



# Diverse species readily acquire copies of novel actions from others that are not achieved through individual learning

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The cultural transmission of behaviour patterns across animal populations and between generations has been rigorously demonstrated in diverse vertebrate species and also in insects, but controversies continue about exactly what distinguishes nonhuman from human cultural learning. A contentious contemporary debate concerns a hypothetical ‘zone of latent solutions’ (ZLS), conceptualized as all that members of a species can acquire by individual learning. The ZLS hypothesis proposes that cumulative culture is restricted to humans because of a unique ability to copy behavioural innovations beyond our species’ ZLS. Apes and other taxa are argued instead to be limited to copying only behaviours that are already within their ZLS, thus constraining their capacity for cumulative culture. Here I suggest that empirical tests of this hypothesis are scattered through the research literature covering social learning experiments and I collate relevant instances. Over 20 such studies spanning mammals, birds, fish and insects demonstrate social learning of novel actions new to the species that no individual acquires through its own efforts. Many offer particularly compelling refutation of the ZLS hypothesis because in addition to documenting an absence of individual level learning, they incorporate designs showing that observers match whichever of two alternative forms of action they witnessed or include multistep actions that are clearly challenging for individuals of the species studied to acquire by individual learning.

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It has taken the study of animal behaviour just a few short decades to decisively challenge the belief that only humans display culture, as research has progressively revealed cultural transmission of behaviour patterns through social learning (learning from others) to be widespread in vertebrates and also evidenced in invertebrates, notably insects (Allen, 2019; Aplin, 2019; Danchin et al., 2004; Duboscq et al., 2016; Lachlan & Whiten, 2020; Whitehead & Rendell, 2015; Whiten, 2017, 2021). That culture is widespread in nonhuman animals (henceforth ‘animals’) is now well supported so long as ‘culture’ is defined in such broad and widely accepted terms as ‘behaviour patterns shared by members of a community, that rely on socially learned and transmitted information’ (Laland & Hoppitt, 2003, p. 151), as opposed to such intrinsically anthropocentric definitions as an early and oft-cited one due to Tylor (1871, p. 1), for whom culture was ‘that complex whole which includes knowledge, belief, art, morals, law, custom, and any other capabilities and habits acquired by man as a member of society’.

Just what distinguishes human culture from that evidenced in animals has long been controversial and remains so. The most common difference currently cited is that human culture is massively cumulative, with layers of cultural advance building on earlier ones, whereas there is sparse and contested evidence for this even in the rich, multiple-tradition cultures of taxa such as chimpanzees, *Pan troglodytes* (Boesch, 2012; Whiten, 2023). The most recent review on this topic (Rawlings et al., 2021) tabulated as many as 26 candidate examples of cumulative cultural evolution (CCE) in mammals, birds and insects, judging these against four core criteria for CCE laid out by Mesoudi and Thornton (2018), namely (1) occurrence of a novel behaviour (innovation), (2) transmission of this to others via social learning, (3) occurrence of a performance improvement of some kind and (4) repetition of these steps, creating sequential improvement over time. While many findings match several of these criteria, only two were so far judged by Rawlings et al. to meet all four criteria (baboons, *Papio papio*, Claidiere et al., 2014; homing pigeons, *Columba livia*, Sasaki and Biro, 2017). The disparity between human and animal cultures in this respect thus begs explanation.

Tomasello et al. (1993) asserted that cumulative culture is uniquely human and hypothesized that this is dependent on

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uniquely high-fidelity transmission of cultural elements to learners. These authors proposed more specifically that imitative learning is key to this, and also uniquely human. A later phase of this theorizing by [Tennie et al. \(2009\)](#) sharpened this perspective by introducing the concept of a 'zone of latent solutions' (ZLS), conceptualized as all that members of a species can learn through their own efforts during their lifetime, without the benefit of cultural inheritance. It was argued that apes are prevented from displaying CCE because they can learn from others only behaviours that are already within their ZLS, whereas 'only humans could copy traits beyond their ZLS' ([Tennie, Hopper et al., 2020](#), p. 430). This latter claim means that although the associated core debates have historically focused on apes, whether the hypothesis is true or false is relevant for our understanding of social learning and culture across the whole field of animal behaviour. Moreover, as I show below, relevant evidence exists for a much wider range of animal taxa than just apes.

I have recently critiqued the ZLS hypothesis on logical grounds ([Whiten, 2022, 2023](#)). I noted that unless a culture has already become an instance of CCE created through a series of innovations by different individuals over time, the behaviour will necessarily have been initiated by one or a few individuals through their own explorations and without benefit of cultural inheritance, which [Tennie et al.](#) class as within the species' ZLS. The hypothesis is therefore simply circular, and inherently irrefutable in this naturalistic context, in which a behaviour new to the species is invented by one or more individuals, and then spreads, by social learning, to meet the definition of culture given above. I argued that this circularity means the hypothesis represents a scientific blind alley. Other authors have critiqued the ZLS hypothesis on a variety of other grounds, such as that the 'lifetime learning' and 'cultural vacuum' criteria are untestable in practice, and that testing the hypothesis requires proving a negative ([Caldwell et al., 2016](#); [Mesoudi & Thornton, 2018](#); [Miton & Charbonneau, 2018](#); [Rawlings et al., 2021](#); [Schofield et al., 2018](#); [Thornton & Mesoudi, 2023](#)).

At first sight paradoxically, the ZLS is nevertheless more directly testable if a human experimenter plays the role of a conspecific innovator, introducing a task that requires a behaviour new to the species to be acquired for successful solution. This challenge can then be presented in experimental contexts that contrast opportunities for social learning with an absence of such opportunities. The latter obviously cannot reasonably span a 'lifetime' but can last for a compellingly long period. One way to address the latter issue is to show that attempts at the task without benefit of a model dissipate over time, so that solution is vanishingly unlikely even if a

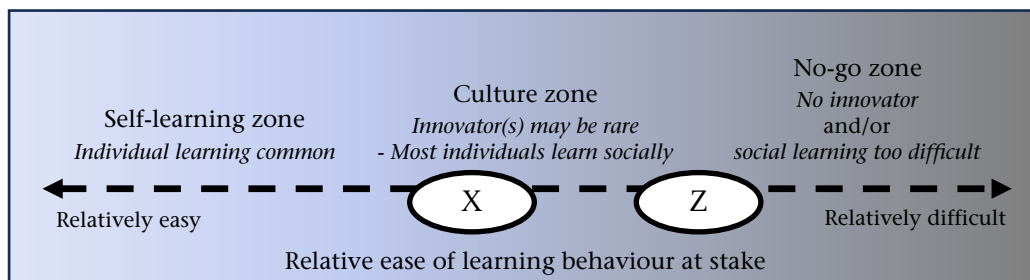
more extended opportunity were offered ([Hopper et al., 2015](#)). Another approach discussed in this paper is testing short-lived animals such as insects ([Alem et al., 2016](#); [Bridges et al., 2024](#); [Thornton, 2024](#)).

Arguing both that the ZLS hypothesis is circular and not scientifically testable in the context of animals' natural lives, and yet that it is testable in the specific, artificial way just outlined, may appear to be in conflict. To explain why this is not the case, I offer a simple model of the occurrence and evolution of animal culture ([Fig. 1](#)), and contrast this with the views of ZLS theoreticians.

[Fig. 1](#) envisages three broad zones, conceptualized to occur along a continuum of graded difficulty in individuals' capacity to acquire the behaviour at stake. The Culture Zone is characterized as one in which the behaviour of interest is relatively difficult or costly to acquire individually compared to in the Self-learning Zone. Initiation or invention of any particular instance of what later spreads to become a cultural behaviour may occur in just a few individuals or even a single one, corresponding to 'Z' in the figure. Studies fortunate enough to document the spontaneous beginnings and later spread of animal cultures are consistent with this latter scenario (e.g. lob-tail feeding in humpback whales, *Megaptera novaeangliae*, [Allen et al., 2013](#); moss-sponging in chimpanzees, [Hobaiter et al., 2014](#); chimpanzees placing a grass-blade leaf in an ear, [van Leeuwen et al., 2014](#)).

