Social learning in a non-social reptile (*Geochelone carbonaria*)

Anna Wilkinson*, Karin Kuenstner, Julia Mueller and Ludwig Huber

Department of Cognitive Biology, University of Vienna,
Althanstrasse 14, Vienna 1090, Austria

*Author for correspondence (anna.wilkinson@univie.ac.at).

The ability to learn from the actions of another is adaptive, as it is a shortcut for acquiring new information. However, the evolutionary origins of this trait are still unclear. There is evidence that group-living mammals, birds, fishes and insects can learn through observation, but this has never been investigated in reptiles. Here, we show that the non-social red-footed tortoise (*Geochelone carbonaria*) can learn from the actions of a conspecific in a detour task; non-observer animals (without a conspecific demonstrator) failed. This result provides the first evidence that a non-social species can use social cues to solve a task that it cannot solve through individual learning, challenging the idea that social learning is an adaptation for social living.

Keywords: social learning; solitary; reptile; tortoise; turtle

1. INTRODUCTION

Learning through observing the behaviour of another individual is adaptive, as it provides a shortcut to finding a solution, and so avoids the costly process of trial and error learning. There is evidence that group-living mammals (Heyes & Galef 1996; Whiten *et al.* 2005; Huber *et al.* 2009), birds (Zentall 2004), fishes (Schuster *et al.* 2006) and insects (Leadbetter & Chittka 2009) can learn socially, however, very little is known about the evolutionary origins of this behaviour despite its prevalence. An almost implicit assumption in the literature is that living in social groups favours the evolution of social learning; this logically leads to the idea that social learning is an adaptation for social living (Klopfer 1961; Templeton *et al.* 1999). The experimental support for this hypothesis, however, is not compelling. The majority of studies investigating the link between social living and social learning have examined social learning abilities in closely related species that differ in sociality. Positive findings (with the exception of Templeton *et al.* 1999) are frequently confounded by species differences in individual learning; those social species that perform better in social tasks also perform better in non-social tasks (see Reader & Lefebvre 2001).

To avoid this problem, we approached the question from a different angle, asking whether a non-social animal could learn to solve a task by observing the actions of a conspecific. The adaptive specialization hypothesis predicts that they could not. However, an

alternative hypothesis, which has received little attention in the literature, is that the ability of an animal to learn socially is simply a reflection of an animal's general ability to learn. Any animal with the capacity to learn is likely to be able to use a wide variety of salient stimuli as cues (Heyes 2003); in this context, social cues can be considered similar to other environmental cues and can thus be learned through associative processes. This hypothesis would predict that any species that has had extensive exposure to a conspecific should be able to learn socially.

Using a non-social species provides an ideal scenario for testing the hypothesis that sociality is directly linked to social learning abilities in animals. Truly solitary species within the mammalian and avian classes, however, remain elusive as those that are solitary in their adult life still receive extensive parental care as infants (Galef & Laland 2005). It is therefore unsurprising that only one study has previously used this approach. Fiorito & Scotto (1992) found evidence of social learning in the solitary common octopus (*Octopus vulgaris*). Though apparently compelling, this study has been widely criticized for failing to control innate species-specific behaviour (e.g. Biederman & Davy 1993).

Social learning has never been previously studied in reptiles. Moreover, some species of reptiles are solitary and exhibit no parental care (Wilson 1998), making them ideal subjects for this experiment. To this end, we examined the social learning abilities of the red-footed tortoise (*Geochelone carbonaria*), a naturally solitary species that inhabits the margins of tropical forests in Central and South America (Strong & Fragoso 2006). Though they may naturally interact with conspecifics (e.g. mating opportunities; Auffenberg 1965), they do not form permanent groups. Indeed, parental care has not been observed in tortoises (Burghardt & Layne 1995): eggs are laid in holes and then left. Once the infants hatch, they dig themselves out of the hole and disperse. Despite their solitary nature, there is evidence that this species possesses a sensitivity to visual social cues (Auffenberg 1965; Wilkinson *et al.* in press). This makes the red-footed tortoise an ideal subject for examining whether a solitary species can use the behaviour of a conspecific to reach a goal.

Eight socially housed red-footed tortoises were presented with a detour task. By presenting this task to both non-observer (control) animals, who had to solve the task through individual learning, and to animals who were able to watch a conspecific demonstrator solve the task before they attempted it themselves, we were able to examine the role that social and individual learning plays on solving a task in this species.

