Social learning in non-grouping animals

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ABSTRACT

Social learning is widespread in the animal kingdom and is involved in behaviours from navigation and predator avoidance to mate choice and foraging. While social learning has been extensively studied in group-living species, this article presents a literature review demonstrating that social learning is also seen in a range of non-grouping animals, including arthropods, fishes and tetrapod groups, and in a variety of behavioural contexts. We should not be surprised by this pattern, since non-grouping animals are not necessarily non-social, and stand to benefit from attending to and responding to social information in the same ways that group-living species do. The article goes on to ask what non-grouping species can tell us about the evolution and development of social learning. First, while social learning may be based on the same cognitive processes as other kinds of learning, albeit with social stimuli, sensory organs and brain regions associated with detection and motivation to respond to social information may be under selection. Non-grouping species may provide useful comparison taxa in phylogenetic analyses investigating if and how the social environment drives selection on these input channels. Second, non-grouping species may be ideal candidates for exploring how ontogenetic experience of social cues shapes the development of social learning, allowing researchers to avoid some of the negative welfare implications associated with raising group-living animals under restricted social conditions. Finally, while non-grouping species may be capable of learning socially under experimental conditions, there is a need to consider how non-grouping restricts access to learning opportunities under natural conditions and whether this places a functional constraint on what non-grouping animals actually learn socially in the wild.

Key words: associative learning, culture, diffusion, grouping, social information, sociality.

CONTENTS

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I. INTRODUCTION

(1) Background

The lives of animals play out in often complex environments. In order to overcome daily problems, such as finding food and avoiding becoming food for others, and recurrent challenges, such as locating mates and undertaking migrations, animals rely on information. Information can come from experience and learning and from cues acquired and continuously updated as they navigate their surroundings. It can also come from the social environment, from other animals. Many animals respond to information gleaned from the behaviour of others. They use it to recognise when others have found food, and to locate profitable foraging patches. They use it to take evasive action from predators, locate mates, to exploit new resources and to travel efficiently. Information provided by other animals is referred to as social information. This can take the form of targeted signals that communicate information from a sender to a receiver, such as a courtship or threat display, or an alarm or recruitment call. Information can also be produced passively and inadvertently, for example through changes in posture as animals feed, or bursts of activity as they flee from danger. These categories are not discreet, and sitting between them, eavesdroppers pay attention to signals for which they are not the intended recipient, acquiring information about resources or risks in the process. Learning that results from animals attending to social information is known as social learning (Heyes, 1994; Valone & Templeton, 2002; Danchin *et al.*, 2004; Seppänen *et al.*, 2007; Hoppitt & Laland, 2008).

More formally, social learning is defined as any influence on learning arising from observing or interacting with another individual or something produced by another individual (Heyes, 1994; Hoppitt & Laland, 2008). Observing can be interpreted broadly to include acquisition of cues through any sensory modality, and the observed individual may be a con- or heterospecific. Interaction can similarly be interpreted broadly, and may refer to direct physical contact, aggression, pursuit or fleeing, maintaining proximity or travelling together. Finally, a product can be anything left in the environment by another individual, such as, but not limited to, a scent cue or signal, faeces or urine, a processed food item or a manufactured artifact such as a nest or shelter.

It has been argued that social learning in many cases can be explained by general learning processes, without the need to invoke adaptive specialisation in cognition, such that social learning can be explained in terms of associative learning, where the stimulus happens to be provided, directly or indirectly, by another animal (Heyes, 2012; Leadbeater, 2015; Reader, 2016). In this sense, the cognitive mechanisms underlying social learning are not subject to natural selection specifically, rather, selection acts on learning performance more generally. Social learning may be shaped by natural selection in other ways however, not through selection on cognitive processes but through selection on input channels. These include the sensory systems and brain regions through which animals perceive social information, processes related to how they attend to social cues relative to other sensory input, and processes that affect how motivated they are to respond to these cues (Heyes, 2012).

Social learning has been documented in a wide range of species, from wood crickets (*Nemobius sylvestris*) and frog embryos learning about predators to French grunts (*Haemulon flavolineatum*) acquiring twilight navigation routes and humpback whales (*Megaptera novaeangliae*) accessing new food resources (Helfman & Schultz, 1984; Coolen, Dangles & Casas, 2005; Mathis *et al.*, 2008; Allen *et al.*, 2013).

