

RESEARCH METHODS GUIDE

Contemporary Methods for Studying Animal Sociality in the Wild

Manipulating actions: A selective two-option device for cognitive experiments in wild animals

Sonja Wild^{1,2}  | Gustavo Alarcón-Nieto²  | Michael Chimento^{1,2}  | Lucy M. Aplin^{1,2,3} 

¹Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Constance, Germany

²Cognitive and Cultural Ecology Research Group, Max Planck Institute of Animal Behavior, Radolfzell, Germany

³Research School of Biology, Australian National University, Canberra, Australian Capital Territory, Australia

Correspondence

Sonja Wild

Email: swild@ab.mpg.de

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Abstract

1. Advances in biologging technologies have significantly improved our ability to track individual animals' behaviour in their natural environment. Beyond observations, automation of data collection has revolutionized cognitive experiments in the wild. For example, radio-frequency identification (RFID) antennae embedded in 'puzzle box' devices have allowed for large-scale cognitive experiments where individuals tagged with passive integrated transponder (PIT) tags interact with puzzle boxes to gain a food reward, with devices logging both the identity and solving action of visitors.
2. Here, we extended the scope of wild cognitive experiments by developing a fully automated selective two-option foraging device to specifically control which actions lead to a food reward and which remain unrewarded. Selective devices were based on a sliding-door foraging puzzle, and built using commercially available low-cost electronics.
3. We tested it on two free-ranging PIT-tagged subpopulations of great tits *Parus major* as a proof of concept. We conducted a diffusion experiment where birds learned from trained demonstrators to get a food reward by sliding the door either to the left or right. We then restricted access of knowledgeable birds to their less preferred side and calculated the latency until birds produced solutions as a measure of behavioural flexibility.
4. A total of 22 of 23 knowledgeable birds produced at least one solution on their less preferred side after being restricted, with higher-frequency solvers being faster at doing so. In addition, 18 of the 23 birds reached their solving rate from prior to the restriction on their less preferred side, with birds with stronger prior side preference taking longer to do so.
5. We therefore introduce and successfully test a new selective two-option puzzle box, providing detailed instructions and freely available software that allows reproducibility. It extends the functionality of existing systems by allowing fine-scale manipulations of individuals' actions and opens a large range of possibilities to study cognitive processes in wild animal populations.

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KEYWORDS

automated data collection, biologging, cognitive experiments, great tits, puzzle box, RFID, selective feeder, two-option device

1 | INTRODUCTION

Advances in biologging have improved our abilities to remotely track individual animals' behaviour and physiology as they move through their natural environment (Evans et al., 2013; Fehlmann & King, 2016; Rutz & Hays, 2009; Whytock & Christie, 2017). Moreover, the increased availability of low-cost electronic devices (Jolles, 2021; Youngblood, 2019) has enabled remote data collection in a wide variety of observational and experimental studies. A popular choice for remote tracking is radio-frequency identification (RFID) technology, a low-cost system consisting of an attached or implanted passive integrated transponder (PIT) tag that transmits a unique code when activated through proximity to a receiving antenna (e.g. Aguzzi et al., 2011; Bridge & Bonter, 2011; Youngblood, 2019). For example, RFID data-loggers at feeders or nest sites have been used extensively to study breeding activity (Bonter & Bridge, 2011; Mariette et al., 2011), build social networks (Aplin, Firth, et al., 2015; Psorakis et al., 2012), estimate mass and energetics (Hou et al., 2015) and study habitat use (Cox et al., 2016). Automated puzzle boxes that incorporate RFID antennae have also been used to extend the scale and scope of cognitive social learning and decision-making experiments (Aplin, Farine, et al., 2015; Chimento et al., 2021; Morand-Ferron et al., 2015; Wild et al., 2021).

Low-cost electronic devices have been further developed into selective systems that allow to control and manipulate experiences based on individuals' unique electronic tag IDs. The potential of such selective or 'smart' systems has been quickly recognized in animal husbandry, zoos, as well as the pet industry to optimize diet (Remus et al., 2020; Vaintrub et al., 2020; Zuidhof et al., 2017), control access through automatic doors (Wicaksono et al., 2019) or provide individually tailored enrichment (Hoy et al., 2010; Kim-McCormack et al., 2016). Selective systems have also been used for cognitive research on captive animals. For example, in studies on primate cognition, individuals were given access to computerized test systems that were controlled by automatic identification of subjects via RFID to provide cognitive puzzles tailored to the specific individual (Fagot & Bonté, 2010; Fagot & Paleressompoulle, 2009). Similarly, in studies on decision making in ants, colony members were equipped with radio tags and their access to food sources controlled through automatic doors (Robinson et al., 2012).

Selective devices are also increasingly used in the field. For example, in wildlife conservation, RFID activated doors were used to provide breeding sites that are protected from predators (Muns et al., 2018; Watson et al., 2021). Similarly, 'smart traps' selectively target specific individuals for capture to minimize unnecessary bycatch and recaptures (Meniri et al., 2019). However, the most frequently used selective system in the wild are selective feeders that can be programmed to grant access to food for particular

individuals. Such selective feeders have, for example, been used to artificially manipulate food preferences for particular sugar water concentrations in hummingbirds (Ibarra et al., 2015), to investigate individual feeding patterns in squirrels (Kenward et al., 2005), to manipulate the foraging social network in communities of songbirds by allowing only certain dyads to co-feed (Firth et al., 2016; Firth & Sheldon, 2015) and for spatial memory tasks in mountain chickadees to compare behavioural flexibility between birds from different age and sex classes, and from different environments (Branch et al., 2020; Croston et al., 2016, 2017; Tello-Ramos et al., 2018). In these studies, selective feeders have been exclusively used to control whether or not individuals get access to food. A study on spatial reversal learning in great tits has taken selective feeding systems a step further by controlling on an individual level which action led to a food reward and which remained unrewarded (Cauchoix et al., 2017). Using an operant conditioning device with three keys, originally developed for a colour-associate learning study in tits (Morand-Ferron et al., 2015), birds were rewarded if they correctly pecked the illuminated key, with illumination governed by internal individualized rules based on the birds' unique PIT tags (Cauchoix et al., 2017).

Here, we extend the functionality of selective feeding systems by developing a selective two-option foraging puzzle, which gives an opportunity to extend the sample size and scope of cognitive experiments. Two-option foraging puzzle boxes ('artificial fruits') are often used in studies on cognition and learning, during which individuals have to perform one of two alternative actions (turn a dial, slide a door etc.) to receive a food reward (Aplin, Farine, et al., 2015; Canteloup et al., 2020; Morand-Ferron et al., 2015). A selective two-option task allows control over whether or not an individual gets access to food, and over which of the two actions leads to a food reward, and which remains unrewarded.