2. MATERIAL AND METHODS

(a) Subjects and apparatus

Eight red-footed tortoises (*G. carbonaria*) participated in this experiment. Subjects were all juvenile or subadult at the time of the study. Individual age was approximated based on inspection of the lower part of their shells (i.e. the plastron), which ranged from 9 to 17 cm in length. Though this species of tortoise is naturally solitary, they were group-housed for two months prior to the start of this experiment to give them experience with the behaviour of other conspecifics. The tortoises were housed in two groups in a heated (29°C ± 4°C) and humidified room. For the experiment, the tortoises were randomly assigned to one of the two testing conditions,

Figure 1. The experimental setup. The arrow indicates the direction in which the demonstrator moved.

the non-observer ($n = 4$) and the observer ($n = 4$) conditions. The groups were size (age)-matched. Six of the tortoises had previously taken part in experiments (e.g. Wilkinson *et al.* in preparation), but were unfamiliar with the present task. Two tortoises were experimentally naive at the onset of the study. One of the experimentally naive individuals was in each group.

The task was run in an arena measuring 120×120 cm, the floor of which was covered with bark chips. In the centre of the arena was a 40 cm high V-shaped fence. Each side was 50 cm long; the angle between the sides was 110° . The setup was situated in a heated room, maintained at approximately 29°C .

(b) Procedure

In each trial a tortoise was placed on the outside of the V-shaped fence and a preferred food was available in the centre. To reach the goal successfully, the tortoise had to move away from the food, circumvent the fence and return to the food on the other side (figure 1 depicts the setup and the experimental group task).

Each animal of the non-observer group received 12 trials (one per day). For each non-observer trial, a tortoise was placed in a small cage in the test arena for 30 s. The bark flooring of the setup was redistributed through the entire arena (to avoid any scent trails in the observer condition) before the tortoise was released from the cage. After release, each animal was allowed 2 min (from when it started to move) to solve the task. Any animal that reached the goal was allowed to eat the reward.

One of the non-observer animals was then trained, using a successive approximation procedure, to make the detour in a rightward direction. It took over 30 sessions (each consisting of five or more trials) to attain reliable performance. The trials of the observer group were identical to those of the non-observer animals except that when each observer animal was placed in the small cage it watched the demonstrator complete the detour and eat the reward. The demonstrator was then removed, the bark redistributed and the reward bowl replenished before the observer tortoise was released. Any trial in which the observer did not watch the demonstration was stopped after the demonstration and repeated. Watching was judged as facing towards the demonstrator for at least 80 per cent of the trial. Any trial in which the demonstrator did not move after 30 s was abandoned and repeated later.

3. RESULTS

None of the four non-observer tortoises reached the goal in any of their 12 trials (figure 2a). They readily approached the fence in front of the reward but were unable to successfully navigate the detour. However, all four of the observer subjects completed the task at least twice, with two completing the detour on the first trial (figure 2b). A Fisher exact test comparing the success of each group on an all or nothing measure of whether an animal was successful or not within the 12 trials (irrelevant of the number of trials it was successful) revealed that the observer group were significantly more successful than the non-observer group ($p < 0.05$). The observer tortoises completed the detour in a leftward as well as the demonstrated

Figure 2. The number of trials in which the tortoises completed the detour and the direction taken for (a) the non-observer group and (b) the observer group. White bars, left; shaded bars, right.

rightward direction (figure 2b). On their first successful trial, three of the observer tortoises went right and one went left. Of the 29 successful trials, the tortoises made the detour 21 times in a rightward direction and 8 times in a leftward direction. A χ^2 test revealed that the tortoises made the detour in a rightward direction significantly more than would be expected by chance ($\chi^2(1) = 5.83$, $p < 0.05$).

4. DISCUSSION

The results show that the solitary red-footed tortoise can learn to solve a task by observing the actions of a conspecific. This task was not solved through individual learning. After observing a demonstrator complete the detour, all the observer tortoises successfully reached the goal while all the non-observer animals failed. Use of a simple strategy, such as following the scent of the demonstrator, can be ruled out as the tortoises made the detour in both the directions. The results may be explained through local or stimulus enhancement brought about by the presence of a conspecific. This possibility can only be entirely ruled out through the use of a two-action procedure (see Zentall 2004). However, we believe that stimulus or local enhancement of some element of the route is unlikely to account for our findings. The demonstration was only made in a rightward direction, but the tortoises' responses were not restricted to this. One of the tortoises went leftward on its first successful detour and two of the other tortoises successfully navigated the

detour in both directions. However, overall there was a significant rightward preference. The role of social facilitation remains unclear, but it seems plausible that the tortoises copied some part(s) of the behaviour of the conspecific. This is the first evidence of social learning in a non-social reptile and reveals that sociality is not a prerequisite for social learning.