The great majority of research into social learning has been conducted using group-living animals as subjects. On the face of it this makes sense, since group-living animals are constantly exposed to cues from their group mates, and access to information may be one of the main benefits of living in groups (Ward & Webster, 2016). In fact, in the mid-20th century some researchers began to propose that social learning might be an adaptive specialisation for group living. Klopfer (1959), for example, predicted a positive correlation between the extent to which species live in groups and their ability to learn socially, and that non-grouping species would be less likely to acquire behaviours through social learning (Klopfer, 1961). Other researchers have advocated for a role of group living in the evolution of social learning, and Giraldeau & Lefebvre (1996) provide a critical evaluation of this discussion. Notwithstanding contemporary perspectives on social learning (that it is mechanistically indistinct from asocial, associative learning at a cognitive level) Giraldeau & Lefebvre (1996) raise a number of methodological concerns over this comparative work; any number of confounding variables related to species-specific differences in factors such as responses to experimental procedure and design, general motivation, responses to food deprivation, neophobia, habituation to humans and handling could also drive species-level differences in social learning. Typically, these are not accounted for by researchers. By the end of the 20th century the idea that proficiency in social learning might be driven by group living had largely fallen away as the predicted relationships between sociality and social learning did not materialise. While noting that comparatively few species had been examined Giraldeau & Lefebvre (1996) concluded that for birds there was no apparent relationship between ecological factors, including gregariousness, and social learning. They highlighted the relationship between learning performance in both asocial and social learning tasks seen in strongly flocking and less-gregarious birds, suggesting that these both reflect general learning ability. Reader & Lefebvre (2001) go further, arguing that group living does not appear to be a defining feature of ability to learn socially, and that the evidence for group social complexity predicting social learning ability is weak. Lending further support to the idea that group living is not a prerequisite for social learning is a growing body of research documenting instances of social learning in animals that do not habitually live in social groups.

(2) Aims of this article

Social learning has been described in a taxonomically broad range of non-grouping animals, and in a variety of contexts ranging from navigation to locating food to learning about predators. This literature is piecemeal, and the first aim of this review is to draw together and summarise representative examples through a non-systematic literature survey. The second aim of this article is to attempt to draw lessons and opportunities from this body of work. Section III begins by arguing that we should not be particularly surprised to observe abundant examples of social learning in non-grouping species, because non-grouping species are likely to be exposed to social cues too and stand to benefit from responding appropriately to social information just as grouping species do. This section goes on to ask whether non-grouping species provide any insights into social learning more generally, and presents opportunities for how non-grouping species might be used to advance our understanding of the origins and development of social learning, particularly with reference to selection on input channels associated with social learning (Heyes, 2012). This section ends by discussing whether not living in groups places a functional constraint on what non-grouping animals actually learn socially in the wild through limiting their opportunities to access social information. Before this, it is necessary to define what we mean by grouping and non-grouping, and to acknowledge the limitations of this binary distinction.

(3) Defining social learning and non-grouping

Clearly defined terminology is essential. 'Social learning' and 'social information use' are sometimes used interchangeably, while what constitutes 'group-living' and 'social' can be interpreted in various ways. This article will also consider cases of social information use by non-grouping animals. *Social learning* is used in accordance with the formal definitions of Heyes (1994) and Hoppitt & Laland (2008) as: any influence on learning arising from observing or interacting with another individual or something produced by another individual. No differentiation is made between cases where the animal socially learns a novel skill (such as how to open a new food item) and cases where the animal learns something about an already-known-about resource (such as a new location of an already-familiar food type). If both cases involve learning arising from an association with a social cue then both are counted as social learning.

The term *social information use* is used here to describe cases where the behaviour of an observer is influenced by another animal, without it necessarily learning something new. For example, an observer might approach a group member that is feeding and in doing so arrive at a food patch it did not previously know existed. Since this can occur without the observer having learned anything (such as the route to the food patch, the memory of the food patch or the association between joining others and finding food), this would be classed as social information use. In this article, when

discussing specific examples, confirmed cases of social learning and instances of social information use where no learning is shown to be involved will be differentiated.

