

How practice makes perfect: the role of persistence, flexibility and learning in problem solving efficiency.

Pizza Ka Yee Chow*, Stephen E. G. Lea, and Lisa A. Leaver

* Corresponding author: kyc202@exeter.ac.uk

Psychology Department

Washington Singer Building

Perry Road

University of Exeter

EX4 4QG

Contact number: +(44) 07785 946 704

ABSTRACT

To fully understand how problem solving ability provides adaptive advantages for animals, we should understand the mechanisms that support this ability. Recent studies have highlighted several behavioural traits including persistence, behavioural variety and behavioural/cognitive flexibility that contribute to problem solving success. However, any increment in these traits will increase time and energy costs in natural conditions, so they are not necessarily advantageous. To examine how behavioural traits vary during learning to solve a problem efficiently, we gave grey squirrels (*Sciurus carolinensis*) a problem solving task that required squirrels to obtain out-of-reach but visible hazelnuts by making a lever drop in the laboratory. We recorded persistence, measured as attempt rate, flexibility, measured as the rate of switching between tactics, and behavioural selectivity, measured as the proportion of effective behaviours, in relation to problem solving efficiency on a trial-by-trial basis. Persistence and behavioural selectivity were found to be directly associated with problem solving efficiency. These two factors also mediated the effects of flexibility and increased experience. We also found two routes that led to more efficient problem solving across learning trials: increasing persistence or increasing behavioural selectivity. Flexibility was independent from learning. Flexibility could increase problem solving efficiency, but it also has a time cost; furthermore it seemed to involve a trade-off with behavioural selectivity, with high flexibility being associated with a higher frequency of some disadvantageous ineffective behaviours. These results suggest that flexibility is an independent cognitive process or behavioural trait that may not always bring advantages to animals.

Keywords: effective behaviour, efficiency, flexibility, grey squirrels, ineffective behaviour, learning, learning ability, persistence, problem solving

INTRODUCTION

Direct demonstrations of correlations, within species, between general cognitive abilities and fitness measures have shown the functional significance of problem solving success (e.g. Cole, Morand-Ferron, Hinks, & Quinn 2012, Keagy, Savard, & Borgia 2009; but also see Isden, Panayi, Dingle, & Madden 2013). The recent focus on individual or species differences in specific behavioural traits that may underlie animals' success or failure in innovative problem solving has helped us to understand some traits that contribute to problem solving success. Examples of behavioural traits that have been implicated in this way include persistence, behavioural variety, behavioural and cognitive flexibility, with each of the trait providing different advantages for an individual during problem solving process:

Persistence: Since complex problems are unlikely to be solved immediately. It is necessary to be persistent in order to solve them. Individuals who persisted longer in their problem-solving attempts have been shown to be more likely to solve a problem, for example among hyenas (Benson-Amram & Holekamp 2012), carib grackles (Overington, Cauchard, Côté, & Lefebvre 2011), great tits (Cauchard, Boogert, Lefebvre, Dubois, & Doligez 2013), and meerkats (Thornton & Samson 2012).

Behavioural variety: In their studies of hyena problem-solving, Benson-Amram & Holekamp (2012) and Benson-Amram, Weldele, & Holekamp (2013) showed that behavioural variety, the number of *types* of contact that an individual employs to manipulate an apparatus, was a good predictor of whether an animal would solve a problem; Griffin, Diquelou, & Perea (2014) obtained a similar result in Indian hill mynas.

Behavioural and cognitive flexibility: Animals may vary in their capacity to change their behaviour as a function of success or failure at solving a problem, or the speed with which they do so. Ramsey, Bastian, & van Schaik (2007) set the capacity to find novel behaviours in response to novel problems at the heart of their analyses of innovation.

Kummer and Goodall (1985) argue that flexibility may also involve the capacity to mobilise old behaviours in new situations. Reader & Laland (2003) consider that both of these conditions could indicate flexibility in problem solving.

Two theoretical difficulties are posed by this list of factors. Firstly, increasing any of them is likely to increase the time and energy spent on finding a solution to a problem. In a natural context, spending extra time or energy solving a problem has a cost, especially when the individual first encounters the novel problem: it decreases the net worth of whatever resource a solution makes available, and it increases exposure to risks such as predation. Secondly, they are to some extent opposed to one another. In particular, persistence could be the opposite of either flexibility or behavioural variety, though it need not be, as we discuss later.

Both these difficulties can potentially be resolved by considering what happens when animals are faced with a problem that allows access to high-value food, and the same problem recurs. Committing time and energy to solving a problem is more worthwhile if the net worth is high and the same problem is likely to recur. Similarly, the apparent contradictions between the needs for behavioural variety and flexibility on the one hand, and persistence on the other, may perhaps be broken down by looking at how they each vary across trials. For example, persistence might be important in the earliest trials with a problem, when the animal has had little experience of obtaining the ultimate reward; flexibility might become more important later, in helping the animal adjust its behaviour to reach the most efficient solution. Griffin et al.'s results on Indian hill mynas (2014) support this idea by showing persistence was important in solving the first problem of a series whereas behavioural variety was important for solving further problems.

The primary goal of the present experiment, using Eastern grey squirrels (*Sciurus carolinensis*) as subjects, was to disentangle these different factors by studying how

flexibility, behavioural variety and persistence vary between individuals and across successive trials on a problem, and then examine how these factors contribute to the efficiency of problem solving (See Methods). To do this, we designed a problem task that afforded specific ineffective and effective contact types for obtaining rewards, although squirrels were allowed to employ any techniques to make a lever drop to obtain visible rewards (see Methods), and we focused on the variations in the time each squirrel took to solve the problem on each trial.

The factors of persistence, variety and flexibility have all been defined in varying and sometimes confused ways in the past and variables may have confounded with the solution time. For example, Griffin et al. (2014) measured persistence, or motivation, as the actual number of attempts to solve a problem on each trial. To examine these variables' separate impacts on the time it takes an animal to solve a problem, it is necessary to define them so that they are logically independent of each other and of solution time. To achieve this, we adopted definition of each factor of interest based on previous studies (details see Methods). In summary, we followed the method of Biondi, Bó, & Vassallo (2008) and Griffin & Diquelou (2015), measuring persistence as the rate at which the squirrels used behaviours directed at the apparatus regardless of what kind of behaviours they were, behavioural variety as the number of different behaviours employed, flexibility as the frequency with which the squirrels changed the behaviour they directed at it, and behavioural selectivity as the proportion of effective behaviours. All these measures were taken trial by trial, so that we could observe how they changed in the course of learning. But how would we expect them each to impact on the efficiency of problem solving?

Since we were measuring persistence in the same way as Biondi et al. (2008) and Griffin & Diquelou (2015), we predicted that persistence would emerge as one of the contributors to problem solving efficiency, as what the authors found in their studies.

