



# From whom do animals learn? A meta-analysis on model-based social learning

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## Abstract

Social learning via the observation of or interaction with other individuals can allow animals to obtain information about the local environment. Once social information is obtained, animals may or may not act on and use this information. Animals may learn from others selectively based on particular characteristics (e.g., familiarity, age, dominance) of the information provider, which is thought to maximize the benefits of social learning. Biases to copy certain individuals over others plays an important role in how information is transmitted and used among individuals, and can influence the emergence of group-level behaviors (i.e., traditions). Two underlying factors can affect from whom animals learn: the population social dynamics – with whom you associate (e.g., familiar), and status of the demonstrator (e.g., dominant). We systematically surveyed the literature and conducted a meta-analysis to test whether demonstrator characteristics consistently influence social learning, and if social dynamics strategies differ from status strategies in their influence on social learning. We extracted effect sizes from papers that used an observer-demonstrator paradigm to test if the characteristics of the individual providing social information (i.e., the demonstrator) influence social information use by observers. We obtained 139 effect sizes on 33 species from 54 experiments. First, we found an effect of experimental design on the influence of demonstrator characteristics on social learning: between-subject designs had stronger effects compared to within-subject designs. Second, we found that demonstrator characteristics do indeed influence social learning. Characteristics based on social dynamics and characteristics based on status had a significant effect on social learning, especially when copying familiar and kin demonstrators. These results highlight the role that demonstrator characteristics play on social learning, which can have implications for the formation and establishment of behavioural traditions in animals.

**Keywords** Biased social learning · Decision making · Model-based social learning · Social information use · Social learning strategies

## Introduction

Acquiring information about the local environment is fundamental for animals to survive and thrive. Information about the local environment can be acquired from observing or interacting with other individuals, or with the products of their behaviour (i.e., social information; Heyes, 1994; Mesoudi et al., 2016). Learning that is influenced by social information is defined as social learning (Heyes, 1994). Social learning occurs across a wide range of species (Hoppitt & Laland, 2013), and across different behavioural

contexts and sensory domains (e.g., visual, auditory). For example, learning what food is safe to eat from observing a conspecific eating a novel food (e.g., Galef & Whiskin, 2004; Guillette & Healy, 2014), learning about suitable egg-laying substrates from observing the choice of other females (e.g., Sarin & Dukas, 2009), or learning the local vocal repertoire from listening to the vocalizations of adults (e.g., Garland & McGregor, 2020). Over the last century, social learning was widely assumed to be inherently beneficial, as it allowed animals to acquire adaptive information while avoiding or reducing the costs of trial-and-error (i.e., asocial) learning (Hoppitt & Laland, 2013). Examples of these costs include time and energy as well as increased predation risk (Kendal et al., 2005; Rendell et al., 2011). However, it is now widely acknowledged that socially learned information comes with potential costs, for example the social information could be

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outdated or wrong (Hoppitt & Laland, 2013). Theoretical work suggests that indiscriminately relying on social learning is maladaptive and that animals should use social information selectively (Boyd & Richerson, 1985; Kendal et al., 2018; Laland, 2004; Rendell et al., 2011; Whiten, 2021a). This selectivity in social learning could be achieved via the implementation of rules (i.e., heuristics) shaped by natural selection that specify under which contexts animals copy the behaviour of others (Boyd & Richerson, 1985; Hoppitt & Laland, 2013; Kendal et al., 2018; Laland, 2004).

These sets of heuristics, sometimes referred to as ‘transmission biases’, are also known as ‘social learning strategies’ (Hoppitt & Laland, 2013). Laland (2004) separated social learning strategies into two broad categories: (i) *when* and (ii) *who strategies*. *When strategies* specify the circumstances under which animals should use social information, for example in situations where asocial learning is costly (Davies & Welbergen, 2009) or when an individual lacks relevant information (Guillette et al., 2016). *Who strategies* specify from whom animals should learn when they are exposed to social information (Boyd & Richerson, 1985; Coussi-Korbel & Fragaszy, 1995). For example, *who strategies* include copying successful (Sarin & Dukas, 2009) or familiar (Swaney et al., 2001) individuals. Here, copying others’ behaviour is equated with using social information. In this meta-analysis, we also employ the term ‘copy’ as synonym for social information use, to mirror how theory presents the different social learning strategies (e.g., *copy when asocial is costly, copy familiar*). However, it must be mentioned that social information use is not limited to copying others as avoiding the behaviour/option demonstrated by another individual (rather than being indifferent) is also evidence of using social information (Guillette & Healy, 2014).

Investigating these social learning strategies has become key for understanding how animals can optimize the benefits of social learning amidst the costs involved in copying others (Rendell et al., 2011). Moreover, synthesizing the body of empirical research on these functional heuristics that underlie social information use is also key for understanding the dynamics of cultural evolution as social learning strategies underlie the transmission and maintenance of behavioural traditions in populations (Kendal et al., 2018; Whiten, 2017, 2021a, 2021b).

### Who strategies of social learning

*Who strategies* of social learning state that the characteristics of the individual providing the information (called the demonstrator hereafter) influence the use of social information by the learner (called the observer hereafter). Both human and non-human animals are selective regarding whom to copy (e.g., friends, relatives, successful individuals; Flynn & Whiten, 2012; Henrich & Broesch, 2011; Wood et al.,

2012), and these social learning biases can vary according to an individual’s life stage (Ehmann et al., 2021; Whiten & van de Waal, 2018). According to social learning theory, the selective copying based on demonstrator characteristics can maximize the benefit of social learning because certain individuals in the population provide more relevant or beneficial information than others. Therefore, these strategies allow animals to acquire the most useful information while avoiding the costs of assessing the payoff of several other individuals’ behaviour (Coelho et al., 2015; Laland, 2004; Seppänen et al., 2011; Swaney et al., 2001). Biases to copy certain individuals over others are proposed to play an important role in how social information is transferred among individuals, with important consequences for the emergence of group-level behaviours, including traditions and animal culture (Bono et al., 2018; Kendal et al., 2018; Laland & Janik, 2006). For example, models suggest that unbiased, random copying is not helpful at establishing useful/adaptive behavioural traits in a population, while biases that influence individuals to copy specific demonstrators according to their characteristics lead to more rapid establishment of a beneficial behavioural trait over generations (Rendell et al., 2011).

In this article, we divide *who strategies* into two categories based on the proposed underlying mechanisms that determine why copying social information provided by one type of demonstrator would be more beneficial than copying others. Here, we call these categories of *who strategies* (i) social dynamics and (ii) status strategies.

*Social dynamics* strategies predict that copying certain individuals should be favoured based on the pre-existing relationship between the observer and the demonstrator. More specifically, the influence of a demonstrator will increase when that demonstrator is an individual that the observer knows or with whom they share a bond, for example kinship (i.e., a genetic bond) or a pair bond (i.e., a social bond). Copying a known demonstrator or a demonstrator with whom the observer shares a bond should be favoured by natural selection since these kinds of demonstrators are more likely to live in the same or more similar environments as the observer compared to unknown individuals, thus rendering the information provided by known demonstrators more relevant than information provided by unknown demonstrators (Coussi-Korbel & Fragaszy, 1995; Hoppitt & Laland, 2013; Laland, 2004). Nest-building zebra finches (*Taeniopygia guttata*), for example, copy the material choices demonstrated by another bird only when the demonstrator is a familiar individual (Guillette et al., 2016). Guppies (*Poecilia reticulata*) learn the route to a food source more effectively from familiar rather than unfamiliar demonstrators (Swaney et al., 2001). Mongolian gerbils (*Merriomes unguates*) copy the food choices of demonstrators that are kin over the food choices of demonstrators that are not (Valsecchi et al.,

1996). In humans, children trust the information provided by a familiar teacher over the information provided by an unfamiliar teacher (Corriveau & Harris, 2009). However, contrary to what would be predicted by theory, the frugivorous Peter's tent-making bat (*Uroderma bilobatum*) was found to copy the food choices from unfamiliar demonstrators over those from familiar demonstrators (Ramakers et al., 2016). Another case of copying unfamiliar individuals was found in zebra finches, who were experimentally exposed to developmental stress. These stressed individuals preferred to forage with and copy non-kin individuals instead of their parents (Farine et al., 2015).

*Status strategies* predict that copying high status or successful individuals should be favoured since the behaviour of successful individuals in a population theoretically yields better payoffs than the behaviour of unsuccessful individuals. These demonstrator biases represent a 'shortcut' towards copying successful behaviour, under the assumption that certain types of individuals (e.g., old, dominant, large) have acquired these characteristics or states because they have been able to accumulate more resources than others. Characteristics of an individual that could be used as cues about the status of that demonstrator include age, dominance rank, body size and other cues of individual success like mating status, reproductive output or foraging proficiency. Fruit flies (*Drosophila melanogaster*), for example, copy the egg-laying substrate of mated over virgin flies, where the mating status of the fly served as cue for the level of success of the demonstrator (Sarin & Dukas, 2009). Another status strategy was found in nine-spined sticklebacks (*Pungitius pungitius*), which copy the foraging path of larger over smaller demonstrators (Duffy et al., 2009). Humans also follow status strategies: children copy adults over same-age peers when learning a skill, thus providing evidence for a strategy to copy older demonstrators (Wood et al., 2012). In Norway rats (*Rattus norvegicus*), however, juveniles equally copied the food choices of adult and juvenile demonstrators (Galef & Whiskin, 2004). Note that in these examples, animals are copying others based on a status cue (e.g., mated vs. virgin females) and not on the success of the behaviour (e.g., selecting a substrate to lay eggs). Copying others based on the success of the demonstrator behaviour would consist of a payoff bias instead of a demonstrator bias. For example, male vervet monkeys (*Chlorocebus pygerythrus*) were found to copy the side of a puzzle box that male demonstrators opened over the side that female demonstrators opened only when the payoff obtained by male demonstrators was higher (five pieces of apple) than the payoff obtained by female demonstrators (one piece of apple; Bono et al., 2018). Although not mutually exclusive, a payoff bias could be harder to implement compared to a demonstrator bias as animals would be required to evaluate the value of a behavioural outcome and keep track of these outcomes

for multiple individuals in their population, which may be cognitively demanding (Bono et al., 2018).

Most of the examples in the two preceding paragraphs provide empirical evidence supporting the theory of social learning strategies that states that animals should be selective with regards to whom they copy. Despite the strong link between theory and empirical work that has characterized the study of social learning strategies, no effort has been made to synthesize these findings and determine the effect that demonstrators' characteristics play on social learning nor which of the *who strategies* (e.g., *copy kin* or *copy older*) have a significant effect on social learning.

## Objectives

In the present meta-analysis, we aimed to systematically examine if and how demonstrator characteristics influence social learning, and whether this influence is consistent across species, sexes, developmental stages, behavioural contexts (e.g., foraging, reproduction) and type of *who strategy* (e.g., different types of social dynamics and different types of status strategies, discussed below). Although other meta-analyses on social learning exist, these meta-analyses examine the factors that influence social learning in specific contexts like foraging (Penndorf & Aplin, 2020) and mate-copying (Davies et al., 2020; Jones & DuVal, 2019). None of these previous meta-analyses, however, examine the influence of demonstrator characteristics on social learning, which comprises a key aspect of social learning theory (Hoppitt & Laland, 2013). Biases to copy certain types of demonstrators can influence the way information is transmitted within a group of animals and, thus, may be the basis of the formation and establishment of behavioural traditions (Rendell et al., 2011; Whiten, 2021b). Therefore, it is essential to synthesize and evaluate the existing empirical evidence on *who strategies* of social learning in order to better understand the processes that shape social information use in animals.