Here the term 'non-grouping' is used to refer to animals that do not actively join and remain with others. Grouping is defined as two or more individuals maintaining proximity in space and time through social attraction to one another (Ward & Webster, 2016). Given this, non-grouping animals are defined as: animals that show no social attraction to others and as such exhibit no tendency to remain close to others that they might encounter for prolonged periods of time, during the life stage of interest.

Specifying no tendency to remain close to others distinguishes groups from aggregations; groups form when individuals come and remain together through social attraction to one another, while aggregations arise because animals are attracted to some feature of the physical environment (for example a food patch, waterhole or shelter). The caveat *life stage of interest* is included to account for the fact that animals may switch between grouping and non-grouping at different stages of their lives, or that they might switch between grouping and living alone opportunistically. Here a species that groups when immature but which lives alone as an adult would be counted as non-grouping if studied when mature. Some authors have used terms like 'non-social' when discussing cases of social learning by solitary animals, but this problematic because it fails to acknowledge the fact that under natural conditions almost all animals are going to be exposed to social cues, such as calls or odours that transmit over long distances, or through artifacts produced by others that have since departed, even if they rarely encounter another individual directly. This is an important point that is discussed in more detail in Section III.1, and for these reasons, the term 'non-grouping' is preferred over 'non-social'.

The binary separation of grouping *versus* non-grouping presented here is problematic in its own right (Doody, Burghardt & Dinets, 2013). First, it is a gross oversimplification that treats grouping as a homogenous social system, when this clearly is not the case. It does not account for group size, the nature of affiliations and relationships between group members, the form and frequency of the interactions that take place between them, or whether group members are capable of recognising one another at some level. It also does not separate groups with stable membership from ephemeral groups, or closed-access groups where would-be newcomers are excluded, or from open groups where new members can join freely (Krause & Ruxton, 2002; Ward & Webster, 2016; Tóth, Jaloveczi & Tarján, 2020). All of these factors can potentially influence how and what kind of information is transmitted between group members. Second, it acknowledges but sidesteps the fact that animals may switch between grouping and non-grouping at different stages of their lives, or that they might sometimes aggregate. Because the literature on social learning in non-grouping species is fragmentary, this binary separation is probably the best that can be achieved at present. It is still useful in the context of thinking about social learning insofar as it allows us to answer

the question of whether animals typically thought of as solitary are capable of socially learning in broadly similar ways to those that habitually form groups. In the future, as data accrues, there exists the possibility for linking finer-grained, more sophisticated measures of grouping to social learning, and Section III.2 returns to this point.

II. EXAMPLES OF SOCIAL LEARNING IN NON-GROUPING SPECIES

This section compiles examples of social learning in non-grouping animals. Studies were identified through database (*Scopus, Google Scholar*) searches and *via* citations by relevant articles. The following search terms were used: 'social learning' AND non-social; 'social learning' AND non-grouping; 'social learning' AND solitary; 'social learning' AND non-colonial. Articles were read and assessed for inclusion based upon whether they documented cases of social learning or social information use when learning was plausible, in non-grouping species, per the definitions specified in Section I.3. No formal meta-analyses were attempted, and the overview presented here is descriptive. In total, 35 papers were identified, describing 46 occurrences or investigations of social learning in 35 species. These are summarised in Table 1, where they are ordered taxonomically for ease of presentation (arthropods, cephalopods, bony fish, rays and sharks, amphibians, snakes and lizards, turtles and tortoises, birds, and mammals). For each example, the behavioural context is described. These are categorised as anti-predator responses, foraging, oviposition/nest-site selection, courtship/mate choice, discrimination/motor tasks, navigation, and shelter selection. These categories are interpreted somewhat broadly, so that anti-predator responses also include responses to parasitoids, foraging incudes non-food resources, and navigation includes local enhancement and obstacle-detour tasks (Table 1). More detailed overviews of each example, including a concise description of the experimental design and any caveats relating to the results are provided as online supporting information in Table S1. Species are classified as non-grouping according to the definition in Section I.3. For some examples it is debatable whether species meet this criterion, and where relevant this is indicated in Table S1. Studies investigating social learning typically do so in only one species. A few have investigated multiple species, and some also quantify social learning in a group-living species by way of comparison. Such cases are highlighted in Table S1.

