1$) $D_2 = 0$ s. These values are based on existing data from a delay-choice experiment run with common marmosets, *Callithrix jacchus* [1]. A_1 and A_2 represent the total energetic value from the food pellets used for each reward option by Stevens *et al.* [1], and handling times h_1 and h_2 are the average handling times across five subjects for each reward option. m is calculated using an equation for basal metabolic rate (BMR) in primates given by Leonard *et al.* [46]. In terms of kcal day^{-1}, the equation is 55× body mass $^{(0.81)}$. Converting to J s^{-1} gives 2.66× body mass $^{(0.81)}$, which for a body mass for *C. jacchus* (0.28 kg) from Stevens *et al.* [1] gives BMR = 0.95 J s^{-1}. To our knowledge, a value for y for *Callithrix jacchus* has not been measured; we therefore use a multiplication value that describes the increase in metabolic rate from rest to sustained metabolic scope in another primate species that is also highly arboreal with similar patterns of locomotion, *Alouatta palliata* [47].

(b) Waiting for longer does not always increase fitness

The critical delay represents the only waiting time for the larger–later reward at which an animal can be indifferent towards which option it chooses while maximizing their net rate of energy intake. When the wait for the larger–later reward is shorter than the critical delay (i.e. when $D_1 < D_1$*), choosing the larger–later reward gives the highest net rate of intake (figure 1a). When the wait for the larger–later reward is longer than the critical delay (i.e. when $D_1 > D_1$*), choosing the smaller–sooner reward gives the highest net rate of intake (figure 1a). Thus, waiting for longer does not always increase fitness. This result is in keeping with previous models that also find a theoretical critical delay (e.g. [1,22,32,35]). The critical delay is also not the same for all animals: it is dependent on handling time (equations (2.8) and (2.9)), which has previously been shown for gross rate of intake by Rosati *et al.* [35], metabolic rate while waiting (equation 2.9) and metabolic rate while handling (equation 2.9). These subject-dependent parameters can vary greatly both within and between species. For example, handling times in cotton-top tamarins (*Saguinus oedipus*) for the larger–later reward varied between 16.5 and 46 s, while those for the smaller–sooner reward varied between 6.7 and 18.3 s [1]. Similarly, metabolic rate at rest (equivalent to metabolic rate while waiting) and increase in metabolic rate while moving have been shown to vary considerably both within and between taxonomic groups ([47]; their table 1).

(c) Minimizing the difference between predicted and observed wait times always increases fitness

If subjects exhibit a shorter wait time than the critical delay, they reduce their net rate of intake in comparison with always choosing the larger–later reward. Similarly, if subjects exhibit a longer wait time than the critical delay, they reduce their net rate of intake in comparison with choosing the smaller–sooner reward. This difference in net rate of intake between the two options reduces with closer proximity to the critical delay (figure 1a); a subject therefore minimizes the net energy intake lost by reducing the difference between the critical delay and their observed wait time. Minimizing this difference will therefore always increase fitness if net rate is the correct currency for assessing fitness. We demonstrate this by plotting the net rate of intake lost from choosing both rewards with equal probability over the option with the largest net rate of intake before and after the critical delay (i.e. when always choosing the larger–later reward before the critical delay and always the small–sooner reward after the delay; figure 1b).

(d) Comparing changes in observed wait times with qualitative predictions from our model

(i) Increasing handling time, h_1

Rosati *et al.* [35] used cottontop tamarins and common marmosets (*Callithrix jacchus*) to explore the influence of handling times on wait times. Subjects were given a choice between two immediate and six delayed food items at three different delays to the larger reward: 5, 10 and 15 s. The researchers increased the handling time required to consume a single food item and measured the proportion of trials in which subjects chose the larger reward at each delay ([35]; their fig. 3). In response to this increase in handling time, subjects reduced their preference for the larger–later reward. Rosati *et al.* ([35], p. 1380) argue that increasing the handling times should produce this result 'because the total amount of time necessary to acquire and process rewards is longer'. The general effect of handling time on wait time can be understood by considering gross rate.