The dominant hypothesis in this field claims that social learning evolved as a result of social living and therefore predicts that the tortoises would have difficulty with this task. They did not. The findings suggest that, in this case, social learning may be the result of a general ability to learn. Although the brain mechanisms that underlie the tortoises' ability to learn socially remain unclear, it seems most likely that it is the product of a general learning mechanism that allows the tortoises to learn, through associative processes, to use the behaviour of another animal just as they would learn to use any cue in the environment.

To further understand the mechanisms controlling social learning in this species, it is necessary to manipulate the amount of social experience that an animal has, as well as to test the importance of the demonstrator being a conspecific (or even an animate object). Further investigation is essential; however, this study provides the first evidence of social learning in a solitary reptile. The findings suggest that, at least in some cases, the ability to learn socially may simply be a reflection of an animal's general ability to learn.

We would like to thank the cold-blooded cognition group (University of Vienna), particularly U. Aust, J. Bryson, O. Fraser and E. Glass for their helpful comments. This work was supported by funding from the Austrian Science Fund (to L.H.) contract number P19574.

- Auffenberg, W. 1965 Sex and species discrimination in two sympatric South American tortoises. *Copeia* **3**, 335–342. (doi:10.2307/1440797)
- Biederman, G. B. & Davy, V. A. 1993 Social learning in invertebrates. *Science* **259**, 1627–1628. (doi:10.1126/science.259.5101.1627)
- Burghardt, G. M. & Layne, D. G. 1995 Effects of ontogenetic processes and rearing conditions. In *Health and welfare of captive reptiles* (eds C. Warwick, F. L. Frye & J. B. Murphy), pp. 165–185. London, UK: Chapman & Hall.
- Fiorito, G. & Scotto, P. 1992 Observational learning in *Octopus vulgaris*. *Science* **256**, 545–547. (doi:10.1126/science.256.5056.545)
- Galef Jr, G. B. & Laland, K. 2005 Social learning in animals: empirical studies and theoretical models. *BioScience* **55**, 489–499. (doi:10.1641/0006-3568(2005)055[0489:SLIAES]2.0.CO;2)
- Heyes, C. M. 2003 Four routes to cognitive evolution. *Psychol. Rev.* **110**, 713–727. (doi:10.1037/0033-295X.110.4.713)
- Heyes, C. M. & Galef Jr, B. G. 1996 *Social learning in animals*. San Diego, CA: Academic Press.
- Huber, L., Range, F., Voelkl, B., Szucsich, A., Virányi, Z. & Miklósi, A. 2009 The evolution of imitation: what do the capacities of non-human animals tell us about the mechanisms of imitation? *Phil. Trans. R. Soc. B* **364**, 2299–2310. (doi:10.1098/rstb.2009.0060)
- Klopfer, P. H. 1961 Observational learning in birds: the establishment of behavioural modes. *Behavior* **14**, 71–80. (doi:10.1163/156853961X00376)
- Leadbetter, E. & Chittka, L. 2009 Bumble-bees learn the value of social cues through experience. *Biol. Lett.* **5**, 310–312. (doi:10.1098/rsbl.2008.0692)
- Reader, S. M. & Lefebvre, L. 2001 Social learning and sociality. *Behav. Brain Sci.* **24**, 353–355. (doi:10.1017/S0140525X01543964)
- Schuster, S., Wohl, S., Griebisch, M. & Klostermeier, I. 2006 Animal cognition: how archer fish learn to down rapidly moving targets. *Curr. Biol.* **16**, 378–383. (doi:10.1016/j.cub.2005.12.037)
- Strong, J. N. & Fragoso, J. M. V. 2006 Seed dispersal by *Geochelone carbonaria* and *Geochelone denticulata* in north-western Brazil. *Biotropica* **38**, 683–686. (doi:10.1111/j.1744-7429.2006.00185.x)
- Templeton, J. J., Kamil, A. C. & Balda, R. P. 1999 Sociality and social learning in two species of corvids. *J. Comp. Psychol.* **113**, 450–455. (doi:10.1037/0735-7036.113.4.450)
- Whiten, A., Horner, V. & de Waal, F. B. M. 2005 Conformity to cultural norms of tool use in chimpanzees. *Nature* **437**, 737–740. (doi:10.1038/nature04047)
- Wilkinson, A., Mandl, I., Bugnyar, T. & Huber, L. In press. Gaze following in the red-footed tortoise (*Geochelone carbonaria*). *Anim. Cogn.*
- Wilkinson, A., Mueller, J. & Huber, L. In preparation. What does a reptile see in a photograph? Picture-object confusion in the red-footed tortoise (*Geochelone carbonaria*).
- Wilson, E. O. 1998 *Sociobiology: the abridged edition*. MA: Harvard College Press.
- Zentall, T. R. 2004 Action imitation in birds. *Learn. Behav.* **32**, 15–23.