We based our design on a sliding-door foraging puzzle that has previously been developed for studying social learning processes in songbirds (Aplin et al., 2017; Aplin, Farine, et al., 2015; Chimento et al., 2021). The original puzzle box allowed birds to obtain a food reward by sliding a door either left or right, while an RFID antenna built into the landing perch registered the birds' unique PIT tags. Combined with sensors and an internal motor, solving actions were registered and the door reset after birds departed. Here, we modified the original design to be able to selectively grant access for each individual bird to either left, right or both sides based on its unique tag. We tested the selective design on two wild subpopulations of great tits *Parus major* in a reversal learning task. Being able to do the opposite of a task that was previously learned is often used in cognitive studies as a measure of behavioural flexibility (Chow et al., 2015; Croston et al., 2017; Lea et al., 2020).

We initially introduced several knowledgeable birds, *demonstrators* hereafter, into the two subpopulations. In the first part of the

experiment, we let the behaviour diffuse naturally through the population. In order to create local side preferences, the demonstrators of one subpopulation were restricted to left, and the other to right. Meanwhile, no restrictions were placed on any of the naïve birds. In the second part of the experiment, after the behaviour had spread, we determined the preferred solving side for each knowledgeable bird and restricted them to their less preferred side. As a measure of behavioural flexibility, we calculated both the latency until the first solve on their less preferred side as well as the latency until birds reached their prior baseline solving rate. We tested whether age, the strength of their prior side preference, whether they were demonstrators, their connection to other informed individuals, the solving rate and the number of solves prior predicted those latencies. We hypothesized that younger, more connected individuals with weaker prior side preferences and higher solving rates would be faster at switching (Aplin et al., 2017). We finish by discussing possible applications and extensions of and limitations to our selective two-option puzzle box design.

2 | MATERIALS AND METHODS

2.1 | Puzzle box design

The design of our experimental device was based on a sliding-door foraging puzzle originally developed for studies on social learning in tits (Aplin, Farine, et al., 2015; Chimento et al., 2021). It consisted of a white acrylic box (30.5 × 20.5 × 24.5 cm—custom ordered) with a receiving antenna (9 × 7 cm, frq 125 kHz, NatureCounters Ltd) built into the landing perch that was attached to the box front (Figure 1a). The box contained a Raspberry Pi 4 micro-computer, and an RFID reader/writer module for data logging (Priority1 Design), and was powered by a 12V 18MAH battery (Figure 1c, Table S1). A sliding door of 30mm width concealed a circular opening (10mm diameter) into a mealworm tray located inside the box, which the birds could slide either left or right to get access to this highly preferred food (Figure 1a,b). All electronic components were commercially sourced, and STL files for 3D printed parts have been deposited on github (Table S1). Costs for all components for one puzzle box were approximately 200 EUR.

The operation of the sliding door mechanism was controlled by software that governed the transition between five different states (Figure 2), based on software developed for a previous experiment (Chimento et al., 2021). In state 0, the opening was concealed by the sliding door with the door held in place by two servo motors on the inside (Figure 1b). If a tagged bird landed on the perch, it transitioned into state 1, during which the bird's ID and time of arrival were recorded and its tag cross-referenced with an internal list that defined side access as either 'right', 'left' or 'both'. Based on the defined restrictions, one or both of the servo motors were operated to selectively unblock the sliding door to the respective side(s) (state 2) (Figure 1b). If the bird then pushed the door open to reveal the opening to the mealworm tray, this was registered as either a 'left' or

'right' solve by triggering infra-red (IR) sensors on the inside of the box front (state 3) (Figure 1b). Departure time was recorded once the tag was no longer detected by the antenna. Following state 3, both servo motors were operated to reset the sliding door (back to state 0). Arrival and departure times of non-solvers were also recorded. In the rare occurrence that the sliding door became stuck open, this was registered by continuous triggering of one of the two IR sensors and both servos were operated at an interval of 10s in an attempt to close the door (state 4). A 'sensor error' was then recorded in the data. The software code was saved on a USB drive inserted into the Raspberry Pi and set up to automatically launch when the Raspberry Pi was powered on (Figure 1b). We used VNC viewer 6.20.113 to access the pi with a field laptop using an Ethernet cable (Figure 1b). The puzzle box software is available on github (see Data Availability Statement).

2.2 | Field methods

The study took place in Radolfzell, Germany, at two separate field sites consisting of mixed woodland (ME: 47.72866, 8.99727; MC: 47.74961, 8.95335 [WGS84]). Great tits were caught in mist nets between September 2019 and December 2020, and each equipped with a uniquely numbered metal leg ring issued by the Radolfzell Bird Observatory, and a passive integrated transponder (PIT) tag (Eccel Technology, EM4102). Birds were ringed under ringing licences held by GAN and SW, granted by the Radolfzell Bird Observatory (55-8841.03; 8853.17), and ethical approval was granted to LMA by the Regierungspräsidium Freiburg (35-9185.81/G-19/159). All birds were sexed and aged (juvenile/adult) based on plumage (Svensson, 1992).

Two puzzle boxes were deployed at each site between 10 December 2020 and 3 March 2021 at a distance of 200–250m apart on wooden platforms (66 × 60cm) at approximately 1–1.3 m height above-ground. Platforms were covered with a cage with 35mm hexagonal mesh (dimensions 66 × 60 × 40cm) to selectively allow small birds to access the experimental device while preventing damage from larger birds and rodents. Puzzle boxes were deployed 5 days per week, followed by 2 days of network data collection to infer social associations (see below; Psorakis et al., 2012; Aplin, Firth, et al., 2015). We additionally added small openly accessible feeder columns (35cm) with a mix of sunflower seed and kibbled peanuts next to the wooden platforms to attract birds to the vicinity of our experimental devices.

At both sites, we then released six knowledgeable *demonstrator* birds that had previously been sourced from these two subpopulations and had learned to solve the sliding-door puzzle in an independent captive experiment. The permit for the captive experiment was obtained from the Regierungspräsidium Freiburg, granted to LMA (35-9185.81/G-20/100). We restricted these demonstrators to one of the two sides ('right' at ME, 'left' at MC), to create artificial local side preferences. All other birds remained unrestricted.

Over the course of 10 weeks, we let the behaviour diffuse through the populations. To adjust difficulty of the task, we

