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A battle of wits? Problem-solving abilities in invasive eastern grey squirrels and native Eurasian red squirrels

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Behavioural flexibility has been argued to be an evolutionarily favourable trait that helps invasive species to establish themselves in non-native environments. Few studies, however, have compared the level of flexibility (whether considered as an outcome or as a process) in mammalian invaders and related native species. Here, we tested whether flexibility differs between groups of free-ranging invasive eastern grey squirrels, *Sciurus carolinensis*, and native Eurasian red squirrels, *Sciurus vulgaris*, in the U.K., using an easy and a difficult food extraction task. All individuals of both species showed flexibility, at the outcome level, in solving the easy task and solution time was comparable between species across a series of successes. A higher proportion of grey squirrels than red squirrels solved the difficult task. However, for those squirrels that did solve the task, solving efficiency was comparable between species on their first success, and a few red squirrels outperformed the grey squirrels in subsequent successes. Between-species analysis showed that instantaneous flexibility, flexibility at the process level that was measured as the rate of switching between tactics after a failed attempt, was higher in red squirrels than in grey squirrels. Within-species analysis also revealed that red squirrel problem solvers showed higher flexibility at the process level than their nonsolver counterparts. Nonsolvers also failed to make 'productive' switches (switching from ineffective to effective tactics). Together, the results suggest that problem-solving ability overlaps in the two species, but is less variable, and on average higher, in grey squirrels than in red squirrels. The superior behavioural flexibility of the grey squirrels, shown here by success at problem solving, may have facilitated their invasion success, but it may also have resulted from selective pressures during the invasion process.

Behavioural flexibility has been argued to be an evolutionarily favourable trait for invasive species, as flexibility helps them adapt to non-native environments (e.g. Jarić, Jaćimović, Cvijanović, Knežević-Jarić, & Lenhardt, 2014; Lefebvre, Reader, & Sol, 2013; Sol & Lefebvre, 2000; Sol, Timmermans, & Lefebvre, 2002; Webb, Letnic, Jessop, & Dempster, 2014). Flexibility has been measured in a number of ways (see review by Audet & Lefebvre, in press), and it has been conceptualized at different levels. On the one hand, it has been conceived as a process (hereafter, 'the process level') through which animals are able to vary their behaviours (e.g. Benson-Amram & Holekamp, 2012; Chow, Lea, Hempel de Ibarra, & Robert, 2017; Chow, Lea, & Leaver, 2016; Griffin, Diquelou, & Perea, 2014). For example, Lefebvre and colleagues have measured flexibility from the incidence of novel foraging techniques per taxon (Lefebvre et al., 2013; Sol & Lefebvre, 2000; Sol et al., 2002). On the other hand, flexibility has been conceived as an outcome of actions observed when animals show variations in responding to challenges (hereafter, 'the outcome level'). For example, flexibility could be measured as the outcome of success or failure in solving artificial problem-solving tasks (review by Griffin & Guez, 2014) in which animals are required to overcome obstacles to obtain food rewards, either by applying previously learned tactics to solve a novel problem, or by developing novel tactics to solve old problems (Kummer & Goodall, 1985; Reader & Laland, 2003). In practice, the process can also be inferred from its behavioural outcome; for example, enhanced flexibility is indicated by success in solving artificial problem tasks.

Both these approaches have been used to suggest a relationship between flexibility and success as an invasive species. Sol et al. (2002) and Sol and Lefebvre (2000) have shown that, across taxa, the incidence of novel foraging techniques reported is correlated

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with the establishment of invasive bird species in new environments, while Griffin and Diquelou (2015) have used artificial problem-solving tasks to examine the level of flexibility in two successfully invasive bird species, Indian mynas, *Acridotheres tristis*, and noisy mynas, *Manorina melanocephala*. In the present paper, we take a more direct approach to the hypothesis of a relationship between flexibility and invasiveness, by comparing the flexibility, both at the outcome and at the process levels, shown by an invasive species and the native species it displaces.

Our study model was a population of free-ranging invasive grey squirrels, *Sciurus carolinensis*, and a population of native red squirrels, *Sciurus vulgaris*, in the U.K., and we compared their flexibility, at the outcome level, by measuring their success in solving food extraction problems in field experiments. Although grey squirrels are larger than red squirrels (Bryce, Speakman, Johnson, & Macdonald, 2001), the two species share many morphological and ecological characteristics, so that niche overlap is high (grey squirrels: Koprowski, 1994; red squirrels: Lurz, Gurnell, & Magris, 2005). Grey squirrels are regarded as one of the '100 World's Worst Invasive Alien Species' (Lowe, Browne, & Boudjelas, 2008). They were introduced to the U.K. and Ireland in the 19th century (Gurnell, 1987) and more recently to Italy (Bertolino, Lurz, Sanderson, & Rushton, 2008; Martinoli, Bertolino, Preatoni, Balduzzi, Marsan et al., 2010), and in all three countries the population of grey squirrels is still expanding (Bosch & Lurz, 2012; Huxley, 2003) and replacing red squirrels. When red squirrels in European countries are sympatric and have to compete with grey squirrels, they spend less time foraging and consume less high-energy food than their counterparts that live without the grey squirrels (Wauters, Gurnell, Martinoli, & Tosi, 2001; Wauters, Tosi, & Gurnell, 2002). Measurable consequences of the competitive interactions between the species include significantly reduced red squirrel reproductive success and juvenile recruitment, leading to a potentially rapid decline of the local red squirrel population (Gurnell, Wauters, Lurz, & Tosi, 2004). The red–grey squirrel system is therefore ideal for investigating whether differences in behavioural flexibility may play a part in the competitive success of the introduced species.