Specifically, we predicted that persistence would increase across trials, and in turn, reduce solution time, since perfect performance would entail a rapid rate of (successful) attempts. The prediction for behavioural selectivity is also straightforward; as the squirrels learn to solve the problem more efficiently, the proportion of effective behaviours should increase across trials, and hence, lead to lower solution time. At least at the beginning of training, behavioural variety and flexibility should also facilitate learning, as having a wide range of contact types available, and switching between them frequently, should assist individuals in identifying the successful behaviours for a task; however, later in training, we might expect to see success associated with lower levels of these variables.

If we have correctly identified these four factors as accounting for problem solving performance and its improvement with experience, we can then investigate which, if any, of the factors we were measuring in fact mediate the effect of experience (operationalised by trial number) on solution time, and how. That is to say, some or all of these factors should be correlated with both trial number and solution time; if the variables of persistence, behavioural variety, flexibility and behavioural selectivity are included as covariates in a model along with trial number, then there should be no remaining correlation of solution time with trial number. Figure 1 illustrates one possible explanatory model for problem solving efficiency. In this model, the four factors introduced above mediate the effect of experience. However, it is not the only possible model; at least some of the four component skills such as persistence and behavioural variety could be personality traits (or behavioural syndromes), and flexibility and behavioural selectivity could be cognitive processes and their contributions to individual differences in problem solving performance are not easily modified by experience.

Grey squirrels are well suited for studies of problem solving ability for several reasons. They have excellent motor skills which they use in natural conditions such as

manipulating twigs and leaves to build dreys, and in anthropogenic situations, for example for extracting food from even the best protected bird feeders. Accordingly, the manipulatory skills of grey squirrels should not be a limiting factor in a problem solving task. Grey squirrels also belong to the family *Sciuridae*, whose members have a comparatively larger brain to body size ratio than other rodents (Mace, Harvey, & Clutton-Brock 1981; Roth & Dicke 2005). Species with relatively larger brains are more successful than those with relatively smaller brains in invading new environments (avian species: Sol, Duncan, Blackburn, Cassey, Lefebvre 2005; amphibians and reptiles: Amiel, Tingley, & Shine 2011). Birds with larger brains relative to body size are also more flexible than those with a smaller brain relative to body size, and more successful in establishing themselves in a new environment (Sol, Timmermans, & Lefebvre 2002; Sol, et al. 2005; Sol, Bacher, Reader, & Lefebvre 2008), surviving in nature (Sol, Székely, Liker, & Lefebvre 2007) and adapting to city life (Sol, Lapiedra, & González-Lagos 2013). In line with this evidence, the relatively large brain to body size of grey squirrels may have facilitated their spread around most of the UK since the 19th century and in Italy since the mid- 20th century. This spread of population has been predicted to continue into other European countries (Huxley 2003). Field studies have shown that grey squirrels are flexible in a social context, employing various food protection strategies to minimise food loss during caching (Hopewell & Leaver 2008; Hopewell, Leaver, & Lea 2008; Leaver, Hopewell, Caldwell, & Mallarky 2007; Steele, et al. 2008). Although it is not clear whether such flexibility is also shown in other cognitive domains such as problem solving, the evidence suggests that squirrels are able to adapt to new environments and can therefore be expected to be good at problem solving.

Figure 1

METHODS

Ethical Note

The study was approved by the Ethical Review Group at the University of Exeter and in accordance with the Association for the Study of Animal Behaviour guidelines on animal welfare and UK law. Five squirrels (three hand-reared and two recused) living in the laboratory at the University of Exeter participated in this study. Squirrels were two females and three males, aged from 2.5-9 years. Details of the housing and test room, see Hopewell, Leaver, Lea, Wills (2010). Squirrels were not food deprived; daily diet included sunflower seeds, pumpkin seeds, tiger nuts, dried vegetables and fresh fruits and water was provided *ad libitum* throughout the experiment. All squirrels were trained to go voluntarily into the test room through an overhead tunnel that connected their home cage with the test room. The laboratory daylight cycle was 12:12 hrs (0700-1900).

Study information

In the experiment, we used hazelnuts as reward, because these are a preferred food for squirrels and were not included in their normal daily diet. Data were collected from 7th July - 27th Sep, 2013. Testing time was within the period 0900-1500 but depended on the active time of each squirrel. A high-resolution digital camera (Panasonic HD) was set up 15 cm away from the testing cage to capture all the behaviours throughout the experiment. Another mini-camera (Samsung HD brand HMX-W190) was also mounted on the mesh of the adjacent cage, 60 cm away from the centre to capture specific behaviours.

Problem solving apparatus

The problem solving apparatus used was a Plexiglas box, which had ten holes randomly located on each side, and a pyramid-shaped base (Fig. 2a). The dimensions of the box were 25 cm x 25 cm x 19 cm, while the base measured 25 cm x 25 cm x 3 cm (Length x Width x Height). The ten holes (2 cm x 0.9 cm, W x H) on each side of the box were horizontally but not vertically aligned with holes on the opposite side (Fig. 2b-d), so that levers could be inserted across the box through holes roughly opposite to each other. The box was secured

above the base by four wooden legs, and this created a 4.5 cm gap between them where a squirrel could obtain hazelnut rewards when it had solved the problem. The shape of the base allowed the hazelnuts to roll down to the squirrel during the testing phase. In the habituation phase, only the transparent box without any levers was presented to each squirrel. During this phase, the base was made of plastic, but this was replaced by a wooden base for the testing phase. The thickness of the Plexiglas box was also changed from 2 mm to 5 mm in the testing phase. These changes were made to steady the apparatus and prevent squirrels knocking it over during the experiment. During the test phase, ten plastic levers were inserted through holes across the box, protruding from the box by 2.5 cm at each end (Fig. 2c). Each lever (1.5 cm x 29.8 cm x 0.5 cm; Length x Width x Thickness) had a 3-sided Plexiglas nut container (back: 2 cm x 1.5 cm; side: 1.5 cm x 1.5 cm) at one end; this was positioned just inside the box. The thickness of each lever was less than the size of the hole, allowing squirrels to smell the hazelnuts when the lever was inserted into a hole. The back of the nut container was transparent and its sides were white, so the squirrel could view the nut from two opposite sides of the box. The design of the apparatus meant that the squirrel could cause the lever to drop, and thereby obtain a nut if there was a nut in the nut container, by pushing the lever end that was near to the nut (henceforth, 'near end'), or by pulling it from the opposite end (hereafter, 'far end'), but not by pulling at the near end or pushing the far end.

Figure 2

Procedures

The whole experiment lasted for 17 days for each squirrel. The experiment included a standardised habituation phase followed by a testing phase. The habituation phase lasted for three consecutive days and the testing phase for 14 days. Squirrels were habituated and tested individually.

Habituation phase. Each squirrel was given a 30-min habituation phase each day for three consecutive days before the testing phase. The habituation phase aimed to minimise the effect of neophobia on performance and so increase the chance of measuring the intrinsic problem solving ability of each individual. During the habituation phase, we placed the puzzle box without levers in the centre of the test room. To motivate squirrels to get close to the apparatus, we placed eight half hazelnuts around the apparatus.