We conducted a systematic literature search and meta-analysis in order to examine how demonstrator characteristics influence social learning. We did so by following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Moher et al., 2009) and extracting the effect sizes from experimental papers that used an *observer-demonstrator paradigm* (described below) to test how the characteristics of the demonstrator influenced social information use by the observer. We did not include experiments that tested demonstrator bias in the vocal learning context since vocal learning is considered a highly specialized type of social learning that involves behavioural, neuronal and anatomical specializations, as well as a sensitive period (for close-ended vocal learners; Brenowitz & Beecher, 2005; Shettleworth, 2010). We aimed to answer

the following questions: (i) Do demonstrator characteristics, in general, influence social information use as predicted by the social learning strategies theory? (ii) Do social dynamics strategies differ from status strategies in their influence on social information use? (iii) Which specific strategies (e.g., copy kin, copy older) influence social information use?

## Methods

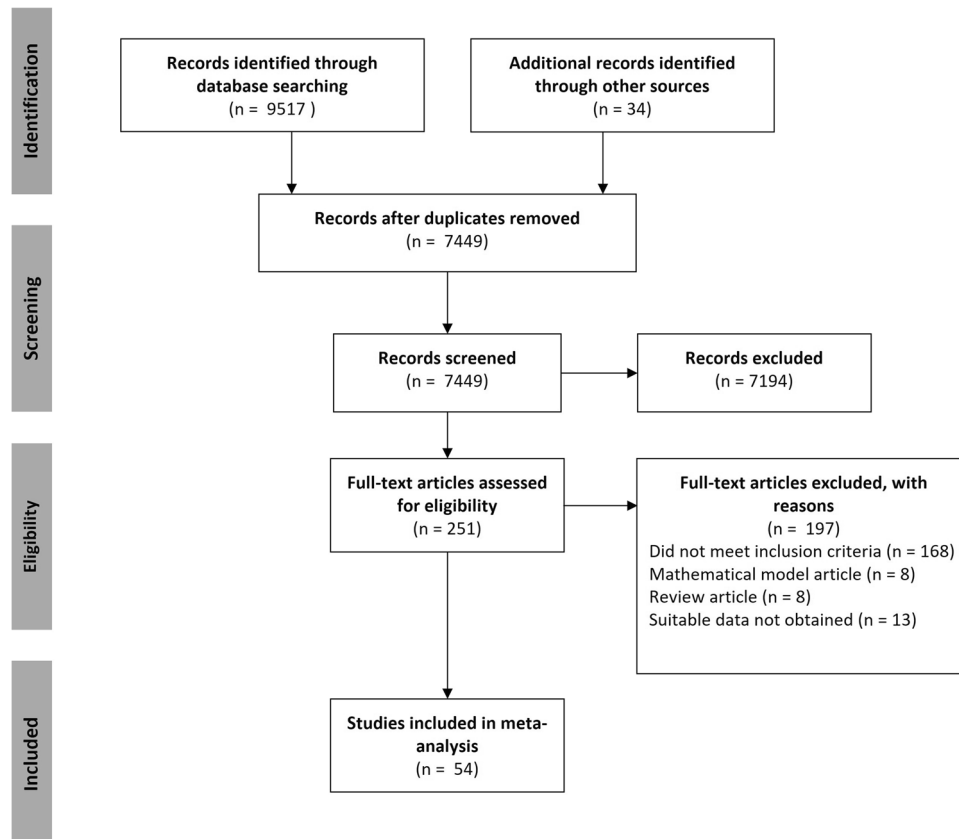
### Search protocol

We followed the PRISMA guidelines (Moher et al., 2009). We searched for published articles on *who strategies* of social learning (aka model-biased social learning) in October 2020 in Web of Science, Scopus and PsychInfo databases. We used search terms pertaining to social learning (e.g., ‘social information’, ‘social transmission’) and to the *who strategies* of social learning (e.g., ‘demonstrator’, ‘social learning strategy’) to search for peer-reviewed scientific papers. We also included papers from a preliminary search that were found outside of these database searches. Figure 1 shows the PRISMA diagram of the systematic

search process. The full list of search terms is available in the Online Supplementary Material (OSM; Supplementary Table 1).

### Criteria for inclusion

In order to be included, papers had to consist of experiments that used an *observer-demonstrator paradigm* to test if the characteristics of the individual providing social information (i.e., the demonstrator) affected social information use in the observer. The social information phase had to include either one or two groups of observers watching or interacting with one or more demonstrators. The different demonstrators had to vary in some characteristic. The social information phase had to be followed by a test phase measuring whether the observers copied (copy = used social information) the demonstrator. In each experiment, the different demonstrator types had to differ in a characteristic based on the *who strategies* of social learning proposed by Laland (2004) and further expanded by Rendell et al. (2011; see below for a detailed description). These strategies are: *copy familiar*, *copy kin*, *copy breeding partner*, *copy successful*, *copy older*, *copy high ranking*, *copy larger*, and *copy male* or



**Fig. 1** PRISMA diagram of the systematic review process beginning with the initial search results and ending with the number of papers included in the meta-analysis. *Note.* n indicates the number of papers

*copy female*. Additionally, we included experiments where demonstrators were of the same or a different species with regards to the observers (i.e., *copy conspecific*). Despite *copy conspecific* not being previously included as a *who strategy*, copying conspecifics could be another demonstrator bias animals employ (Avarguès-Weber et al., 2013; Sasvári, 1979).

We included experiments that used a within-subject methodology in which each observer had access to two or more types of demonstrators that differed in one of the characteristics mentioned above (e.g., kin vs. non-kin). Experiments using a within-subject design could have two types of methodologies where demonstrators were presented either: (1) simultaneously, or (2) sequentially. Alternatively, we also included experiments that used a between-subject methodology in which some observers had access to only one kind of demonstrator (e.g., kin) and other observers had access to the other kind of demonstrator (e.g., non-kin). For experiments using a between-subject design, groups of observers had to be consistent in their age and sex in order to ensure that any difference in copying was due to characteristics of the demonstrator and not those of the observer. For example, we excluded experiments that had juveniles observe one type of demonstrator (e.g., older) and adults observe the other type (e.g., younger, as in Rørvang et al., 2015). We did not include experiments comparing how animals responded to a signal (e.g., alarm calls), since signals have evolved to elicit a response in the receiver (Maynard-Smith & Harper, 2003), and responding to these stimuli is not considered social learning. We excluded experiments that used Network Based Diffusion Analysis because these statistical methods use mathematical models in order to infer biases in social learning instead of an *observer-demonstrator paradigm*.

In the test phase of experiments, copying behaviour was tested in two ways. In the first type, copying was tested by comparing behaviour matching between the observer and the demonstrator. Behaviour matching was measured by quantifying the extent to which observers chose the same option as the demonstrator (e.g., selecting feeder A over feeder B). This quantification was made by counting how many observers performed the same behaviour as the demonstrator (e.g., number of individuals choosing demonstrated feeder), or by measuring the fear response (e.g., freezing duration) of observers after being put in the same context where observers watched a demonstrator being exposed to an adverse stimulus (e.g., a foot shock). In the second type of experiment, copying was tested by comparing the performance of observers at solving a task after observing either one of two kinds of demonstrators (e.g., kin or non-kin) solving that same task. For example, latency to solve a foraging task after observing a demonstrator that is kin versus latency to solve a foraging task after observing a non-kin demonstrator. Experiments that measured attention towards demonstrators

as a proxy for social learning were excluded as they do not show whether observers acted upon the socially provided information, and the focus of this meta-analysis is on the effect of demonstrator characteristics on social information use. As mentioned in the *Introduction*, we excluded experiments in the vocal learning context as vocal learning can be considered a very specialized type of learning and is usually studied as its own research field separate from the field of social learning.

Experiments had to provide enough data or statistical information to allow for calculation of an effect size. If an experiment was missing the required statistical information in the text, we used the online tool WebPlotDigitizer v4 (Rohatgi, 2015) to extract means and standard deviations from plots. We obtained data for 93 effect sizes in 27 experiments in this way. If we needed additional data, we contacted authors and asked for any missing information or the raw data. We obtained data for two effect sizes from one experiment in this way. We only included experiments in non-human animals. See OSM Supplementary Table 2 for a list of papers not included in the meta-analysis and their reason for exclusion.

### Primary moderator: Strategy type

We propose two general categories of *who strategies* based on social learning theory (Boyd & Richerson, 1985; Coussi-Korbel & Fragaszy, 1995; Hoppitt & Laland, 2013; Laland, 2004). These categories are based on the proposed underlying factors that determine why it would be more beneficial to copy one type of demonstrator over another.

### Social dynamics strategies

The first category has to do with the social dynamics between the observer and the demonstrator. In this category, particular individuals are more influential demonstrators to certain observers as a consequence of pre-existing social relationships between the two (Coussi-Korbel & Fragaszy, 1995). The influence of a demonstrator increases when that demonstrator is an individual that the observer knows or shares a bond with, for example kinship or a pair bond. Information from known individuals should be preferred over information from strangers because known individuals are more likely to live in and experience the same environment as the observer, thus rendering the information that a known demonstrator provides more relevant than information provided by an unknown demonstrator (Coussi-Korbel & Fragaszy, 1995; Hoppitt & Laland, 2013; Laland, 2004). *Who strategies* that fit into the social dynamics category are *copy familiar*, *copy kin*, *copy breeding partner* and *copy conspecific*. Although a bias towards copying conspecifics does not necessarily involve some kind of pre-existing



social relationship between observer and demonstrator, social learning is assumed to occur mostly between conspecifics based on the idea that resource needs are shared more between conspecifics than between heterospecifics (Avarguès-Weber et al., 2013; Jaakkonen et al., 2015). For this reason, we decided to categorize *copy conspecific* as a social dynamics strategy. Each of these social dynamics strategies are described in greater detail below.

**Copy familiar** This strategy predicts that an observer has a bias to copy a familiar over an unfamiliar demonstrator, therefore copying a familiar demonstrator was coded as a positive effect and copying an unfamiliar demonstrator as a negative effect (Fig. 2). A familiar demonstrator is one with whom the observer has interacted at some point of their lives and is therefore known to the observer (Guillette et al., 2016; Ramakers et al., 2016). An unfamiliar individual is one that, prior to the experiment, had never interacted with the observer. Some experiments combined familiarity and another demonstrator characteristic like kinship ( $k = 9$  experiments,  $n = 26$  effect sizes; e.g., Galef & Whiskin, 2008) or breeding partner ( $k = 2$  experiments,  $n = 12$  effect sizes; e.g., Munch et al., 2018) in the same experiment – for example, by using demonstrators that were familiar/kin to the observers and demonstrators that were unfamiliar/non-kin. If the experimental groups differed in more than one demonstrator characteristic (e.g., familiarity and kinship), the effect size was classified into both of the social learning strategies being tested (i.e., learning strategies were not considered as mutually exclusive).

