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Diffusion of Novel Foraging Behaviour in Amazon Parrots through Social Learning

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Abstract

While social learning has been demonstrated in species across many taxa, the role it plays in everyday foraging decisions is not well understood. Investigating social learning during foraging could shed light on the emergence of cultural variation in different groups. We used an open diffusion experiment to examine the spread of a novel foraging technique in captive Amazon parrots. Three groups were tested using a two-action foraging box, including experimental groups exposed to demonstrators using different techniques and control birds. We also examined the influence of agonistic and pilfering behaviour on task acquisition. We found evidence of social learning: more experimental birds than control birds interacted with and opened the box. The birds were, however, no more likely to use the demonstrated technique than the non-demonstrated one, making local or stimulus enhancement the most likely mechanism. Exhibiting aggression was positively correlated with box opening, whilst receiving aggression did not reduce motivation to engage with the box, indicating that willingness to defend access to the box was important in task acquisition. Pilfering food and success in opening the box were also positively correlated; however, having food pilfered did not affect victims' motivation to interact with the box. In a group context, pilfering may promote learning of new foraging opportunities. Although previous studies have demonstrated that psittacines are capable of imitation, in this naturalistic set-up there was no evidence that parrots copied the demonstrated opening technique. Foraging behaviour in wild populations of Amazons could therefore be facilitated by low-fidelity social learning mechanisms.

Keywords: social learning, open diffusion, two-action test, parrots, *Amazona amazonica*

Discoveries of locale-specific, or group-typical, behavioural patterns among wild populations of animals have been the source of fascination and debate for several decades. Often referred to as 'cultural variations' or 'traditions,' regional variations among wild populations have been found in a diversity of taxa, including mammalian, avian, and fish species (Laland and Hoppitt 2003; Swaddle et al. 2005; van de Waal et al. 2013; van Schaik et al. 2003; Witte and Ryan, 2002; Yurk et al. 2002). They are considered significant because of the insight they may provide into the evolution of culture. These discoveries have led to speculations about the parallels that may exist between the development of animal 'traditions' and the emergence of human culture (Galef 1992; Heyes 1993; Laland and Hoppitt 2003). By conducting research aimed at understanding the spread of novel behaviour in animals, we may gain insight into the cognitive and socio-ecological processes that supported and shaped the evolution of human culture (Galef 1992; Laland and Hoppitt 2003).

Social learning provides a way of transmitting a novel behaviour, such as an effective foraging technique, that is more rapid than genetic transmission and can be more efficient than individual trial-and-error learning. Social learning can occur via a variety of different mechanisms, and may involve high or low fidelity copying; in the former, the details of an action are precisely replicated, while in the latter behaviour is replicated with some modification or variation in the action sequence (Lewis and Laland 2012; Whiten and Ham 1992). Identifying which social learning mechanisms are available to (and used by) different species has important consequences for whether new behaviours are faithfully transmitted and maintained within a population. The development and maintenance of human culture is believed by many to rely upon high-fidelity social learning underpinned by imitation, or 'action learning' (seen when individuals copy motor patterns they have observed) (Legare and Nielson 2015; Tennie et al. 2009; Whiten and Mesoudi 2008; Whiten et al. 2009). This is distinct from mechanisms that may result in low-fidelity transmission, such as stimulus or local enhancement, which occurs when an observer’s attention is drawn to a particular area or object due to another individual’s presence. This increases their chances of learning something valuable about that object or area, such as the availability of food in a specific location (Caldwell and Whiten 2002). An observer may also gain information about the function or affordances of an object as a result of another’s actions, referred to as emulation (Whiten et al., 2004). In such cases, an observer achieves the same goal as the observed individual, but may do so by engaging in a different behaviour (Caldwell and Whiten 2002; Heyes and Saggerson 2002; Tennie et al. 2006). In order to fully understand how animal traditions emerge and are sustained, it is necessary to identify which types of social learning mechanisms are involved in the acquisition and spread of novel behaviour.

The two-action test is one of the most widely used paradigms in the experimental investigation of social learning mechanisms (e.g. Aplin et al. 2013, 2015; Campbell et al. 1999; Dindo et al. 2008; Galef et al. 1986; Huber et al. 2001; Whiten et al. 2005). In this paradigm, subjects are presented with a baited apparatus containing a manipulandum that can be operated using two alternative methods (e.g. pull or push) to gain access to food (Dindo et al. 2009). If subjects are found to use the method they observed being employed by demonstrators significantly more than the alternate (non-observed method), it would suggest that they learned something about the technique, either by imitating the actions used or emulating their effects.

Testing demonstrator-observer dyads on two-action foraging tasks has provided evidence of social learning in avian, primate, and reptile species. Evidence has been found of task acquisition by means of imitation or possible emulation learning (European starlings: Akins and Zentall 1998, Campbell et al. 1999; pigeons: Zentall et al. 1996; budgerigars: Heyes and Saggerson 2002; capuchins: Dindo et al. 2009; chimpanzees: Horner et al. 2006; bearded dragons: Kis et al. 2015; kea: Huber et al. 2001). However, while tightly controlled dyadic tasks may reveal species' social learning capacities, this experimental approach does not reveal anything about the social factors that may influence learning processes within a natural foraging context. In many species, natural foraging parties involve several observers being simultaneously exposed to the same event, who can all then react to the demonstration and potentially become demonstrators themselves. Additionally, behaviours such as aggression or scrounging are highly relevant to the diffusion of novel foraging behaviour in a natural group context. Willingness to enter into aggressive encounters, for instance, may ensure sufficient exploration opportunity to acquire behaviour that was previously observed (Schnoell and Fichtel 2012). Further, gaining rewards from the actions of others (scrounging) may either inhibit social learning (Giraldeau and Lefebvre 1987) or help focus individuals' attention on demonstrators' actions (e.g., nut cracking behaviour in sub-adult chimpanzees; Inoue-Nakamura and Matsuzawa 1997). Experimental designs that provide conditions that more closely resemble species' natural social environment are therefore vital for understanding how different types of social learning may function in a more natural foraging context.