The conception illustrated in [Fig. 1](#) differs radically from that of the proponents of the ZLS hypothesis, for whom the occurrence of a behaviour in just two independent individual learners is immediately attributed to the species as a whole: it is categorized as within the species' ZLS ([Tennie, Hopper et al., 2020](#); [Tennie, Bandini et al., 2020](#)). I suggest such an inference is not logically tenable and goes against all we know of the interindividual variance in cognitive capacities and learning abilities within many animal taxa ([Lambert & Guillette, 2021](#); [Naug & Tait, 2021](#); [Thornton & Lukas, 2012](#); [Fig. 1](#) in [Whiten, 2023](#)). The conception in the present [Fig. 1](#) better reflects this reality, as well as what field research has revealed about cultural phenomena in the wild ([Gruber & Biro, 2023](#); [Koops, Arandjelovic et al., 2023](#); [Koops, Biro et al., 2023](#) and references above on spontaneous invention and diffusion of novel behaviours).

Adopting the perspective of [Fig. 1](#), in the kind of experiment outlined above and reviewed in this paper, a human researcher is essentially playing the part of an animal somewhat more innovative than those being tested; in the social learning conditions of the experiment, the researcher is presenting models trained to solve tasks that individuals fail to acquire unless witnessing the



**Figure 1.** A simple model for the occurrence of culture and cultural evolution. Any particular behaviour in a particular species may fall within a Self-learning Zone in which learning at the individual level is relatively easy, and hence common. In the Culture Zone, where individual learning is more challenging, innovators of the behaviour may be relatively rare but socially learning from them can be common, followed by further cultural transmission. 'Z' indicates a situation where invention of the behaviour will be very rare, whereas at 'X', invention will likely be more common and occur on multiple occasions: but in both cases, a majority of those in the population may then acquire the behaviour by learning from those already performing it. In the No-go Zone, either innovation is beyond any individual's capacity, and/or social learning of any such innovation may not occur. These zones are envisaged as lying along a continuum, so grade into each other, as discussed further in the text. The model is simple, but the underlying causal phenomena are of course complex and will vary by species and ecology. Individual differences mean that any one species should be envisaged as lying along a horizontal band of the continuum. Both organic and cultural evolution may shift the transition zones between the three highlighted here.

know-how of the model, corresponding to a position like that marked 'Z' in Fig. 1. To put this another way, these experiments can be thought of as simulating a situation like that in a potential first step in the emergence of a new culture, or even cumulative culture, in which the model trained by an experimenter provides the novel 'step-up' to a behaviour new for the species, and the capacity of participants to acquire this through social learning is tested, given that no other individuals can master it by their own unaided efforts.

In this article I collate and summarize studies scattered in the scientific literature that meet the criterion of demonstrating social learning of such a novel task provided by experimenters, contrasting with failure at the same task in conditions that permit individual learning only. There are many other studies that demonstrate better learning in social than asocial conditions, but here I include only studies in which no individual learns in the no-model condition.

## METHOD

Ideally, one might approach the task of collating studies meeting the criteria above through a systematic search of the literature using a database such as Web of Science. Unfortunately, it seems an impossible task to design terms (keywords or phrases) that can direct such a search at all efficiently, given the nature of the criteria. ChatGPT declines a request to do this. I have instead adopted a

simple two-step procedure. First, I assembled and tabulated those studies by my own research group or known to me in the existing research literature. Second, I circulated this to an online list of over 300 researchers I have accumulated that includes most of the senior figures in this field known to me, plus associated early career researchers, asking for help in identifying further studies that meet the criteria I set ('experiments in which animals acquire behaviour matching a model that none do in a no-model control condition'). My hope is that presenting the results collated so far in this paper will encourage other readers to draw attention to further studies, old or new, that may match the criteria or otherwise cast light on the empirical issues at stake.

In the resulting Table 1, I highlight 'two-action studies' (or 'two-option', or 'two-target' studies, marked '2A' in Table 1) which seed each of two experimental groups with conspecific models applying one of two spatiotemporally different forms of behaviour to gain rewards from the same task. This is significant because [Tennie, Bandini et al. \(2020\)](#) state that the ZLS hypothesis hinges on 'direct copying of form' defined as 'a measurably matched resemblance between the specific form of input A to the specific form of output B, where this matched resemblance between A and B is and must be, at least in part, causally due to the specific form of the input' (p. 29). Two-action experiments follow a design that tests this, by measuring whether 'inputs' (demonstrations) by models, of behaviour X versus behaviour Y, generate matched resemblance to

**Table 1**  
Experiments in which animals acquire behaviour matching a model that none acquire in no-model control conditions

Article	Species			Behaviour
<b>Baseline controls</b>				
<a href="#">Bonnie et al. (2007)</a>	Chimpanzees	<b>2A</b>	x	Posting tokens in receptacle A vs B
<a href="#">Craist et al. (2010)</a>	Capuchin monkeys	<b>2A</b>	x	Operating juice dispenser using method A vs B
<a href="#">Hopper et al. (2015)</a>	Chimpanzees		V	Using tool to 'Lift' blockage in 'panpipes'
<a href="#">Lefebvre (1986)</a>	Urban pigeons		x	Piercing a cover to obtain hidden grain
<a href="#">Mennill et al. (2018)</a>	Savannah sparrows		–	Young birds learning novel simulated songs that none sang in years before the experiments
<a href="#">Whiten et al. (2007)</a>	Chimpanzees	<b>2A</b>	V	Extracting food from one device by tool method A vs B, from second device by sequence of A-X vs B-Y
<a href="#">Van Leeuwen et al. (2024)</a>	Chimpanzees			Extracting food from a container by collecting tokens, opening a drawer, posting the token and closing the drawer
<b>Parallel controls</b>				
<a href="#">Alem et al. (2016)</a>	Bumble bees		V	Pulling a string to access artificial flower hiding food
<a href="#">Aplin et al. (2013)</a>	Blue tits	<b>2A</b>	x	Extract food items by method A vs B
<a href="#">Diez &amp; MacDougall-Shackelton (2020)</a>	Zebra finches	<b>2A</b>	–	Effects of wild-type, isolate and heterospecific song models on song learning
<a href="#">Feher et al. (2009)</a>	Zebra finches		–	Wild-type song vs effects of vocal isolation
<a href="#">Hopper et al. (2007)</a>	Chimpanzees	<b>2A</b>	V	Extracting food with tool method A vs B
<a href="#">Kis et al. (2015)</a>	Bearded dragons	<b>2A</b>	V	Pushing door to left vs right
<a href="#">Koops et al. (2022)</a>	Chimpanzees		x	Nut cracking in the wild
<a href="#">Nottebohm (1968)</a>	Chaffinches		–	Wild-type song vs effects of vocal isolation
<a href="#">Picard et al. (2017)</a>	Parrots	<b>2A</b>	x	Opening door using method A vs B
<a href="#">Stanley et al. (2008)</a>	Guppies		x	Unusual swimming vertically up a tube to feed
<a href="#">Thorpe (1958)</a>	Chaffinches		–	Wild-type song vs effects of vocal isolation
<a href="#">Voelkl &amp; Huber (2007)</a>	Marmosets		M	Precise form of unusual manipulation
<a href="#">Whiten et al. (2005)</a>	Chimpanzees	<b>2A</b>	V	Extracting food with tool method A vs B
<a href="#">Wild et al. (2021, p. 5)</a>	Great tits	<b>2A</b>	x	(1) Adding a second technique to a first, to create a two-step act gaining greater rewards from a puzzle box (2) Using the two-step solution when it alone gained a food reward from a feeding device
<a href="#">Wild et al. (2021, p. 6)</a>	Great tits	<b>2A</b>	x	
<a href="#">Wilkinson et al. (2010)</a>	Tortoises	<b>2A</b>	V	Detour around barrier to left or right
<a href="#">Bridges et al. (2024)</a>	Bumble bees		VM	Pushing a first barrier out of the way so that a second barrier could be pushed to access a drinking hole beneath
<b>Both types</b>				
<a href="#">Marshall-Pescini and Whiten (2008)</a>	Chimpanzees		x	Nut cracking using rock hammers
<a href="#">Spiteri (2009)</a>	Chimpanzees	<b>2A</b>	V	Extracting food from one device by tool method A vs B, from second device by sequence of A-X vs B-Y