Testing phase. After the habituation phase, each squirrel went through three blocks of four learning trials of a problem solving task, with one learning trial each day and each trial lasting for a maximum of 45 minutes. Each block lasted for four consecutive days and there was a one-day break between blocks. The apparatus was placed at the same location as in the habituation phase, but ten levers (five functional and five non-functional) were inserted into the box. Each functional lever contained a hazelnut in its shell in the nut container while each non-functional lever was empty (Fig. 2a). We performed the following additional randomisations so as to minimise the probability that an individual would use the positions or direction of the apparatus and levers as a cue to solve the task. In each learning trial, the side of the box presented to the front of the test room was chosen randomly, except that each side of the box was presented once in a block. We also pseudo-randomised the functionality of each lever (with or without a hazelnut) and the direction it faced. Each lever and nut container combination was used as functional twice and non-functional twice within each block of trials. Therefore, no lever could be reliably predicted to be functional or non-functional.

During a learning trial, the squirrels were free to interact with the apparatus without disturbance. The trial began when a squirrel first interacted with the apparatus with any of its body parts. If the squirrel did not interact with the puzzle box for 15 minutes, the trial was terminated and repeated the following day (this only occurred in one trial with one squirrel).

The trial ended when the individual obtained all five nuts, when the squirrel had stopped interacting with the apparatus for 15 minutes, or when 45 minutes had elapsed, whichever happened first. Successful problem solving was defined as the squirrel obtaining a nut or causing a lever to drop, whether it was functional or non-functional (see Table 1 for full operational definitions).

Table 1

Measurements

Problem solving efficiency

Problem solving efficiency was recorded in three ways. All these solution times included only the time when a squirrel was in contact with the levers. The first measure was the total time spent on solving the entire task in each trial (hereafter ‘solution time for the entire task’). This included the start time that a squirrel manipulated any functional (with hazelnuts) or non-functional levers (without hazelnuts) until the squirrel obtained all the five nuts or stopped working for 15 minutes. The second measure recorded the total time spent interacting only with functional levers in each trial (hereafter ‘solution time for functional levers’). The final measure was the mean time spent on solving each lever per trial for each squirrel (hereafter ‘solution time per lever’). We divided the solution time for the entire task by the total number of levers that an individual caused to drop in that trial.

Persistence

To measure persistence, we followed the method of Biondi et al. (2008) and Griffin & Diquelou (2015), measuring the rate of attempts during problem solving to minimise confounding between the number of attempts and overall problem solving efficiency (measured by solution time). This rate of attempts could reflect squirrels were either showing high frequent of attempts within a short period of time or spending a longer amount of time

for each attempt. We first measured the total number of attempts in each learning trial. An attempt was defined as a squirrel starting to use any of its body parts to contact a lever and continued until the squirrel stopped contacting the same lever. If squirrels switched contact from one lever to another that was counted as a new attempt. Then we divided the total number of attempts by the solution time for the entire task.

Behavioural variety

This was measured by the number of different *types* of contact with the apparatus that a squirrel exhibited during problem solving (as listed in Table 1). The observed total scores of contact types for a trial ranged from 0 to 9. Behaviours included pull, push in, push up, push down, shake, claw, tilt up, lick and any combination of these such as “tilt up and push in” or “pull and push down” on a lever. Higher scores indicated that an individual exhibited more types of contact during problem solving. We also calculated the rate of behavioural variety, dividing the total number of exhibited types of behaviours by the solution time for the entire task.

Flexibility

Roth & Dicke (2005) suggested that switching between contact types is a measure of intelligence, and this measure is likely to be useful in relation to learning, since it addresses the individual’s tendency to employ alternative means to solve the problem. However, Mery & Burns (2010) have argued that one criterion for adapting to environmental demands is being able to directly observe the consequence of one’s action. It follows that changing the means used to solve a problem should be due to the observed failure of current strategy. Accordingly, we measured flexibility in terms of the number of changes, as a result of failure, between defined contact types the squirrel made in a given trial. Unlike Ramsey et al. (2007),

we do not completely insist that such alternative means should be entirely novel: they could include novel strategies as well as strategies that an animal has tried on a previous trial, or a previous problem (Kummer & Goodall 1985; Reader & Laland 2003). Nor did we consider whether the behaviours concerned were potentially effective or not. The number of switches between contact types does not depend on an individual's behavioural repertoire size, as an individual with a limited repertoire could make numerous switches between its few available behaviours, whereas an individual with a large repertoire might make very few switches between its many available behaviours. However, it is clear that, as with persistence, the number of switches between contact types on a trial will almost inevitably be confounded with the solution time for the trial – the longer it takes the animal to solve the problem, the more chance it has to switch contact types. Accordingly, we measured flexibility by the rate of switching, calculated by dividing the number of switches between contact types on a trial by the solution time for the entire task. This measure examined switches *between* the types of contact used to measure behavioural variety during problem solving. A switch was recorded whenever the current contact type was different from the previous contact type. Only switches as a result of failure were counted, so no switch was recorded if a squirrel had obtained a nut through the immediate previous contact.

Behavioural selectivity

With experience at a task, individuals should learn to narrow down the behavioural types employed to task-relevant behaviours. Benson-Amram & Holekamp (2012) showed that in successive trials on a problem, hyenas showed reduced behavioural variety across trials on a problem, as they learned to employ fewer ineffective behaviours (as was also found by Thornton & Samson 2012, in meerkats). They also showed more effective behaviours for the task (as was also found by Manrod, Hartdegen, & Burghardt 2008, in

monitor lizards, and Millot et al. 2014, in cod). In light of this literature, we were interested in the proportion of the behaviours used that were effective. We defined behavioural selectivity as the proportion of the contacts that were effective type. We categorised behaviours as ineffective or effective based on the way that the apparatus design specified ineffective and effective behaviours for solving the problem. We focused on the pull and push contact types which, when correctly applied, led to the most efficient problem solving. These two behaviours were classified as correct or incorrect, based on which end of the lever a squirrel manipulated (Table 1). Ineffective behaviours consisted of contact types that were incompatible with the task requirements, including pulling levers on the near end and pushing them at the far end. These actions could not result in problem solving success. Effective behaviours were contact types that were compatible with the task requirements and were the most efficient behaviours for solving the task in one action. These effective behaviours including correctly pushing the near end or pulling the far end of a lever.

Data analysis

To examine learning, we used non-parametric tests including Page's trend test (Page 1963) and exact binomial tests. Page's test was applied to examine changes in behaviour across 12 trials (three blocks of four trials each) by examining: solution time for the entire task, solution time for functional levers, solution time per lever, persistence (rate of attempts), flexibility (switch rate), behavioural variety and behavioural selectivity (the proportion of effective behaviours). Exact binominal tests were used to assess whether the distribution of solving attempts between functional and non-functional levers differed from chance for each individual in the first trial. All tests were carried out on individuals, and then we pooled the P -values using Fisher's formula $\chi^2 = -2 \sum \ln(P)$ (Sokal & Rohlf 1995 p. 794).