From $D_g = Ah_2 - h_1$,
we see that $\mathrm{d}D_g/\mathrm{d}h_2 = A$
and $\mathrm{d}D_g/\mathrm{d}h_1 = -1$.

Because $A > 1$, a given increase in h_2 results in a greater increase in D_g than the decrease produced by the same increase in h_1. Thus, if both handling times are increased by the same amount, D_g will increase. If the handling time of option 1 is increased by t_1 and the handling time of option 2 is increased by t_2 then D_g will decrease if $t_2 < t_1/A$ and increase if $t_2 > t_1/A$.

Rosati *et al.* [35] increased the handling time of each option by adding an inter-pellet interval between each piece of food and the next one (see their fig. 1). This increases the immediate option by one inter-pellet interval and the delayed option by five inter-pellet intervals, which means that $t_2 < t_1/A$ and so D_g should decrease. To replicate Rosati *et al.*'s [35] experiment with our model, we have to move from establishing whether it is better to take the larger option to predicting the probability that this option will be chosen. If the optimal policy is followed exactly, the probability will be either zero or one, depending on whether the waiting time is smaller or larger than the critical time. The same sort of problem occurs in predicting the probability that a given type of prey is accepted [48]. One approach is to follow McNamara & Houston [48] and Houston [49] in using a softmax rule [50,51], which involves a parameter whose value we are free to choose. Instead, we take a simpler approach that involves no free parameters. (A softmax model can give qualitatively similar results.)

We assume that the probability p of choosing the larger–later reward is given by dividing the net rate of energy intake from choosing the larger–later reward, γ_1, by the sum of the net rate of energy intake of taking the larger–later and smaller–sooner options $\gamma_1 + \gamma_2$, i.e.

$$p = \frac{\gamma_1}{\gamma_1 + \gamma_2} \tag{2.14}$$

(cf. [52]).

We use this equation to investigate the effect of increasing both h_1 and h_2. The results are shown in figure 2. When we increase the handling time for the larger–later reward, we find the same qualitative effect as Rosati *et al.* [35]—the probability of choosing the larger–later reward decreases (figure 2a). The change in probability of choosing the larger–later reward generated from our model therefore matches the change in preference for the larger–later reward observed in Rosati *et al.*'s [35] experiment, suggesting that this change in preference can be explained on the basis of maximizing net rate of energy intake. However, if Rosati *et al.* [35] had increased handling times in such a way as to make $t_2 > t_1/A$ then the effect should be reversed (figure 2b).

(ii) Increasing the energetic costs as represented by *y* and *m*

It follows from equations (2.8) and (2.9) that $D_1{}^*$ increases with y and with m. We look at each of these parameters and compare their effects with changes in observed wait times from existing data. Chelonis *et al.* [53] gave male Sprague-Dawley rats a choice between a small reward after 0.1 s and a larger reward after 6 s; rewards were accessed by pulling a lever uniquely associated