Studies are listed alphabetically by first author name. 2A: two-action experimental designs in which different groups are seeded via one or more models displaying alternative forms of action in each group. **2A** in bold: behaviour of each group showed significant matching to whichever action option they had been exposed to. For study descriptions, see text. V: reward visible; x: reward not visible; -: not applicable in birdsong experiments; M: participants had already learned of reward availability in box; VM: participants had learned of reward hole before it was protected in test by a transparent cover, so still visible.

X versus Y in the respective outputs of members of their group. In this case, the matching resemblance to X or Y is clearly caused by whichever of the two options the experimental participants had observed.

Tennie, Hopper et al. (2020a) wrote that 'we know of no two-target test that, to date, has successfully tested apes' copying of traits beyond their ZLS' (p. 440). In what follows I therefore begin with such studies with apes, then turn to other two-action studies with species other than apes, and finally to experimental designs that contrast social learning with an individual learning condition.

Also marked in the table are those studies in which a desirable reward is visible to participants in the no-model condition. This is because in response to a study by Koops et al. (2022) that showed non-nut-cracking wild chimpanzees failing to nut-crack despite being supplied with the necessary raw materials, Tennie and Call (2023) argued that the test was not valid because chimpanzees did not eat the shelled nuts also provided, so were unlikely to be motivated to discover nut cracking (a reply to this in turn was offered by Koops, Arandjelovic et al., 2023; Koops, Biro et al., 2023). In the present table, rewards are recorded as having been visible (marked 'V'), with no-model control participants actively exploring means to obtain them, in six of the nine chimpanzee studies and (leaving aside the five birdsong studies where the question is not relevant) in four of the remaining 10 studies. In two other cases (marked 'M') individuals had already learned that motivating rewards were available, although hidden.

However, I urge that the cases where the task set-up is opaque with respect to the rewards obtainable should by no means be set aside. To the contrary, they are important because opacity with respect to rewards available, and what actions cause which functional outcomes, characterize much of the human cumulative culture that provides the theoretical framework for interest in these experiments. Henrich's (2015) volume on human CCE, for example, is replete with such examples. To take just one illustration, in his ethnographic work Henrich asked a Mapuche man why he took ash from burned wood and added it to a corn dish he was preparing, to be told only 'it's our custom' (p. 102). In other words, humans will frequently copy causally opaque actions like this, with unknown payoffs, which they would be unlikely to invent themselves, and our human predilection to do so is seen as particularly striking evidence for the power of cultural inheritance in our lives (Henrich, 2015). Similarly, many of the contexts in which wild chimpanzees use tools, and particularly where they use multitool toolsets, proposed to be the most likely instances of CCE (Boesch, 2012), are likewise inherently causally opaque. They are concerned with harvesting termites, ants and honey that do not become visible until a complex sequence of behaviours has been accomplished (Sanz et al., 2009) and these are far from the only kinds of animal behaviour to harvest resources that are initially hidden. Accordingly, the cases in Table 1 that incorporate opacity, and test whether social learning operates even in these circumstances, where individual learning fails, should be of interest in their own right.

## RESULTS

Table 1 lists 26 experimental findings in a variety of species, reported in 24 peer-reviewed journal articles and one PhD thesis. In what follows I briefly summarize the key findings of each, starting with studies on apes, since apes have been the core focus of presentations of the ZLS hypothesis and debates about its significance (Tennie et al., 2009; Tennie, Hopper et al., 2020; Tennie, Bandini et al., 2020; Whiten, 2022).

During the review and revision stages of this paper, two new studies were published that meet the criteria of Table 1, so they have been added (Bridges et al., 2024; van Leeuwen et al., 2024). A

further article links and comments on both these experiments and their significance (Thornton, 2024). These two experimental studies are distinctive in that unlike all the others in Table 1, they have been designed to test the ZLS hypothesis, based on a theoretical focus on the conditions for CCE in nonhuman species. Except for these new studies, the experiments in Table 1 were not designed to test the ZLS hypothesis: the model-present and model-absent conditions were simply included to test for social learning by measuring whether a novel behaviour was more successfully acquired by social than asocial learning. It just so happened that in the cases included here, learning in the asocial (no-model) condition turned out to be not merely less than in the social condition, but absent. Eleven of the studies were completed before 2009, so their authors were oblivious to the ZLS hypothesis which was first proposed that year.

### Ape Two-Action Experiments

#### Bonnie et al. (2007)

In the experimental phase of this study, each of two groups of chimpanzees was seeded with a model trained to place plastic tokens cast into their enclosure either into a hole in a lidded bucket, or instead into the top of a nearby pipe that slid them into another container. Either option was rewarded by an experimenter throwing food from an overlooking tower to any individual who posted one of 25 tokens provided, into either container.

In a prior baseline phase with no rewards given, one individual posted a token in the transparent bucket, after which two more looked into this bucket and each added a token. Both containers were then made opaque, after which no token was posted. In the experimental phase, once models began to post tokens in their assigned container and were rewarded for doing so, all nine chimpanzees who posted tokens in the group seeded with the 'bucket' model followed suit, whereas five of the six who posted in the group seeded with the 'pipe' did so, the exception being one of the chimpanzees who had posted in the bucket in the baseline phase, and who repeated this. The chimpanzees posting in the 'pipe' group thus learned to do this through observation, an action no chimpanzees did in the baseline control session.

#### Whiten et al. (2005)

Two groups of chimpanzees were seeded with models trained to use a stick tool in either of two different ways to free food rewards from behind a blockage in the upper of two pipes ('panpipes'): the tool either hooked a 'twig' on top of the blockage and pulled it up so the reward was released ('Lift') or entered the top pipe and pushed the blockage backwards so the reward fell into the bottom pipe and rolled out ('Poke'). Fifteen of the 16 chimpanzees in each group mastered the task, with a highly significant tendency to match the form of technique seeded in their group. By contrast, six chimpanzees exposed to the panpipes individually for 1 h and then as a group for 4.5 h failed to free any reward, although all repeatedly applied the stick tool to the device. Thus, chimpanzees could readily learn novel tool use techniques through social learning that their motivated peers failed to acquire by their own efforts.

#### Hopper et al. (2007)

This replicated the 2005 panpipes poke/lift study in a second research facility. Here, findings were different as one individual in the no-model control group discovered the Poke technique and it spread in her group. In the group seeded with Lift, the Lift technique likewise spread, significantly more commonly than in the other group, but Poke was also discovered and became the dominant approach. These effects were suggested to be related to the common use of probe sticks to obtain juice as enrichment in this

facility, although it is impossible to test and confirm that. Lift occurred just four times in the group that had no Lift model, apparently accidentally among chimpanzees proficient in the Poke technique, and it was not repeated, so was never ‘acquired’ other than after observing a Lift model. Following this finding, ‘ghost experiments’ were conducted to test whether chimpanzees would learn the Lift technique if they saw the blockage rise up and release the reward, or saw this done by the stick tool, but with no chimpanzee or other agent responsible. Of the 18 chimpanzees tested, none displayed ‘emulation’, recreating these outcomes; none performed the Lift action. The two panpipes lift/poke studies thus converged in demonstrating that chimpanzees could readily learn the Lift technique by observation of a skilled model, despite not acquiring it through individual learning, even having seen key movements of tool and panpipes blockage that released the reward.