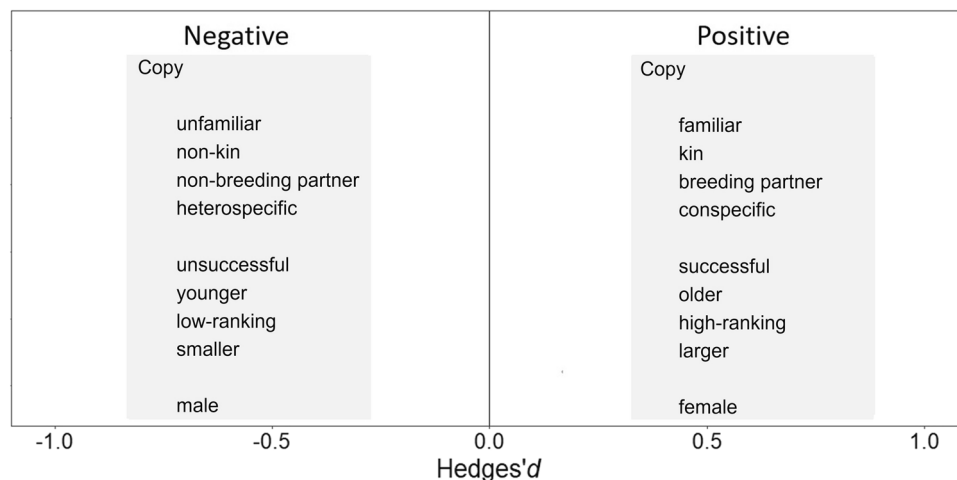
**Copy kin** This strategy predicts an observer has a bias to copy a demonstrator that is kin over a non-kin demonstrator (Hoppitt & Laland, 2013), therefore copying a kin demonstrator was coded as a positive effect and copying a non-kin demonstrator as a negative effect (Fig. 2). There were no experiments in our sample that used social kin (i.e., cross fostering).

**Copy breeding partner** This strategy predicts that an observer has a bias to copy a demonstrator that is their breeding partner compared to a non-breeding-partner demonstrator, therefore copying the breeding partner was coded as a positive effect and copying a non-breeding partner demonstrator was coded as a negative effect (Fig. 2). Two experiments combined familiarity and breeding partnership using familiar/breeding-partner demonstrators and unfamiliar/non-breeding-partner demonstrators (Jeon et al., 2010; Munch et al., 2018). The effect sizes extracted from experiments that combined familiarity and breeding partnership were classified into both learning strategies and were not considered mutually exclusive.

**Copy conspecifics** This strategy predicts that an observer has a bias to copy a conspecific over a heterospecific demonstrator, therefore copying a conspecific demonstrator was coded as a positive effect and copying a heterospecific demonstrator as a negative effect (Fig. 2).

### Status strategies

The second category of *who strategies* has to do with copying high status or successful individuals, as copying the



**Fig. 2** Diagram showing how effect direction was assigned within each who strategy. *Note.* Positive effect sizes were assigned when observers showed a bias towards copying the demonstrator predicted by the social learning strategies literature (Boyd & Richerson, 1985; Coussi-Korbel & Frigaszy, 1995; Hoppitt & Laland, 2013; Laland,

2004). Negative effect sizes were assigned when observers copied the demonstrator that is not predicted by the social learning strategies literature. Females arbitrarily assigned a positive value. Spaces between groupings of strategies indicate the different strategy types: social dynamics strategies, status strategies and other strategies, respectively

behaviour of individuals that are more successful than others in a population would theoretically yield the better payoff (Boyd & Richerson, 1985). Status strategies include *copy successful*, *copy older*, *copy high-ranking* and *copy larger*, and we discuss each strategy, in turn, below.

**Copy successful** This strategy predicts that an observer has a bias to copy a more successful over a less successful demonstrator. Therefore, preference for copying a more successful demonstrator was coded as a positive effect and preference for copying an unsuccessful demonstrator as a negative effect (Fig. 2). Each of the experiments testing the *copy successful* strategy used experimental manipulations to establish some demonstrators as successful individuals and others as unsuccessful or less successful individuals. Manipulations to establish the success of the demonstrators occurred either prior to or during the social information phase. Manipulations included foraging success (e.g., having access to food items of high value vs. not having this access; Nicol & Pope, 1999), mating status (e.g., mated vs. non-mated; Sarin & Dukas, 2009), or breeding success (e.g., large quantity vs. small quantity of eggs in nests; Forsman & Seppänen, 2011; Loukola et al., 2012; Seppänen et al., 2011).

**Copy older** This strategy predicts that an observer has a bias to copy an older (adult) over a younger (juvenile) demonstrator as older individuals should be more experienced and successful (e.g., Kendal et al., 2018; Laland, 2004). Therefore, copying an older demonstrator was coded as a positive effect and copying a young demonstrator was coded as a negative effect (Fig. 2).

**Copy high-ranking** This strategy predicts that an observer has a bias to copy a high-ranking over a low-ranking demonstrator. Therefore, copying high-ranking demonstrators was coded as a positive effect and copying low-ranking demonstrators as a negative effect. Each experiment used demonstrators that differed in their dominance status, while the dominance status of observers was kept consistent or a mixture of low-ranking and high-ranking observers in the same experiment. Dominance rank of both observers and demonstrators in each experiment was assessed before the start of the experiment. Depending on the experiment, observers could be in the middle of the hierarchy and observe demonstrators that ranked higher or lower than them (e.g., Baciadonna et al., 2013; Nicol & Pope, 1994, 1999; Watson et al., 2017), or there could be a combination of low-ranking and high-ranking observers observing low-ranking or high-ranking demonstrators (e.g., Brotcorne et al., 2020).

**Copy larger** This strategy predicts that an observer has a bias to copy a large over a smaller demonstrator, as demonstrator

size could be used as a proxy for demonstrator success (e.g., Kendal et al., 2018; Laland, 2004). Therefore, copying a larger demonstrator was coded as a positive effect and copying a smaller demonstrator as a negative effect (Fig. 2). The size of the observers was kept consistent across experimental groups.

## Other learning strategies

We analyzed one additional *who strategy* that does not fall under the social dynamics or status strategies discussed above.

**Copy female/male** Experiments in the *copy female/male* category tested whether animals have a bias towards copying male versus female demonstrators. Sex-based strategies can depend on the interaction between the observer and demonstrator's sex and do not have a clear prediction in the literature (Katz & Lachlan, 2003). For that reason, we arbitrarily assigned preference for copying female demonstrators as a positive effect and preference for copying male demonstrators as a negative effect.

## Secondary moderators

We obtained information on 12 moderator variables related to experimental design and observer characteristics that might influence the effect size of demonstrator characteristics on social learning.

## Experimental design

Experiments used either a within-subject or a between-subject design. These designs differ not only in their methodology but also in the basic question each address. Within-subject design experiments ask the observers to choose whether to copy demonstrator A or demonstrator B (they ask which demonstrator does the observer copy, assuming social learning always occurs). Between-subject design experiments ask one group of observers to copy demonstrator A or not, and another group of observers to copy demonstrator B or not (they ask if the observer will copy if the demonstrator is A or B, not assuming social learning will occur). Moreover, a within-subject design allows for direct comparison of both types of demonstrators, whereas in a between-subject design each observer only gets to interact with/observe one of the demonstrator types, and does not allow for a direct demonstrator comparison. We coded experiments as either within-subject or between-subject, and tested for the influence of study design in the effect of demonstrator characteristics on social learning.

## Demonstrator presentation

Within-subject designs differed in the experimental paradigm used during the social information phase. Some experiments had observers watch demonstrators simultaneously, whereas other experiments had observers watch each demonstrator sequentially. A meta-analysis on mate choice found that experimental design played a significant role in the strength of mating preferences in non-human animals (Dougherty & Shuker, 2015). More specifically, the mean strength of mating preferences was larger in experiments where potential mates were presented to subjects simultaneously, compared to experiments where potential mates were presented sequentially. We tested for the influence of demonstrator presentation (simultaneous vs. sequential) on the effect of demonstrator characteristics on social learning.

## Observer characteristics and other moderators

Three moderators were concerned with characteristics of the observers, these were: taxonomic group at the class level, sex of the observers (female, male or both) and age group of the observers (juvenile – before sexual maturity, adult – once sexual maturity is reached, or both). We examined the effect of experiment location on effect size (laboratory vs. field). We also examined how the type of access to demonstrators during the social information phase influenced effect size. During the social information phase, observers could: freely interact with the demonstrator(s) – coded as interaction, interact with the demonstrator(s) in a restricted way (e.g., through a holed barrier) – coded as restricted interaction, have only visual access to the demonstrator(s) – coded as observation. Additionally, observers could have visual access not to a live demonstrator but to a video – coded as video observation or have access to the product of the demonstrator's behaviour (e.g., nest with eggs) – coded as behavioural product. We tested whether the influence of demonstrator characteristics on copying were affected by the behavioural context of the experiment. We coded the behavioural context as either foraging, aversion/predator avoidance, or reproduction.

Finally, we examined whether having a wider time window to acquire social information affects model-based social learning by examining the influence of the duration of the social information phase on the effect size. The duration of the social information phase could be determined either by time in hours, controlling for species differences in developmental rates and lifespans (by dividing the duration of the social information phase by the average days of the species to reach sexual maturity, and then calculating the square root of that number to normalize the data; Lambert & Guillette, 2021), or by number of actions performed by the demonstrator (number of events). We also tested if the bias to copy

one type of demonstrator is affected by the delay (in hours) between the end of the social information phase and the start of the test phase.

## Effect size calculation

We quantified the influence of demonstrator characteristics on social learning by comparing the mean copying of the predicted demonstrator to the mean copying of the non-predicted demonstrator according to the *who strategies* theory and used Hedges'  $d$  as our effect size (Hedges & Olkin, 1985; Koricheva et al., 2013). To calculate  $d$ , the mean copying value obtained for the demonstrator type that is not predicted to be copied by the social learning strategies literature (e.g., non-familiar or unsuccessful demonstrators) was used as the baseline mean. Therefore, if observers copied non-predicted demonstrators (e.g., non-familiar) more than predicted demonstrators (e.g., familiar) the effect was negative, and if observers copied in the predicted direction, the effect size was positive (Fig. 2). Similar levels of copying of each kind of demonstrator result in an effect size near zero.

We obtained the effect sizes in different ways. When means, standard deviations and sample sizes were available, we calculated Hedges'  $d$  directly from these values using the equations in Koricheva et al. (2013). When copying was quantified as the number of individuals that copied each demonstrator, we first calculated the odds ratio and converted the value obtained to Hedges'  $d$  using the formula in Polanin and Snilstveit (2016).

## Phylogeny

Our sample included 33 species from five taxonomic groups: invertebrates, fish, reptiles, birds and mammals. In order to control for non-independence as a result of shared evolutionary history (Koricheva et al., 2013), we created a phylogenetic tree of the study species by downloading a subset of a supertree from TimeTree on 4<sup>th</sup> October, 2021 (Hedges et al., 2006; Hedges et al., 2015; Kumar et al., 2017; Supplementary Fig. 1). Two species were not in the database, and so we used closely related species as substitutes to build the phylogenetic tree.

## Statistical analysis

All analyses were performed using R v.4.0.3 (R Core Team, 2020). We ran multivariate meta-analysis models that included study ID and species as random effects to control for potential non-independence associated with multiple effect sizes from one study or species. Our models included a covariance matrix of our phylogeny to control for the shared evolutionary history of the species (Nakagawa & Santos, 2012). We conducted a main set of analyses using



the directional effect sizes, and ran another set of analyses using the absolute effect sizes with a folded distribution (Morrissey, 2016a). We present the  $I^2$  value of the base models as a measure of model heterogeneity.