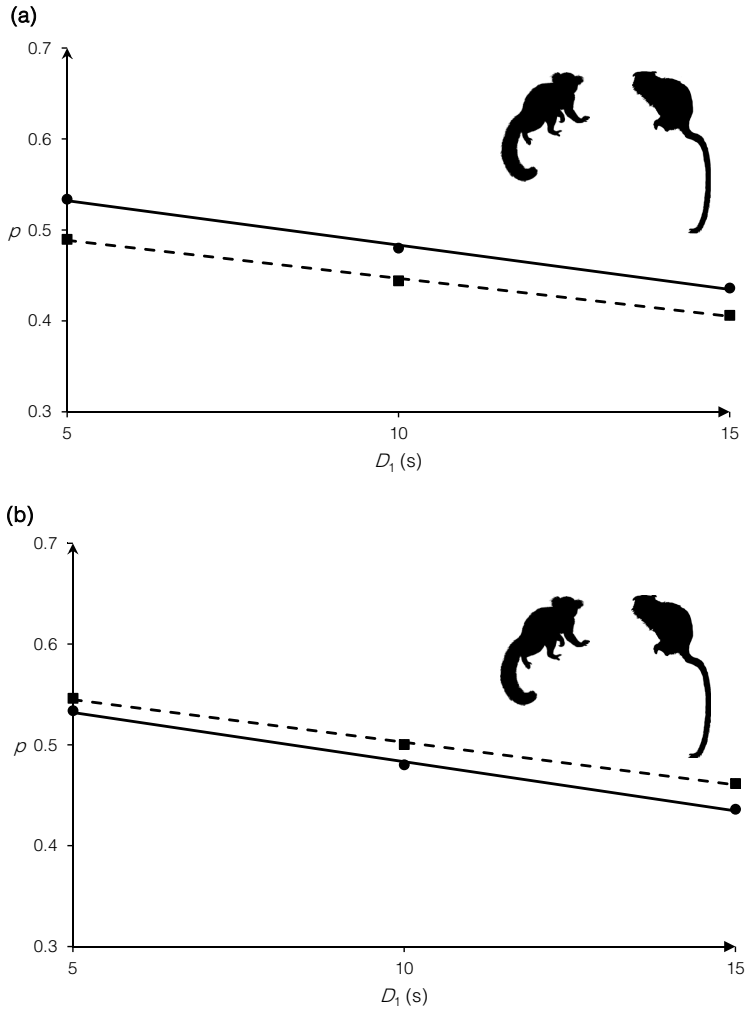

Figure 2. Probability of choosing the larger–later reward over the smaller–sooner reward, $p = \gamma_1/(\gamma_1 + \gamma_2)$, in food-based self-control tasks at three different delays to the larger–later reward. (a) A case where only h_1 increases while h_2 remains fixed ($h_2 = 8$ s). The circular markers joined by the black line show the probabilities generated when handling time for the larger–later reward is shorter ($h_1 = 16$ s). The square markers joined by the dashed line show probabilities generated when handling time for the larger–later reward is longer ($h_1 = 20$ s). (b) A case where both h_1 and h_2 increase. The circular markers joined by the black line show the probabilities generated when handling time for both rewards are shorter ($h_1 = 16$ s, $h_2 = 8$ s). The square markers joined by the dashed line show probabilities generated when handling times for both rewards are longer ($h_1 = 20$ s, $h_2 = 10$ s). Parameter values are the same as those used in figure 1 to aid comparability of these results across figures ($A_1 = 3900$ J, $A_2 = 1300$ J, $m = 0.95$ J s^{-1}, $y = 0.5$, $D_2 = 0$ s). Silhouette illustrations obtained from PhyloPic (http://phylopic.org), from various authors under Public domain licence.

with each reward, both of which required the same force to activate. The proportion of choices that subjects made for the larger–later reward was measured in response to increasing the force required to pull the levers. Subjects chose the larger–later reward with increasing probability as the force required to pull the levers increased. This is equivalent to a subject increasing their wait time in self-control tasks. For convenience, we represent this procedure by increasing the multiplication of metabolic rate while handling food items compared with waiting (y). We find the same qualitative effect as Chelonis *et al.* [53]—when y increases, the critical delay and therefore the expected wait time increases too (see equations 2.8 and 2.9 and figure 3). Thus, our predicted change in wait times matches observed changes in preference for the larger–later reward, again suggesting that the animals' change in preference is to maximize net rate of energy intake.

Tobin & Logue [55] compared the proportions of choices made by rats (*Rattus norvegicus*), pigeons (*Columba livia*) and humans (*Homo sapiens*) in response to a larger–later reward in comparison with a smaller–sooner reward. They argued that species with a high metabolic rate might need to take a small item with a short delay to avoid starvation, and so self-control would decrease across species as metabolic rate increased. By contrast, their data showed that species with higher metabolic rates at rest had a greater preference for the larger–later reward than species with lower metabolic rates. The authors did not come to this conclusion themselves because they used mass-specific metabolic rate instead of metabolic rate, but as McNab [56] points out, mass-specific metabolic rate is not appropriate. We fix all the parameters of our model while increasing body mass (which affects our model by increasing m) for two values of y, and find the same qualitative effect—critical delay, and therefore predicted wait time, increases when metabolic rate increases (figure 3). It is possible that parameters other than m will change with mass and this seems very likely if we compare pigeons and humans. To make the assumption more plausible, we have used a range of primates up to the mass of a chimpanzee (about 45 kg; table 1). Our results match observed behaviour, suggesting that interspecific variation in wait times could be a function of differences in metabolic rate. That our results match observed behaviour could also explain why species with a larger body mass (that also tend to have larger brains) have longer