#### Hopper et al. (2015)

To check that the ghost experiment results summarized above were not due to isolate testing, further chimpanzees were tested on the panpipes Lift option in a group context (19 in four small groups). None acquired the Lift technique in baseline control tests that permitted only individual learning, and the same was true following exposure to ghost controls, as found in the 2007 study. In a subsequent series of social learning contrasts hypothesized to be likely to offer escalating support to learning, individuals in two of the four groups began to acquire the Lift technique after observing a human demonstrator, others in a third group learned after further watching a chimpanzee model on video, and chimpanzees in the final group learned once a live chimpanzee model became available, with 14 of the 19 participants in the four groups successful in gaining rewards using Lift. Summing the results across the three main experimental phases, all 35 chimpanzees failed to acquire the Lift technique when limited to individual learning or ghost condition experiences, whereas 33 of 43 did so after witnessing a model perform the action.

#### Whiten et al. (2007), Spiteri (2009)

These reports described two experiments that used more challenging tasks than the panpipes lift/poke apparatus, requiring the participants to perform a sequence of two different actions, and also investigated whether these sequences would be transmitted from group to group. Two separate action sequences allowed successful performers to extract a food reward. In one (‘turn-ip’), either a large disk could be manually rotated until two holes aligned to allow the reward to drop, followed by pressing down a red lever to finally release the food, or instead a handle could be manipulated ratchet-fashion to turn the disk so that the holes aligned to let the reward drop, followed by sliding a yellow lever for final reward release. The other task (‘probe task’) could be solved by either opening a hatch on top and using a tool to stab food items and pull them out, or by raising a different hatch on the side and using a different tool slid into it to push food rewards out of a tunnel. Both devices are illustrated in Fig. A1. To test intergroup transmission, once half the group had mastered the task, irrespective of the techniques they had acquired, a second group was allowed to watch them, and similarly once half of them exposed to the task had mastered it, a third group could watch this second group; finally, the actions of this third group were recorded. The results of these two-action cultural transmission experiments were that, for both devices, the alternative options seeded in the first group diffused across the other two groups to become the dominant traditions (Whiten et al., 2007).

Turning to the control tests for individual learning, Whiten et al. (2007) reported that in 2 h baseline tests with each group prior to the cultural transmission experiment, in which they had seen food

items dropped into the test device, remaining visible, none of the 55 chimpanzees managed to extract a reward from either the turn-ip or probe task. This was despite the fact that most chimpanzees were motivated to manipulate both tasks (Table 2): note, for example, that many manipulated parts of the turn-ip, yet none discovered either of the two-step sequences of actions required to extract a reward. Compare the occurrence of the two-step sequences seeded in the model that began the cultural diffusion they became involved in, shown in the last two lines of the table.

In addition to these baseline control results, Spiteri (2009) described the results of parallel control conditions that Whiten et al. had not reported, since their focus was on the cultural transmission results. In these parallel control conditions, two groups of nine and 12 chimpanzees, respectively, were exposed to each baited device for 8 h, which appeared to exhaust their exploratory actions. None of these chimpanzees achieved any success, except for one chimpanzee who once did the necessary two steps but appeared not to recognize what was required for success and did not repeat the sequence. The sequence was thus ‘performed’ (once) but could not be described as having been ‘acquired’.

#### Ape Complex Sequence Learning with a Long Prior Individual Learning Period: van Leeuwen et al. (2024)

Chimpanzees in two enclosures in an African sanctuary were provided with a box containing visible nuts and small balls strewn

**Table 2**  
Summary results from experiments in Whiten et al. (2007) and Spiteri (2009)

	Group					
	B1	B2	B3	C1	C2	C3
Number of chimpanzees in group	8	8	11	10	8	10
<b>Baseline phase</b>						
Probe task						
Number manipulating task	7	4	6	6	7	6
<b>Number gaining reward</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>
Turn-ip task						
Number manipulating task	8	8	9	7	8	8
Number using ratchet	4	6	4	3	4	4
Number turning wheel	2	4	1	2	0	3
Number sliding yellow lever	6	6	8	5	5	4
Number pressing red lever	8	7	5	6	8	7
<b>Number gaining reward</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>
<b>Experimental phase</b>						
Probe task						
Number manipulating task	8	8	10	9	8	8
Number gaining reward	5	7	9	9	7	8
<b>Median open-top-stab actions</b>	<b>55</b>	<b>75</b>	<b>67</b>	<b>0</b>	<b>0</b>	<b>0</b>
<b>Median raise-hatch-slide actions</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>60</b>	<b>66</b>	<b>103</b>
Turn-ip task						
Number manipulating task	8	8	11	10	8	9
Number gaining reward	8	7	9	5	7	8
<b>Median ratchet then slide yellow lever</b>	<b>97</b>	<b>116</b>	<b>108</b>	<b>0</b>	<b>0</b>	<b>0</b>
<b>Median turn disk then press red lever</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>140</b>	<b>125</b>	<b>143</b>

Most chimpanzees manipulated both tasks in the Baseline phase and as illustrated for the turn-ip task, many explored and moved all four elements of the two-step series of actions needed to extract the food item (shown in Fig. A1). However, no chimpanzee was successful in performing two actions sequentially to gain the food reward. By contrast, after a single model was trained to either ratchet-and-slide in the turn-ip task in group B1 or turn-and-press in group C1, these solutions spread among observers in these groups and their neighbours, B1-2-3, C1-2-3 (last two lines of data) and 44 of the 55 chimpanzees in these groups (and of the 51 who manipulated the tasks) successfully gained food rewards. For the probe task, following the introduction of alternative models in B1 and C1, these likewise spread in the respective groups, with 45 chimpanzees now successfully gaining food rewards. Summary numbers in bold highlight the contrasts between the performances in asocial control conditions and the two, two-action experimental conditions. Groups labelled B4-6 in the original study have been changed for clarity here to C1-3.

among the vegetation. Gaining nuts from the box required a multistep sequence of collecting a ball, taking it to the box, opening a small drawer, dropping the ball in and closing the drawer. In a baseline no-model condition of 3 months, many chimpanzees expressed strong motivation to gain the nuts they could see inside the box, including collecting balls and hitting them on the box. However, none did the behavioural sequence required to gain nuts. A chimpanzee in each enclosure was then laboriously trained to complete the task and performed it in their enclosure. After observing this, 14 of 66 residents mastered the whole routine. This study stands out from the rest in the long duration of the baseline phase, which leaves little room for doubt that individual learning failed to generate the behaviour sequence required. This was not a two-action study, but social learning of the four-step action sequence provides compelling evidence that observers learned by copying what the trained experts knew how to do.

#### *Other Two-Action Experiments Demonstrating Matching to the Option Performed by the Model*

##### *Aplin et al. (2013)*

This study built on the celebrated earlier evidence for cultural diffusion of milk bottle top opening by tits across the U.K. (Fisher & Hinde, 1949). Aplin reported that over half of blue tits, *Cyanistes caeruleus*, in experimental groups seeded with models that either pierced a cover or flipped a lid to access a reward underneath gained rewards, whereas none of the 32 birds in four no-model control groups did so during a similar 4 h of exposure to the baited test boxes. There was a significant match between the technique that experimental birds were exposed to and the technique they went on to use. The task was challenging insofar as only 61% of birds exposed to piercing were successful, and only 36%, exposed to lid flipping were successful; nevertheless, these birds could learn a technique socially that none achieved when no model was available to learn from.