The open diffusion design, involving the simultaneous exposure of a group of naive subjects to trained conspecifics engaging in novel behaviour, has greater ecological validity than dyadic testing (Whiten and Mesoudi 2008), and has provided further evidence of high fidelity copying in chimpanzees and capuchins (Dindo et al. 2009; Whiten et al. 2005). Only a few studies have used two-action tests to investigate transmission of behaviour through open diffusion in birds (Aplin et al. 2013, 2015). We believe it is important to do so in order to adequately understand the transmission of behaviour in birds that are social foragers. This approach not only makes it possible to investigate the social learning mechanisms that are in operation, but also allows for investigation of various social factors that may influence behaviour acquisition in natural conditions. Studies of captive and wild tits reveal that experimental birds were significantly more likely to use the solution demonstrated by trained birds than the alternate one (Aplin et al. 2013, 2015). Furthermore, the foraging techniques that were introduced into wild tit populations were found to be stable over two generations (Aplin et al. 2015). This suggests that high fidelity copying could have adaptive value for these birds.

The occurrence of group-specific behaviours in wild avian populations, along with experimental findings that provide evidence of social learning capacities in a range of birds, suggest that this group can make a significant contribution to the development of a broad comparative framework aimed at understanding the emergence of culture. In discussions of primate and avian cognitive convergence, parrots are often cited alongside corvids as examples of birds that possess high-level, ‘primate-like,’ cognition (Emery and Clayton 2004; Emery et al. 2007; van Horik et al. 2012). Like primates and corvids, parrots are highly social, long lived, and have large relative brain sizes (Seibert 2006; Shultz and Dunbar 2010), yet they remain comparatively understudied in most aspects of cognition and behaviour; only a small proportion of more than 350 extant parrot species have been the subject of any field or laboratory research.

Parrots are widely known for their capacity to engage in vocal learning, a trait that relies on social learning mechanisms. Vocal imitation has been documented in various species, such African greys, yellow-naped Amazons, budgerigars, and orange-fronted conures (Balsby et al. 2012; Bradbury 2004; Cruickshank et al.1993; Hile et al. 2000; Pepperberg 2006; Rowley and Chapman 1986; Wright 1996). However, evidence for imitation of motor patterns, such as those associated with foraging, is less abundant. Moore (1992) reports imitation of both words and actions by a captive African grey housed in a laboratory by itself. After regular exposure to a keeper engaging in repetitive word-behaviour sequences, the bird began to replicate these vocal and motor patterns in the absence of social or food rewards. In the foraging domain, kea have been found to be capable of learning through stimulus enhancement and likely emulation in a dyadic transmission experiment that required subjects to manipulate a series of locking devices on a baited apparatus (Huber et al. 2001). Experimental birds showed significantly shorter latency to approach locking devices, greater persistence in manipulation of the apparatus, and greater success in opening the locks, than control birds. Evidence of imitative capacities have been found in budgerigars (Dawson and Foss 1965; Heyes and Saggerson 2002). Heyes and Saggerson tested subjects using a two-action/two-object test. They were presented with baited boxes containing lids with two holes; holes were obstructed by distinctly coloured plugs, which could be removed by pulling or pushing. Subjects were found to remove the same coloured plug in the same manner as observed individuals, revealing evidence for imitation. A recent study with Goffin cockatoos showed that whilst they failed to learn to obtain food through novel tool use in a ghost control condition (whereby an observer is exposed to the movement of a manipulandum in the absence of a demonstrator), half the birds succeeded when observing a trained conspecific demonstrator. The tool-using techniques of demonstrators and observers, however, varied greatly, indicating that both stimulus enhancement and emulation were the most likely mechanisms underlying the successful performance (Auersperg et al. 2014). Psittacines seem to have the capacity to acquire novel motor and foraging behaviour from the observation of others; however, it is unknown what type of social learning occurs in the diffusion of a novel foraging technique in a naturalistic group setting.

The present study aimed to address this issue by investigating the transmission of a novel foraging technique in captive orange-winged Amazon (OWA) parrots (*Amazona amazonica*) using an open diffusion design. A Neotropical species, OWAs demonstrate characteristics typical of most parrots, including being highly social and having a long life history, a large relative brain size, and a monogamous breeding system (Hoppe 1992). In the wild, OWAs rely on fruits and seeds that vary spatially and temporally and form foraging parties in order to locate food sources (Bonadie and Bacon 2000). They are also commonly regarded as agricultural pests because they tend to exploit novel food sources as their natural ones are replaced with farm land (Hoppe 1992). OWAs have vocal mimicry abilities (Hoppe 1992) and their socio-ecology indicates that it is likely that learning to exploit novel foraging opportunities by observation of others would be highly adaptive in this species. It would likely provide a more efficient way of learning about suitable food sources (e.g., location, types, extraction methods) than individual learning.

We tested social transmission of foraging behaviour in OWAs using a two-action foraging box based on the design used by Dindo and colleagues (2008, 2009). Two OWA groups were exposed to a group member who was trained to open the apparatus, each using a different technique (slide or pull the door). As a third group of OWAs was not available to use as a control group, we used one OWA group as both a control and an experimental group (control trials were completed prior to experimental trials). If stimulus or local enhancement occurred, we would expect birds to approach and make physical contact with the foraging box more often in experimental trials (after seeing the trained demonstrator interact with it), than during control trials.

We could not use the OWA amazon control group to assess whether observing a skilled demonstrator increased the likelihood of an animal solving the task because the apparatus was locked during the control trials (locks were invisible to the birds) to ensure that the first exposure that group had to solving the novel foraging task would be as a result of the trained demonstrator’s behaviour during experimental trials. We therefore used a group of blue-fronted Amazons (BFA; *Amazona aestiva*) to assess how likely the box was to be successfully opened in the absence of a trained demonstrator. BFAs are closely related to OWAs, and share various socio-ecological traits with OWAs (including habitat, diet, and social composition; Hoppe 1992). If imitation, emulation or individual learning following stimulus enhancement occurred after observation of a trained demonstrator we expected more birds in the OWA experimental groups to solve the task than the BFA group.