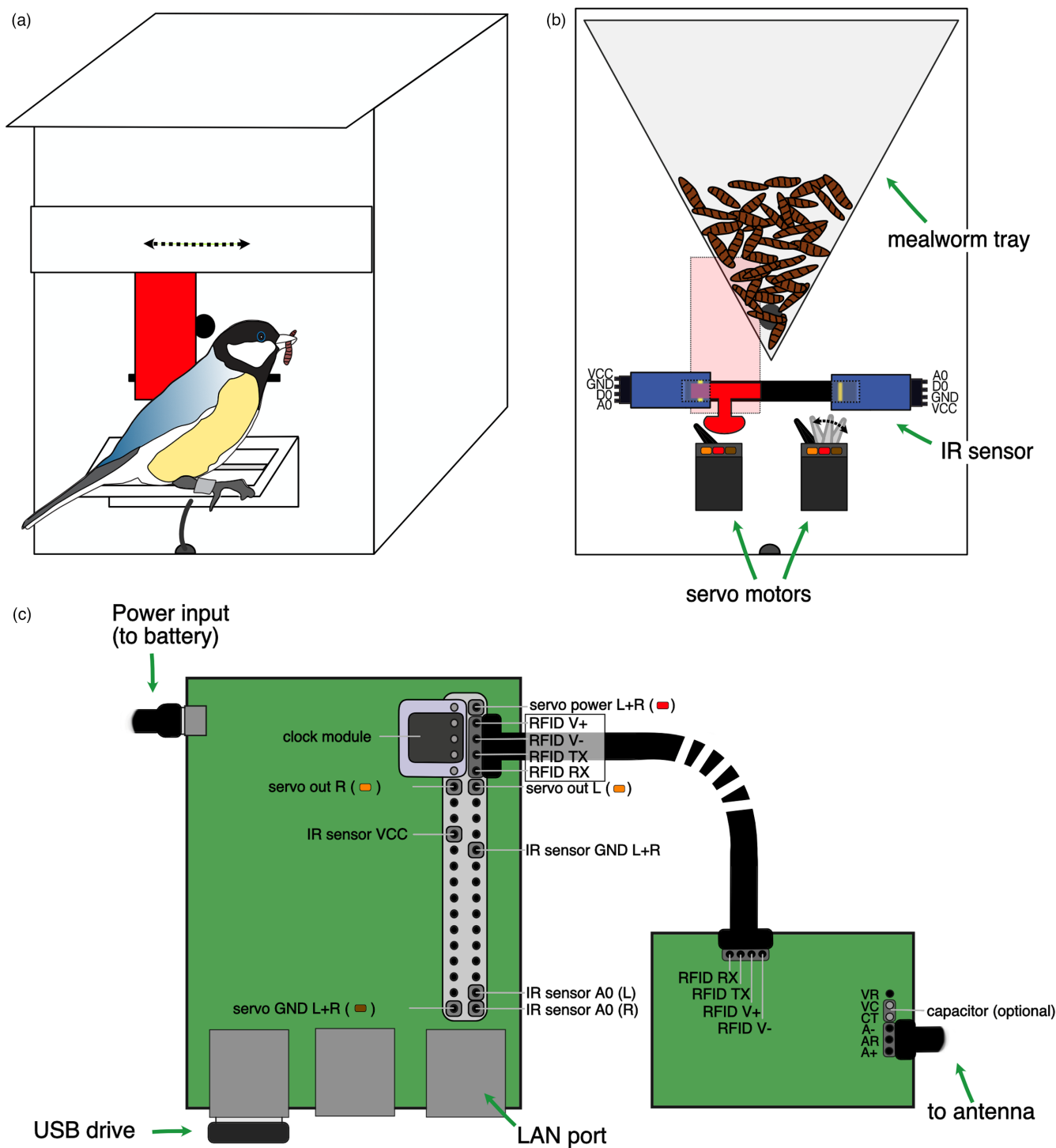


FIGURE 1 Schematic drawing of the selective puzzle box. (a) Front view: Birds' unique alphanumeric PIT tags were recorded with the RFID antenna built into the landing perch. By pushing the sliding door either to the left or the right, birds could uncover a hole leading to a concealed mealworm tray. (b) Inside view: The rotating arms of two servo motors selectively allowed access for individual birds as defined on an internal access list. Following a solve—registered by IR sensors on each side—the servo motors moved the sliding door back to the original position to conceal the opening. (c) Internal set-up: A Raspberry Pi 4 computer was connected to an RFID reader/writer module (Priority1 Design), which connected to an RFID receiving antenna (125 kHz—NatureCounters Ltd) built into the landing perch to register visiting birds' PIT tags. The Raspberry Pi was equipped with a clock module and connected to the servo motors and IR sensors via GPIO pins. All electronics were powered through a 12V 18mAh battery.

tested several modifications to the box design, including changing the door width and colour (SI). After the diffusion, we then modified the access lists on all puzzle boxes to restrict access

for all knowledgeable birds with at least 10 solves to their less preferred side, including the initial demonstrators, who had been restricted throughout the experiment. We continued to record

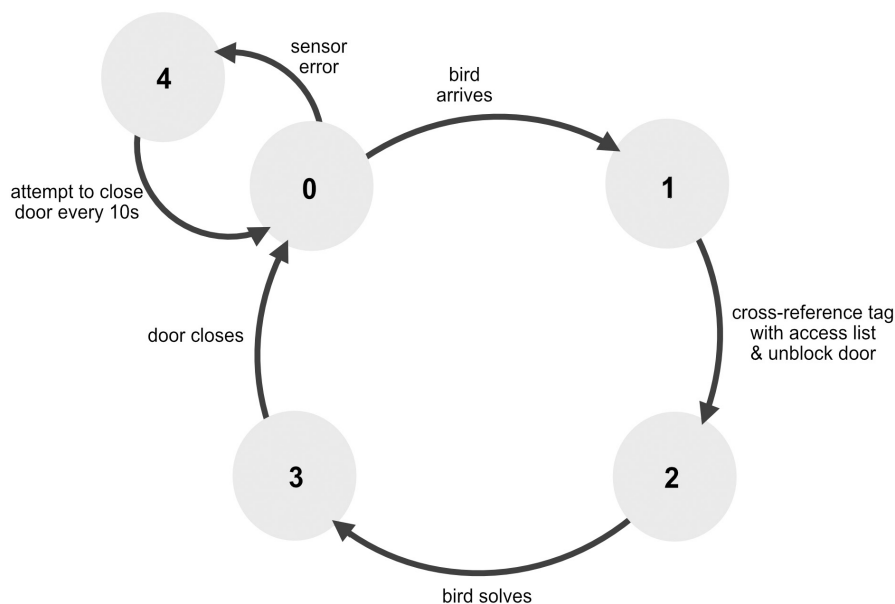


FIGURE 2 Flowchart of the software controlling puzzle box operations. As birds landed on the receiving RFID antenna (stage 0 → stage 1), their PIT code was cross-referenced with an internal access list, triggering operation of the servo motors to selectively allow access to one or both sides (stage 1 → stage 2). Following a successful solve (registered through activation of IR sensors), doors were subsequently closed by operating the servo motors (stage 3 → stage 0). Bird ID, arrival and departure time, as well as solving side were recorded. In the case of departure of the bird or displacement by another bird at any stage, the software was set up to transition back to stage 0. In the rare event of the sliding door getting stuck—indicated by continuous triggering of the IR sensor—servo motors were operated at a 10-s interval in an attempt to close the door (stage 4 → stage 0).

birds' visits and solving behaviour during 10 experimental days until 3 March 2021.