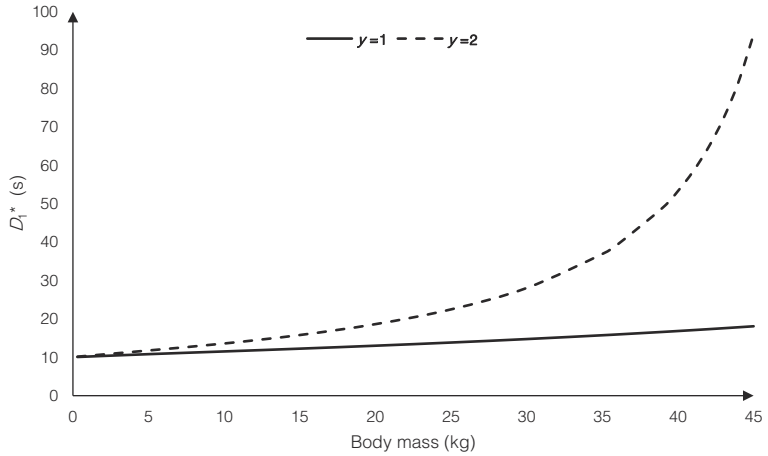

Figure 3. Critical delay in food-based self-control tasks, D_1*, with body mass (kg). The range of body mass is based on primates (common marmoset 0.32 kg to chimpanzee 45 kg; see table 1). Mass affects D_1* through metabolic rate for which we have used the equation for primates—2.66 x body mass$^{0.81}$ (J s^{-1}) [54]. Body mass may also increase the multiplication in metabolic rate required to handle food rewards, y. Wait times are therefore given for both a low- and high-value y, shown by the black line ($y = 1$) and the dashed line ($y = 2$), respectively. $A_1 = 3900$ J, $A_2 = 1300$ J, $h_1 = 20$ s, $h_2 = 10$ s, $D_2 = 0$ s.

wait times (table 1)—because species with a larger body mass have a higher metabolic rate [56,57] and therefore a longer predicted wait time.

When comparing wait times across species, it is also likely that y will vary as a function of different body masses and body plans. To demonstrate the influence of y on wait times, we use both a low and a high value of y when investigating the effect of mass (figure 3). The effect of y on wait times is far more pronounced at higher body masses (figure 3). Detecting differences in wait times as a function of changes in y may therefore be difficult when comparing smaller species.

Because the metabolic parameters m and y are hard to measure, we find the sensitivity of D_1* to variation in them by means of a dimensionless measure known as elasticity. In the case of infinitesimal changes, elasticity (the point elasticity) is the differential of the function with respect to the parameter, multiplied by the parameter and divided by the function. Elasticity has been used to investigate how hard animals work for rewards [58–60]. In the current context, the function is D_1* and the parameters are m and y. It follows that the elasticity of both m and y is $z/(1 - z)$. As we have pointed out, z is very small for the species studied by Stevens *et al.* [1] and Rosati *et al.* [35] ($z = 0.003$ for the common marmoset parameters in the caption to figure 1), so the elasticities are small. ($z/(1 - z)$ is approximately equal to z when z is very small.) By contrast, the elasticity of A is $Ah_2/(D_1^* (1 - z))$, which is much larger (about 4 for the common marmoset). Although the elasticity for small primates is low, it can be substantial for larger primates. For a black lemur with mass 2.39 kg, $z = 0.083$ and D_1* = 10.90, whereas $z = 0.8$ and D_1* = 49.4 for a bonobo (39.1 kg) and $z = 0.89$ and D_1* = 93.69 for a chimpanzee (44.97 kg) (parameters as in figure 3 with $y = 2$). For the bonobo, elasticity = 4 when $y = 2$, whereas when $y = 1$, $z = 0.2$ and elasticity = 0.25.