We then investigated whether experimental subjects that successfully opened the box showed evidence of imitation of the door-opening method (slide or pull) that they had observed or if they used the same body parts used by the demonstrator to manipulate the door (beak or beak and foot). If imitation was occurring, then we expected the method and body part to match that of the trained demonstrator the birds had observed. If birds discovered and used both methods, we aimed to examine whether they were more likely to conform to the method of the trained demonstrator (using the same action as observed) when the demonstrator was present in the immediate vicinity of the foraging box. Conformity to an observed action, even when an alternative is discovered has been found in a number of species (chimpanzees: Whiten et al. 2005; vervet monkeys: van de Waal, Claidière et al. 2013; tits: Aplin et al. 2015). Finally, we assessed whether subject engagement with or acquisition of the task was influenced by aggression or ‘pilfering’ (scrounging behaviour consisting of taking food from the apparatus after another bird opened the apparatus or taking a food reward from another bird’s physical possession). Whilst scrounging has previously been shown to both inhibit (Giraldeau and Lefebvre 1987) and facilitate (Inoue-Nakamura and Matsuzawa 1997) learning in those who gain food in this manner, we predicted pilfering and aggression may decrease the victims’ motivation to engage with the box.

Methods

Study groups

Research was conducted at Lincolnshire Wildlife Park, UK: a parrot sanctuary and licensed zoo. Parrots were voluntarily surrendered by owners who were unable to continue to care for them. Aviary group composition varied regularly at the sanctuary as newly surrendered parrots joined groups and thus it is highly unlikely that any individuals within a single group were related. We used three independent groups of captive parrots (two OWA groups, one BFA group); each group's composition was kept stable throughout data collection periods. One group of OWAs (*N* = 22) served as the 'slide' experimental group, and the other OWA group (*N* = 15) served as both the 'pull' experimental group and the OWA control group. The BFAs (*N* = 20) were used in order to assess the likelihood that birds would solve the task in the absence of a trained demonstrator (a third group was necessary for this assessment as the box door was kept locked during OWA control trials and a third group of OWAs were not available). We collected data on the slide OWA group in July 2012 and both the pull OWA group and the BFA group in August 2013.

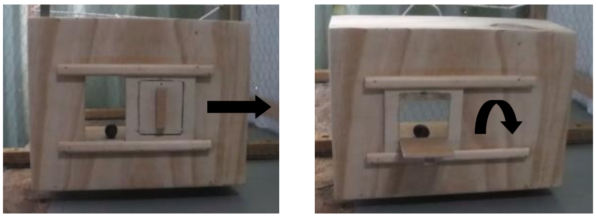
All subjects were believed to be adults, although their exact ages were unknown. Only the sexes of the OWA slide group were known (9 females and 14 males) due to their participation in an observational study on social behaviour. All subjects were identified by coloured leg rings.

Each of the three groups of parrots was housed in its own outdoor aviary (2.3 (h) x 2.4 (w) x 5.5 m (l)) containing natural wood perches. The enclosures contained covered areas that provided shelter from wind and rain and could be freely accessed by birds. The enclosure OWAs were housed in had an indoor training compartment (1.2 (h) x 1.8 (w) x 2.2 m (l)); the OWA slide group were housed in that enclosure in 2012 and the OWA pull group were housed in it in 2013. Food and water were provided ad libitum. Subjects' diets consisted of approximately 70% fresh fruit (fed in afternoon after testing) and 30% seed (fed in morning after testing).

Experimental box

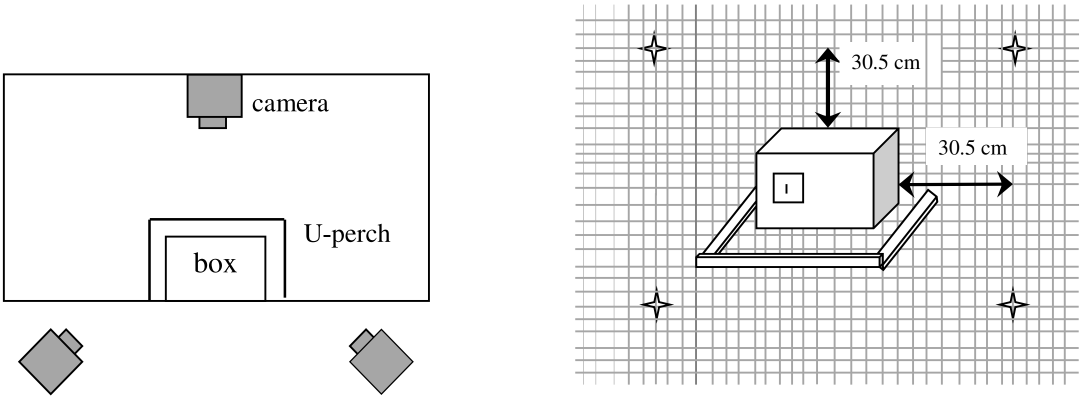
The two-action task consisted of a baited opaque apparatus that could be opened using two alternate methods. A wooden box measuring 11.4 (h) x 30.5(w) x 20.3 cm (l) was used.

The back of the box contained an opening (9.5 (w) x 10cm (l)) through which food could be inserted, and the front contained a door (9 (w) x 9 cm (l)) with a handle (4 (h) x 1.75 (w) x 1.75 cm(l)) that could be opened by either pulling it or by sliding it (see Fig. 1).



(a) (b)

Fig. 1 Photographs illustrate the foraging box and both methods of opening it - the slide method (a) and the pull method (b)



(a) (b)

Fig. 2 Representations of the experimental setup. A top view of the aviary (a) illustrates the position of the cameras in relation to the box. The camera in the aviary was protected with a camera box. A front view of the experimental box from the parrots' perspective (b) illustrates the position of the U-shaped perch and target zone boundary markers on the mesh in relation to the box

Procedure

Training. Habituation to three cameras mounted on tripods (see Fig. 2), as well as an observing researcher occurred for two 30-minute periods daily in the two weeks prior to test trials starting. We selected one bird in each experimental group to be a demonstrator; the birds selected met the following criteria: they showed high levels of food motivation, social tolerance, willingness to remain in the training compartment and low levels of neophobia.

We used a successive approximation procedure to train demonstrators to perform the task. Training took place in the training compartment, out of sight of other individuals. The foraging box was mounted on the outside of a wire cage (64.8 (h) x 53.3 (w) x 45.7 cm (l)). A T-perch mounted on a base was placed in front of the box door, allowing demonstrators to open the door while standing on the perch. During initial training, the alternate method was locked (locking mechanism was invisible to the birds). The demonstrators were required to successfully open the box using the desired method (slide or pull) in 10 consecutive trials with the alternate door locked; this prevented the demonstrators from accidentally discovering the alternate solution before fully mastering the desired method. They were then required to complete a further 10 consecutive trials using the desired method, with the alternate method unlocked.