2.3 | Social associations

Throughout the experiment, puzzle boxes were removed for 2 days each week for data download, cleaning and repairs. During these 2 days, we installed three openly accessible feeder columns spaced around each of the two sites at approximately 125 m distance, giving a total of 20 days of data. All feeders had two feeding holes, both equipped with RFID antennas to record visits. We then used Gaussian mixture models to locate spatio-temporal clusters in the data-stream and identify visiting groups (Psorakis et al., 2012). Following previous work on this species, we created social networks using a gambit of the group approach and the simple ratio index (SRI: Cairns & Schwager, 1987), where social associations between any two birds varied between 0 (never observed in the same group) and 1 (always observed in the same group) (Aplin, Farine, et al., 2015; Aplin, Firth, et al., 2015; Farine, 2013).

2.4 | Statistical analyses

In our analysis of behavioural flexibility, we only included birds that were both present in the 10 days before and after the restriction date and that had solved at least five times in the 10 days prior to the

restriction. For each bird, we extracted several characteristics on its visiting and solving behaviour and network position from before the restriction. From the 10 days prior, we extracted: (a) each bird's total number of solves, (b) the solving rate as the number of solves divided by the number of visits, (c) the strength of the side preference before the restriction as the proportion of solves on their preferred side across all solves and (d) each bird's summed association strength to other knowledgeable birds. The solving rate was used as a baseline to investigate whether birds managed to reach the same solving rate on their less preferred side (see next paragraph). Social measures were calculated using social association data from four 2-day periods before the restriction was put in place.

Next, we calculated two different latencies based on solving behaviour after the restriction as measures of behavioural flexibility. (a) The latency until birds produced the first solution on their less preferred side; and (b) the latency until birds reached their solving rate from prior to the restriction. For both latencies, we used the number of visits that were not followed by solve as a proxy for unsuccessful solving attempts. To determine the visit on which birds reached their prior solving rate (second latency), we calculated birds' solving rate after the restriction over blocks of 40 visits (SI) using a sliding window, and compared the resulting rates to the prior solving rate. We considered a bird to have reached its prior solving rate, if the calculated solving rate within the block of visits was at least 90% of the one prior to the restriction. We allowed for this 10% decrease in solving rate to account for noise in the data. To exemplify, let us assume a hypothetical bird with a solving rate of 0.5 prior to

the restriction. According to our defined criterion, it would need to reach a solving rate of 0.45 (90% of 0.5) after the restriction. Starting with its first solve after the restriction, we would calculate the bird's solving rate over the next 40 visits. Assuming it solved 10 of 40 times during that first block (solve rate of 0.25), we would conclude that it had not reached 90% of its prior solving rate. We would then recalculate the solving rate from the second solve over the next block of 40 visits—then the third, fourth, etc—until a solving rate of at least 0.45 had been reached. The first solve of the block within which the solving rate had been reached was then taken as the latency.

We investigated which factors predicted both latencies (until the first solve and until the prior solving rate was reached) in two separate cox proportional hazard models, including all knowledgeable individuals regardless of whether they managed to produce a solution on their less preferred side and/or reached their solving rate from prior. Cox proportional hazard models are used to model time-to-event (survival) data by estimating the hazard rate for each covariate as a ratio relative to a reference level (Moore, 2016). A hazard rate (HR) > 1 indicates a decrease in 'survival'—here decreased latency—and a HR < 1 an increased survival—here increased latency. Cox models explicitly consider events that never occur as censored data, in this particular case if no solves were produced on the less preferred side or the solving rate from prior was not reached until the end of the experiment respectively.

We included several predictors in the models: (a) age of the individual (adult/juvenile); (b) whether it was a demonstrator (yes/no); (c) the summed association strength with informed individuals (based on SRI, see above); (d) the prior solving rate and (e) the number of solves in the 10 days before the restriction. As sex could not

be assigned with certainty for all individuals, we did not include it as a predictor variable. We first tested for multi-collinearity among these predictor variables by calculating variance inflation factors (VIFs) (Fox & Weisberg, 2018) and for the proportional hazards assumption (Therneau & Lumley, 2014) (SI). We then built the two cox proportional hazard models (one for each latency) controlling for site as a random effect and compared all possible models containing subsets of variables in all possible combinations using the Akaike information criterion corrected for sample size (AICc) (Anderson & Burnham, 2004; Barton, 2014). We obtained relative support for each predictor (as summed AICc weights across all models), and effect sizes (as model averaged estimates), and 95% confidence intervals were estimated across models within $\Delta AICc > 4$ from the best performing model (Anderson & Burnham, 2004).

All analyses were performed in R v4.0.5 (R Core Team, 2021), and the code is available on github (see Data Availability Statement).

3 | RESULTS

At ME, 87 tagged great tits visited the puzzle box, of which 36 birds with at least 10 solves produced a total of 11,649 solutions. Of the 36 birds, three were demonstrators and 33 birds learned to solve the puzzle box during the diffusion period. At MC, 74 tagged birds visited the puzzle box, of which 33 produced at least 10 solutions, resulting in a total of 13,431 solves. Of the 33 birds, six were previously knowledgeable demonstrators and 27 were birds that learned during the diffusion period. Similar to a prior study using a sliding-door