##### *Wild et al. (2021)*

Before this study, Aplin et al. (2015) had reported that wild great tits, *Parus major*, exposed to pairs of models that gained mealworms from a feeding device by either pushing a cover on its red side to the left, or on its blue side to the right, showed high fidelity in acquiring the alternative they were exposed to, continuing into a second season of testing. Some individuals in control populations with no model eventually mastered the task through individual learning. Building on this, Wild et al. (2021) introduced another two-action variant in which a small dial could be spun either clockwise or anticlockwise, and again found evidence of corresponding differential cultural spread (initiated in three groups by trained models and in one by an independent innovator). The experimenters then introduced a more complex task in which both pairs of options were in play, and a higher reward was obtainable for performing a sequence of both (e.g. slide left, dial right), while a smaller reward remained for a single action. No model was provided for this, but a small number of birds discovered the two-step solution, with 5.7% of birds eventually acquiring it in groups that had previously learned the slide-door and/or disk techniques. By contrast, no birds in a control group that was never seeded with either of the two actions in the sequence achieved a two-step solution of the complex task. But was it the case that some birds acquired the complex task that was apparently beyond individual learning, through social learning? The answer is somewhat complex in that social network analyses revealed slightly more support for asocial than social models; in other words, despite strong evidence for social learning of one-step techniques, birds tended to produce the full two-step approach by themselves, combining the one-step techniques they

had acquired. However, '13 birds were able to acquire the two-step solution without having produced either component, suggesting that a small percentage of birds were able to learn the two-step solution through observation alone' (p. 8). Accordingly, this contrasted with control birds, which were unable to do so through individual learning alone.

A similar contrast was demonstrated in a 'second complex generation' experiment in the following season, in which rewards were made available only for full two-step solutions, again with no trained models involved. Among populations that included 17 birds that knew two-step solutions, 14 new, naïve birds learned the full two-step solution. By contrast, no birds in a control group lacking knowledgeable models were able to do so.

##### *Kis et al. (2015)*

Bearded dragon lizards, *Pogona vitticeps*, were exposed to a conspecific model shown on a video screen, which used its head to nudge a wire-mesh door to either left or right, giving access to a dish containing a mealworm. In all cases observer participants' first response when given this choice matched whichever alternative they had been exposed to. In marked contrast, no control participants that saw a lizard in a central position and the door moving by itself (thus a 'ghost' scenario) learned to open the door. The authors concluded that 'A key difference between the control and the experimental groups was that, while a sliding head movement occurred in the case of all experimental subjects, it was never observed in the control subjects. As this was the movement that the demonstrator performed in order to open the sliding door, this suggests that experimental subjects copied an action that was not part of their spontaneous behavioural repertoire' (p. 329).

##### *Wilkinson et al. (2010)*

Red-footed tortoises, *Chelonoidis carbonaria*, that saw a conspecific progress around one side of a barrier to reach a food reward showed a significant tendency to match the side followed by the model; by contrast, no control tortoises lacking a model individually learned to negotiate the barrier. The model in this study only ever went to one side of the barrier, but it represents a two-action test insofar as observers could go to either side yet matched the side shown by the model.

#### *Two-Action Experiments Not Recording a Match to the Option Observed*

##### *Crast et al. (2010)*

This was a two-action study in which adult capuchins, *Sapajus capella*, obtained juice from a device that was selectively locked such that one group learned to press a lever, while capuchins in the second group turned a small wheel to elicit the flow of juice. Young capuchins could also enter an adjacent 'crèche' where juice could be obtained by either method from a similar device. Evidence was provided that the young capuchins socially learned how to obtain juice: 'Results from this study support the implications from field research that wild groups of capuchin monkeys can develop behavioural traditions that are maintained over time' (p. 962). Evidence for adherence to the adults' specific method of obtaining juice in an infant's group was more ambiguous. However, by contrast with the evidence for social learning, in baseline control tests in the crèches, there was no discovery of the lever method, and just one infant turned the wheel once, another one turned it twice, and they did not repeat these actions. Accordingly, they did not acquire the technique until they could learn along with adults.

*Picard et al. (2017)*

Each of two groups of orange-winged Amazonian parrots, *Amazona amazonica*, was seeded with a model that either pulled open a small door or slid the door to one side, to obtain food rewards inside. Ten conspecifics learned to open the door after exposure to these models, whereas none of 15 did so during nine 30 min control trials with no model; nor did a further 20 of a different species exposed to the box, without benefit of a model. Accordingly, some (10) birds were able to learn socially, whereas none did so through individual learning. However, there was no significant tendency for experimental birds to adopt the technique shown by their group model.

*Birdsong experiments, 1958–2020*

Table 1 includes five birdsong studies, beginning with the foundational experiments of Thorpe (1958), which demonstrated that chaffinches, *Fringilla coelebs*, reared in isolation from singing conspecifics did not acquire the typical three-part structure of songs produced by birds that were exposed to chaffinch song. Nottebohm (1968) replicated and extended these findings, reporting that chaffinches totally deprived of conspecific song early in life ‘produced a virtually structureless song’ containing only a single recognizable ‘chirrup’ element (p. 560). Supplementing this captive work, Mennill et al. (2018) showed that wild Savannah sparrows, *Passerculus sandwichensis*, would learn novel, simulated conspecific songs that no birds in prior generations sang.

All these birdsong studies are included here for two principal reasons. The first is simply that they meet the criteria of Table 1: the birds learned songs matching a (vocal) model that none produced in a no-model control (isolate) condition. Second, Tennie, Hopper et al. (2020) themselves accepted that these results are counter to the ZLS hypothesis, as the birds learned songs from models that, in the terms of Tennie et al., were beyond their ZLS, which was investigated in the isolate experiments. However, we should note the birdsong studies are different to all the others in one important respect. While all the other studies were focused on learning actions novel to the participants, and likely to the whole species (and so particularly relevant in relation to CCE), the birds with conspecific models learned songs characteristic of their species. I return to these issues in the Discussion.

A further complication is that Feher et al. (2009) reported similar results to Thorpe and Nottebohm for zebra finches, *Taeniopygia castanotis*, but also the intriguing finding that a diffusion chain of conspecifics, initially learning from the deficient songs of isolates, can eventually recreate a characteristic zebra finch song. This complicates the issue of what may be ‘latent’ in relation to social learning, and in the Discussion, I also return to this interesting discovery. Diez and MacDougall-Shackleton (2020) extended this work, contrasting the effects on 11 variables characterizing zebra finch song of exposure to wild-type songs, isolate conspecific songs or the heterospecific songs of Bengalese finches, *Lonchura striata domestica*. Accordingly, this can be regarded as a ‘two-options’ experiment in the realm of birdsong. Songs were found to converge on wild-type songs within one or two cultural generations in both the latter conditions, but less quickly for some aspects of heterospecific song. The authors reported that ‘both experimental lineages, isolate-tutored and heterospecific-tutored, from the first generation shifted towards wild-type song features at the song-bout level. However, at the song-motif level the shift took one extra generation in the heterospecific-tutored lineage compared to the isolate-tutored lineage. At the syllable level, it took two generations for both groups to shift towards the wild-type zebra finch song features. Therefore, the rates of cultural evolution differ across lineages and levels of song’. The authors concluded that ‘zebra

finches have a strong predisposition to imitate song elements with particular parameters’ (p. 262).

*Other Experiments, Lacking a Two-Action Design**Lefebvre (1986)*

In this pioneering field experiment, a novel behaviour of piercing covers to access food items diffused efficiently, through social learning, across flocks of both captive and feral pigeons. This was not a two-action design, but control conditions lacking a model showed that ‘trial-and-error learning and natural shaping can be ruled out as mechanisms of diffusion in the present case’ (p. 295).