Testing. Set up was the same for control and experimental trials. The foraging box was placed in the centre of the ‘target zone’ that extended 30.5 cm from all sides of the box. Target zone corners were marked with coloured plastic zip-ties or electrical tape so that the boundaries were clearly visible. The box was visually accessible to subjects perched outside the target zone. A U-perch (23. 5 (w) x 43.8 cm (l)) was mounted underneath the box (see Fig. 2). All trials were videoed from three angles using two Panasonic SDRH40 cameras and one Panasonic HCW570 camera (see Fig. 2). Trials began when the foraging box was mounted and baited inside the aviary target zone. Two experimenters stood outside the aviary and provided real time commentary of behaviour in the target zone onto the video recordings (including identifying which individuals entered and exited the target zone and made contact with the box, and describing the type of contact made with the box). One of the experimenters re-set and re-baited the box after every successful opening. The box door was also re-set after unsuccessful attempts (see Table 1). Peanuts and grapes, favoured food items, were used as rewards for all trials. The box was baited with one food item at a time. Birds could obtain a food reward by flying or climbing into the target zone and opening the box door (using a slide or pull action). As group members were simultaneously exposed to the box, it was also possible for birds to obtain food items by scrounging - either pilfering (retrieving food from the box after the door was opened by another bird or taking it from another bird's physical possession) or by retrieving food from the ground that was dropped by another bird.

Twelve peanuts and 12 grape halves were available in each experimental trial. Trials ended when (i) all 24 pieces of food were successfully retrieved from the foraging box or (ii) if 20 min elapsed since the last interaction with the box. In cases in which there was no interaction with the box at all, trials ended after 30 min. We ensured both experimental groups retrieved the same number of pieces of food from the box (216 pieces) across all their trials. It took the slide experimental group a total of nine trials and the pull experimental group a total of 13 trials to retrieve all pieces of food.

A total of nine control trials were run on both the OWA pull group and the BFAs. As experimental trials had to be conducted on the OWAs after control trials were completed, the foraging box door was kept locked for the OWA control trials. The locking device was located on the inside of the box and was not visible to subjects; thus, the box's outward appearance was the same in control and experimental trials. As no OWAs attempted to open the box in control trials they did not learn that the box was un-openable prior to their experimental trials. Performance of the OWAs in control and experimental trials were compared to assess whether stimulus or local enhancement occurred after observation of a trained demonstrator. During BFA control trials the box was unlocked, as it was in OWA experimental trials, thus comparison of BFA and OWA experimental trials enabled assessment of how observation of a trained demonstrator influenced the likelihood of successfully opening the box. All control trials lasted 30 min.

All trials (experimental and control) were performed in the morning (between 7:30 and 9:00 am) and the afternoon (between 4:30 and 6:00 pm) when the zoo was closed to visitors. A maximum of two trials (one in the morning; one in the afternoon) were performed per day. For the OWA pull group experimental trials started the day after the last control trial.

Table 1

Behaviours Coded from the Videos During Social Learning Test Trials.

Behavioural category and behaviours		Definition
Target zone	Inside target zone	50% or more of a subject's body is within the boundaries of the target zone area; subjects are coded as either being on the perch that surrounded the box (having at least one foot on the perch) or being elsewhere in the target zone.
Attempts	Touches box	Subject makes contact with the box; area touched (door handle, front of box, or other part of box (not front) and body part(s) used (beak, foot, or beak and foot) are coded.
	Unsuccessfully opens	Subject partially opens box door; method (slide, pull, or slide-pull) and body part(s) used (beak, foot, or beak and foot) are coded.
	Opens successfully	Subject fully opens box door, but food is pilfered; method (slide or pull) and body part(s) used (beak, foot, or beak and foot) are coded.
	Fully successful	Subject fully opens box door and retrieves food; method (slide or pull) and body part(s) used (beak, foot, or beak and foot) are coded.
Agonistic	Unidirectional	A subject directs aggression (squawking, pecking, forcing off perch, or raising a foot at another individual) towards another subject; roles of individuals are coded (demonstrator or observer; victim or aggressor).
	Mutual	Two subjects direct aggression (see above) towards each other; role of individuals is coded (demonstrator or observer).
	Involving pilfering	There is an agonistic interaction between two subjects in the context of a successful or unsuccessful pilfering attempt.
Pilfer	Inside box	A subject takes food from inside the box after the box door has been opened by another bird; roles of individuals are coded (victim or pilferer).
	Outside box	A subject takes food from a bird after that bird successfully retrieved it from the box; roles of individuals are coded (victim or pilferer).

Video coding

The Observer XT 10 program was used to code recorded subject behaviour that occurred within the target zone (see Table 1). Methods used for unsuccessful attempts that included both slide and pull actions were coded as ‘slide-pull.’ Methods used for successful attempts that included both slide and pull actions were coded according to whether subjects retrieved food through the opening that resulted from a pull or slide action. Subject attempts were coded as separate behaviours if a minimum of 3 s elapsed between behaviours. This rule also applied to agonistic behaviours involving the same individuals. In cases of unidirectional or mutual aggression (and only in these cases), subjects were considered observers if they were not in physical contact with the box door at the start of the aggression; any bird (trained or non-trained) that was in physical contact with the box door was considered a demonstrator.

To test the accuracy of video coding, a second independent individual blind to the experimental group coded a random sample of 6 (2 control and 4 experimental) of the 38 trials (16%) with the full coding scheme (Table 1) in Observer XT, and a Cohen’s kappa test was run to assess inter-observer reliability. The mean kappa score was 89.33, indicating a high level of agreement between coders and that the videos had been coded accurately.