3. Discussion

Performance in self-control tasks is often used as the basis to compare cognition between species. These comparisons rely on the assumption that waiting longer for a larger–later food reward at the expense of a smaller–sooner food reward is a sign of greater self-control. By contrast, optimal foraging theory predicts that beyond a sufficient delay, subjects increase their rate of energy intake by choosing the smaller–sooner food reward, not the larger–later food reward ([1,32]; this study). However, previous attempts to use rate-maximization models to predict observed wait times have failed to do so consistently (e.g. [1,22,35]). That a difference is sometimes found between predicted and observed wait times has left the field of comparative self-control in search of alternative explanations that focus on non-energetic costs associated with time (lost opportunities to increase fitness elsewhere and the risk of interruption and reward loss [61]). We do not believe that this difference means that we should reject the insights that optimal foraging theory can offer.

We built a model of net rate of energy intake for food-based self-control tasks that are typically used to generate wait times. Unlike many previous attempts to model rate of energy gain in self-control tasks [1,22,35], we followed Kacelnik [32] in including both the energy gained and lost when exploiting each reward—without the latter, it is difficult to make accurate predictions. This is particularly important when metabolic costs and the cost of handling, as reflected by m and y, are large because, all else being equal, this produces a greater difference in predicted wait times between models of gross and net rate of intake (as shown by equation 2.13). To simulate the task, we fixed all parameters of our model while increasing the delay to the larger–later reward (thereby simulating many self-control tasks). In line with previous work [1,32], we found a critical delay (D_1*) beyond which animals maximize their rate of energy intake by choosing the smaller–sooner reward. Importantly, minimizing the difference between a subject's critical delay and observed wait time *always* reduces the net rate of energy intake lost from failing to match the critical delay. Finally, we compared changes in observed wait times in response to specific parameters—handling time (h_i), metabolic rate at rest (m) and increase in metabolic rate when handling (y)—in empirical studies and found that the qualitative trends matched changes in wait time predicted by our model. Our model predicts that the critical delay is longer than the critical delay predicted by maximizing gross rate D_g* if $y > 0$ (i.e. metabolic rate while handling is greater than rate while waiting). By contrast, the critical delay is shorter if $y < 0$. When $y = 0$, $z = 0$ and so the critical

delays are equal. A similar result holds in the context of exploiting depleting patches of food: whether the optimal patch time under maximization of net rate is greater or lesser than the time that maximizes gross rate depends on the metabolic rate while travelling between patches minus the metabolic rate while on a patch. If this difference is positive, net rate predicts a longer patch time but if it is negative, net rate predicts a shorter patch time [62,63]. For small primates, z is likely to be close to zero and so the difference between D_1* and D_g* will not be noticeable. This means that the maximization of net rate cannot explain the data from tamarins and marmosets. A general point is that the waiting time procedure may not correspond to the circumstances in which waiting evolved [33,64]. Although this leads us to expect that there are other aspects of the data that rate maximization will not explain, the qualitative success of our model suggests that energetic costs are important.

Equation (2.12) shows that under the maximization of gross rate of energetic gain, the only effect of body mass could be associated changes in handling time. In contrast to this, under the maximization of net rate, there is a more direct effect of mass through its relationship to metabolic rate, as represented by z in equation (2.8). As far as we are aware, this is the first consistent argument for the effect of metabolic rate on optimal waiting time. It is illustrated in figure 3; the line for $y = 2$ shows how strong the effect of mass can be.