*Stanley et al. (2008)*

The authors asserted that ‘this is the first study to show the social transmission of information too difficult to learn asocially, in fish’ (p. 571). The latter took the uncharacteristic form of behaviour in the two species tested (guppies, *Poecilia reticulata*, and southern platyfish, *Xiphophorus maculatus*), of swimming vertically up inside a tube to obtain a food reward. Diffusion chains seeded with a model gradually trained to do this showed clear evidence of cultural transmission through social learning, contrasting with individual control fish lacking a model. The authors concluded that ‘Both experiments provide evidence that information that is difficult for individual fish to learn asocially can readily be learned socially and can be transmitted along chains of individuals in a population of changing composition’ (p. 571).

*Alem et al. (2016)*

Each of three laboratory colonies of bumble bees, *Bombus terrestris*, were seeded with an individual that had been trained, stepwise, to pull a string that dragged an artificial flower from beneath a Plexiglas cover, making a food reward available. Other bees observing this were able to acquire the skill, some going on to act as models for others, such that the behaviour diffused over as many as four such cultural transmission steps. By contrast, ‘none of the bees from eight colonies in which individuals were tested singly ( $n = 291$ ) could solve the string-pulling task on their first 5-min attempt. Naïve to the string task but attracted to the artificial flowers, these bees tried to reach the reward from the top of the table through the Plexiglas cover’ (p. 11). In three control colonies in which, as for the model-seeded colonies, pairs of bees were observed across 1505 min foraging bouts in the arena, no bees acquired string pulling. This was in marked contrast to the cultural diffusion that occurred in the model-seeded colonies.

*Voelkl and Huber (2007)*

In an earlier study (Voelkl and Huber, 2000), the authors had reported that while marmosets, *Callithrix jacchus*, in a no-model control condition tended to use their hands to prise a cap off a canister to access the food inside (only two of 11 used their mouths), others that witnessed a model using their mouth tended to do the same, leading the authors to include ‘true imitation’ in their study title. In the 2007 paper, uniquely, these authors conducted a detailed, frame-by-frame analysis comparing the topography of an unusual mouth technique displayed by a trained model with the later actions of observers of the model and nonobservers which used an oral technique. Based on discriminant analysis scores, 13 of the 14 observers were classed as matching the model’s action topography, but none of the nonobservers did so. The authors concluded that ‘the high matching degree suggests that marmosets possess the neuronal mechanism to code the actions of others and to map them onto their own motor repertoire, rather than priming existing motor-templates’ (p. e611).

### *Marshall-Pescini and Whiten (2008)*

In this study, social learning by young chimpanzees witnessing a model proficient in nut cracking using a stone hammer was contrasted with no-model control conditions. First, all but one youngster exposed to the model learned to nut-crack, whereas none in a parallel no-model control condition did so. This was then treated as a baseline control condition, as these, as well as the original experimental participants, were further exposed to the model's nut cracking. In this phase all acquired nut cracking, with those exposed in the first phase of the experiment becoming more proficient and cracking nuts at a higher frequency.

### *Koops et al. (2022)*

Complementing the study above, Koops et al. provided a non-nut-cracking subpopulation of chimpanzees in Guinea, living close to some of the nut-cracking communities common across West Africa, with clusters of two appropriate species of nuts, hammer stones and already cracked nuts, echoing the affordances experienced by young chimpanzees in nut-cracking communities. This is the first and only study to test for innovation of a cultural behaviour in wild primates, and the only one of the studies in [Table 1](#) to explicitly test the ZLS hypothesis. Thirty-five parties of chimpanzees visited the samples and members of 11 of these investigated them: they 'closely explored the experimental items' (p. 489) in 19 of 99 visits, including sniffing or touching them, but no attempts at nut cracking were made. This contrasts with the routine acquisition of nut cracking in numerous nut-cracking communities in West Africa ([Carvalho & McGrew, 2010](#)) as well as the findings of the experimental study of [Marshall-Pescini and Whiten \(2008\)](#) and others (lacking a no-model control condition) reviewed therein.

In a critique of this study, [Tennie and Call \(2023\)](#) argued that because the chimpanzees ate no nuts, the ZLS hypothesis was not truly tested. [Koops, Arandjelovic et al. \(2023\)](#), [Koops, Biro et al. \(2023\)](#) replied that Tennie and Call defined latent solutions as 'behavioral and/or artefact forms whose underlying know-how can be *spontaneously innovated* [italics added] by ecologically relevant individuals ... in the absence of cultural access' (p. 89) and noted that in their nut-cracking study, this did not occur. There is not the space here to summarize further critiques and the multiple counterarguments delivered in this exchange.

### *Bridges et al. (2024)*

For a bumble bee to gain a reward of sugar solution it had to complete a two-step procedure. The second step required the bee to push a small barrier until it revealed access to sweet liquid to drink. Before this could be done, a first barrier had to be pushed away to the side to allow the second barrier to be moved. In control conditions of up to 24 days (involving 72 h of exposure) no bee performed this sequence. This experiment thus comes closest to the 'lifetime' of opportunities envisaged in ZLS theory, because a bumble bee's foraging life is only about 8 days ([Thornton, 2024](#)). After laborious training of model bees to complete the required two-step sequence, five bees exposed to them learned the sequence, which none had done in the no-model condition. They learned to do so by following the knowledgeable bees performing each act of the sequence in turn, and thus acquired a successful action sequence matching that of the model they had followed.

## DISCUSSION

### *Birdsong*

I first discuss the birdsong research because it is arguably a special case in relation to the controversies at stake in this review,

for several reasons. One, as noted earlier, is that [Tennie, Hopper et al. \(2020, p. 446\)](#) are prepared to accept the results of birdsong experiments such as those summarized above as special cases of failing to conform with the ZLS hypothesis, saying that 'one animal culture domain in which the main tenet of the ZLS account is not (always) applicable is vocal culture ... some animal vocalizations are most likely (at least partly) copied (e.g. in some cetaceans and birds) and have led to CDTs (e.g. there is little chance that a specific humpback whale song will ever be spontaneously innovated in the same form by another naïve whale ([Garland et al., 2011](#); see also [Tennie, Caldwell and Dean, 2018](#))' (CDT stands for 'culturally dependent trait': a behaviour that can emerge only if culturally acquired). That this is true for humpback whale song has, unsurprisingly, yet to be experimentally confirmed, but this has been done rigorously in vocal isolation studies with songbirds, notably those reviewed above.

Two key findings that all this rests on both merit discussion: first, that certain songs cannot be learned without a model; and second, that these same songs can be learned from a model. With respect to the latter social learning aspect, there is a major contrast with other cases in [Table 1](#): these all concern the learning of novel behaviours that are new to the species, whereas the birdsong studies reviewed are about learning behaviour, 'wild-type song', that, to the contrary, is normally characteristic of the species. However, there is also experimental evidence for songbirds learning aspects of the songs of other species, such as zebra finches acquiring from strawberry finch, *Amandava amandava*, tutors some of their unusually high-pitched songs, which zebra finches do not otherwise produce ([Price, 1970](#)). This is arguably more equivalent to the learning of elements new to the species in the other kinds of studies in [Table 1](#).

Another consideration in interpreting the birdsong experiments in relation to the ZLS hypothesis is that vocal learning has long been interpreted as being cognitively 'easier' than in the domain of manipulation. According to [Heyes \(2023\)](#) 'Vocal imitation, which is said to occur when birds, cetaceans, and humans copy elements and sequences of speech and songs (but see [Byrne & Russon, 1998](#)), is not thought to be a sign of cognitive complexity because it does not pose the correspondence problem. I hear similar things when I listen to your vocalisation and when I produce the same vocalisation myself. Therefore, I could copy a sound you make by simple trial-and-error, varying my vocal output until it matches my memory of the sounds you made' (p. 45). This can be contrasted with copying a manipulative task, requiring a transformation from seeing the other's action to performing it from one's own perspective (contemplate copying how someone else ties their shoelaces, or other knots). Another way to portray this contrast is to interpret the perceptual requirements for vocalizations as representable in two dimensions (as in a two-dimensional spectrograph) whereas manipulations are inherently three-dimensional. If this is true, it might be inherently 'easier' for an animal to copy vocalizations it cannot generate itself, than to copy manipulations it cannot generate itself, and the latter have been the main focus of debates about the ZLS hypothesis.