### Absolute effect size analyses

We used absolute effect (i.e., using only positive values,  $|d|$ ) as a response variable in model analyses in order to determine whether demonstrator characteristics in general influenced social learning, regardless of the predictions about which demonstrator type should be copied. We conducted this analysis with the MCMCglmm package (Hadfield, 2010) using generalized linear models with a Bayesian framework by using Markov Chain Monte Carlo (MCMC). Absolute effect models included the three random variables listed above (study ID, species and phylogeny). We ran our models using 3,000,000 iterations, a thinning interval of 2,000, and a burn-in period of 2,000,000 (Dougherty & Guillette, 2018; Lambert & Guillette, 2021), and fitted the models using the inverse-Wishart prior (Noble et al., 2018). We applied a folded normal distribution to the posterior means of our models in order to account for the use of absolute values of effect sizes ( $|d|$ ), using the ‘analyze and transform’ method (Morrissey, 2016a, 2016b; Noble et al., 2018). We examined the MCMC time series to check for convergence of all models and checked model mixing by checking the autocorrelation between the samples in the chain. Finally, we checked for model convergence by running each model three times and using the Gelman-Rubin diagnostics (Gelman, 2008).

### Directional effect size analyses

We performed analyses using directional effect sizes as a response variable to determine whether demonstrator characteristics affect social learning following the predictions of the social learning strategies (Fig. 2; Coussi-Korbel & Frigaszy, 1995; Hoppitt & Laland, 2013; Laland, 2004). For these analyses we performed multi-level mixed effects models using the Metafor package (Viechtbauer, 2010), using a subset of our dataset which excluded effect sizes calculated from *copy male/female* studies as the directionality of this strategy was arbitrarily assigned and was not based on theory. We first ran a model on the data subset using study ID, with species and phylogeny as random factors and without any fixed factors, in order to determine the overall mean directional effect of the combined demonstrator characteristics on social learning. Then, we grouped *who strategies* into social dynamics and status strategies and ran a model that included strategy type (social dynamics vs. status) as a fixed factor to test for the effect of each type of strategies and compare their effect size to determine which strategy type had a larger influence on social learning. We also

examined, using independent models, the effect of each *who strategy* separately: *copy familiar*, *copy kin*, *copy breeding partner*, *copy conspecific*, *copy successful*, *copy older*, *copy high-ranking* and *copy larger*. An effect size was considered to significantly differ from zero when the 95% confidence intervals (CIs) did not overlap zero (Koricheva et al., 2013; Lambert & Guillette, 2021).

We examined the influence of our secondary moderator variables on the mean effect size using models that included the same four random variables presented above plus one of the moderator variables (categorical or continuous) as a fixed factor. To determine whether a moderator significantly influenced the overall mean effect size, we used the QM statistic (Koricheva et al., 2013). Statistical significance for QM tests was set at  $\alpha = 0.05$ . We obtained estimates of the mean effect size for each level of the categorical moderators by running the same models as above but excluding the model intercept. We searched for potential publication bias by running an Egger’s test and a trim-and-fill analysis on a model without random effects (Egger et al., 1997; Sterne & Egger, 2006).

## Results

### Search results and dataset

We extracted a total of 139 effect sizes from 54 publications (Fig. 1) that included experiments on 33 species (invertebrates,  $n = 3$ ; fish,  $n = 5$ ; reptiles,  $n = 5$ ; birds,  $n = 37$ ; and mammals,  $n = 93$ ). The number of effects per paper ranged from 1 to 18. Most of the studies took place in the laboratory ( $n = 45$ ), while a smaller number took place in the field ( $n = 9$ ; see Table 2). Eight of the laboratory studies used wild-caught subjects and one used a combination of wild-caught and zoo-bred subjects. An Egger’s test found asymmetry in the directional effects of a simple model (no random variables), suggesting potential publication bias to publish significant results ( $z = 3.35$ ,  $p < 0.01$ ). A z-test of sample variance in the multivariate model also identified asymmetry ( $z = 2.71$ ,  $p < 0.01$ ). However, a trim-and-fill test did not estimate any missing studies on either side of the funnel plot (OSM Supplementary Fig. 2).

### Effect sizes

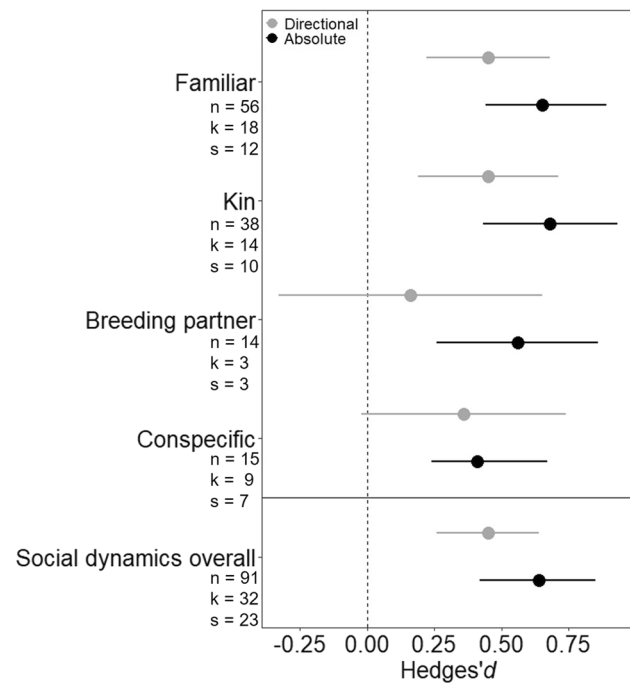
#### Overall effect sizes

We found a significant overall absolute effect (derived from all 139 effect sizes) of  $|d| = 0.58$  (95% CI = 0.39, 0.79), which is considered a medium to large effect. The overall heterogeneity was  $I^2 = 47.0$ , with the three random factors

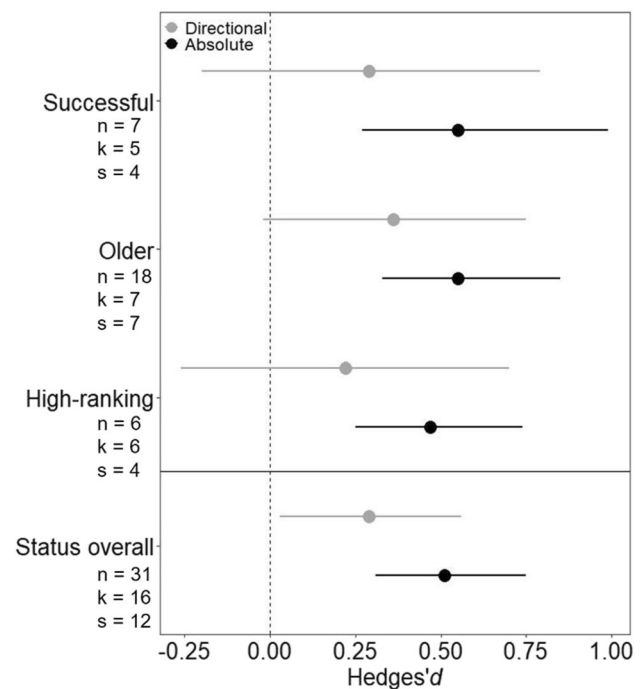
explaining a portion of this heterogeneity (phylogeny:  $I^2 = 11.4$ , species:  $I^2 = 13.9$ , and study:  $I^2 = 13.9$ ). We also found an overall directional effect size of  $d = 0.39$  (95% CI = 0.24, 0.54), derived from a data subset ( $n = 122$  effect sizes) that excluded *copy male/female* effect sizes because the direction of the effect size in this strategy (male = negative effect, female = positive effect) was arbitrarily assigned, which corresponds to a medium effect. A significant directional effect means that demonstrator characteristics influence social learning in the direction predicted by social learning strategies (Hoppitt & Laland, 2013; Kendal et al., 2018; Laland, 2004; Rendell et al., 2011). The overall directional effect size had a heterogeneity of  $I^2 = 67.0$ .

### Primary moderators – who strategies

The overall effect of social dynamics strategies on social learning was  $d = 0.44$  (95% CI = 0.26, 0.64), a medium



**Fig. 3** Forest plot of the mean directional effect size estimate (grey circles) and the mean absolute effect size estimates (black circles) with their 95% confidence intervals (horizontal lines) for the social dynamics strategies. Note. n indicates the number of effect sizes per strategy, k indicates the number of papers per strategy, s indicates number of species per strategy. The dashed line indicates 0 and the dotted line indicates the overall effect size estimate for social dynamics strategies grouped together. An effect was considered statistically significant if its 95% Confidence Interval did not overlap 0. Note that the strategies *copy familiar*, *copy kin* and *copy breeding partner* are not mutually exclusive. *Copy familiar* and *copy kin* share 26 (of 56 for familiar and 38 for kin) effect sizes and *copy familiar* and *copy breeding partner* share 12 (of 56 for familiar and 14 for breeding partner) effect sizes



**Fig. 4** Forest plot of the mean directional effect size estimate (grey circles) and the mean absolute effect size estimates (black circles) with their 95% confidence intervals (horizontal lines) for the status strategies. Note. n indicates the number of effect sizes per strategy, k indicates the number of papers per strategy, s indicates number of species per strategy. The dashed line indicates 0 and the dotted line indicates the overall effect size estimate for status strategies grouped together. The status overall effect size includes the effect size calculated for the *copy-larger* strategy however the *copy-larger* strategy effect size was not included due to the low sample size ( $n = 1$  effect size,  $k = 1$  paper)

effect (Fig. 3). The effect of status strategies was also significantly different from no effect at  $d = 0.29$  (95% CI = 0.03, 0.56; Fig. 4), a small effect. The effect sizes for social dynamics strategies and status strategies did not significantly differ from each other ( $z = 0.94$ ,  $p = 0.35$ ).

Regarding each *who strategy*, we found a significant effect in the predicted direction for *copy familiar* ( $d = 0.45$ , 95% CI = 0.22, 0.68) and *copy kin* ( $d = 0.45$ , 95% CI = 0.19, 0.71) strategies (Fig. 3). The effect size of each of these two strategies was still significantly different from no effect even when the shared effect sizes between the two ( $n = 26$ ) were excluded (*copy familiar*:  $d = 0.48$ , 95% CI = 0.19, 0.77,  $n = 30$ ; *copy kin*:  $d = 0.56$ , 95% CI = 0.16, 0.96,  $n = 12$ ). The effect size estimates for remaining *who strategies* did not significantly differ from zero: *copy breeding partner* ( $d = 0.16$ , 95% CI = -0.33, 0.65); *copy conspecific* ( $d = 0.36$ , 95% CI = -0.02, 0.74); *copy successful* ( $d = 0.29$ , 95% CI = -0.20, 0.79); *copy older* ( $d = 0.36$ , 95% CI = -0.02, 0.75); and *copy high-ranking* ( $d = 0.22$ , 95% CI = -0.26, 0.70). The *copy larger* strategy effect size was not included in Fig. 4

due to its low sample size ( $n = 1$  effect size,  $k = 1$  paper;  $d = 0.44$ , 95% CI = -0.70, 1.58).