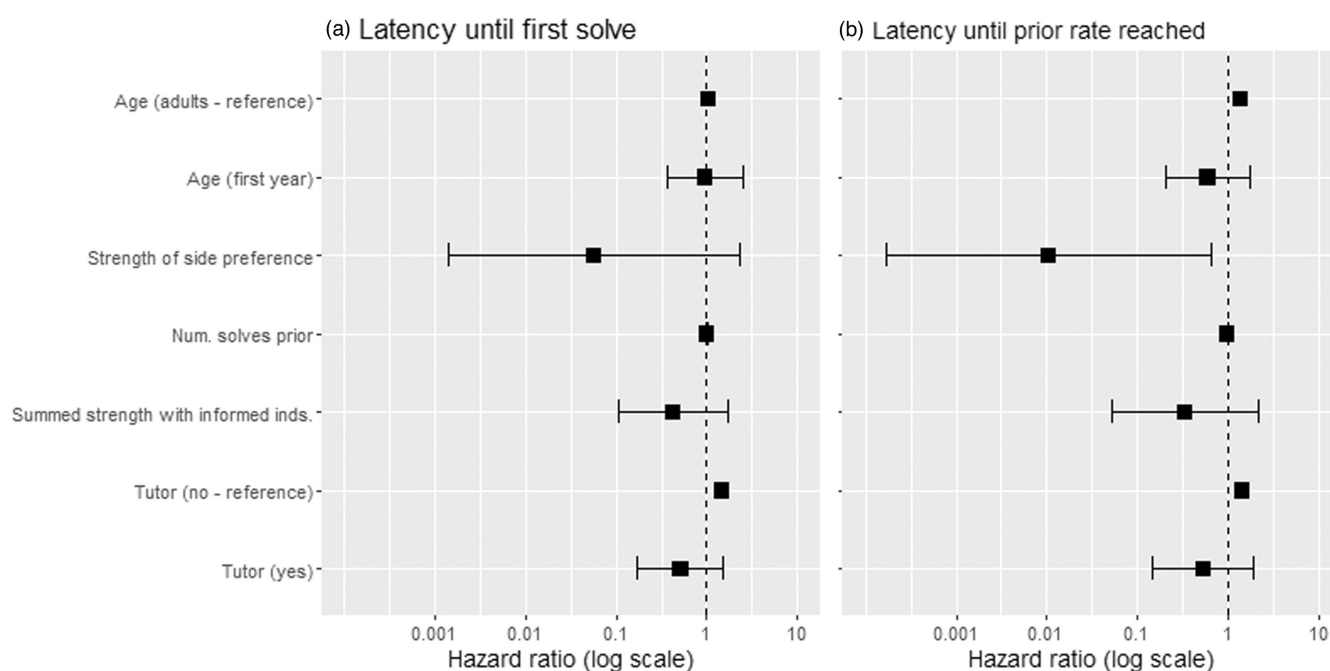


FIGURE 3 Hazard ratios of covariates including 95% confidence intervals. (a) For predicting the latency until the first solve on the less preferred side. (b) For predicting the latency until birds reached the solving rate from prior to the restriction. Hazard ratios and corresponding 95% confidence intervals were averaged across models within $\Delta AICc < 4$ of the best performing model. Hazard ratios < 1 indicate reduced latency while those > 1 indicate increased latency.

TABLE 1 Support and model averaged estimates including 95% confidence intervals for covariates predicting latency with supported variables (summed Akaike weights >0.5) in bold

	Num. solves 10 days prior	Strength preference	Demonstrator (yes/no)	Summed association strength w. informed inds.	Age (juveniles/adults)
Latency until first solve					
Summed Akaike weights ^a	0.91	0.42	0.34	0.34	0.21
Hazard ratio with 95% CI ^b	1.003 [1.001–1.005]	0.057 [0.001–2.298]	0.514 [0.173–1.532]	0.426 [0.105–1.722]	0.961 [0.359–2.572]
Latency until rate from prior reached					
Summed Akaike weights ^a	0.24	0.67	0.28	0.30	0.27
Hazard ratio with 95% CI ^b	1.001 [0.999–1.003]	0.010 [0.0001–0.666]	0.537 [0.149–1.935]	0.339 [0.052–2.214]	0.603 [0.209–1.741]
Num. models	16	16	16	16	16

^aAcross all models.

^bAveraged across models with deltaAICc < 4.

puzzle box (Aplin, Farine, et al., 2015), the majority of solutions produced during the diffusion occurred on the side demonstrators had been restricted to (MC: 93.7%; ME: 82.1%).

Across both sites, a total of 23 birds were present both before and after the restriction and had produced a least five solves in the 10 days prior to the restriction. Of those, 22 produced at least one solution on their less preferred side after the restriction. On average, they produced their first solve after 12 unsuccessful solving attempts [range 1st–43rd] after the restriction was put in place. Birds with more solves prior to the restriction were marginally faster at switching sides (summed Akaike weight $\sum w_i = 0.91$; HR = 1.003 [95% CI 1.001–1.005] per solve; Figure 3; Table 1). This corresponds to a decrease in latency of 1.7 [0.5–2.5] visits per increase of 500 solves prior to the restriction. Age, demonstrator status, the strength of the prior side preference or a bird's association strength with other informed individuals did not influence the latency until the first solve (all $\sum w_i < 0.5$; Table 1; Figure 3).

Eighteen of the 23 birds reached their previous solving rate after the restriction, on average after 60 unsuccessful solving attempts (range: 1st–223rd). Across those 18 birds, there was no significant difference in solving rate from before and after they switched (within 10%) (Wilcoxon signed rank test: $V = 66.5$; $N = 18$; $p = 0.420$), indicating that overall, they retained solving rates even when forced to switch sides. Birds with stronger prior side preference were significantly slower to reach their solving rate from prior to the restriction ($\sum w_i = 0.67$; HR = 0.011 [95% CI 0.0002–0.670]), while none of the other predictors (number of solves, demonstrator status, summed association strength, age) were correlated with the latency to reach the prior solving rate (all $\sum w_i < 0.5$; Table 1; Figure 3).

4 | DISCUSSION

While in the past, selective systems have usually been based on differences in physical features between target and non-target animals, such as body size, physical strength or weight (Massei et al., 2010;

Zielinski et al., 2020), the use of biologging technologies has revolutionized selective systems by allowing for a much more refined selection of target animals, based on individuals' unique electronic tag IDs (e.g. Meniri et al., 2019; Remus et al., 2020). Here, we have developed a selective two-option foraging device that extends the functionality of available selective feeding systems (e.g. Croston et al., 2017; Firth et al., 2016; Ibarra et al., 2015). It not only allows controlling whether or not specific individuals get access to food, but also to manipulate on an individual level which specific action(s) are rewarded.

We have successfully tested our new design on wild great tits that had previously socially learned to prefer one of two possible actions (e.g. Lea et al., 2020). After the restriction, 22 of 23 knowledgeable birds managed to produce at least one solution of their less preferred action and 18 of 23 birds even reached their previous solving rate within a 10-day period. This not only demonstrates the extent of behavioural flexibility in this species (Cauchoix et al., 2017), but also demonstrates the utility of a selective two-option device to manipulate and change behaviour. We show that, even in the case of demonstrator birds who had been restricted to one side for several weeks, prior learned preferences could be updated within only a few days.

This behavioural change was not significantly affected by most individual characteristics, with no effect of age, demonstrator status or connection to knowledgeable individuals on either latency to try the alternative side or reach prior solving rates. The lack of an effect of social associations indicates that, perhaps surprisingly, there was no or little social influence on birds' latency to switch to their less preferred side. However, we found that birds that solved at high frequencies prior to the restriction were faster at producing the first solution on their less preferred side, which potentially reflects both higher motivation to find a solution to the new challenge as well as increased levels of solving experience in those birds. By contrast, birds with a stronger prior side preference were slower to regain their solving rate after restriction. These results are in contrast to a previous study on wild great tits in which

the locally established solution was subjected to a reduced payoff. There, younger individuals were faster to switch, and neither the number of solves nor the strength of the prior preference had an effect on whether birds would switch from the lower-payoff to the higher-payoff solution (Aplin et al., 2017). Unlike in our experiment, however, birds in this study were still rewarded for producing the previously preferred solution. In fact, our results are in line with a study on reversal learning of a spatial task in great tits, during which the incorrect behaviour was also no longer rewarded (Cauchoix et al., 2017). They found that 59% of birds successfully completed a first reversal task, and performance improved over successive trials as they gained more experience (Cauchoix et al., 2017). Together, these might suggest that variation in behavioural flexibility in this species, for example related to age, might be more related to cognitive biases than learning abilities (Aplin et al., 2017; Morand-Ferron et al., 2015).