We first examined whether flexibility, at the outcome level, was different in the two species, using the food extraction problem paradigm (review by Griffin & Guez, 2014). Based on invasion history in the U.K. (e.g. Gurnell, Lurz, & Bertoldi, 2014), we predicted that grey squirrels would be more successful and efficient than the congeneric red squirrels in solving problems. It has already been shown that grey squirrels show better spatial memory than red squirrels (Macdonald, 1997), but this may be an example of niche-specific cognition since red squirrels are less dependent on recovering scatter-hoarded caches than grey squirrels (Bosch & Lurz, 2012).

We then investigated whether flexibility, considered as a process, was a trait that predicts the differences in problem-solving performance at both between-species and within-species levels. To examine this, we followed Chow et al. (2016), by measuring this 'flexibility' as the rate of switching between tactics after a failed attempt (hereafter 'instantaneous flexibility') to solve a given problem. Across species, problem-solving performance is not always a function of instantaneous flexibility: other traits such as persistence (rate of attempts), motor diversity (rate of performing new types of behaviour), and selectivity (the proportion of effective behaviours performed) have often been implicated. For example, successful problem solvers showed increased persistence (Benson-Amram & Holekamp, 2012; Biondi, Bo, & Vassallo, 2008; Chow et al., 2016; Griffin et al., 2014; Van Horik & Madden, 2016) and/or high motor diversity (Benson-Amram & Holekamp, 2012; Diquelou, Griffin, & Sol, 2016; Griffin & Diquelou, 2015; Griffin et al., 2014). Enhanced efficiency as a result of practice can be related to increased persistence and increased selectivity (Chow et al., 2016), or decreased motor diversity with increased experience (Griffin et al., 2014). Accordingly, we included these three behavioural traits, alongside instantaneous flexibility, when examining between- and within-species differences in problem solving.

Ideally, we would have compared red and grey squirrels living in the same habitat, to avoid any confound between environmental and species differences. However, this is not possible because once grey squirrels enter red squirrel habitats, either the number of red squirrels declines (often rapidly due to the added risk of squirrel pox virus disease transmission; Rushton, Lurz, Gurnell, & Fuller, 2000; Sainsbury, Nettleton, Gilray, & Gurnell, 2000) or the greys are removed by humans in an effort to prevent that happening (for an overview of the current removal project in Scotland, control operations and the pox issue, see https://scottishsquirrels.org.uk/about/project-overview/). We therefore had to study separate populations of the two species. Within the range of habitats currently occupied by red and grey squirrels in the U.K., we matched our study sites as closely as we could for climate, season, vegetation types, predation risk, the number of foraging squirrels and the level of human activity. We also used study sites as widely spread as possible within each habitat, to maximize the genetic diversity within our sample and to avoid sampling the same individuals from each population.

METHODS

Ethical Note

Our study was approved by the Ethical Review Group at the University of Exeter (no. 2012/533). Experiments were carried out in accordance with the ASAB/ABS Guidelines on the treatment of animals and U.K. law. Initially, we trapped squirrels to mark and identify individuals. Between April and September, 12 traps were set at different locations in the University of Exeter campus from dawn to dusk. Traps were checked every 1.5–2 h. When a squirrel was captured, we transferred it to a mesh cylinder-shaped tube (or a handling cone). We PIT tagged and marked each squirrel with a different pattern on different body parts, using commercial hair dye. Individuals were released once they had been sexed and weighed. No deaths occurred as a result of trapping. As the trapping process appeared to deter squirrels from participating in these experiments (only four of 43 trapped squirrels interacted with the test apparatus), we used the individuals' unique characteristics for identification for the rest of the experiment (see Animal Identification below). The experiments did not involve invasive methods; squirrels voluntarily approached and left the apparatus. The apparatus was placed away from roads and in locations with a low risk of predation to avoid exposing the squirrels to added risk from participating in the experiments.

Study Habitats, Study Sites and Study Populations

We collected data from two free-ranging squirrel populations in habitats that contained either grey squirrels or red squirrels exclusively. The grey squirrel habitat consisted of woodlands neighbouring the University of Exeter campus, Devon, U.K. (50.74°N, 3.54°W), or on the campus itself. Data were collected from eight sites within this habitat, between October 2013 and January 2014, and between December 2014 and February 2015. The red squirrel habitat consisted of woodlands around Brodick castle and country park (55.59°N, 5.15°W), Brodick, Isle of Arran, U.K. Data were collected from seven sites within this habitat, from September