Data Analyses

Analyses were conducted using data from nine OWA control trials and nine experimental trials from the OWA slide group. The OWA pull group completed 13 experimental trials, but only 11 were analysed; in the two excluded trials no bird (neither trained demonstrator nor subject) entered the target zone. The IBM SPSS Statistics 21 program was used to run the majority of analyses, which were nonparametric due to small sample sizes and because data were not normally distributed. Our analyses focussed on the behaviour of subjects which were defined as all birds in the aviary except the trained demonstrator. We used two-tailed Fisher’s exact tests to compare the proportions of subjects that (i) entered the target zone and (ii) that made contact with the box in the OWA slide experimental group and the OWA control group. As the OWA control group also served as the pull experimental group, we also assessed whether they showed significantly more interest in the box during experimental trials than control trials; McNemar's tests were used to compare proportions of birds that entered the target zone and that made contact with the box in the two conditions. Focussing on the subjects that successfully opened the box, we used a two-tailed Wilcoxon signed-ranks test and a binomial test to assess if subjects used door opening methods that matched those of their trained demonstrator. We used two-tailed Wilcoxon signed-ranks tests to compare the number of subjects' attempts 1 min before and 1 min after being victims of unidirectional aggression or pilfering. Kendall's tau tests were run to investigate possible relationships between attempts and agonistic or pilfering behaviour across trials (for both victims and aggressors). As recommended by Field (2009), we report r values as measures of effect sizes. We report Hodges-Lehmann and exact binomial 95% confidence intervals (CIs). A web-based calculator was used to calculate exact binomial CIs (Pezzullo 2009).

We also used a generalized linear mixed-effects model (GLMM) with a binomial error structure and a logit link function to investigate whether the subject door-opening method ($N = 278$ full opens by non-trained birds) matched their respective trained demonstrator method or not (binary dependent variable) was influenced by the presence or absence (0/1) of the trained demonstrator in the target zone (categorical explanatory variable). We ran the GLMM in R Version 3.1 (R Core Team 2014) and used the package lme4 (Bates et al. 2015) to run random intercepts models. In order to control for pseudoreplication; subject ID ($N = 10$) and trial number ($N = 16$) were entered as random factors to account for multiple data points being taken from each individual and each trial. To assess the significance of the explanatory variable, we compared the model containing this variable with a null model, comprising only the intercept and random effects, using a likelihood ratio test.

Results

Trained demonstrator performance

Both of the trained demonstrators consistently used the trained method to open the foraging box during test trials, although overall the slide trained demonstrator provided more demonstrations than the pull trained demonstrator, particularly in the first two trials (see Table 2). All of the interactions with the box and successful opening attempts in the experimental groups occurred after demonstrations by the trained demonstrators (Table 3).

Table 2

Box opens by trained demonstrator across all trials and in each of the first three trials.

	Total				
Trained method	Slides	Pulls	Trial 1	Trial 2	Trial 3
Slide	80	2	11 (all slides)	15 (all slides)	8 (all slides)
Pull	2	66	3 (all pulls)	5 (all pulls)	20 (all pulls)

Table 3

Number of times trained demonstrators (TD) demonstrated before subjects' first interactions with the foraging box.

Type of initial interaction with the box	Demonstrations by Slide TD	Trial in which interaction occurred	Demonstrations by Pull TD	Trial in which interaction occurred
First physical contact	3	Trial 1	4	Trial 2
Door handle touched with beak	7	Trial 1	6	Trial 2
Unsuccessful attempt to open door	8	Trial 1	14	Trial 3
Door successfully opened	17	Trial 2	37	Trial 4

Is there evidence of local or stimulus enhancement?

To determine whether subjects' interest in the foraging box was influenced by exposure to trained demonstrators' successful manipulation of it, the number of OWAs that entered the target zone and made contact with the box in control and experimental trials were compared. Fisher's exact tests showed that significantly greater proportions of OWAs entered the target zone (20/22; proportion 0.91 with 95% confidence limits of .71 and .99) and made contact with the box (18/22; proportion .82 with 95% co0nfidence limits of .60 and .95) in the experimental slide group than the proportions of birds that entered the target zone (3/16; proportion 0.19 with 95% confidence limits of .04 and .46; $p < .001$) and made contact with the box (0/15; proportion 0.00 with 95% confidence limits of .00 and .22; $p < .001$) in the OWA control group. OWAs (N =15) that completed control trials, followed by experimental (pull) trials, also showed changes in their responses. McNemar's tests revealed there was a significant increase in the number of subjects that entered the target zone from control (3/16) to experimental trials (13/16; $p = .039$), as well as a significant increase in the number of subjects that touched the box from control (0/15) to experimental trials (8/15; $p = .008$). As can be seen in Figure 3, we found that as the frequency of trained demonstrator box door opens increased, as did the number of subjects that made contact with the box.

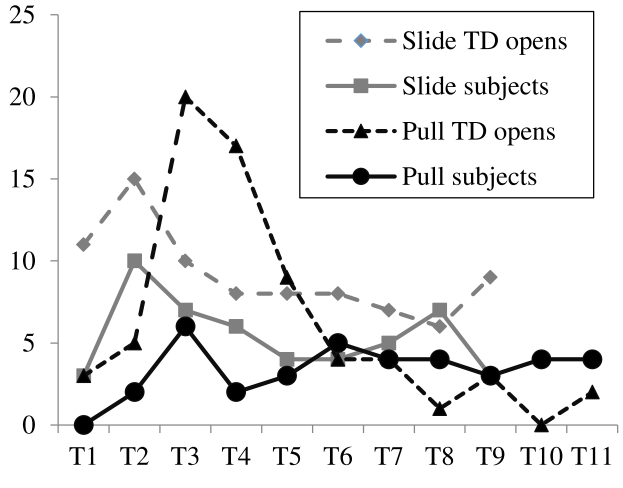


Fig. 3 Number of demonstrations by trained demonstrators (TD) and number of subjects that made contact with the box in each trial for experimental groups

Comparison of box opens by OWA experimental birds and BFAs

Seven slide experimental birds and three pull experimental birds successfully opened the box at least once (see Table 4). The total time it took for each successful bird to enter the target zone from the start of the first trial is listed in Table 5. The time that elapsed between subjects' first target zone entry and subjects' first box contact, and the time that elapsed between subjects' first box contact and first successful box open, can also be seen in Table 5.

As the box door was kept locked during the control trials the OWA pull group completed, we used a group of BFAs to assess the likelihood that subjects would open the box without exposure to a trained demonstrator. Similar to the OWA control trials, few BFAs entered the target zone (8/20) and crucially whilst 10/37 experimental OWA subjects opened the box at least once, 0/20 BFAs opened the box and no OWA attempted to do so during the control trials. A total of three BFAs made contact with the box; only one made contact with the door handle with the tip of its beak, but did not manipulate the door in anyway.

Table 4

Frequency of box opens slide and pull experimental subjects completed using the slide method and the pull method, and the method they used for first opens.