The use of selective two-option devices opens up new avenues for studying a range of socio-cognitive processes in wild animal populations, as they allow for fine-scale manipulation of what each individual experiences. The nature of questions that can be addressed is manifold. By restricting access for some individuals, for example, one can introduce local artificial side preferences to manipulate the social information that is available to others. This can be used to study social learning biases or decision-making processes, such as whether naïve individuals preferentially copy the side choice of particular demonstrators based on their phenotypes (e.g. rank, age or sex-biased transmission: Laland, 2004; Kendal et al., 2018) or whether individuals update their preference as a response to artificially introduced side preferences of close associates (e.g. stability of conformist traditions within a population: Aplin, Farine, et al., 2015). In combination with statistical methods like experience-weighted attraction models (Barrett et al., 2017; McElreath et al., 2005, 2008), selective two-option tasks provide a powerful tool to understand the mechanisms underlying behavioural decisions on an individual level, and how these translate to emergent population-level outcomes.

In our current system, restrictions are controlled through an internal list defining side access for each individual bird based on its PIT tag. In theory, restrictions could also be based on updating internal models—for example, that consecutive solves need to occur on opposite sides—which then takes individuals' previous actions into account and updates access lists in real-time. Such updating rules have been implemented at the individual level in operant chambers ('Skinner boxes') used for cognitive tasks in captivity (Devarakonda et al., 2016; Pineño, 2014). In the wild, to our knowledge, individualized programmes have only been implemented in a spatial reversal-learning study in great tits, using an operant conditioning device (Cauchoix et al., 2017). Extending this approach to a two-option foraging puzzle would provide a multitude of ways to control and manipulate individuals' experiences or, on a population level, mimic environmental changes.

While our design was tested on great tits, it could likely be used for birds of similar size. Indeed, nuthatches *Sitta europaea*, blue tits *Cyanistes caeruleus*, coal tits *Periparus ater* and marsh tits *Poecile*

palustris have all participated in previous experiments using similar sliding-door puzzles (Aplin, Farine, et al., 2015). Alternatively, the hardware could be scaled up or down to accommodate body size, strength and cognitive abilities of different target species. In fact, various studies have used a very similar sliding-door paradigm in socio-cognitive studies in other species, such as chimpanzees (Sánchez-Amaro et al., 2018), parrots (Picard et al., 2017) or vervet monkeys (van de Waal et al., 2013).

One of the limitations to our current device is its inability to register unsuccessful solving attempts, for which in our study we have used the number of visits registered by the antenna that were not followed by a solve as a proxy. However, this could easily be solved by adding a motion triggered Raspberry Pi camera to the system, which allows more fine-scale tracking of individual birds' behaviour as they interact with the puzzle box (e.g. Chimento et al., 2021). Furthermore, unlike the original sliding-door puzzle (Aplin, Farine, et al., 2015), our selective device does not allow for untagged birds to solve the puzzle box as they are not recognized by the RFID antenna and the sliding-door mechanisms will therefore remain closed. Experiments could of course be restricted to tagged birds only, or the landing perch could additionally be fitted with a scale or sensor that registers the presence of untagged individuals, with a software modification specifying side access for these untagged individuals.

Safe methods for PIT tagging for a wide range of species are well-established, and participation in such experiment occurs on an entirely voluntary basis. For capturing and tagging birds for this study, we followed well-established protocols that minimize negative impacts on individuals: Mist netting for capturing birds is a widely used technique for monitoring avian populations, with injury and mortality rates below 1% (Spotswood et al., 2012)—in our study population below 0.05%. Potential negative long-term effects of attaching metal rings or PIT tags are considered mild. Incident rate of leg injuries that were potentially related to tagging in our study population were below 0.005%. Furthermore, a study on small passerine birds found no differences in survival or body condition of tagged versus untagged individuals (Farr et al., 2021), indicative of no negative long-term effects of tagging. The use of puzzle boxes in combination with RFID technology therefore not only provides a low-cost method for conducting socio-cognitive experiments on wild animals in their natural environment, but is also of low ethical concern.

In conclusion, our puzzle box design extends the functionality of currently available selective feeding systems by adding selectivity to a two-option puzzle box often used in studies on animal cognition and learning. It allows to systematically control which individual-level actions lead to a food reward. This can potentially be used not only to change the personal information that individuals receive, but also the social information available to others. Our device is fully reproducible: we provide comprehensive instructions on both the hardware and software associated with this task in the supplementary materials and associated data. All components are commercially available, providing a low-cost, fully automated device for studying a broad range of social learning and decision-making processes in wild animals.

AUTHORS' CONTRIBUTIONS

L.M.A. and S.W. conceived the study; G.A.-N. and S.W. built the puzzle boxes, M.C. and G.A.-N. wrote the puzzle box software; G.A.-N. and S.W. tagged birds, S.W. collected puzzle and network data; S.W. ran analyses and drafted the manuscript, all authors contributed to writing and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no competing interest.

DATA AVAILABILITY STATEMENT

All data and code for have been archived and are publicly available on <https://doi.org/10.5281/zenodo.6470325> for replication of analyses (Wild et al., 2022a) and on <https://doi.org/10.5281/zenodo.6504283> for puzzle box software respectively (Wild et al., 2022b).