To examine the variables that were related to problem solving efficiency (Fig. 1), we applied a Generalised Estimating Equation (GEE) with exchangeable 'working' correlation

(Hardin & Hilbe 2003; Liang & Zeger 1986). GEE is a quasi-parametric statistical test that takes individual correlations under repeated measurements into account and has been proven to yield robust results as long as there are no missing data, even if the sample size is small, as in our case (Wang & Long 2011). The dependent variable was solution time for the entire task in each trial (i.e. including functional and non-functional levers, until squirrels obtained all the five hazelnuts or stopped working for 15 minutes). Covariates included trial number, persistence, flexibility and behavioural selectivity. Behavioural variety was found to be highly correlated with behavioural selectivity ($r=0.68$) and persistence ($r=-0.64$). This correlation held true even after we expressed behavioural variety as rate with selectivity ($r=-0.56$) and persistence ($r=0.67$), and so behavioural variety was dropped from the model to avoid multicollinearity. As small sample size can lead to underestimating the variance in calculation, an adjusted robust variance (Wang & Long 2011) was applied to calculate the P-values. All the results reported are two-tailed and results were considered as significant when alpha was <0.05 . Statistical analyses were performed in R (version 2.15.2, R Development Core Team, 2012); the ‘gee’ package was used to apply GEE (Carey 2012) and the ‘crank’ package was used to apply Page’s trend test (Lemon 2014).

RESULTS

Figure 3

Trends across trial blocks

All the squirrels solved the entire task and obtained all five nuts on their first trial, with solution time ranging from 38.1 seconds to 69.6 seconds (see Supplementary material for video S1a shows an example for one squirrel, Leonard, solving the puzzle box in his first trial). Variations in solution time also persisted to the last trial, ranging of solution times from 8.4 seconds to 68.8 seconds (see Supplementary material for video S1b shows Leonard solving the puzzle box in his last trial). Fig. 3a shows that in the first trial, squirrels

approached the functional levers (with hazelnuts) more often than the non-functional levers (without hazelnuts); 84.1% of all approaches were to functional levers, and this proportion is significantly different from 50% (pooled $\chi^2_{10}=35.04$; $P<0.001$). This indicates that squirrels were motivated by the food reward since the beginning. Figs. 3b, 3c and 3d shows that solution time for the entire task, solution time for functional levers, and solution time per lever decreased across trials (Page's trend tests: $\chi^2_1=8.8$, 14.1 and 13.8 respectively, $P<0.005$ in all cases). Figs. 4b and 4c show that the change of behavioural variety and flexibility across the 12 trials. Neither behavioural variety nor flexibility showed significant changes across trials (Page's trend tests: $\chi^2_1=0.5$ and 0 respectively, $P>0.05$ in both cases). Figs. 4a and 4d show the change of persistence and behavioural selectivity across trials. Both persistence and behavioural selectivity showed significant increased across trials (Page's trend tests: $\chi^2_1=9.8$ and 20.83, respectively, $P<0.005$ in both cases), indicating that squirrels gradually increased their attempts and exhibited more effective behaviours. Fig. 5 shows scatterplots, across all trials and subjects, of the relationship between flexibility and selectivity (Fig. 5a) and persistence (Fig. 5b), and of the relationships between those two variables and solution time (Figs. 5cd).

Figure 4& 5

Predicting problem solving efficiency

The GEE model for the predictors of solution time (Table 2 Path 1) showed that two factors, persistence ($\chi^2_1=7.48$, $P=0.006$) and behavioural selectivity ($\chi^2_1=3.98$, $P=0.046$), were significant predictors of solution time. Specifically, persistence was negatively related to the solution time, indicating that increased rate of attempts led to lower solution time.

Behavioural selectivity was also negatively associated with solution time, with a higher proportion of effective behaviour associated with lower solution time. However, flexibility ($\chi^2_1=0.51$, $P=0.474$) was not a significant predictor of solution time. Moreover, with the

component skill variables included in the model, trial number ($\chi^2_1=0.20$, $P=0.656$) was not a significant predictor of solution time either.

Table 2

Relationships between independent variables: mediation analysis

Although trial number was individually correlated with solution time (see Fig. 3b), the lack of any effects of trial number and flexibility on problem solving efficiency in the full model suggests that persistence and behavioural selectivity might mediate the effects of experience, and perhaps flexibility (Fig. 5a and 5b), on solution time (Fig. 5c and 5d). Therefore, we ran two further GEE analyses to test these mediational analyses, including trial number and flexibility as covariates factor and predict persistence for one model (Path 2) and behavioural selectivity in the other model (Path 3). Results confirmed that persistence (Path 2) and behavioural selectivity (Path 3) were both significantly predicted by trial number and flexibility, with opposite directions of effect, such that persistence increased across trials and decreased with higher flexibility whereas behavioural selectivity increased across trials and decreased with higher flexibility. We then ran the final analysis to assess whether trial number and flexibility were independent from each other. Results showed no evidence that they were dependent on each other ($\chi^2_1=0.33$, $P=0.565$). This is the pattern of results that would be expected if persistence (Path 2) and behavioural selectivity (Path 3) mediate the effects of trial number and flexibility on solution time. Fig. 6 shows the causal structure corresponding to those results, and the standardised beta weights (β) of the indirect paths from the GEE analyses. According to this analysis, two routes were involved in the improvement of problem solving efficiency across learning trials. First, persistence increased across learning trials, leading to reduced solution time ($\beta = 0.41 \times -0.43 = -0.18$), and secondly behavioural selectivity increased, increasing the proportion of effective behaviours

and again reducing solution time ($\beta = 0.36 \times -0.40 = -0.14$). The total effects of each factor on problem solving efficiency are shown in Table 3.

Table 3

Figure 6

DISCUSSION

In the present experiment, we have been able to fully account for the improvement in problem solving efficiency that occurred with experience in terms of two intermediate factors, persistence and behavioural selectivity. We have also shown that an additional relevant factor, flexibility, may be an independent cognitive process, since it was unaffected by experience on the task.

A priori, the first of the two key mediating factors, persistence, could have either positive or negative effects on problem solving. But, at least in the present task, persistence (measured, following Biondi et al. 2008, as the rate of attempts), increased across trials and was an important positive factor in learning, as it was related to decreased solution time (Path 1). This is consistent with the results of Sol et al. (2012), who showed that an increased attempt rate over trials was associated with an increased probability of task completion: here, we extend their result by showing that such increased persistence mediates the improvement of performance that occurs over learning trials. This result reflects that squirrels showed more attempts with improved solution time to complete the task, which is what should be expected in an instrumental task once at least some success has been achieved: the reward delivered on success in the task should reinforce both the specific effective behaviour, and also the more general behaviour of interacting with the apparatus, which we recorded as attempt rate. In addition rewards will increase incentive motivation. The present task was solved (albeit inefficiently) on the first trial by all squirrels, allowing reinforcement to take effect. In a task

where some animals are not unsuccessful in initial trials, persistence might have more negative effects.