Experimental Group	Subject	Slides observed	Pulls observed	Method of first open
Slide	GYLSR	63	34	Slide
	OL	28	5	Slide
	PIL	46	18	Slide
	PUR	17	0	Pull
	RL	23	3	Slide
	SL	98	69	Pull
	SR	36	9	Pull
Pull	LGR	2	31	Slide
	RBN	1	37	Slide
	RR	14	68	Pull

Table 5

Number of minutes it took for successful subjects to first enter the target zone (TZ), seconds between subjects' first TZ enter and the first contact they made with the box, and seconds between subjects' first box contact and their first successful open.

Subject	Time to 1st TZ enter (min)	TZ to 1st contact (s)	1st contact to 1st box open (s)
GYLSR	13	2705	191
OL	10	60	36
PIL	30	28	37
PUR	13	694	5
RL	12	17	28
SL	28	24	89
SR	13	599	31
LGR	117	8	50
RBN	117	72	55
RR	111	36	101

Did subjects imitate the door opening methods they observed?

The methods used by subjects who solved the task, in all successful openings (including those where the food was pilfered from the bird that opened the box) were compared to methods used by their group's trained demonstrators to determine whether they matched. A two-tailed Wilcoxon signed-rank test showed that subjects that successfully opened the box (N =10) did not use the demonstrated method (*Mdn* = 5.50, *IQR* = 22) significantly more than the non-demonstrated method (*Mdn* = 5.50; *IQR* = 40), z = - 0.36, p = .720, r = - .11, 95% Hodges-Lehmann CI [– 3, 17.5] (see Fig. 4); six subjects used both methods to open it. As individuals may have developed a preference for the alternative method through individual learning during the course of the experiment, subjects' initial attempts were also analysed; a binomial test (0.5) showed that the number of OWAs whose first successful open matched the demonstrator's method (6/10) was not above that expected by chance (p = .754).

In this open diffusion setting, non-trained birds became demonstrators once they successfully opened the box. As such, we tested whether birds were influenced by the last demonstration they were exposed to before their successful attempts (or first successful attempt if they produced a sequence of attempts without intervening demonstrations from others). A Wilcoxon signed-rank test for the 10 birds that succeeded in opening the box showed that the number of attempts that matched (*Mdn* = 4.50, *IQR* = 17) the most recently used method by any (trained and non-trained) demonstrator did not significantly differ from the number of non-matching attempts (*Mdn* = 8; *IQR* =28), $z = -1.13$, $p = .258$, $r = -.36$, 95% Hodges-Lehmann CI [-6, 1]. We also examined whether the door-opening method that was used during an individual's first successful door-opening attempt matched the method that had been most frequently used up to the point those first solves were made (including across all previous trials). A Binomial test (.50) showed that the number of birds that used the dominant technique (6/10) was not significantly greater than chance, $p = .754$ (see Table 4).

We investigated whether subjects replicated their trained demonstrators' pattern of body part use when opening the box. The trained demonstrators interacted with the apparatus in different ways, the slide trained demonstrator used only his beak and the pull trained demonstrator used both his beak and a foot in the majority of successful attempts. In contrast, subjects in both groups showed a similarly high preference for beak-only opens (see Table 6). Across both groups the beak only was used in 99% of opens that used the slide method opens and 92% of pull method opens. There was no instance in which a bird used only its foot to open the box door.

We conducted a GLMM to assess if subjects were more likely to use the trained demonstrator's method of box opening when he was present in the target zone. The GLMM indicated that the trained demonstrator presence in the target zone during or shortly before a subject's attempt did not affect the likelihood of the subject using the box-opening method that matched that of the trained demonstrator (X^2 (1) = 0.09, $p = .761$).

Table 6

Total opens and percentage of beak only opens per group using each method (TD = trained demonstrator).

Method	Group	Number of opens	% beak only
Slide	Slide TD	80	100
	Slide subjects	35	97
	Pull subjects	77	10
Pull	Pull TD	66	8
	Slide subjects	86	95
	Pull subjects	79	89

Did aggression influence subjects' interactions with the box?

As the presence of a food source that could be monopolized created a competitive social environment, we examined the role that aggression may have played in task acquisition. Agonistic behaviour was seen in the target zone in all slide experimental group trials and in 10 of 11 trials in the pull experimental group. Both groups displayed similar total instances of aggression (slide group *N* = 172 agonistic events involving 15 individuals (including the trained demonstrator); pull group *N* = 178 agonistic events involving seven individuals (including the trained demonstrator); see Fig. 5); no aggression was observed in control groups. A total of 19 experimental subjects were the victims of unidirectional aggression, with each victim receiving aggression from an average of 2.74 birds (*SD* = 1.09).

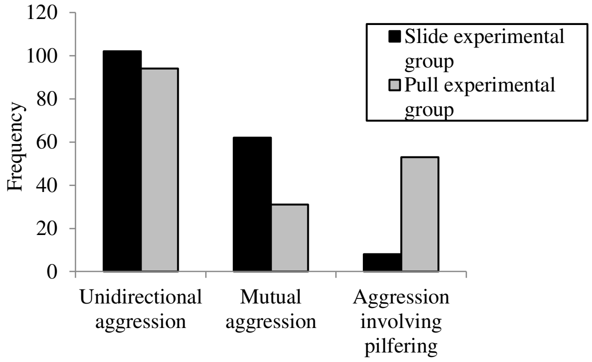


Fig. 5 Frequency of each type of aggression in each experimental group

In order to determine whether subjects were less likely to make contact with the box immediately (up to 1 min) after being the victims of aggression, we focused on the 19 subjects who received unidirectional aggression in the target zone (not including trained demonstrators or subjects that were in physical contact with the box at the start of the agonistic interaction). For each agonistic event, we calculated the number of victims' attempts to open the box (see Table 1: all categories were included except 'touch other part of box') 1 min before and 1 min after the aggression. For each victim (N =19) we then took mean values across all instances where they received aggression. A Wilcoxon signed-rank test showed there was no significant difference between victims' mean number of contacts with the front of the box 1 min before the aggression (Mdn = 1.00, IQR = 1.88) and 1 min after the aggression (Mdn = 1.00, IQR = 1.50; z = - .18, p = .859, r = .04, 95% Hodges-Lehmann CI [-.25, .33]).