ORCID

Sonja Wild  <https://orcid.org/0000-0002-5904-0096>

Gustavo Alarcón-Nieto  <https://orcid.org/0000-0003-4076-3750>

Michael Chimento  <https://orcid.org/0000-0001-5697-1701>

Lucy M. Aplin  <https://orcid.org/0000-0001-5367-826X>

REFERENCES

- Aguzzi, J., Sbragaglia, V., Sarriá, D., García, J. A., Costa, C., del Río, J., Manuel, A., Menesatti, P., & Sardà, F. (2011). A new laboratory radio frequency identification (RFID) system for behavioural tracking of marine organisms. *Sensors*, 11(10), 9532–9548.
- Anderson, D., & Burnham, K. (2004). *Model selection and multi-model inference* (2nd ed.). Springer-Verlag.
- Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2015). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, 518(7540), 538–541.
- Aplin, L. M., Firth, J. A., Farine, D. R., Voelkl, B., Crates, R. A., Culina, A., Garroway, C. J., Hinde, C. A., Kidd, L. R., Psorakis, I., Milligan, N. D., Radersma, R., Verhelst, B. L., & Sheldon, B. C. (2015). Consistent individual differences in the social phenotypes of wild great tits, *Parus major*. *Animal Behaviour*, 108, 117–127.
- Aplin, L. M., Sheldon, B. C., & McElreath, R. (2017). Conformity does not perpetuate suboptimal traditions in a wild population of songbirds. *Proceedings of the National Academy of Sciences of the United States of America*, 114(30), 7830–7837.
- Barrett, B. J., McElreath, R. L., & Perry, S. E. (2017). Pay-off-biased social learning underlies the diffusion of novel extractive foraging traditions in a wild primate. *Proceedings of the Royal Society B: Biological Sciences*, 284(1856), 20170358. ISSN: 0962-8452. <https://doi.org/10.1098/rspb.2017.0358>
- Barton, K. (2014). *MuMIn package: Multi-model inference*. CRAN Project, USA.
- Bonter, D. N., & Bridge, E. S. (2011). Applications of radio frequency identification (RFID) in ornithological research: A review. *Journal of Field Ornithology*, 82(1), 1–10.
- Branch, C. L., Sonnenberg, B. R., Pitera, A. M., Benedict, L. M., Kozlovsky, D. Y., Bridge, E. S., & Pravosudov, V. V. (2020). Testing the greater male variability phenomenon: Male mountain chickadees exhibit larger variation in reversal learning performance compared with females. *Proceedings of the Royal Society B*, 287(1931), 20200895.
- Bridge, E. S., & Bonter, D. N. (2011). A low-cost radio frequency identification device for ornithological research. *Journal of Field Ornithology*, 82(1), 52–59.
- Cairns, S. J., & Schwager, S. J. (1987). A comparison of association indices. *Animal Behaviour*, 35(5), 1454–1469.
- Canteloup, C., Hoppitt, W., & van de Waal, E. (2020). Wild primates copy higher-ranked individuals in a social transmission experiment. *Nature Communications*, 11(1), 1–10.
- Cauchoux, M., Hermer, E., Chaine, A. S., & Morand-Ferron, J. (2017). Cognition in the field: Comparison of reversal learning performance in captive and wild passerines. *Scientific Reports*, 7(1), 1–9. ISSN: 20452322. <https://doi.org/10.1038/s41598-017-13179-5>
- Chimento, M., Alarcón-Nieto, G., & Aplin, L. M. (2021). Population turnover facilitates cultural selection for efficiency in birds. *Current Biology*, 31, 2477–2483.e3. ISSN: 18790445. <https://doi.org/10.1016/j.cub.2021.03.057>
- Chow, P. K. Y., Leaver, L. A., Wang, M., & Lea, S. E. G. (2015). Serial reversal learning in gray squirrels: Learning efficiency as a function of learning and change of tactics. *Journal of Experimental Psychology: Animal Learning and Cognition*, 41(4), 343–353.
- Cox, D. T. C., Inger, R., Hancock, S., Anderson, K., & Gaston, K. J. (2016). Movement of feeder-using songbirds: The influence of urban features. *Scientific Reports*, 6(1), 1–9.
- Croston, R., Kozlovsky, D. Y., Branch, C. L., Parchman, T. L., Bridge, E. S., & Pravosudov, V. V. (2016). Individual variation in spatial memory performance in wild mountain chickadees from different elevations. *Animal Behaviour*, 111, 225–234.
- Croston, R., Branch, C. L., Pitera, A. M., Kozlovsky, D. Y., Bridge, E. S., Parchman, T. L., & Pravosudov, V. V. (2017). Predictably harsh environment is associated with reduced cognitive flexibility in wild food-caching mountain chickadees. *Animal Behaviour*, 123, 139–149.
- Devarakonda, K., Nguyen, K. P., & Kravitz, A. V. (2016). Robucket: A low cost operant chamber based on the arduino microcontroller. *Behavior Research Methods*, 48(2), 503–509.
- Evans, K., Lea, M. A., & Patterson, T. A. (2013). Recent advances in bio-logging science: Technologies and methods for understanding animal behaviour and physiology and their environments. *Deep Sea Research Part II: Topical Studies in Oceanography*, 88–89, 1–6.
- Fagot, J., & Bonté, E. (2010). Automated testing of cognitive performance in monkeys: Use of a battery of computerized test systems by a troop of semi-free-ranging baboons (*Papio papio*). *Behavior Research Methods*, 42(2), 507–516.
- Fagot, J., & Paleressompoulle, D. (2009). Automatic testing of cognitive performance in baboons maintained in social groups. *Behavior Research Methods*, 41(2), 396–404.
- Farine, D. R. (2013). Animal social network inference and permutations for ecologists in R using *asnipe*. *Methods in Ecology and Evolution*, 4(12), 1187–1194.
- Farr, J. J., Haave-Audet, E., Thompson, P. R., & Mathot, K. J. (2021). No effect of passive integrated transponder tagging method on survival or body condition in a northern population of black-capped chickadees (*poecile atricapillus*). *Ecology and Evolution*, 11(14), 9610–9620.