The other key mediating factor, behavioural selectivity, was measured as the proportion of effective behaviours observed on a trial. This would be unambiguously expected to be associated with increased efficiency, and it was (Path 1). Again, operant conditioning provides a straightforward account of this change, with reinforcement increasing the rates of effective behaviours and extinction decreasing the rates of ineffective behaviours. The cognitive factors underlying such reinforcement processes are likely to include attention to the subject's own behaviour. Heightened attention to relevant exteroceptive cues has been shown to be important for successful problem solving (St Clair & Rutz 2013), as has attention to movement cues (Overington et al 2011), but attention to the individuals' own movements has not been investigated and would be a promising area for future study. Experiments on stimulus-response overshadowing (e.g. Roberts, Tarpy & Lea 1984) show that common attentional processes apply to both exteroceptive and interoceptive cues.

In our experiment, flexibility, measured as the rate of switching between contact types as a result of failure to solve the current problem, did not vary as a function of the squirrels' experience at the task (Fig. 4*b*). Increased flexibility was not associated directly with greater efficiency at problem solving (Path 1): instead, it was related to both decreased persistence (Path 2) and lower behavioural selectivity (Path 3). These results reflect that the ability to learn is not the same thing as showing flexibility within a single encounter with a problem solving task and such flexibility could be an independent cognitive process in problem solving that does not involve learning, but it facilitates animals to cope with the demand with an instant modification of behaviours after a failed attempt. Our finding of flexibility is contrary to other studies that have suggested that flexibility brings clear advantages for animals, through its contribution to successful innovation (e.g. Benson-Amram & Holekamp

2012). Under natural conditions, individuals who spend a long time with a given problem also put themselves at predation risk, perhaps for little nutritional gain. A resolution of this apparent paradox is possible if increased flexibility is associated with lower competitive ability in the wild. Indeed, it has been shown that the individuals that commit time to solve problems are those that have lower competitive ability in foraging than their counterparts or are subordinates in their group (Cole & Quinn 2011; Thornton & Samson 2012). Thus increased flexibility might be an adaptive foraging strategy for individuals who have no alternative, enabling them to access food sources that more dominant individuals are less bother with. Such plasticity of behaviour can bring individuals adaptive advantages in various fitness measures such as learning ability in harsh environments (Roth, LaDage, & Pravosudov 2010), species richness (Nicolakakis, Sol, & Lefebvre 2003), and mating success (Keagy, Savard, & Borgia 2009; but also see Isden et al. 2013); see Dukas (2013) for a review.

A limitation of the present study is that it is based on a small sample size, so only limited degrees of freedom were available for exploring how other interaction effects might have contribute to problem solving efficiency. We also need to be cautious in generalising the results to the whole species. Nevertheless, the study provides insights into the underlying mechanisms in problem solving. Given that grey squirrels have successfully invaded several European countries and the Western United States, future research should use a larger sample size and investigate their flexibility and problem solving ability under conditions where innovative foraging is essential to survival; this might help us to gain a better understanding of the basis for their invasive success and give insight into the success of other invasive species. Like other scatter hoarders, grey squirrels undoubtedly have unusual capacities for spatial cognition (e.g. Smulders, Gould, & Leaver 2010). It remains an open question whether this exceptional ability is domain-specific. Their capacity for exploiting

anthropogenic food sources suggests that grey squirrels may also be unusually good problem solvers; if in fact they have high cognitive capacity over a range of domains, this would be a good candidate as an explanation for their invasive success.

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Figure captions

Figure 1. This figure shows all the predicted directions and the correlations between all the behavioural traits that vary across time and solution time. Traits include persistence, behavioural variety, flexibility and behavioural selectivity. Persistence is measured as the rate of attempts, behavioural variety is measured as the number of types of contact, flexibility is measured as the rate of switching between contact types and behavioural selectivity is measured as the proportion of effective behaviours.

Figure 2. (a) figure shows the front side of the puzzle box. This box is constructed as a transparent box (25cm x 19 cm x 25 cm) with ten holes (2 cm x 0.9 cm) located randomly on each side. The holes are horizontally but not vertically aligned to the holes in the opposite side. The pyramidal shape base (25 cm x 3 cm x 25 cm) is to facilitate hazelnuts to roll down the apparatus. Each lever (1.5 cm x 29.8 cm each) has a nut container (back dimension: 2 cm x 1.5 cm; side dimension: 1.5 cm x 1.5 cm). The sides of the container are a solid colour while the back of the container is transparent; (b) the back side of the puzzle box; (c) side view of the puzzle box, levers are positioned horizontally; (d) top view of the puzzle box.

Figure 3. (a) Proportion of choices of functional levers (■) and non-functional levers (■) in the first trial. Numbers above bars indicate the actual number of times that each squirrel approached functional and non-functional levers. (b) median, maximum and minimum of total solution time in seconds (\pm s.e.) to solve the entire task, including functional and non-functional levers across trials. (c) median, maximum and minimum of total solution time in seconds (\pm s.e.) on solving the *functional* levers across trials. (d) median, maximum and minimum of average solution time in second (\pm s.e.) in solving *any* lever across blocks. N=5.

* $p < 0.05$

Figure 4. Boxplots show how each behavioural trait varied across the 12 trials. Tails for each box show maximum and minimum, the top and bottom of each box show the 2nd and 4th squirrels' data respectively; thus the data of the five squirrels could be read from the graph (a) persistence, measured as the rate of attempts across the 12 trials; (b) behavioural variety, measured as the number of types of contact across the 12 trials; (c) flexibility, measured as the rate of switching between contact types across the 12 trials; and (d) behavioural selectivity, measured as the proportion of effective behaviours across the 12 trials. N=5.

* $p < 0.005$

Figure 5. Scatter plots showing relationships between (a) flexibility (rate of switching) and behavioural selectivity (proportion of effective behaviours); (b) flexibility (rate of switching) and persistence (rate of attempts); (c) behavioural selectivity (proportion of effective behaviours) and the solution time for the entire task; (d) persistence (rate of attempts) and the solution time for the entire task. Noted that each plot uses the raw data across all subjects and trials to show the general trends between variables.

Figure 6. Standardised beta weights (β) of all the direct and indirect effects between factors. The dependent variable is the total solution time (including solving both functional and non-functional levers) of each trial for each squirrel. Covariates are trial numbers, flexibility, persistence and behavioural selectivity. Thick solid lines show the route to achieve efficient problem solving. Solid lines indicate significant effects while dash lines indicate non-significant effect. * < 0.05 , ** < 0.01 , *** < 0.005

Table 1. Operational definitions for coding the behaviours in the problem solving task.