Turning to lack of individual learning, the startling results of experiments such as those of [Feher et al. \(2009\)](#) and [Diez and MacDougall-Shackelton \(2020\)](#) suggest that the appearance of wild-type song in transmission chains that began with only the impoverished songs of isolate birds could, ironically, perhaps, given the statement of Tennie et al. cited above, be interpreted as implying that wild-type song must in some sense be 'latent' in the species. Nevertheless, these phenomena do not fit the ZLS hypothesis because of the results of the experiments confirming the songs are not generated by isolated individuals, and indeed the acceptance by [Tennie et al. \(2020a\)](#) of these as refutation of the



hypothesis. It might be argued that the ensemble of a Feher et al. transmission chain ‘as a whole’ is consistent with the ZLS hypothesis, but I suggest that this merely obfuscates the inherent and challenging complexity of the innate and learned influences that unfold in these studies. Instead, the results of Feher et al., and replications of the effect they reported, indicate intricate interactions between what is innate and what is socially learned, which remain to be empirically dissected and explained.

#### *Does the Corpus of Studies in Table 1 Refute the ZLS Hypothesis?*

All the studies in Table 1 have been included because they demonstrate acquisition via social learning of some behaviour that is not acquired in a corresponding no-model control condition. However, Tennie, Hopper et al. (2020), Tennie, Bandini et al. (2020) are at pains to emphasize that the ZLS hypothesis is focused not on social learning per se, but on what they call ‘form-copying’ observational learning: that is, acquiring the spatiotemporal form of the behaviour of a model. Accordingly, the hypothesis is to be empirically tested by checking experimentally for learning in the species concerned that (as quoted in my introduction) displays ‘a measurably matched resemblance between the specific form of input A to the specific form of output B, where this matched resemblance between A and B is and must be, at least in part, causally due to the specific form of the input’. All the experiments in Table 1 meet this criterion of demonstrating social acquisition of behaviour that matches the behaviour of the model witnessed, but they vary in their power to demonstrate that a significant match depends causally on the form of behaviour witnessed. I submit that, logically, the strongest evidence for this will be obtainable through the two-action designs marked ‘2A’ in the table, because these test whether the spatiotemporal form of a behaviour in learners matches whichever of the two different forms of model behaviour they were exposed to, above chance levels. This occurred in the 10 cases marked ‘2A’ in bold in the table, spanning mammalian, avian and reptilian examples. These accordingly challenge the ZLS hypothesis for the species and contexts concerned.

Tennie, Bandini et al. (2020) object to this interpretation of the findings of two-action tests in apes, because ‘the tasks are typically grounded in demonstrated action techniques as well as differences in physical techniques’ (p. 55). But the logic of this objection is unclear, because actions, tool movements and the movements of objects by actions all have variable forms that can be copied, and thus can meet the criterion of matching the witnessed form of what a model did in the relevant part of a two-action experiment (Whiten, 2002; Whiten et al., 2009). Tennie, Hopper et al. (2020) themselves describe ‘copying observational learning’ as ‘the transmission of the form of a behavior or artifact (or artifact production)’ (p. 429: my italics), which presumably count as ‘physical techniques’.

In addition to making ‘form-copying observational learning’ (contrasting with other kinds of observational learning) the focus of the ZLS hypothesis, Tennie, Hopper et al. (2020), Tennie, Bandini et al. (2020) employ what they see as a related contrast between social learning of ‘know-how’ and alternatives such as learning ‘what’, ‘where’ or ‘that’. The ZLS hypothesis expressed in these terms is thus that only humans can, through observation, learn know-how from others that they could not acquire by their own efforts. Adopting this terminology, the ZLS hypothesis again appears to be refuted by the cases marked ‘2A’ in Table 1, because the alternative options represent different ‘know-hows’. For example, in the panpipes experiment (Whiten et al., 2005), chimpanzees acquired the know-how to apply either the Lift technique or the Poke technique; in Aplin et al. (2013), the birds adopted the know-

how to either flip or pierce lids, and so on for the other two-action studies.

Just what information is processed to shape the local know-how acquired is a further empirical question: in principle it could include any mix of the varied kinds of social learning distinguished in the literature, such as bodily imitation, emulation of results of actions and/or local enhancement (Whiten et al., 2009; Hoppitt & Laland, 2013). The bees in the experiment of Bridges et al. (2024), for example, acquired their matching copy of what the model did by simply following the model as they completed the task and thus learning the sequence of behaviour required. Tennie and colleagues offer no suggestions for how experiments that aim to test their hypothesis, like those in Table 1, could evaluate form copying, or copying of ‘know-how’, in any way superior to two-action designs. Operational criteria for identifying form-copying and copying of know-how, and distinguishing them from alternatives, are essential.

Birdsong studies aside, the six experiments in Table 1 that do not rest on two-action designs can claim to demonstrate copying of form in a different way, which hinges on the complexity and novelty of the form of action copied, for the species concerned. In Stanley et al. (2008), for example, fish acquired the behaviour, very novel for them, of swimming vertically up into a tube. A check on such novelty of form is provided by the no-model control conditions, given the behaviour fails to occur there (Hopper et al., 2015; Lefebvre, 1986; Marshall-Pescini and Whiten, 2008). Structural complexity is what appears to make the two most recent experiments compelling cases. The bumble bee experiment of Bridges et al. (2024) required a sequence of two steps and the chimpanzee experiment of van Leeuwen et al. (2024) required a sequence of four steps, which in both studies could be acquired only by social learning. The same was true for multistep sequences of actions in the two experiments of Whiten et al. (2007). Van Leeuwen et al. conclude that in their experiment ‘the chimpanzees used social learning to acquire a skill that seems beyond their zone of latent solution and thus that chimpanzees can master copying-dependent forms. This suggests that chimpanzees use know-how copying to expand their skill-set, which has been argued to form an important mechanism underlying the ensuing of CCE’ (p. 7). Note that Call, one of the architects of the ZLS hypothesis (Tennie et al., 2009), is one of the co-authors endorsing this conclusion in the 2024 report.

#### *Studies in Table 1 Vary in Meeting the Criteria Required to Refute the ZLS Hypothesis*

Aside from the birdsong studies, most of the experiments in Table 1 demonstrate copying of alternative options through two-action designs, coupled with evidence that there is no learning in no-model control conditions. Some of these studies are weaker on one or other of these criteria for refutation of the ZLS hypothesis. Taking the social learning side first, Crast et al. (2010) demonstrated a social learning effect in the young capuchins studied, but there was no significant matching to the action option they had been exposed to. Picard et al. (2017) reported a similar result in their two-action study with parrots. More generally, the evidence for copying the form of the model’s behaviour in those studies that lack a two-action design hinges on judging how novel the actions are in the species concerned, although lack of learning in the no-model condition supports this.

Turning to the evidence concerning a failure to learn without a model, Bonnie et al. (2007) noted that in baseline tests with transparent containers, three chimpanzees posted tokens in one of them (a bucket), although this ended once the containers were made opaque, and there was no performance of the more unusual

alternative option of posting the tokens down a pipe. Alem et al. (2016) reported that hundreds of bees in their control, no-model tests failed to perform string pulling, but they also reported some extended tests in which two naïve bees managed to succeed. The authors noted that ‘These two bees were exceptionally explorative, trying a wide variety of methods, and solved the task in several attempts by moving the string accidentally while trying to reach the flower under the table’ (p. 5). This finding leads us directly onto the final but important topic for discussion.