Although receiving aggression did not affect interactions with the box in the short term, we also examined whether the amount of aggression received was related to box interactions across trials. We focussed on subjects that were the victims of unidirectional aggression and/or touched any portion of the front of the box for this analysis. Only subjects that had data points for at least one of these two behaviours in seven trials or more were included in this analysis (N = 6). We ran correlational analyses for each of these birds individually, and despite small sample sizes (N = trials), Kendall's tau tests showed significant positive associations between the duration of unidirectional aggression received and the number of victims' attempts to interact with the front of the box for three birds (see Table 7). For those three OWAs, making more attempts to interact with the front of the box was significantly correlated with receiving more aggression (see Table 7). We found no evidence on either a short or long term basis that receiving aggression reduced victims' motivation to interact with the box.

Table 7

Results of Kendall Tau correlations between duration of aggression received and number of physical contacts with the front of the box across trials. Analysis only run for individuals that interacted with the box and/or were victims of unidirectional aggression in seven trials (N) or more.

Subject ID	*N* (trials)	τ value	*p* value
GYLSR	7	.76	.007
RR	8	.65	.008
PUR	8	.67	.020
RBN	8	.37	.142
LGR	9	.33	.194
OL	9	-.09	.741

An additional analysis was conducted to determine whether there was a relationship between successfully opening the foraging box and giving aggression to other group members in the target zone. All subjects that displayed unidirectional aggression and/or successfully opened the box were included in this analysis ($N = 14$), with the total number of successful openings and incidences of being aggressive to others were entered for each bird. A Kendall's tau correlation revealed a significant positive relationship between the frequency of directing aggression towards others and the frequency of successfully completing the foraging task ($\tau = .52$, $p = .015$, $N = 14$ birds).

Insufficient win-lose agonistic interactions within each group were observed to calculate reliable dominance hierarchies, so it was not possible to assess the influence of dominance on performance in this task.

Did pilfering influence subjects' interactions with the box?

As pilfering victims did not benefit from their successful door-opening attempts, while pilferers gained rewards as a result of others' successful door-opening attempts, we examined whether victims' and pilferers' motivation to interact with the box may have been impacted by this behaviour. A total of 83 instances of pilfering were recorded across both experimental groups (slide $N = 39$; pull $N = 44$) and the majority of these ($n = 63$) involved the pilfering of food from inside the box (slide $n = 33$; pull $n = 30$). To assess whether having food stolen had a short term effect on the victim's motivation to engage with the box, for each pilfering event we calculated the number of times victim subjects (excluding trained demonstrators) successfully opened the box door in the 1 min before and 1 min after being pilfered. For each victim ($N = 8$), we then took mean values across all instances where they experienced pilfering. A Wilcoxon signed-rank test showed no significant difference between the mean number of times victims opened the box before they were pilfered ($Mdn = 1.21$, $IQR = 1.00$) and after they were pilfered ($Mdn = 1.75$, $IQR = .62$; $z = -1.36$, $p = .176$, $r = -.48$, 95% Hodges-Lehmann CI [-.16, 1]).

All eight subjects that pilfered food from inside the box also opened the box. To assess whether successful pilfering food from another was related to successfully opening the box across trials, we conducted a correlational analysis. All subjects that pilfered from inside the box and/or successfully opened the box were included in this analysis ($N = 10$). A Kendall's tau test showed that there was a significant positive relationship between total number of times subjects pilfered food from inside the box and total number of times they successfully opened the box ($\tau = .87$, $p = .001$, $N = 10$ birds).

Discussion

Our study provides further evidence of social learning capacities in psittacines, and to our knowledge, is the first to present evidence of this capacity in OWAs in a foraging context. The results obtained indicate that OWAs benefit from stimulus and/or local enhancement. Significantly more birds in experimental trials were found to approach and make physical contact with the testing apparatus than in control trials. This suggests that subjects' interest in the foraging box was increased due to trained demonstrators' interactions with it. More subjects in the slide group were found to have approached and touched the box in the first few sessions as compared to the pull group. This is likely due to the greater number of learning opportunities provided by the slide trained demonstrator in the initial sessions compared to the pull trained demonstrator. However, some of this variation may also be attributable to the pull group's prior experience as a control group, where they may have learnt the box was an irrelevant stimulus, and thus needed more time to overcome this. It is important to note though, that none of the OWAs in the pull group made contact with the locked box during control trials. As such, it was not necessary for them to overcome learning that the box door did not open.

Whilst none of the OWAs made contact with the box in control trials and 0/3 BFAs who made contact with the box in control trials solved the task, 10 OWA experimental birds acquired this novel foraging technique. Although the comparison of BFA and OWA performance needs to be considered with caution, due to the species difference, these findings are consistent with previous avian research, which commonly reports significant differences between performance in experimental and control conditions in social learning tests (Fritz and Kotrschal 1999; Huber et al. 2001; Langen 1996; Midford et al. 2000). It is possible that successful acquisition of the task was influenced by emulation in addition to stimulus/local enhancement. By observing skilled demonstrators, experimental OWAs could have learned about the affordances of the box, in that movement of the box door revealed food. Alternatively, successful performance by the birds that opened the testing apparatus may have relied on trial and error individual learning once they were attracted to the apparatus through stimulus/local enhancement. Unfortunately, it is not possible to distinguish between the influences of local/stimulus enhancement and emulation on subject performance in the present study: future studies could address this with a ghost control condition.

Interestingly, no evidence of imitation was found. Both door-opening techniques (slide and pull) were used by OWAs in both experimental groups, and no connection was found between methods used by subjects and methods used by their groups' trained demonstrators, either in their overall performance or in their very first successful opening (before individual reinforcement for that behaviour had occurred). In this open diffusion setting, other birds who acquired the task then became demonstrators, however, there was no evidence that birds copied the method they last observed (from a trained or non-trained demonstrator) before each attempt. Additionally, no evidence was found that birds used the dominant method (technique that had been used most often by group members up to that point of subjects' first attempts) significantly more than the non-dominant method. Experimental subjects also showed no inclination to use the trained demonstrator's method when he was present with the subject in the target zone. As both trained demonstrators consistently and repeatedly obtained food from the testing apparatus using the method they were trained to use, it is unlikely that the absence of imitation was due to poor performance of the trained demonstrators. Overall, subjects used the pull method about a third more often than the slide method. Despite efforts to have two actions that were equally easy to execute, it may be that this motion, pulling with the beak, is more similar to actions required for natural foraging such as the extraction of seeds and nuts from hard shells, than the slide action. The slide action was, however, clearly within the capacity of OWA, as 9/10 birds (three from pull group) who learnt to open the box used this method at least once. In the future, it may be interesting to consider using novel actions that are not likely to be used in natural feeding behaviour, but are within the scope of subjects' motor capacities.