Given that the effect of all but the *copy familiar* and *copy kin* strategies were not significantly different from no effect, we calculated the absolute effect of the *who strategies* listed in the above paragraph. In doing so we can determine whether the non-significance of the directional effects is due to our sample including a similar number of studies showing positive and negative effects (which would result in a significant absolute effect), or due to our sample including many studies with effects that do not differ from zero (which would result in a non-significant absolute effect). We found a significant absolute effect for each of the *who strategies* (Figs. 3 and 4; OSM Supplementary Table 3).

With regards to the sex of the demonstrator ( $n = 17$  effect sizes,  $k = 8$  papers), we found a significant positive effect, meaning that females were copied more than males across these studies ( $d = 0.46$ , 95% CI = 0.07, 0.85).

## Secondary moderators

**Experimental design and demonstration presentation** Directional effect size was significantly influenced by study design (QM = 4.22,  $df = 1$ ,  $p = 0.04$ ). The influence of demonstrator characteristics on social learning was greater in between-subject than in within-subject designs ( $z = 2.05$ ,  $p = 0.04$ ; Table 1). Moreover, while between-subject designs had a significant medium effect ( $d = 0.47$ , 95% CI = 0.31, 0.63), the effect of within-subject designs did not significantly differ from no effect ( $d = 0.14$ , 95% CI = -0.13, 0.42; Table 1). Demonstrator presentation (simultaneous vs sequential) did not affect the effect of demonstrator characteristics on social learning (QM = 0.13,  $df = 1$ ,  $p = 0.72$ ; Table 1).

**Observer characteristics and other moderators** The only secondary moderator that significantly influenced the strength of directed social learning was behavioural context (QM = 14.6,  $df = 2$ ,  $p < 0.01$ ), where predator/aversion avoidance experiments had a significantly larger effect than

experiments in the foraging or reproduction context ( $z = 3.20$ ,  $p < 0.01$ ; Table 2). None of the factors observer taxonomic group, observer sex, observer age group, experiment location, access to demonstrators, delay between observation and test, nor any measure of observation duration influenced the effect of demonstrator characteristics on social learning (OSM Supplementary Table 4). See Table 2 for mean effect size estimates and sample sizes for each category for the categorical moderator variables.

## Discussion

### Overall absolute and directional effect sizes

This meta-analysis shows that demonstrator characteristics influence social information use in animals, with a medium-to-large effect (0.60) in the absolute scale (i.e., without giving any directionality to effect size), and a medium directional effect (0.37) of demonstrator characteristics in the predicted direction (i.e., a positive effect) on social information use. Directional effects can be positive or negative and are based on social learning theory that observers have a bias to copy specific types of demonstrators (e.g., familiar over unfamiliar; Fig. 2). The significant directional effect shows that certain types of demonstrators are copied more than others, and in the direction predicted by theory (Boyd & Richerson, 1985; Hoppitt & Laland, 2013; Laland, 2004). The smaller directional effect compared to the absolute effect, however, indicates that animals often copy selectively but not necessarily in the predicted direction. For instance, copying in the non-predicted direction occurred in bats, who were found to copy the food choice of unfamiliar demonstrators over familiar demonstrators (Ramakers et al., 2016). In this particular model system, copying unfamiliar demonstrators could increase the chance of finding previously unknown food sources. Copying unfamiliar individuals is beneficial in species that feed from widely dispersed food sources, for example very specific kinds of fruit (Ramakers et al., 2016). Another example of copying in the non-predicted direction

**Table 1** Mean effect size estimates and 95% confidence intervals for each category of the ‘experimental design’ moderator (between-subject and within subject) and each category of the ‘demonstrator presentation’ moderator (simultaneous and sequential)

Moderator	Category	Effect sizes, n	Studies, n	Species, n	Effect type	Hedges' $d$	95% CI lower	95% CI upper
Experimental design	Between-subject	114	40	27	Absolute	0.62	0.39	0.81
					Directional	0.47	0.31	0.63
	Within-subject	24	17	12	Absolute	0.49	0.29	0.70
					Directional	0.14	-0.13	0.42
Demonstrator presentation	Sequential	3	3	3	Directional	-0.03	-0.75	0.70
	Simultaneous	21	14	10	Directional	0.22	-0.16	0.59

Table includes the sample sizes, number of studies, and number of species included in each category

**Table 2** Mean effect size estimates and 95% confidence intervals for each category of the seven extant moderators

Moderator	Category	Effects, n	Studies, n	Species, n	Hedges' <i>d</i>	95% CI lower	95% CI upper
Taxonomic	Mammals	89	28	15	0.39	0.20	0.58
Group	Birds	37	19	12	0.37	0.11	0.63
	Reptiles	5	2	2	-0.04	-0.73	0.65
	Fish	5	3	3	0.84	0.27	1.40
	Insects	3	2	1	0.25	-0.38	0.88
	Both	75	30	23	0.37	0.18	0.57
Observer sex	Female	37	21	11	0.3	0.06	0.53
	Male	27	10	5	0.67	0.3	1.05
	Both	15	9	8	0.3	-0.07	0.67
Observer age	Juvenile	29	12	11	0.54	0.21	0.87
	Adult	95	33	20	0.37	0.17	0.57
	Both	12	9	6	0.57	0.15	0.99
Location	Laboratory	127	45	28	0.37	0.2	0.53
	Interaction	67	25	21	0.42	0.21	0.63
Demonstrator Access	Restricted interaction	18	4	3	0.4	0.01	0.63
	Restricted observation	48	24	15	0.36	0.12	0.61
	Restricted video	4	1	2	0.24	-0.62	1.11
	Behavioural product	2	2	2	0.47	-0.48	1.42
Behavioural	Foraging	108	42	27	0.26	0.11	0.41
Context	Predator/aversion avoidance	22	6	5	0.93	0.6	1.26
	Reproduction	9	7	5	0.39	0.04	0.74

Table includes the sample sizes, number of studies, and number of species included in each category

comes from chimpanzees, which copy the method used by low-ranking demonstrators to retrieve food from a puzzle box over the method used by high-ranking demonstrators (Watson et al., 2017). Here, copying low-ranking demonstrators might occur when copying high-ranking demonstrators increases the chance of antagonistic interactions between observer and demonstrator. Despite some cases of animals copying in the non-predicted direction, however, the positive directional effect indicates that, in most cases animals copy as predicted by theory.

### Social dynamics strategies

We found a medium directional effect for social dynamics strategies (0.44) that was positive. This result means that, as predicted by theory, the pre-existing relationship between observer and demonstrator affects social information use because observers have a bias to copy demonstrators they know or with whom they share a bond. Because they live in the same environment as the observers, known or related demonstrators likely provide more relevant information than unknown demonstrators (Coussi-Korbel & Fragaszy, 1995; Hoppitt & Laland, 2013; Laland, 2004). When examining each of the specific social dynamics strategies, however, not all of the strategies had a significant directional effect on social information use.

The only specific social dynamic strategies with significant positive effects were *copy familiar* and *copy kin*: animals copied more when the demonstrator was familiar or kin than when the demonstrator was unfamiliar or non-kin. Biased copying of familiar or kin individuals under natural settings (e.g., learning from mothers over other adults; Krützen et al., 2005; Van de Waal et al., 2014) might reflect nothing more than social learning being driven by opportunity since individuals spend more time in the presence of familiar individuals or kin. However, our sample only included studies in which opportunity to acquire social information from the different types of demonstrators was equal between observer groups. Therefore, our meta-analysis provides solid evidence for a social information use bias towards familiar individuals and kin. These results could also be the consequence of selective attention towards individuals with whom an observer shares a bond (Range et al., 2009; Van De Waal et al., 2010). For example, ravens (*Corvus corax*), but not jackdaws (*Corvus monedula*), pay more attention to food and object manipulation by individuals with whom they shared a high rate of socially positive behaviours like allopreening (Scheid et al., 2007) compared to other individuals in the social group. Therefore, it is possible that familiar and kin demonstrators are copied more because observers pay more attention to them than to unfamiliar or non-kin demonstrators.

Biased copying of familiar and kin demonstrators suggests that transfer of information within a group of animals may often start among familiars and kin, and from there spread along the whole group (Aplin et al., 2014; Van De Waal et al., 2013). This transfer of information among kin and especially familiar individuals resembles Network Based Diffusion Analyses, as these models infer circumstantial evidence of social learning if a behavioural variant spreads along a social network (individuals that are familiar to each other (Hoppitt & Laland, 2011)). Transfer of information among familiars and kin could represent an early stage in the formation of behavioural traditions. This selective copying could also explain why certain traditions remain group-specific, as a bias to copy known over unknown individuals could limit the spread of behavioural variants among distinct animal groups, even when groups come in contact (Laland, 2008; Laland & Janik, 2006; Whiten, 2021b).

The directional effects of two other social dynamics strategies, *copy breeding partner* and *copy conspecific*, were not significant. Despite the non-significant directional effect, the *copy breeding partner* strategy had a significant absolute effect, indicating that biased copying occurred but that who was copied varied: in some cases observers showed a bias to copy their breeding partner and in other cases observers showed a bias to copy the non-partner demonstrator instead. In zebra finches, for example, female observers fed from the feeder demonstrated by their male partner over the feeder demonstrated by a non-partner male. However, male observers fed more from the feeder demonstrated by a non-partner female than from a feeder demonstrated their female partner (Templeton et al., 2017). One possible explanation for the behaviour of males is that it could be advantageous to ensure that their female partner has unrestricted access to food resources during the breeding stage, which demands high energy investments from females. Therefore, as copying their partner could increase competition for valuable food resources within the pair, males might be more prone to copy non-partner females instead and avoid copying their partners. Another possible explanation for copying non-partner females is that males might be seeking opportunities to mate with other females. This biased copying of non-partner individuals suggests that not all kinds of social bonds will necessarily have the same effect on social learning (i.e., copying the demonstrator who shares the closest bond). In some cases, for example when female partners act as demonstrators, competition for resources might affect whether one type of demonstrator is copied or not.

The non-significant directional effect for the *copy conspecific* strategy was unexpected given that all but one of the papers in our sample had positive effects, which indicates a bias to copy conspecifics over heterospecifics. The non-significance of the *copy conspecific* strategy directional effect might, therefore, be driven by one single negative effect.

This interpretation is supported by the significant absolute effect of the *copy conspecific* strategy, showing that when the one negative effect is turned to a positive one, the overall effect becomes significant. The negative effect in our sample corresponds to an experiment on shiny cowbirds (*Molothrus bonairensis*) who acquired a pecking response in slightly fewer trials after observing a heterospecific demonstrator (screaming cowbird, *Molothrus rufoaxillaris*) compared to a conspecific demonstrator (May & Rebores, 2005). In this specific example, copying heterospecific demonstrators might be influenced by the fact that cowbirds often give lots of attention to other bird species for nest prospecting, which could translate into other social learning behaviors. Thus, showing that under some circumstances the behaviour of heterospecifics can also constitute a useful source of information, and animals can make use of this kind of information, even when conspecific information is also available (Avarguès-Weber et al., 2013; Hämäläinen et al., 2020; Slagsvold & Wiebe, 2017). Nevertheless, in most cases within our sample animals seem to show a bias to copy conspecifics over heterospecifics.