Behaviours	Definitions
Identifying a nut	A squirrel orients its head towards a lever and sniffs within 0.5 cm of a lever more than 1 seconds.
An attempt	A squirrel uses any of its body part including nose, mouth, teeth, tongue, paw or chin to contact a lever.
Pull	<p>Effective* A squirrel uses its teeth to make an <u>outward</u> movement and a lever subsequently moves outside the box. This pulling behaviour must be performed on the <u>near</u> end of the nut container.</p> <p>Ineffective# A squirrel uses its teeth to make an <u>outward</u> movement and a lever does not move out of the box. This pulling behaviour must be performed on the <i>far</i> end of the nut container.</p>
Push	<p>Effective* A squirrel uses any of its body part, including nose (usually), teeth, paw or chin to make an <u>inward</u> movement of a lever and the lever subsequently moves inside the box. This pushing behaviour must be performed on the <i>near</i> end of the nut container.</p> <p>Ineffective# A squirrel uses any of its body part, including nose (usually), mouth, teeth, paw or chin to make an <u>inward</u> movement of a lever and the lever would not moves. This pushing behaviour must be performed on the <u>far</u> end of the nut container.</p>
Push up	A squirrel uses its nose to make a push under an end of a lever.
Push down	A squirrel puts force on a lever end with its paws or teeth. This behaviour makes the lever appears in a curve shape.
Tilted up	A squirrel uses its nose to level up a lever end. This behaviour makes a lever turns 45 degrees.
Claw	A squirrel uses it front paws to scratch a lever end.
Lick	A squirrel uses its tongue to touch a lever end.
Shake	A squirrel uses its teeth to bite a lever end and makes an up-and-down movement.
Combined behaviours	At least two of the behavioural types that mentioned above appear.

* indicated as direct effective contact types.

indicated as non-effective contact types.

Table 2. This table shows the summary of three GEE models.

Path no.	Predictors	DV	Estimates	χ^2	df	Z	P
1	Trial numbers	Problem solving efficiency	0.27	0.20	1	0.44	0.656
	Persistence		-51.38	7.48	1	-2.74	0.006***
	Flexibility		-3.30	0.51	1	-0.72	0.474
	Behavioural selectivity		-41.15	3.98	1	-2.00	0.046*
2	Trial numbers	Persistence	0.03	9.10	1	3.02	0.003***
	Flexibility		-0.19	6.26	1	-2.50	0.012*
3	Trial numbers	Behavioural selectivity	0.03	41.68	1	6.46	<0.001***
	Flexibility		-0.10	5.01	1	-2.24	0.025*

Path 1. This table shows the summary of the GEE model that examines the covariates for solution time. The model shows that only persistence and behavioural selectivity are the significant covariates for efficient problem solving. **Path 2.** Summary of the GEE model that examines the covariates for persistence. **Path 3.** Summary of the GEE model that examines the covariates for behavioural selectivity. The table shows estimated coefficients, χ^2 , *df*, Z values and P values. Values are based on an adjusted variance for small sample size. * $p < 0.05$, *** $p < 0.005$

Table 3. The total effects, shown as standardised beta weight (β), of each predictor on solution time.

Predictors	Total effect (β)
Trial numbers	-0.28
Persistence	-0.43
Flexibility	0.20
Behavioural selectivity	-0.40

Figure 1.

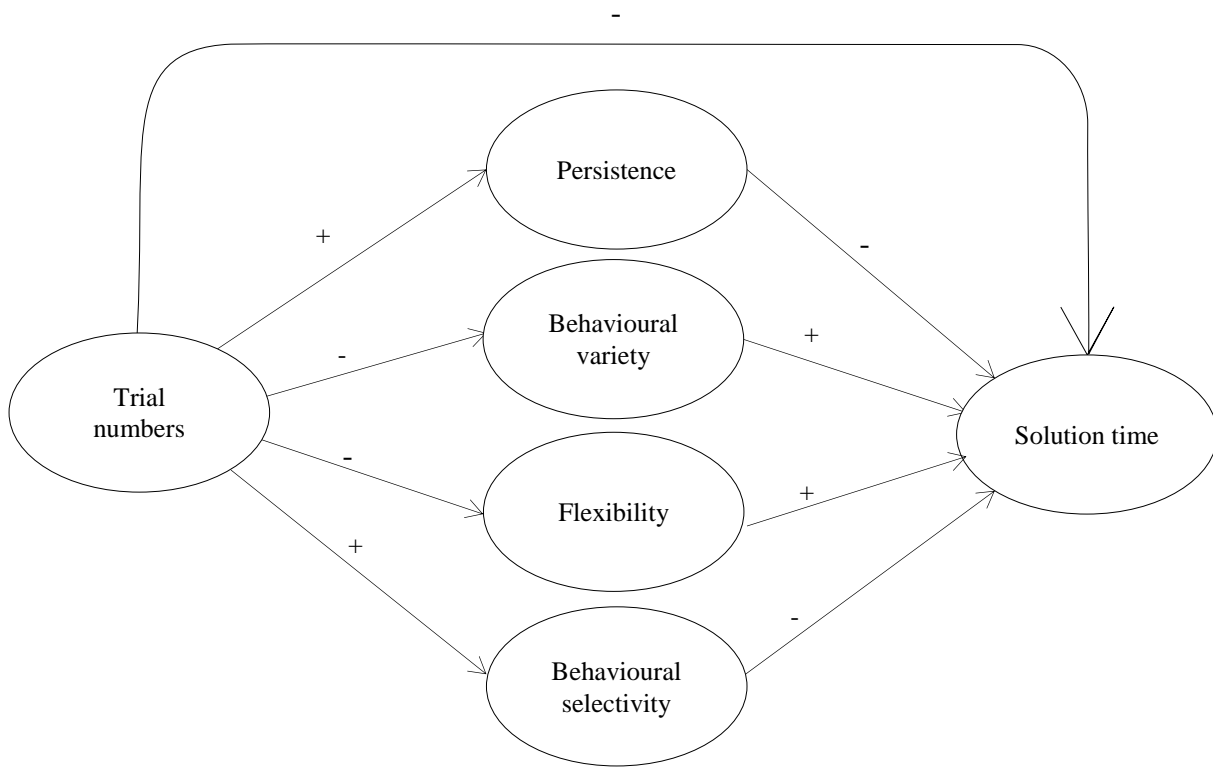


Figure 2.