Our findings have potentially wide-reaching consequences for tests of cognitive evolution that have assumed that waiting for longer is a sign of better self-control. Interspecific comparisons of wait times have been used, for example, to establish a relationship between cognition and brain size, to investigate the likely drivers of cognitive evolution and to consider both the evolution of self-control itself and the behaviours that may enhance it [3,4,22,29]. For instance, species with larger bodies and larger brains have been found to have longer wait times [4,22]. This result has been used as evidence that larger brains could confer greater cognitive abilities [4]. Our work suggests that this relationship could be a reflection of larger species with larger brains having higher metabolic rates, not necessarily enhanced cognition. This finding also suggests that the metabolic hypothesis—species with higher metabolic rates will be more likely to choose the smaller–sooner reward as they have a more urgent need to replenish their energy reserves [9]—is not correct because species with higher metabolic rates have longer predicted and observed wait times. When investigating the drivers of cognitive evolution, longer wait times exhibited by species living in more complex societies and with specific foraging niches have been used as evidence to support both the social intelligence hypothesis and the ecological intelligence hypothesis, respectively [1,3]. However, we have shown that longer wait times should not be assumed to be a measure of good performance. Instead, performance should be based on the ability to match observed wait times to the critical delay. Finally, self-distracting behaviours have been observed during the delay experienced before receiving the larger–later reward [11,29,65,66] and have been found to increase an animal's wait time [29,67]; 'self-distraction' has been suggested as an adaptive behaviour that has evolved to help animals increase their wait times. We have shown that waiting for longer is not always adaptive, thus, the adaptive significance of waiting for longer as a result of self-distraction will need to be reassessed.

While it is not correct to assume that waiting longer is necessarily a sign of greater self-control, wait times can still be used as the basis for comparing self-control between species. Using predictions from our model, we demonstrated that minimizing the difference between the critical delay and observed wait time always increases fitness. Furthermore, by comparing predictions generated from our model with existing data, we showed that animals change their observed wait times in some contexts as if to minimize this difference. We therefore think that the ability to minimize this difference is an appropriate measure of performance that captures how selection acts on self-control. We suggest calculating a delta value ΔD_1* by subtracting critical delay from the observed wait time, W, ($\Delta D_1^* = W - D_1^*$), for use in future interspecific comparisons. Positive values demonstrate that an animal has waited too long to match the critical delay, while negative values demonstrate that an animal has not waited long enough. As an example, we use data from table 1 and figure 3. For a black lemur, $D_1^* = 10.90$ and $W = 14.8$, so $\Delta D_1^* = 3.9$, whereas for a bonobo, $D_1^* = 49.4$ and $W = 74.4$, so $\Delta D_1^* = 30$. In both cases, the delta value is positive (i.e. the waiting time is too long). We suggest that animals with the same loss in net rate of energy intake from a negative ΔD_1* value have performed better than those with a positive value because they experience a reduction in other costs associated with waiting. These costs include lost opportunities to maximize fitness elsewhere and the risk of being interrupted and losing the larger–later reward [32,33,61]. Comparisons of delta values will be a good starting point to understand how successfully animals are using self-control to maximize their foraging returns.

From here, we can start to focus on the role that the two core cognitive abilities required for self-control—future planning and inhibitory control—have in performance. To test future planning, D_1* can be experimentally moved into the future and ΔD_1* values measured in response. A simple way of doing this will be to increase the ratio between the two rewards (i.e. increasing A in equation 2.8), which will increase the critical delay (as shown by equation 2.10). To test the influence of inhibitory control, ΔD_1* values in the delay-choice procedure can be compared with those in the delay-maintenance procedure. The latter differs in that a subject can take the smaller–sooner reward and forfeit the larger–later reward for the entirety of the delay to the larger–later reward. Given that a subject would be required to resist the immediacy of the smaller–sooner reward for longer in the delay-maintenance task, it is likely that any change in wait time will be a reduction (i.e. ΔD_1* will become more negative). Thus, variation in this reduction will reflect a subject's inhibitory control. Finally, understanding how close an animal's wait time is to their critical wait time will allow testing of the adaptive significance of self-distracting behaviour. If self-distracting behaviours move an animal's wait time closer to the critical delay, then they may represent an adaptation to overcome a lack of self-control. Alternatively, self-distracting behaviours may be maladaptive if they move an animal's wait time further away from the critical wait time, particularly if their ΔD_1* value becomes more negative.