### Status strategies

We found a small directional effect for status strategies (0.29) that was positive and significantly different from zero. This result means that, as predicted by theory, individuals have a bias to copy high-status demonstrators over low-status demonstrators. This result is expected because copying high-status demonstrators would theoretically yield the better payoff (Boyd & Richerson, 1985; Hoppitt & Laland, 2013; Laland, 2004). The size of the status strategies effect, however, was a small one, which was unexpected as status or success biases theoretically represent the most beneficial way to use social information and therefore be favored by selection (Boyd & Richerson, 1985; Hoppitt & Laland, 2013). This claim, however, assumes that high-status individuals (e.g., larger individuals or dominant individuals) have reached that condition because they have accumulated more resources due to their ‘successful behaviour’, which is not necessarily true. It is not always clear what factors are the source of an individual’s high-status condition, and the high-status condition could be based on factors that are not directly related to an individual’s behaviour (Hoppitt & Laland, 2013; Laland, 2004). Body size, for example, often correlates positively with social dominance (Huntingford et al., 1990) and is significantly influenced by genetics in species like grass frog tadpoles (*Rana temporaria*; Pakkasmaa et al., 2003) and collared flycatchers (*Ficedula albicollis*; Kruuk et al., 2001), therefore, showing that certain high-status characteristics like body size and social dominance are based not on behaviour but on other non-behavioural factors that cannot be socially learned. Consequently, copying the



behaviour of high-status individuals does not necessarily equal copying beneficial behaviors that lead to these high-status conditions (i.e., successful behaviour).

Each specific effect size within status strategies (e.g., *copy high-ranking*, *copy older*), was not significantly different from no effect in the directional scale. Each of these strategies, however, was significant in the absolute scale. This indicates that each of these status strategies had negative effects, reflecting a bias to copy low-status individuals. The bias to copy low-status individuals could be related to the kind of interactions that observers have with high-status demonstrators. Antagonistic interactions between observers and high-status demonstrators could limit the acquisition and use of information provided by high-status demonstrators. In the *copy high-ranking* strategy for example, if dominant individuals tend to be aggressive towards others, then observers might actually avoid copying high-ranking demonstrators, as doing so could lead to attacks from the dominant individuals if observers join them in their foraging patch, and copy low-ranking demonstrators instead (Thornton & Malapert, 2009). A similar effect could occur in the *copy older* strategy, where adults might have low tolerance towards younger individuals and attack them if approached (Coussi-Korbel & Fragaszy, 1995). It is possible, then, that antagonistic interactions with certain types of high-status individuals weaken the effect of status strategies on social information use, despite the assumed benefits of copying high-status demonstrators.

### Copy females

We found a significant medium effect (0.46) reflecting a bias to copy females over males in our sample. That females were copied more than males could be explained by different factors. In mammals for example, a bias to copy females could be due to females acquiring some sort of higher affective value than males, which might be related to the weaning period where individuals form a strong bond with their mothers (Schumacher & Moltz, 1985). An experiment on the African striped mouse (*Rhabdomys pumilio*), for example, found that juveniles preferably acquired information on novel food from their mothers compared to their fathers, who also provide parental care in this species (Rymer et al., 2008). In group-living species like vervet monkeys where females remain in their native group while males disperse, bias towards copying females might actually reflect a strategy to copy the philopatric sex (Bono et al., 2018; Van De Waal et al., 2010). Because members of the philopatric sex are the ones that remain in their natal group, they might provide more relevant information about the environment than dispersing individuals, thus making *copy philopatric sex* a type of social dynamic strategy. If *copy philopatric sex* were indeed a social learning strategy, then we would predict

that where there is male philopatry, like in chimpanzees, males might be preferred as models, at least after maternal attachments wane (Lawson Handley & Perrin, 2007). These examples suggest that, at least in mammals, mother-offspring relationships and group-level dynamics can influence biased copying toward females.

The few cases of males being copied more than females in our sample all occurred in zebra finches, and mostly when the observers were females (Benskin et al., 2002; Guillette & Healy, 2014; Katz & Lachlan, 2003). One possibility is that in some cases, the bias to copy a specific sex is related to the observer's sex (Katz & Lachlan, 2003). If this were the case, some observers might have a bias to copy members of the opposite sex, as demonstrators of their same sex could be perceived as direct competitors.

### Experimental procedure and other moderators

Experimental design significantly influenced directional effect size, with between-subject designs having a larger – and positive medium – directional effect than within-subject designs, which had a non-significant directional effect. These two designs differ in the basic question they are asking. Within-subject designs ask which of the two demonstrators the observer will copy, and therefore, assume that any choice made by the observer is social learning. Between-subject designs, on the other hand, do not assume social learning is occurring and ask whether the observer will copy a specific kind of demonstrator or not. Another difference between the two experimental designs is that in within-subject designs observers can directly compare both demonstrators, whereas in between-subject designs observers only get access to one type of demonstrator and cannot compare between demonstrator types. It might be possible that when directly comparing demonstrators (as in within-subject designs), factors other than the identity of the demonstrator (e.g., the demonstrator's behaviour) become more relevant in determining which demonstrator is copied. Moreover, the fact that each experimental design is underlined by a different question suggests that the influence of demonstrator characteristics on social learning is stronger when observers are making the decision to copy a demonstrator or not (as in between-subject designs), than when using social information is the only option available the observers (as in within-subject designs). It is still unclear, however, why demonstrator characteristics would influence social learning especially when deciding whether to copy a demonstrator or not, and further study on the topic could be relevant to better understand social learning mechanisms.

In a meta-analysis on the effect of experimental design on mate-choice experiments, it was found that mating preferences were stronger when tested using a *choice design* in which subjects get to choose between two potential mates,

than when tested using a *no-choice design* in which subjects only get access to one potential mate and decide whether to mate with it or not (Dougherty & Shuker, 2015). The reason for this, the authors argue, could be due to an increased cost of rejecting potential mates in no-choice tests. How choice and no-choice designs differ in the access they get to potential mates (two potential mates to choose from, or one potential mate with whom to mate or not respectively) makes within-subject designs analogous to choice designs, and between-subject designs analogous to no-choice designs. According to this analogy, our finding that observers were the most selective when deciding whether to copy or not in between-subjects designs contradicts the finding that subjects were less selective when choosing whether to mate or not in no choice designs (Dougherty & Shuker, 2015). This contradiction might have occurred because rejecting a breeding partner in no-choice designs could be considered costly if not given the opportunity afterwards to mate with another and miss the opportunity to mate altogether. On the other hand, not copying a demonstrator is a less costly decision since observers also have the option to use social information, thereby giving observers the freedom to be more selective with whether to copy a demonstrator or not in between-subject designs (Czaczkes et al., 2019; Dall et al., 2005; Danchin et al., 2004).

The other secondary moderator with a significant effect was behavioural context, where the predator/aversion avoidance context had a significantly larger effect compared to the foraging and reproduction context. This result means that individuals copied more in the predicted direction in predator/aversion avoidance contexts, which constitutes an unexpected result as we would have predicted indiscriminate social learning in these kinds of aversive situations (Hoppitt & Laland, 2013). The reason behind this prediction is that when high costs are involved (e.g., being predated), it would be beneficial to learn from others' experience, regardless of who they are. However, it might be possible that in some high-cost situations, copying specific individuals is more beneficial. For example, Siberian jay (*Perisoreus infaustus*) juveniles copied the movements of kin adults more than the movements of non-kin adults in their flock upon a predator encounter (Griesser & Suzuki, 2016). In these types of situations, where multiple individuals are responding to a predator encounter in an aroused manner, having a bias to copy specific individuals might be better than copying indiscriminately. Moreover, 20 out of 22 of the studies in the predator/aversion avoidance context tested for a *copy familiar* or a *copy kin* bias, which are the strategies with the strongest effect on social learning (e.g., Agee et al., 2019; Griesser & Suzuki, 2016; Kavaliers et al., 2005). It could be then that during aversive situations it is beneficial to bias attention and social information use towards specific types of demonstrators.

## Conclusions

1) Our meta-analysis provides the first quantitative review of the effects of demonstrator characteristics on social learning. Our results support the role that demonstrator characteristics play on the use of social information in animals. Moreover, demonstrator characteristics were found to influence social information use in the direction predicted by theory (e.g., copying familiar over unfamiliar demonstrators).

2) Social dynamics strategies have a medium directional effect on social learning, in particular animals have strong biases to copying others that are familiar or kin.

3) Status strategies have a weak directional effect on social learning, which is likely due to status strategies containing a relatively large number of experiments in which animals copied in the non-predicted direction.

4) Experimental design plays a role in the effect of demonstrator characteristics on social learning: between-subject experiments had stronger effects compared to within subject experiments. This result could mean that when observers have the opportunity to compare both types of demonstrators at the same time (as in within-subject designs), demonstrator characteristics become less relevant when selecting whom to copy.

5) Overall, our findings support a role of demonstrator characteristics on social learning with strong implications on the formation and establishment of cultural traditions in animals. The familiarity and kinship of the demonstrators seem to be key factors for the transfer of information within a group of animals. These findings also provide groundwork for future studies that might explore (a) how demonstrator characteristics promote and/or limit the spread of information in a population, and (b) how these who strategies influence the formation and establishment of cultural traditions.

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**Authors' contributions** ACA and LMG conceived and designed the project. ACA collected the data. ACA analyzed the data. ACA wrote the manuscript with input from LMG. All authors read and approved the final manuscript.

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**Data availability** All data generated and analysed for this experiment are included as supplementary material.