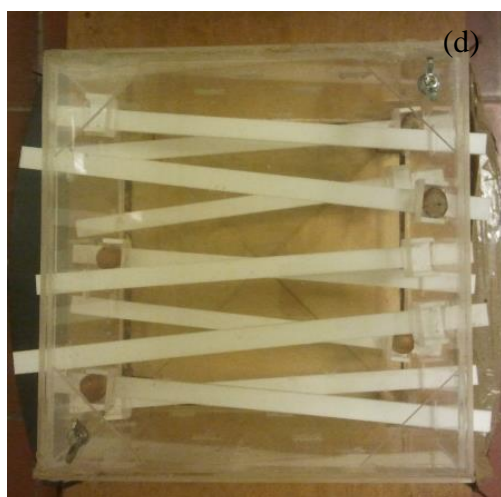
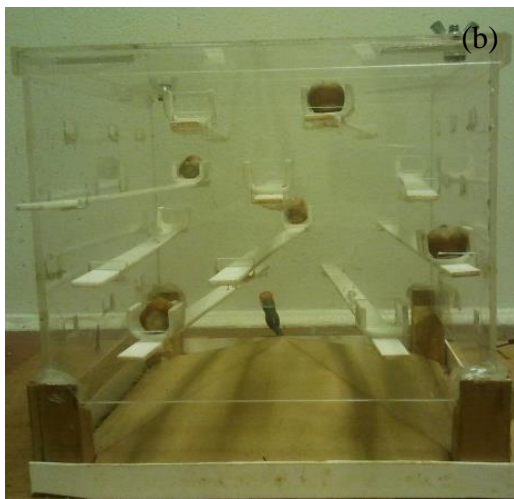
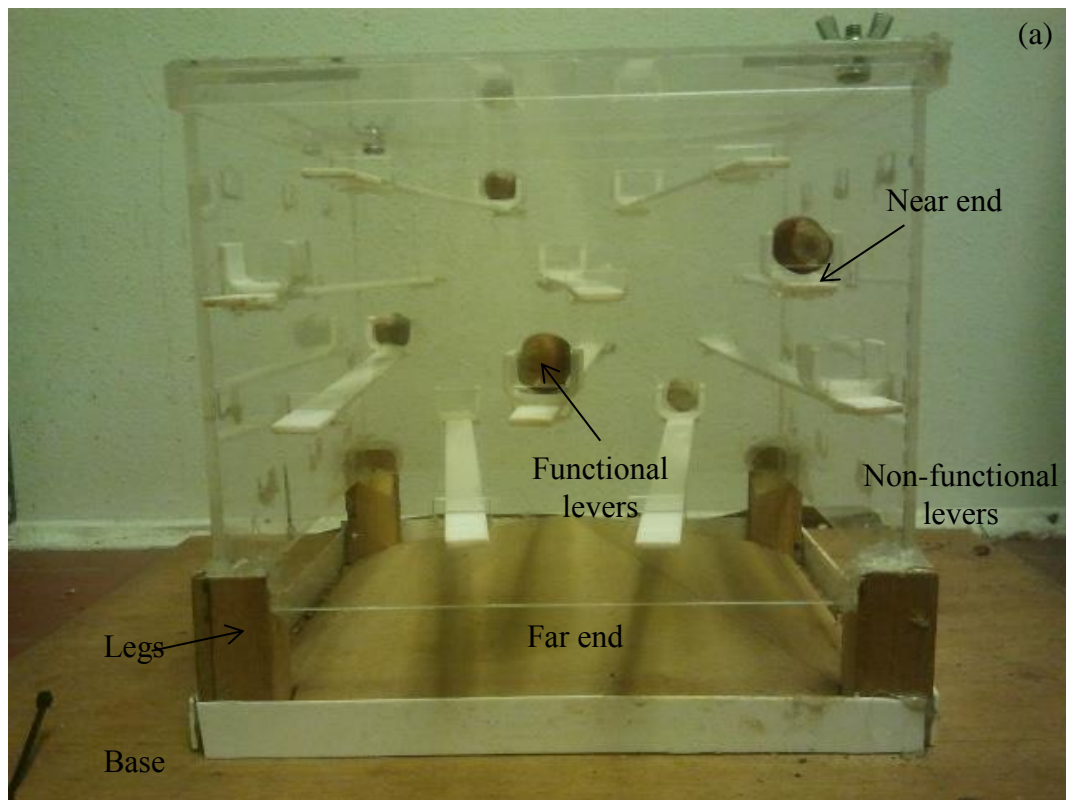


Figure 3.

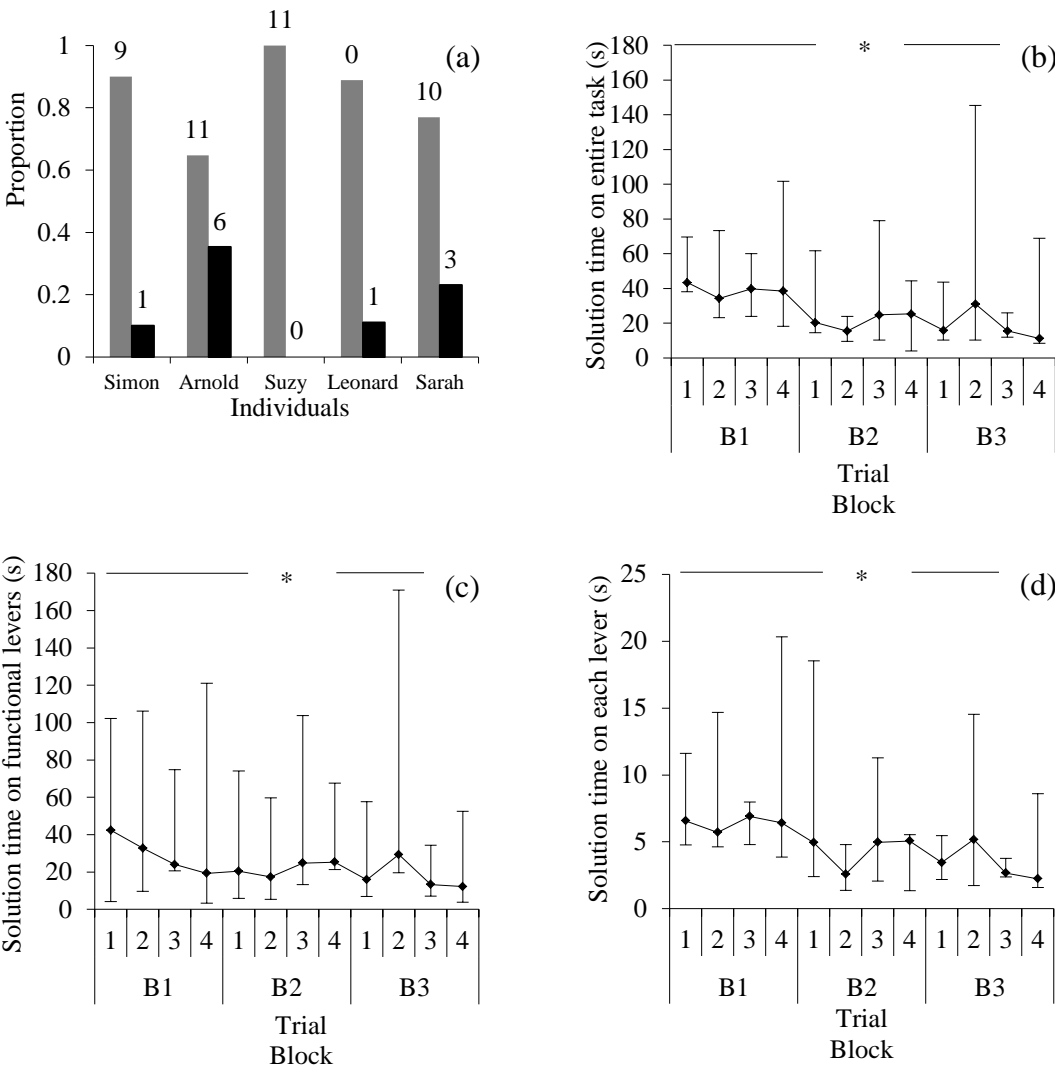


Figure 4.