Compelling evidence of complex social learning capacities has been reported in several parrot studies (Auersperg et al. 2014; Heyes and Saggerson 2002; Moore 1992; Pepperberg 2006), it may therefore be surprising that the present study failed to find evidence of imitation. Although it is possible that OWAs lack the capacity for motor imitation, we suggest that these results are more likely explained by the experimental design used. The two-action task we used may have been too easy, allowing birds to mainly rely on individual learning to acquire the task. Tennie et al. (2006) identified this as potential explanation for failure to find imitation in great apes in a push-pull task. Furthermore, disparities in findings between field and laboratory research with kea parrots indicate that social learning capacities detected in highly controlled testing, may not be observed under more naturalistic conditions (Gajdon et al. 2004; Huber et al. 2001).

Across animal species, imitation has been most commonly observed in highly controlled dyadic experiments. Under such testing conditions, there is little to distract an observer's attention from the demonstrator and testing apparatus, and crucially, there is no social competition when the observer is given access to the apparatus. In contrast, our subjects were tested in their aviaries, with all group members being given simultaneous access to the foraging box, therefore several factors may have influenced what subjects ultimately learned about the foraging task. First, it is much more likely in an open diffusion set-up that subjects obtain less consistent information about the method used by demonstrators to obtain food. Subjects in our study were exposed to alternate task solutions as a result of group members' task acquisition. It is also difficult to know what aspects of each demonstration each subject could observe from their position in the aviary. Subjects also had many more competing stimuli to attend to, including a range of social interactions. It is possible, for instance, that patterns of social association may have influenced task acquisition. As studies have found that the spread of novel behaviour can be predicted by social networks (e.g., lobtail feeding in humpback whales, Allen et al. 2013), future studies that use the open diffusion experimental approach to study social learning may benefit from engaging in network-based analyses. Furthermore, in our study, social competition for access to the foraging box meant that subjects had limited time to interact with the box before being displaced or receiving aggression. This may have encouraged the rapid use of multiple strategies to gain access to the box, rather than careful copying of the demonstrator's technique. Equally, the positive relationship we found between observers displaying aggression to others and successfully opening the box suggests that the most successful birds directed a great deal of their attention towards individuals that came in close proximity to the apparatus. They may therefore have been more interested in displacing group members in the target zone, including the trained demonstrator, than in observing the trained demonstrator's manipulation of the box door. Individual factors such as dominance, boldness and motivation to obtain food are also likely to have impacted on individual engagement in agonistic interactions and task acquisition in this experimental setting and we recommend that future researchers assess these factors to investigate their influence on task acquisition. This complex set of issues and factors are likely to also be present and constrain the types of social learning that influence the transmission of group-specific behaviours in the wild, so using open diffusion designs in experimental work is vital in order to better understand the social learning mechanisms underlying these cultural variants in animals.

Our analyses concerning the effect of aggression and pilfering on subjects' performance indicate that individual characteristics influence the likelihood of an individual acquiring a novel foraging technique from others. The positive relationship we found between observers displaying aggression to others and successfully opening the box indicates that willingness to defend access to the resource from others is important in a highly competitive social situation in terms of ensuring sufficient exploration opportunity to acquire the task solution. Equally, birds who successfully pilfered food from others who opened the box also had high levels of their own successful foraging attempts with the box. Pilfering may be an important scaffolding behaviour in the acquisition of novel foraging techniques. However, this relationship could also be a product of aggressive birds defending an area close to the box door, providing them with a lot of opportunities to open it themselves and pilfer from others. Related to pilfering behaviour, we also anecdotally observed that some individuals in the present study spent more time scrounging for dropped food rewards on the ground below the target zone, than they did attempting to open the box themselves. Thus, for some subjects, benefiting from group members' successful manipulation of the box may have had an inhibitory effect on their task acquisition, in line with previous studies (Beauchamp and Kacelnik 1991; Giraldeau and Lefebvre 1987; Munkenbeck Fragaszy and Visalberghi1990). Unfortunately, because this behaviour occurred outside the target zone, it was not captured on video and could not be systematically examined. Contrary to our predictions, receiving aggression or having food stolen did not appear to deter subjects' efforts to interact with the box. However, it could be that only the more socially confident birds that were relatively resilient to aggression and pilfering chose to regularly enter the target zone to interact with the box. The use of multiple foraging boxes in future studies may reduce aggression and social competition, possibly yielding different results.

In conclusion, the present study found that social facilitation occurred, but high fidelity imitation copying did not. This narrows the space of mechanisms that could account for the social learning observed (local/stimulus enhancement; emulation), but does not distinguish between these low-fidelity social learning mechanisms. In this open diffusion set up experimental birds who could watch a trained demonstrator were more likely than control birds to approach the box and successfully extract food from it; however, we found no evidence that they imitated the method used to open the box. Aggression was relatively frequent as individuals competed to gain access to the monopolisable food source. Surprisingly, subjects were not deterred from making physical contact with the box as a result of receiving aggression from or having food stolen by group members; however, subjects that frequently displayed aggression towards others and pilfered food from others also had high numbers of successful box opens. This indicates that propensity for aggression may play a role in the extent to which birds are able to capitalise on opportunities to learn about, and compete for, monopolisable food, and that imitation is not necessary for the spread of exploitation of a novel food source when relatively basic extractive behaviours are required. While some species may show greater reliance on high fidelity copying (e.g., great tits; Aplin et al. 2015), which would allow adaptive behaviour to spread more rapidly through populations, others may rely more heavily on individual learning and thus may show greater propensity for innovative behaviour. A trade-off may therefore exist between innovative behaviour and social learning. Our open diffusion study highlights important social and individual factors that constrain and promote learning from others in a naturalistic context, as well as the possibility that although tightly controlled dyadic social learning paradigms have shown many animals to be capable of imitation, group-specific behavioural variations observed in the wild could result from lower-fidelity copying processes.

Ethical approval: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the University of York. Approval for this study was obtained by the Department of Biology Ethics Committee (Case KS230512), at the University of York.

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