**Code availability** R Code is included as supplementary material.

## Declarations

**Conflict of interest** We declare no conflicts of interest.

**Ethics approval** Not applicable.

**Consent to participate** Not applicable.

**Consent for publication** Not applicable.

## References

- Agee, L. A., Jones, C. E., & Monfils, M. H. (2019). Differing effects of familiarity/kinship in the social transmission of fear associations and food preferences in rats. *Animal Cognition*, 22(6), 1013–1026.
- Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A., & Sheldon, B. C. (2014). Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature*, 518(7540), 538–541.
- Avarguès-Weber, A., Dawson, E. H., & Chittka, L. (2013). Mechanisms of social learning across species boundaries. *Journal of Zoology*, 290(1), 1–11.
- Baciadonna, L., McElligott, A. G., & Briefer, E. F. (2013). Goats favour personal over social information in an experimental foraging task. *PeerJ*, 2013(1), 1–16.
- Benskin, C. M. H., Mann, N. I., Lachlan, R. F., & Slater, P. J. B. (2002). Social learning directs feeding preferences in the zebra finch, *Taeniopygia guttata*. *Animal Behaviour*, 64(5), 823–828.
- Bono, A. E. J., Whiten, A., van Schaik, C., Krützen, M., Eichenberger, F., Schneider, A., & van de Waal, E. (2018). Payoff- and Sex-Biased Social Learning Interact in a Wild Primate Population. *Current Biology*, 28(17), 2800–2805.e4.
- Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process*. University of Chicago Press.
- Brenowitz, E. A., & Beecher, M. D. (2005). Song learning in birds: Diversity and plasticity, opportunities and challenges. *Trends in Neurosciences*, 28(3), 127–132.
- Brotcorne, F., Holzner, A., Jorge-Sales, L., Gunst, N., Hambuckers, A., Wandia, I. N., & Leca, J. B. (2020). Social influence on the expression of robbing and bartering behaviours in Balinese long-tailed macaques. *Animal Cognition*, 23(2), 311–326.
- Cadiou, N., & Cadiou, J. C. (2004). The influence of free interactions and partner familiarity on social transmission in the young canary. *Animal Behaviour*, 67(6), 1051–1057.
- Chesler, P. (1969). Maternal Influence in Learning by Observation in Kittens. *Science*, 166(3907), 901–903.
- Choleris, E., Guo, C., Liu, H., Mainardi, M., & Valsecchi, P. (1997). The effect of demonstrator age and number on duration of socially-induced food preferences in house mouse (*Mus domesticus*). *Behavioural Processes*, 41(1), 69–77.
- Coelho, C. G., Falótico, T., Izar, P., Mannu, M., Resende, B. D., Siqueira, J. O., & Ottoni, E. B. (2015). Social learning strategies for nut-cracking by tufted capuchin monkeys (*Sapajus* spp.). *Animal Cognition*, 18(4), 911–919.
- Corriveau, K., & Harris, P. L. (2009). Choosing your informant: Weighing familiarity and recent accuracy. *Developmental Science*, 12(3), 426–437.
- Coussi-Korbel, S., & Frigaszy, D. M. (1995). On the relation between social dynamics and social learning. *Animal Behaviour*, 50(6), 1441–1453.
- Czaczkas, T. J., Beckwith, J. J., Horsch, A.-L., & Hartig, F. (2019). The multi-dimensional nature of information drives prioritization of private over social information in ants. *Proceedings of the Royal Society B: Biological Sciences*, 286(1909), 20191136.
- Dall, S. R. X., Giraldeau, L. A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, 20(4), 187–193.
- Damas-Moreira, I., Oliveira, D., Santos, J. L., Riley, J. L., Harris, D. J., & Whiting, M. J. (2018). Learning from others: An invasive lizard uses social information from both conspecifics and hetero-specifics. *Biology Letters*, 14(10), 20180532.
- Danchin, E., Giraldeau, L. A., Valone, T. J., & Wagner, R. H. (2004). Public information: From nosy neighbors to cultural evolution. *Science*, 305(5683), 487–491.
- Danchin, E., Nöbel, S., Pocheville, A., Dagaëff, A.-C., Demay, L., Alphand, M., Ranty-Roby, S., van Renssen, L., Monier, M., Gazagne, E., Allain, M., & Isabel, G. (2018). Cultural flies: Conformist social learning in fruitflies predicts long-lasting mate-choice traditions. *Science*, 362(6418), 1025–1030.
- Davies, A. D., Lewis, Z., & Dougherty, L. R. (2020). A meta-analysis of factors influencing the strength of mate-choice copying in animals. *Behavioral Ecology*, 31(6), 1279–1290.
- Davies, N. B., & Welbergen, J. A. (2009). Social transmission of a host defense against cuckoo parasitism. *Science*, 324(5932), 1318–1320.
- Dougherty, L. R., & Guillelte, L. M. (2018). Linking personality and cognition: a meta-analysis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1756), 20170282.
- Dougherty, L. R., & Shuker, D. M. (2015). The effect of experimental design on the measurement of mate choice: A meta-analysis. *Behavioral Ecology*, 26(2), 311–319.
- Duffy, G. A., Pike, T. W., & Laland, K. N. (2009). Size-dependent directed social learning in nine-spined sticklebacks. *Animal Behaviour*, 78(2), 371–375.
- Egger, M., Smith, G. D., Schneider, M., & Minder, C. (1997). Bias in meta-analysis detected by a simple, graphical test. *British Medical Journal*, 315(7109), 629–634.
- Ehmann, B., van Schaik, C. P., Ashbury, A. M., Mörchen, J., Musdarlia, H., Utami Atmoko, S., et al. (2021). Immature wild orangutans acquire relevant ecological knowledge through sex-specific attentional biases during social learning. *PLOS Biology*, 19(5), e3001173.
- Farine, D. R., Spencer, K. A., & Boogert, N. J. (2015). Early-life stress triggers juvenile zebra finches to switch social learning strategies. *Current Biology*, 25(16), 2184–2188.
- Figuerola, J., Solà-Oriol, D., Manteca, X., & Pérez, J. F. (2013). Social learning of feeding behaviour in pigs: Effects of neophobia and familiarity with the demonstrator conspecific. *Applied Animal Behaviour Science*, 148(1–2), 120–127.
- Flynn, E., & Whiten, A. (2012). Experimental “microcultures” in young children: Identifying biographic, cognitive, and social predictors of information transmission. *Child Development*, 83(3), 911–925.
- Forestier, T., Féron, C., & Gouat, P. (2018). Transmission of food preference between unfamiliar house mice (*Mus musculus domesticus*) is dependent on social context. *Journal of Comparative Psychology*, 132(3), 268–279.

- Forsman, J. T., & Seppänen, J. T. (2011). Learning what (not) to do: Testing rejection and copying of simulated heterospecific behavioural traits. *Animal Behaviour*, *81*(4), 879–883.
- Galef, B. G., Kennett, D. J., & Wigmore, S. W. (1984). Transfer of information concerning distant foods in rats: A robust phenomenon. *Animal Learning & Behavior*, *12*(3), 292–296.
- Galef, B. G., Rudolf, B., Whiskin, E. E., Choleris, E., Mainardi, M., & Valsecchi, P. (1998). Familiarity and relatedness: Effects on social learning about foods by Norway rats and Mongolian gerbils. *Animal Learning & Behavior*, *26*(4), 448–454.
- Galef, B. G., & Whiskin, E. E. (2004). Effects of environmental stability and demonstrator age on social learning of food preferences by young Norway rats. *Animal Behaviour*, *68*(4), 897–902.
- Galef, B. G., & Whiskin, E. E. (2008). Effectiveness of familiar kin and unfamiliar nonkin demonstrator rats in altering food choices of their observers. *Animal Behaviour*, *76*(4), 1381–1388.
- Garland, E. C., & McGregor, P. K. (2020). Cultural transmission, evolution, and revolution in vocal displays: Insights from bird and whale song. *Frontiers in Psychology*, *11*. <https://doi.org/10.3389/fpsyg.2020.544929>
- Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine*, *27*(15), 2865–2873.
- Griesser, M., & Suzuki, T. N. (2016). Kinship modulates the attention of naïve individuals to the mobbing behaviour of role models. *Animal Behaviour*, *112*, 83–91.
- Guillette, L. M., & Healy, S. D. (2014). Mechanisms of copying behaviour in zebra finches. *Behavioural Processes*, *108*, 177–182.
- Guillette, L. M., Morgan, K. V., Hall, Z. J., Bailey, I. E., & Healy, S. D. (2014). Food preference and copying behaviour in zebra finches, *Taeniopygia guttata*. *Behavioural Processes*, *109*(PB), 145–150.
- Guillette, L. M., Scott, A. C. Y., & Healy, S. D. (2016). Social learning in nest-building birds: A role for familiarity. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1827), 20152685.
- Hadfield, J. D. (2010). MCMCglmm: MCMC Methods for Multi-Response GLMMs in R. *Journal of Statistical Software*, *33*(2), 1–22.
- Hämäläinen, L., Mappes, J., Rowland, H. M., Teichmann, M., & Thoroughgood, R. (2020). Social learning within and across predator species reduces attacks on novel aposematic prey. *Journal of Animal Ecology*, *89*(5), 1153–1164.
- Hatch, K. K., & Lefebvre, L. (1997). Does father know best? Social learning from kin and non-kin in juvenile ringdoves. *Behavioural Processes*, *41*(1), 1–10.
- Hedges, S. B., Dudley, J., & Kumar, S. (2006). TimeTree: A public knowledge-base of divergence times among organisms. *Bioinformatics*, *22*(23), 2971–2972.
- Hedges, S. B., Marin, J., Suleski, M., Paymer, M., & Kumar, S. (2015). Tree of life reveals clock-like speciation and diversification. *Molecular Biology and Evolution*, *32*(4), 835–845.
- Hedges, L. V., & Olkin, I. (1985). *Statistical Methods for Meta-Analysis*. In *Statistical Methods for Meta-Analysis*. Academic Press. <https://doi.org/10.1016/C2009-0-03396-0>
- Henrich, J., & Broesch, J. (2011). On the nature of cultural transmission networks: Evidence from Fijian villages for adaptive learning biases. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1567), 1139–1148.
- Heyes, C. (1994). Social learning in animals: Categories and mechanisms. *Biological Reviews of the Cambridge Philosophical Society*, *69*(2), 207–231 <http://www.ncbi.nlm.nih.gov/pubmed/8054445>
- Hoppitt, W., & Laland, K. N. (2011). Detecting social learning using networks: a users guide. *American Journal of Primatology*, *73*(8), 834–844.
- Hoppitt, W., & Laland, K. N. (2013). *Social Learning*. Princeton University Press. <https://doi.org/10.23943/princeton/9780691150703.001.0001>
- Horner, V., Proctor, D., Bonnie, K. E., Whiten, A., & de Waal, F. B. M. (2010). Prestige affects cultural learning in chimpanzees. *PLoS ONE*, *5*(5), 1–5.
- Huntingford, F. A., Metcalfe, N. B., Thorpe, J. E., Graham, W. D., & Adams, C. E. (1990). Social dominance and body size in Atlantic salmon parr, *Salmo solar* L. *Journal of Fish Biology*, *36*(6), 877–881.
- Jaakkonen, T., Kivela, S. M., Meier, C. M., & Forsman, J. T. (2015). The use and relative importance of intraspecific and interspecific social information in a bird community. *Behavioral Ecology*, *26*(1), 55–64.
- Jeon, D., Kim, S., Chetana, M., Jo, D., Ruley, H. E., Lin, S. Y., Rabah, D., Kinet, J. P., & Shin, H. S. (2010). Observational fear learning involves affective pain system and Ca v 1.2 Ca 2+ channels in ACC. *Nature Neuroscience*, *13*(4), 482–488.
- Jones, B. C., & DuVal, E. H. (2019). Mechanisms of social influence: A meta-analysis of the effects of social information on female mate choice decisions. *Frontiers in Ecology and Evolution*, *7*. <https://doi.org/10.3389/fevo.2019.00390>
- Jones, C. E., Riha, P. D., Gore, A. C., & Monfils, M. H. (2014). Social transmission of Pavlovian fear: Fear-conditioning by-proxy in related female rats. *Animal Cognition*, *17*(3), 827–834.
- Katz, M., & Lachlan, R. F. (2003). Social learning of food types in zebra finches (*Taeniopygia guttata*) is directed by demonstrator sex and feeding activity. *Animal Cognition*, *6*(1), 11–16.
- Kavaliers, M., Colwell, D. D., & Choleris, E. (2005). Kinship, familiarity and social status modulate social learning about “micro-predators” (biting flies) in deer mice. *Behavioral Ecology and Sociobiology*, *58*(1), 60–71.
- Kendal, R. L., Boogert, N. J., Rendell, L., Laland, K. N., Webster, M., & Jones, P. L. (2018). Social Learning Strategies: Bridge-building between fields. *Trends in Cognitive Sciences*, *22*(7), 651–665.
- Kendal, R. L., Coolen, I., van Bergen, Y., & Laland, K. N. (2005). Trade-offs in the adaptive use of social and asocial learning. *Advances in the Study of Behavior*, *35*(05), 333–379.
- Koricheva, J., Gurevitch, J., & Mengersen, K. (Eds.). (2013). *Handbook of Meta-analysis in Ecology and Evolution*. Princeton University Press. <https://doi.org/10.1515/9781400846184>
- Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L., & Sherwin, W. B. (2005). Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(25), 8939–8943.
- Kruuk, L. E. B., Merilä, J., & Sheldon, B. C. (2001). Phenotypic selection on a heritable size trait revisited. *The American Naturalist*, *158*(6), 557–571.
- Kumar, S., Stecher, G., Suleski, M., & Hedges, S. B. (2017). TimeTree: A resource for timelines, timetrees, and divergence times. *Molecular Biology and Evolution*, *34*(7), 1812–1819.
- Laland, K. N. (2004). Social learning strategies. *Animal Learning & Behavior*, *32*(1), 4–14.
- Laland, K. N. (2008). Animal cultures. *Current Biology*, *18*(9), 366–370.
- Laland, K. N., & Janik, V. M. (2006). The animal cultures debate. *Trends in Ecology and Evolution*, *21*(10), 542–547.
- Lambert, C. T., & Guillette, L. M. (2021). The impact of environmental and social factors on learning abilities: A meta-analysis. *Biological Reviews*, *96*(6), 2871–2889.
- Lawson Handley, L. J., & Perrin, N. (2007). Advances in our understanding of mammalian sex-biased dispersal. *Molecular Ecology*, *16*(8), 1559–1578.
- Loukola, O. J., Seppänen, J.-T., & Forsman, J. T. (2012). Intraspecific social information use in the selection of nest site characteristics. *Animal Behaviour*, *83*(3), 629–633.
- Lupfer, G., Frieman, J., & Coonfield, D. (2003). Social transmission of flavor preferences in two species of hamsters (*Mesocricetus*