- Fehlmann, G., & King, A. J. (2016). Bio-logging. *Current Biology*, 26(18), R830–R831. ISSN: 09609822. <https://doi.org/10.1016/j.cub.2016.05.033>
- Firth, J. A., Sheldon, B. C., & Farine, D. R. (2016). Pathways of information transmission among wild songbirds follow experimentally imposed changes in social foraging structure. *Biology Letters*, 12(6), 20160144.
- Firth, J. A., & Sheldon, B. C. (2015). Experimental manipulation of avian social structure reveals segregation is carried over across contexts. *Proceedings of the Royal Society B: Biological Sciences*, 282(1802), 20142350.
- Fox, J., & Weisberg, S. (2018). *An R companion to applied regression*. Sage Publications.
- Hou, L., Verdirame, M., & Welch, K. C., Jr. (2015). Automated tracking of wild hummingbird mass and energetics over multiple time scales using radio frequency identification (RFID) technology. *Journal of Avian Biology*, 46(1), 1–8.
- Hoy, J. M., Murray, P. J., & Tribe, A. (2010). The potential for microchip-automated technology to improve enrichment practices. *Zoo Biology*, 29(5), 586–599.
- Ibarra, V., Araya-Salas, M., Tang, Y.-p., Park, C., Hyde, A., Wright, T., & Tang, W. (2015). An RFID based smart feeder for hummingbirds. *Sensors*, 15(12), 31751–31761.
- Jolles, J. W. (2021). Broad-scale applications of the raspberry pi: A review and guide for biologists. *Methods in Ecology and Evolution*, 12(9), 1562–1579.
- Kendal, R. L., Boogert, N. J., Rendell, L., Laland, K. N., Webster, M., & Jones, P. L. (2018). Social learning strategies: Bridge-building between fields. *Trends in Cognitive Sciences*, 22(7), 651–665. ISSN: 1879307X. <https://doi.org/10.1016/j.tics.2018.04.003>
- Kenward, B., Kenward, R. E., & Kacelnik, A. (2005). An automatic technique for selective feeding and logging of individual wild squirrels. *Ethology Ecology & Evolution*, 17(3), 271–277.
- Kim-McCormack, N. N. E., Smith, C. L., & Behie, A. M. (2016). Is interactive technology a relevant and effective enrichment for captive great apes? *Applied Animal Behaviour Science*, 185, 1–8.
- Laland, K. N. (2004). Social learning strategies. *Learning & Behavior*, 32(1), 4–14. ISSN: 1543-4494.
- Lea, S. E. G., Chow, P. K. Y., Leaver, L. A., & McLaren, I. P. L. (2020). Behavioral flexibility: A review, a model, and some exploratory tests. *Learning & Behavior*, 48(1), 173–187. <https://doi.org/10.1109/ICEEI47359.2019.8988788>
- Mariette, M. M., Pariser, E. C., Gilby, A. J., Magrath, M. J. L., Pryke, S. R., & Griffith, S. C. (2011). Using an electronic monitoring system to link offspring provisioning and foraging behavior of a wild passerine. *The Auk*, 128(1), 26–35.
- Massei, G., Coats, J., Quay, R., Storer, K., & Cowan, D. P. (2010). The board-operated-system: A novel method to deliver baits to Wild pigs. *Journal of Wildlife Management*, 74(2), 333–336. ISSN: 0022-541X. <https://doi.org/10.2193/2008-489>
- McElreath, R., Bell, A. V., Efferson, C., Lubell, M., Richerson, P. J., & Waring, T. (2008). Beyond existence and aiming outside the laboratory: Estimating frequency-dependent and pay-off-biased social learning strategies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1509), 3515–3528. ISSN: 09628436. <https://doi.org/10.1098/rstb.2008.0131>
- McElreath, R., Lubell, M., Richerson, P. J., Waring, T. M., Baum, W., Edsten, E., Efferson, C., & Paciotti, B. (2005). Applying evolutionary models to the laboratory study of social learning. *Evolution and Human Behavior*, 26(6), 483–508. ISSN: 10905138. <https://doi.org/10.1016/j.evolhumbehav.2005.04.003>
- Meniri, M., Farley, A., Helfenstein, F., & Fasel, N. (2019). A guide for ecologists to build a low-cost selective trap using radio frequency identification detection. *Behavioral Ecology and Sociobiology*, 73(6), 1–8.
- Moore, D. F. (2016). *Applied survival analysis using R*. Springer.
- Morand-Ferron, J., Hamblin, S., Cole, E. F., Aplin, L. M., & Quinn, J. L. (2015). Taking the operant paradigm into the field: Associative learning in wild great tits. *PLoS ONE*, 10(8), e0133821.
- Muns, S. J., Hoy, J. M., & Murray, P. J. (2018). Microchips for macropods: First use of a microchip-automated door by a bridled naitail wallaby (*Onychogalea fraenata*). *Zoo Biology*, 37(4), 274–278.
- Picard, A. M., Hogan, L., Lambert, M. L., Wilkinson, A., Seed, A. M., & Slocombe, K. E. (2017). Diffusion of novel foraging behaviour in amazon parrots through social learning. *Animal Cognition*, 20(2), 285–298.
- Pineño, O. (2014). Arduipod box: A low-cost and open-source skinner box using an ipod touch and an arduino microcontroller. *Behavior Research Methods*, 46(1), 196–205.
- Psorakis, I., Roberts, S. J., Rezek, I., & Sheldon, B. C. (2012). Inferring social network structure in ecological systems from spatio-temporal data streams. *Journal of the Royal Society Interface*, 9(76), 3055–3066.
- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Remus, A., Hauschild, L., Letourneau-Montminy, M.-P., Andretta, I., & Pomar, C. (2020). Feeding behavior of growing and finishing pigs fed different dietary threonine levels in a group-phase feeding and individual precision feeding system. *Translational Animal Science*, 4(4), txaa177.
- Robinson, E. J. H., Feinerman, O., & Franks, N. R. (2012). Experience, competence and decision making in ant foraging. *Journal of Experimental Biology*, 215(15), 2653–2659.
- Rutz, C., & Hays, G. C. (2009). New frontiers in biologging science. *Biology Letters*, 5(3), 289–292.
- Sánchez-Amaro, A., Duguid, S., Call, J., & Tomasello, M. (2018). Chimpanzees' understanding of social leverage. *PLoS ONE*, 13(12), e0207868.
- Spotswood, E. N., Goodman, K. R., Carlisle, J., Cormier, R. L., Humple, D. L., Rousseau, J., Guers, S. L., & Barton, G. G. (2012). How safe is mist netting? Evaluating the risk of injury and mortality to birds. *Methods in Ecology and Evolution*, 3(1), 29–38.
- Svensson, L. (1992). *Identification guide to European passerines*. The author.
- Tello-Ramos, M. C., Branch, C. L., Pitera, A. M., Kozlovsky, D. Y., Bridge, E. S., & Pravosudov, V. V. (2018). Memory in wild mountain chickadees from different elevations: Comparing first-year birds with older survivors. *Animal Behaviour*, 137, 149–160.
- Therneau, T. M., & Lumley, T. (2014). Package 'survival'. *Survival Analysis Published on CRAN*, 2(3), 119.
- Vaintrub, M. O., Levit, H., Chincarin, M., Fusaro, I., Giammarco, M., & Vignola, G. (2020). Precision livestock farming, automats and new technologies: Possible applications in extensive dairy sheep farming. *Animal*, 15, 100143.
- van de Waal, E., Claidière, N., & Whiten, A. (2013). Social learning and spread of alternative means of opening an artificial fruit in four groups of vervet monkeys. *Animal Behaviour*, 85(1), 71–76.
- Watson, S. J., Hoy, J. M., Edwards, M. C., & Murray, P. J. (2021). In situ training of brushtail possums to use microchip-automated doors. *Wildlife Society Bulletin*, 45(3), 390–395. <https://doi.org/10.1002/wsb.1217>
- Whytock, R. C., & Christie, J. (2017). Solo: An open source, customizable and inexpensive audio recorder for bioacoustic research. *Methods in Ecology and Evolution*, 8(3), 308–312.
- Wicaksono, M. A., Subekti, L. B., & Bandung, Y. (2019). Development of cat care system based on internet of things. In *2019 international conference on electrical engineering and informatics (ICEEI)* (pp. 483–488). IEEE.
- Wild, S., Chimento, M., McMahon, K., Farine, D. R., Sheldon, B. C., & Aplin, L. M. (2021). Complex foraging behaviours in wild birds emerge from social learning and recombination of components. *Philosophical Transactions of the Royal Society B*, 377(1843), 20200307.
- Wild, S., Alarcón-Nieto, G., Chimento, M., & Aplin, L. M. (2022a). Code and data for: Manipulating actions: A selective two-option device for cognitive experiments in wild animals. *Zenodo*, <https://doi.org/10.5281/zenodo.6470325>

- Wild, S., Alarcón-Nieto, G., Chimento, M., & Aplin, L. M. (2022b). Code and data for: Manipulating actions: A selective two-option device for cognitive experiments in wild animals. *Zenodo*, <https://doi.org/10.5281/zenodo.6504283>
- Youngblood, M. (2019). A raspberry pi-based, RFID-equipped bird-feeder for the remote monitoring of wild bird populations. *Ringed & Migration*, 34(1), 25–32.
- Zielinski, D. P., McLaughlin, R. L., Pratt, T. C., Goodwin, R. A., & Muir, A. M. (2020). Single-stream recycling inspires selective fish passage solutions for the connectivity conundrum in aquatic ecosystems. *Bioscience*, 70(10), 871–886. ISSN: 15253244. <https://doi.org/10.1093/biosci/biaa090>
- Zuidhof, M. J., Fedorak, M. V., Ouellette, C. A., & Wenger, I. I. (2017). Precision feeding: Innovative management of broiler breeder feed intake and flock uniformity. *Poultry Science*, 96(7), 2254–2263.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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