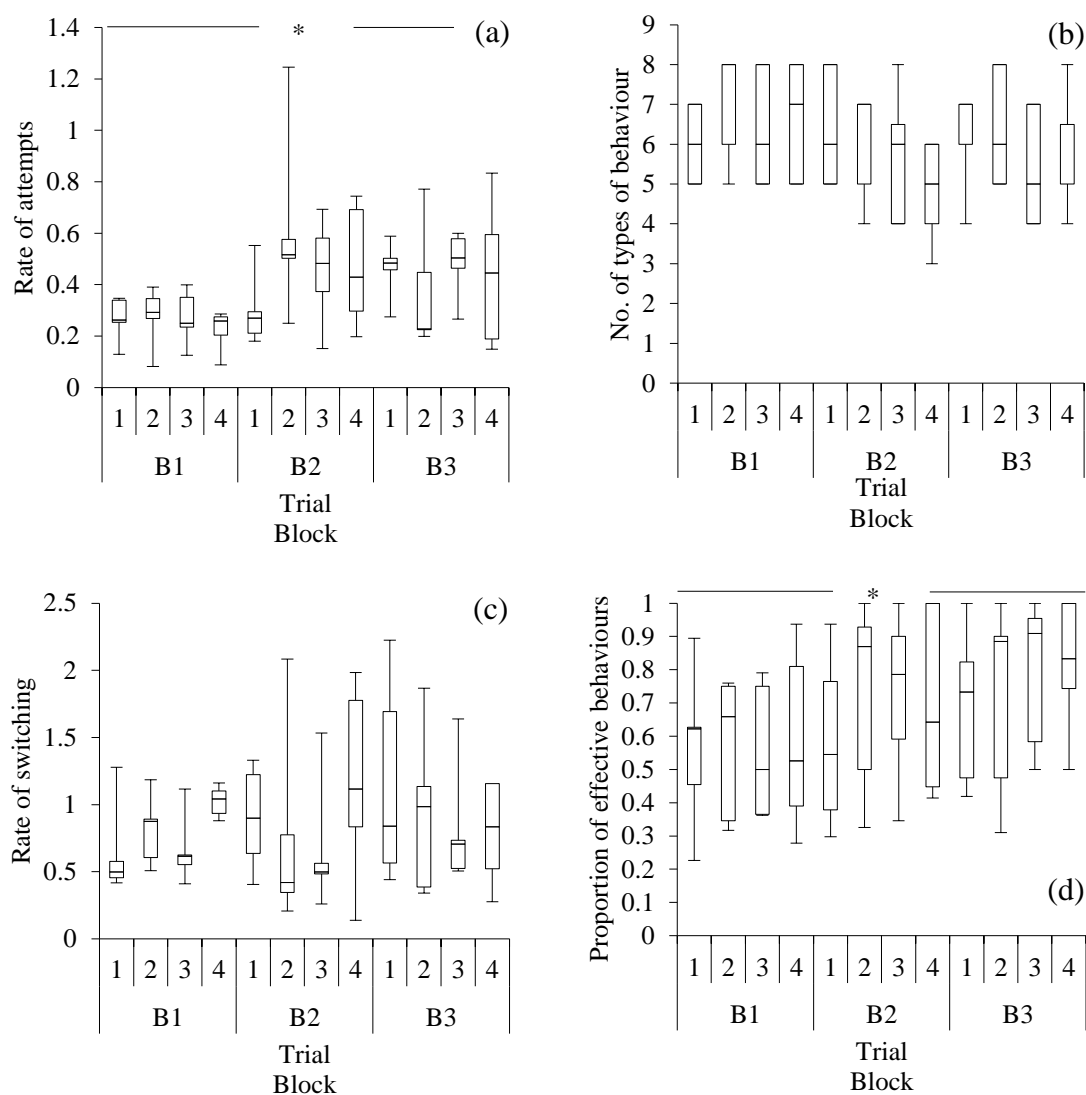


Figure 5.

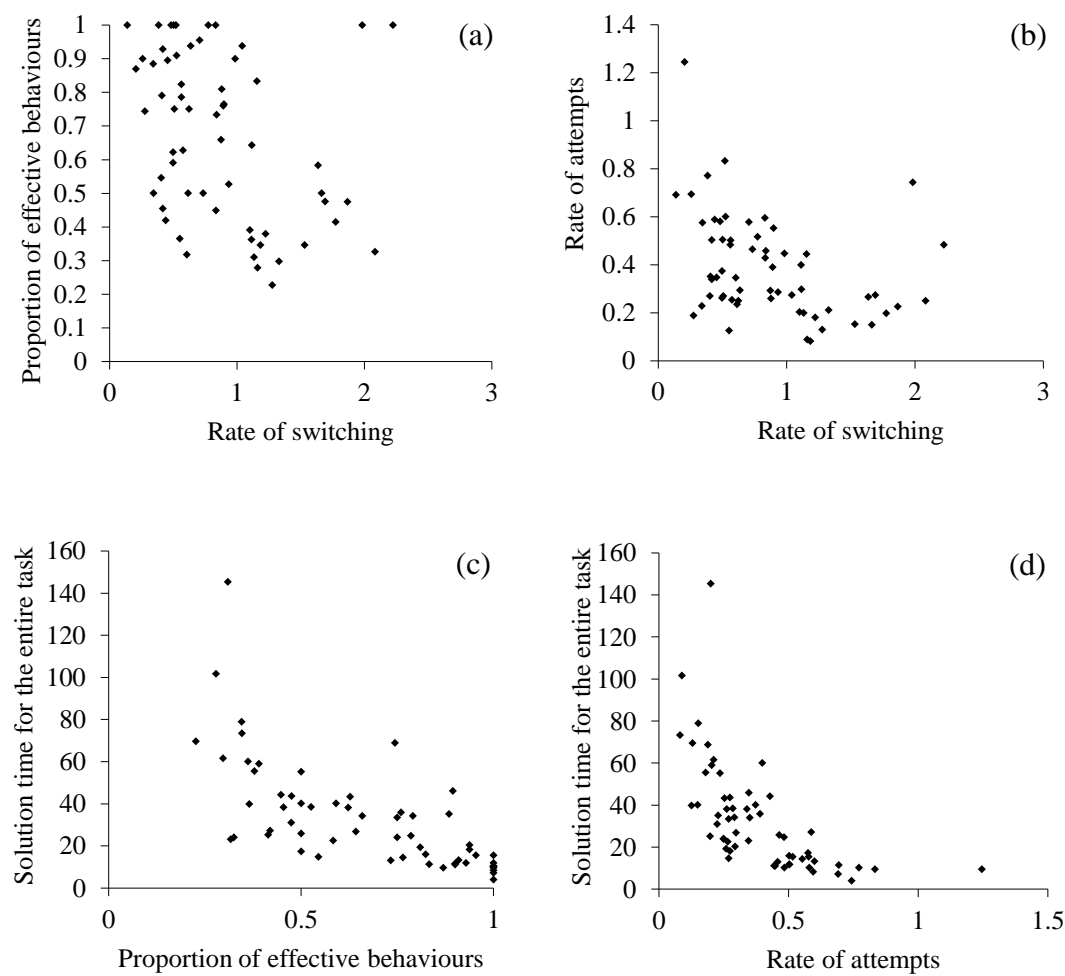


Figure 6.