- auratus* and *Phodopus campbelli*). *Journal of Comparative Psychology*, 117(4), 449–455.
- May, D., & Reboresda, J. C. (2005). Conspecific and heterospecific social learning in shiny cowbirds. *Animal Behaviour*, 70(5), 1087–1092.
- Maynard-Smith, J., & Harper, D. (2003). *Animal Signals*. Oxford University Press.
- Mersmann, D., Tomasello, M., Call, J., Kaminski, J., & Taborsky, M. (2011). Simple mechanisms can explain social learning in domestic dogs (*Canis familiaris*). *Ethology*, 117(8), 675–690.
- Mesoudi, A., Chang, L., Dall, S. R. X., & Thornton, A. (2016). The evolution of individual and cultural variation in social learning. *Trends in Ecology and Evolution*, 31(3), 215–225.
- Moher, D., Liberati, A., Tetzlaff, J., Altman, D. G., Altman, D., Antes, G., Atkins, D., Barbour, V., Barrowman, N., Berlin, J. A., Clark, J., Clarke, M., Cook, D., D'Amico, R., Deeks, J. J., Devereaux, P. J., Dickersin, K., Egger, M., Ernst, E., et al. (2009). Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. *PLoS Medicine*, 6(7). <https://doi.org/10.1371/journal.pmed.1000097>
- Morrissey, M. B. (2016a). Meta-analysis of magnitudes, differences and variation in evolutionary parameters. *Journal of Evolutionary Biology*, 29(10), 1882–1904.
- Morrissey, M. B. (2016b). Rejoinder: Further considerations for meta-analysis of transformed quantities such as absolute values. *Journal of Evolutionary Biology*, 29(10), 1922–1931.
- Munch, K. L., Noble, D. W. A., Wapstra, E., & While, G. M. (2018). Mate familiarity and social learning in a monogamous lizard. *Oecologia*, 188(1), 1–10.
- Nakagawa, S., & Santos, E. S. A. (2012). Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology*, 26(5), 1253–1274.
- Nicol, C. J., & Pope, S. J. (1994). Social learning in small flocks of laying hens. *Animal Behaviour*, 47(6), 1289–1296.
- Nicol, C. J., & Pope, S. J. (1999). The effects of demonstrator social status and prior foraging success on social learning in laying hens. *Animal Behaviour*, 57(1), 163–171.
- Noble, D. W. A., Stenhouse, V., & Schwanz, L. E. (2018). Developmental temperatures and phenotypic plasticity in reptiles: A systematic review and meta-analysis. *Biological Reviews*, 93(1), 72–97.
- Pakkasmaa, S., Merilä, J., & O'Hara, R. B. (2003). Genetic and maternal effect influences on viability of common frog tadpoles under different environmental conditions. *Heredity*, 91(2), 117–124.
- Penndorf, J., & Aplin, L. (2020). Environmental and life history factors, but not age, influence social learning about food: A meta-analysis. *Animal Behaviour*, 167, 161–176.
- Polanin, J. R., & Snijlsteit, B. (2016). Converting between effect sizes. *Campbell Systematic Reviews*, 12(1), 1–13.
- Pongrácz, P., Miklósi, Á., Timár-Geng, K., & Csányi, V. (2004). Verbal attention getting as a key factor in social learning between dog (*Canis familiaris*) and human. *Journal of Comparative Psychology*, 118(4), 375–383.
- Pongrácz, P., Vida, V., Bánhegyi, P., & Miklósi, Á. (2008). How does dominance rank status affect individual and social learning performance in the dog (*Canis familiaris*)? *Animal Cognition*, 11(1), 75–82.
- R Core Team. (2020). *R: A Language and Environment for Statistical Computing*. <https://www.r-project.org/>
- Ramakkers, J. J. C., Dechmann, D. K. N., Page, R. A., & O'Mara, M. T. (2016). Frugivorous bats prefer information from novel social partners. *Animal Behaviour*, 16, 83–87.
- Range, F., Horn, L., Bugnyar, T., Gajdon, G. K., & Huber, L. (2009). Social attention in keas, dogs, and human children. *Animal Cognition*, 12(1), 181–192.
- Range, F., & Virányi, Z. (2013). Social learning from humans or conspecifics: Differences and similarities between wolves and dogs. *Frontiers in Psychology*, 4(DEC), 1–10.
- Rendell, L., Fogarty, L., Hoppitt, W. J. E., Morgan, T. J. H., Webster, M. M., & Laland, K. N. (2011). Cognitive culture: Theoretical and empirical insights into social learning strategies. *Trends in Cognitive Sciences*, 15(2), 68–76.
- Rohatgi, A. (2015). WebPlotDigitizer User Manual Version 3.4. URL <http://Arohatgi.Info/WebPlotDigitizer/App>, 1–18. <https://doi.org/10.5281/zenodo.10532>
- Rørvang, M. V., Ahrendt, L. P., & Christensen, J. W. (2015). Horses fail to use social learning when solving spatial detour tasks. *Animal Cognition*, 18(4), 847–854.
- Rørvang, M. V., & Christensen, J. W. (2018). Attenuation of fear through social transmission in groups of same and differently aged horses. *Applied Animal Behaviour Science*, 209(September), 41–46.
- Rymer, T., Schradin, C., & Pillay, N. (2008). Social transmission of information about novel food in two populations of the African striped mouse. *Rhabdomys pumilio*. *Animal Behaviour*, 76(4), 1297–1304.
- Sarin, S., & Dukas, R. (2009). Social learning about egg-laying substrates in fruitflies. *Proceedings of the Royal Society B: Biological Sciences*, 276(1677), 4323–4328.
- Sasvári, L. (1979). Observational learning in great, blue and marsh tits. *Animal Behaviour*, 27(PART 3), 767–771.
- Scheid, C., Range, F., & Bugnyar, T. (2007). When, what, and whom to watch? Quantifying attention in ravens (*Corvus corax*) and jackdaws (*Corvus monedula*). *Journal of Comparative Psychology*, 121(4), 380–386.
- Schumacher, S. K., & Moltz, H. (1985). Prolonged responsiveness to the maternal pheromone in the postweanling rat. *Physiology & Behavior*, 34(3), 471–473.
- Schwab, C., Bugnyar, T., Schloegl, C., & Kotrschal, K. (2008). Enhanced social learning between siblings in common ravens, *Corvus corax*. *Animal Behaviour*. <https://doi.org/10.1016/j.anbehav.2007.06.006>
- Seppänen, J. T., Forsman, J. T., Mönkkönen, M., Krams, I., & Salmi, T. (2011). New behavioural trait adopted or rejected by observing heterospecific tutor fitness. *Proceedings of the Royal Society B: Biological Sciences*, 278(1712), 1736–1741.
- Shettleworth, S. J. (2010). *Cognition, evolution and behaviour* (2nd ed). Oxford University Press.
- Slagsvold, T., & Wiebe, K. L. (2017). On the use of heterospecific information for nest site selection in birds. *Journal of Avian Biology*, 48(7), 1035–1040.
- Sterne, J. A. C., & Egger, M. (2006). Regression methods to detect publication and other bias in meta-analysis. *Publication Bias in Meta-Analysis: Prevention, Assessment and Adjustments*, 99–110. <https://doi.org/10.1002/0470870168.ch6>
- Swaney, W., Kendal, J., Capon, H., Brown, C., & Laland, K. N. (2001). Familiarity facilitates social learning of foraging behaviour in the puppy. *Animal Behaviour*, 62(3), 591–598.
- Templeton, C. N., Philp, K., Guillette, L. M., Laland, K. N., & Benson-Amram, S. (2017). Sex and pairing status impact how zebra finches use social information in foraging. *Behavioural Processes*, 139, 38–42.
- Thornton, A., & Malapert, A. (2009). Experimental evidence for social transmission of food acquisition techniques in wild meerkats. *Animal Behaviour*, 78(2), 255–264.
- Trapp, R. M., & Bell, A. M. (2017). The effect of familiarity with demonstrators on social learning in three-spined sticklebacks (*Gasterosteus aculeatus*). *Ethology*, 123(3), 213–220.
- Valsecchi, P., Choleris, E., Moles, A., Guo, C., & Mainardi, M. (1996). Kinship and familiarity as factors affecting social transfer of food



- preferences in adult Mongolian gerbils (*Meriones unguiculatus*). *Journal of Comparative Psychology*, 110(3), 243–251.
- Van De Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent social learning and conformity shape a wild primate's foraging decisions. *Science*, 340(6131), 483–485.
- Van de Waal, E., Bshary, R., & Whiten, A. (2014). Wild vervet monkey infants acquire the food-processing variants of their mothers. *Animal Behaviour*, 90, 41–45.
- Van De Waal, E., Renevey, N., Favre, C. M., & Bshary, R. (2010). Selective attention to philopatric models causes directed social learning in wild vervet monkeys. *Proceedings of the Royal Society B: Biological Sciences*, 277(1691), 2105–2111.
- Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, 36(3), 1–48.
- Watson, S. K., Reamer, L. A., Mareno, M. C., Vale, G., Harrison, R. A., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2017). Socially transmitted diffusion of a novel behavior from subordinate chimpanzees. *American Journal of Primatology*, 79(6), 1–10.
- Whiten, A. (2017). A second inheritance system: The extension of biology through culture. *Interface Focus*, 7(5), 20160142.
- Whiten, A. (2021a). The psychological reach of culture in animals' lives. *Current Directions in Psychological Science*, 30(3), 211–217.
- Whiten, A. (2021b). The burgeoning reach of animal culture. *Science*, 372(6537), eabe6514.
- Whiten, A., & van de Waal, E. (2018). The pervasive role of social learning in primate lifetime development. *Behavioral Ecology and Sociobiology*, 72(5), 80.
- Wood, L. A., Kendal, R. L., & Flynn, E. G. (2012). Context-dependent model-based biases in cultural transmission: Children's imitation is affected by model age over model knowledge state. *Evolution and Human Behavior*, 33(4), 387–394.

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