#### *Studies Recording Rare Successes in the No-Model Condition are Instructive*

From the perspective of the conception advocated in Fig. 1, cultural transmission experiments that report evidence of rare inventions of the behaviour of interest in no-model control conditions, dismissed as within-ZLS by proponents of the ZLS hypothesis (Tennie, Hopper et al., 2020; Tennie, Bandini et al., 2020), instead become of particular interest. For example, commenting on the two inventors of string pulling noted above in the bumble bee study, Alem et al. (2016) wrote that ‘string pulling can be learned individually by some bumblebees, but this may be an exceptionally rare ability. Across experiments, 291 naïve individuals were tested once, and a total 110 were tested twice, but no further ‘innovators’ were found. In one experiment, bees were given extensive opportunities. After 5 days of foraging, with a maximum number of 18 foraging bouts per individual, no single bee learned to pull the string. Of the 165 bees tested in this experiment in total, nine individuals were tested more than 10 times, and 26 more than 5 times, but all were invariably unsuccessful. Thus, solving a string-pulling task spontaneously is a relatively rare occurrence in bumblebees (p. 5). Yet we know from the transmission experiments that if a hive comes to contain such a special bee, the skill will diffuse widely. Contra the ZLS thinking, this does not mean that string pulling is latent in all bees: instead, a rare few can achieve it individually and all the rest can learn the skill by observing them, consistent with the Culture Zone envisaged in Fig. 1, and with a variety of studies tracing cultural diffusion from initially rare innovations, such as in the sweet potato washing and other foraging techniques of Japanese monkeys, *Macaca fuscata*, invented by the juvenile, Imo (Kawai, 1965), and other cases in humpback whales (Allen et al., 2013) and cockatoos, *Cacatua galerita* (Klump et al., 2021).

These considerations are relevant to a deeper debate over the interpretation of chimpanzee experiments. Tennie, Hopper et al. (2020) acknowledged that in Whiten et al. (2005) no chimpanzee extracted rewards from the panpipes if they lacked a model to learn from, but once most of each group had adopted the technique seeded in their group, some discovered the alternative method. Tennie et al. interpreted this as meaning ‘that the demonstrated technique forms do not causally require copying social learning, as they can be individually learnt’ (Tennie, Bandini et al., 2020, p. 55). These authors proposed that these actions are thus within chimpanzees’ ZLS, consistent with their hypothesis. I submit that this neglects that (1) the control tests showed that the techniques could not be individually learned from scratch and (2) the occurrence of culturally nonmatching behaviour was rare, occurring in less than 1% of actions (and it appeared accidental), so that as argued further above, generalization to the species as a whole is not valid. Moreover, in the case of the more challenging two-step techniques reported in Whiten et al. (2007) and Spiteri (2009), just two individuals in the trio of groups originally seeded with ratchet-and-slide in the turn-ip task discovered the alternative turn-and-press technique (but overwhelmingly stuck to performing ratchet-and-slide) and none of the 27 individuals who had not witnessed turn-and-press in others acquired the technique. Including the

similar outcomes in the baseline and long exposure tests, this means the turn-and-press, two-step technique did not appear spontaneously in 77 chimpanzees. Nevertheless, the behaviour spread across 25 chimpanzees in the three groups seeded with a model expert in the technique, contrary to the ZLS hypothesis. This squares with the results of the chimpanzee study of van Leeuwen et al. (2024).

#### *Conclusions*

Taken together, findings of papers scattered in the research literature, here collated in Table 1, indicate that animals from diverse species can readily learn behaviours matching a model that they (or conspecifics in parallel control conditions) fail to acquire if limited to individual learning only. This capacity is thus not unique to humans (see also Thornton, 2024), and these findings are counter to the ZLS hypothesis. I suggest that these conclusions are consistent with numerous results from the wider literature in animal social learning in which limited success at the task at stake also occurs in no-model tests. In these, it is also a common finding that social learning of novel behaviour is more effective than individual learning (e.g. Voelkl & Huber, 2000; Huber et al., 2001; for reviews see Galef & Laland, 2005; Galef & Whiten, 2017; Whiten & Mesoudi, 2008). Such studies will not meet the criteria for Table 1, but they are in line with the Culture Zone envisaged in Fig. 1, and from this perspective contribute findings no less important for the field of animal social learning and culture. Those studies that do merit a place in Table 1 stand in direct refutation of the ZLS hypothesis, both in respect of chimpanzees, which proponents of the hypothesis have focused on, and a diverse array of other, nonprimate species.

#### *Author Contributions*

**Andrew Whiten:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Data curation, Conceptualization.

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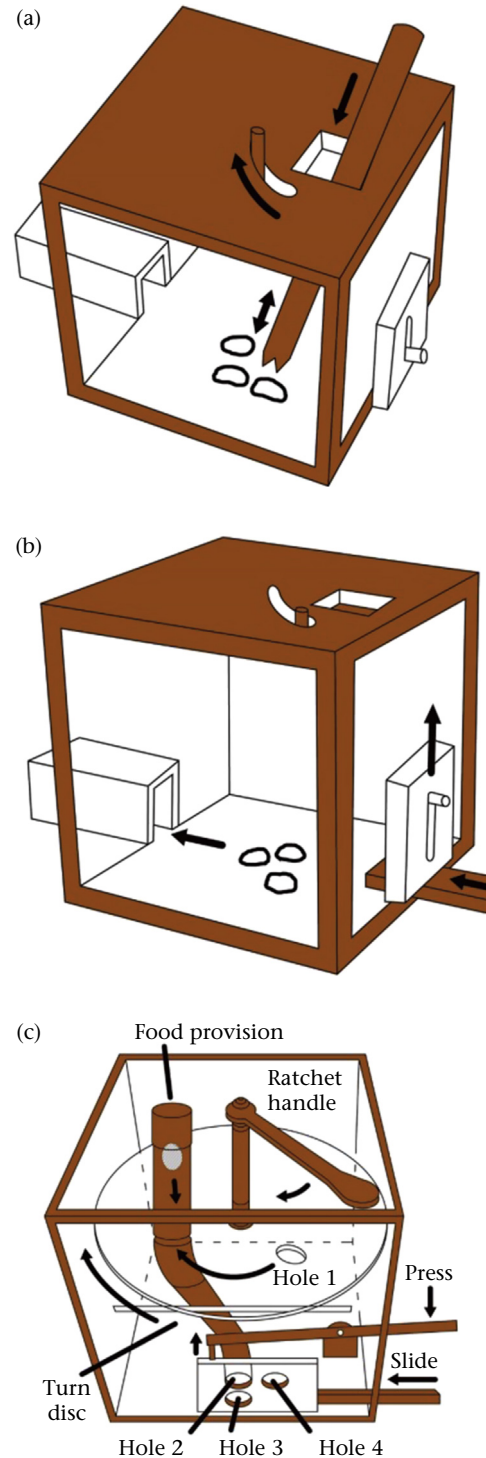
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## Appendix



**Figure A1.** Alternative solutions for gaining food items from the probe task and turn-ip task (after Whiten et al., 2007). (a) Pushing a stub on top of the probe task box opens a hole through which a stick tool can be inserted to stab food items such as grapes or dates. (b) Alternatively, a hatch on the side of the box can be raised, and a flat, ruler-like tool inserted to push the food items into a tunnel from which they fall onto a sloping ramp (not shown) that delivers them to the chimpanzee. (c) To allow food items dropped into the pipe to pass further down in the turn-ip task, the disc must be rotated so Hole 1 aligns with the pipe. This can be achieved either by manually turning the part of the disc that protrudes, or repeatedly operating a ratchet handle on top of the box. The food item can then be released by either pressing a lever (handle marked in red in the study) so Hole 3 aligns with Hole 2 or sliding an alternative lever (handle marked yellow in the study) so Hole 4 aligns with Hole 2.