We have focused on food-based self-control tasks because food is the most common reward in non-human animal studies and because use of the same food items differing in size for both rewards allows net energy gained over time to be calculated as a proximate measure of fitness. However, other reward paradigms have featured in self-control tests with non-human animals: for example, different food items that differ in their nutritional content (e.g. [11]), as well as symbolic tokens that can be

exchanged for food (e.g. [68]). With human subjects, hypothetical or real monetary rewards are common (e.g. [69]). Regardless of the reward type or the procedure, the costs of waiting for the larger–later reward increase as the delay extends. Thus, the result that there will probably be a wait time past which a subject increases their fitness by choosing the smaller–sooner option is likely to hold true.

Broadly speaking, work in the field of self-control has two traditions. The operant psychology tradition has emphasized descriptive models of behaviour in experiments that typically control the time for which subjects have access to food. These descriptive models are not designed to assess performance in an evolutionary context because they do not assess the fitness consequences of different waiting times. By contrast, the tradition within behavioural ecology has been to produce models that are related to natural selection with the use of optimal foraging theory (e.g. [1,2,35]). These optimal foraging models are normative in that they specify the best waiting time to adopt (see [70] for further discussion). Working in this latter tradition, we have extended the approach of Kacelnik [32] by developing a model that predicts the waiting time that maximizes net rate of gain. A key feature of our analysis is that the optimal waiting time depends on metabolic rate while handling as opposed to waiting, which we expect to depend on body mass. We have shown that the optimal time is similar to the time that maximizes gross rate if an animal's mass is low but can be significantly greater when mass is large. A drawback of our ΔD_1^* value is that it requires knowledge of both a metabolic cost and the energy content A_2 of the smaller reward. Our analysis shows that the implications of varying handling time are more complicated than suggested by Rosati *et al*. [35]. It would be worth comparing how animals respond to adding a given time to handling times and adding a given time to delays (e.g. [71,72]). Although there are formal analogies between the two manipulations, animals may treat them in a different way. We also think that further empirical work on the effect of costs would shed light on the validity of our approach.

What we have not done is to attempt to relate our model to the descriptive equations that have emerged from the operant psychology tradition. Kacelnik [32] argues that the basic discount equation of Mazur [18] follows from rate maximization. By contrast, Sozou [73] showed that the equation could be derived by assuming there is uncertainty about the discount rate (see [74] for a review and extension). In addition, we have followed Kacelnik [32] in ignoring the time delay between trials (the inter-trial interval); other approaches are possible (e.g. [2,38]). In terms of gross rate, adding an inter-trial interval is equivalent to increasing both handling times by a given amount T, and the consequence is to increase D_g^* by $T(A_1/A_2 - 1)$. Quantitative predictions will require careful consideration of the inter-trial interval. Perhaps most fundamentally, we have not addressed the fact that rate-based models do not predict choice when an option may give more than one reward (e.g. [75,76]).

We have shown that, when considering self-control, it is most appropriate to compare animals on their ability to minimize the difference between their predicted wait time (i.e. the wait time that maximizes their net rate of energy intake) and their observed wait time. Hence, we suggest that previous comparisons of wait times making the assumption that waiting longer is better (i.e. indicating better self-control) need to be revisited. We also believe that the cognitive significance of having good self-control should be reconsidered because observed behaviours suggest that taxonomically diverse species may be equivalent in their self-control capability. Finally, we advise that future research take into consideration how behaviour in cognitive tasks would be selected for and that performance reflects adaptive behaviour. Since most cognitive tasks in non-human animals assess individuals on their ability to obtain food rewards, optimal foraging models that consider energy gain and costs over time [34,77,78] are a good place to start in understanding the fitness consequences of performance.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. This article has no additional data.

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. H.F.S.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; A.N.R.: funding acquisition, supervision, validation, writing—original draft, writing—review and editing; A.I.H.: conceptualization, formal analysis, investigation, methodology, supervision, validation, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This work was supported by the European Research Council (grant number: 682253).

Acknowledgements. We thank John M. McNamara and Patrick Kennedy for valuable discussions about the project, and all members of Andy N. Radford's and Martin J. Whiting's research groups for their constructive feedback throughout the development of this work.

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