Animal Behaviour 112 (2016) 273–283

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

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

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ARTICLE INFO

Article history:
Received 20 May 2015
Initial acceptance 22 July 2015
Final acceptance 22 October 2015
Available online
MS. number: 15-00439R

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

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 them 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.

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 trait providing different advantages for an individual during the 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 that persisted longer in their problem-solving attempts have been shown to be more likely to solve a problem, for example among hyaenas, *Crocuta crocuta* (Benson-Amram & Holekamp, 2012), carib grackles, *Quiscalus lugubris* (Overington, Cauchard, Côté, & Lefebvre, 2011), great tits, *Parus major* (Cauchard, Boogert, Lefebvre, Dubois, & Doligez, 2013) and meerkats, *Suricata suricatta* (Thornton & Samson, 2012).

Behavioural variety: in their studies of hyaena problem solving, Benson-Amram and Holekamp (2012) and Benson-Amram, Weldele, and 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, and Perea (2014) obtained a similar result in Indian hill mynas, *Gracula religiosa*.

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, and 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) argued that

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http://dx.doi.org/10.1016/j.anbehav.2015.11.014

flexibility may also involve the capacity to mobilize old behaviours in new situations. Reader and Laland (2003) considered that both of these conditions could indicate flexibility in problem solving.

Two theoretical difficulties are posed by this list of factors. First, 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. Second, they are to some extent opposed to one another. In particular, persistence could be the opposite of either flexibility or behavioural variety, although 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 each varies 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 (2014) results on Indian hill mynas 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 might have been 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 a definition of each factor of interest based on previous studies (for details see Methods). In summary, we followed the method of Biondi, Bó, and Vassallo (2008) and Griffin and 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 and Diquelou (2015), we predicted that persistence would emerge as one of the contributors to problem-solving efficiency, as this is what the authors found in their studies. Specifically, we predicted that persistence would increase across trials, and, in turn, would 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 (operationalized 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, Bacher, Reader, & Lefebvre, 2008; Sol, et al. 2005; Sol, Timmermans, & Lefebvre, 2002), 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 U.K. 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 minimize 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.