The pattern that emerges is that social learning has been described for a taxonomically broad range of non-grouping species (Fig. 1A), and in a variety of behavioural contexts (Fig. 1B). Almost half of the cases documented in Tables 1 and S1 concern arthropods (Fig. 1A). Of these the majority focus on *Drosophila* species, which aggregate around oviposition sites. Most of the examples of social learning reflect this, being concerned with laying preferences and parasitoid

avoidance (see also Nieberding *et al.*, 2021). Other arthropods represented include species of cricket, solitary bee, damselfly larvae, spiders and hermit crabs. Among vertebrates, fishes and cartilaginous fish are represented, as are, strikingly, numerous examples from lizard and turtle species, animals that have been somewhat overlooked in cognitive research (Doody *et al.*, 2013; Burghardt, 2021).

Predator and parasitoid avoidance, and foraging, are the commonest contexts in which social learning is reported (Fig. 1B). Numerous studies have also focussed on discrimination and motor tasks. The distribution of social learning contexts across the different taxonomic groups in presented in Fig. 2. It seems plausible that the focus on different contexts might reflect the backgrounds of the research groups behind the work (e.g. behavioural ecology, comparative psychology or behaviour genetics), although this is conjecture.

Almost all of the cases presented in Table 1 and Fig. 2 found evidence for social learning (35 out of 46 cases). A further eight cases demonstrate social information use, where social learning is suspected or plausible, but not demonstrated. In only three cases was no evidence for social learning found. (In one further case, a discrimination and motor task involving turtles in which demonstrators knocked over coloured bottles for a food reward (Davis, 2009; Davis & Burghardt, 2011), test subjects socially learned to approach the correct coloured bottles but failed to learn to knock them over, presenting evidence for social learning in one phase of the task but not the other, Tables 1 and S1). This high proportion of positive findings for social learning (and social information use, Fig. 2) is almost certainly an over-estimate, stemming from the 'file-drawer effect' where negative findings are less likely to be accepted for publication by editors and less likely to be submitted to journals by authors, compared to positive findings (Fanelli, 2010).

There are few examples from birds or mammals, groups well represented in the literature on social learning in group-living species. This may reflect the fact that the majority of bird and mammal models studied by social learning researchers, principally passerines, rodents and primates, are group living. Some researchers focussing on bird and mammal species have compared grouping species against species that live in smaller groups or pairs. This falls outside of the definition on 'non-grouping' used here, so these cases are excluded. For example, Günther's dik-dik (*Madoqua guentheri*), a small, territorial, non-herding antelope that occurs in monogamous pairs responded to alarm calls of heterospecifics that share common predators (Lea *et al.*, 2008). Clark's nutcrackers (*Nucifraga columbiana*) live in territorial pairs or small family groups. Templeton, Kamil & Balda (1999) compared the performance of Clark's nutcrackers in a motor and discrimination task against that of pinyon jays (*Gymnorhinus cyanocephalus*), which occur in large groups. The pinyon jays learned these tasks in fewer trials when using social information than when learning individually, while there was no difference between these rates for the Clark's nutcrackers. Pinyon jays learned the motor task through social learning in fewer trials than did the Clark's

Table 1. List of studies that investigated social learning in non-grouping species. Behavioural contexts: A-P, anti-predator; C/MC, courtship/mate choice; F, foraging; M/D, motor/discrimination; N, navigation; O/N, oviposition/nest-site selection; S, shelter selection. 'SL' indicates evidence for social learning, 'SI-use' identifies cases where only social information use was shown, and 'No learning' is used for cases where no social learning or social information use was evident. These examples are described in more detail in Table S1.

Species	Context	SL or SI-use	Reference	Notes
Arthropods				
Damselfly (larvae) *Enallagma boreale*	A-P	SL	Wisenden *et al.* (1997)	Conditioning of con- and heterospecific injury cue and predator chemical cue.
Wood cricket *Nemobius sylvestris*	A-P	SL	Coolen *et al.* (2005)	Conditioning of hiding response following exposure to conspecific hiding behaviour.
Wool-carder bee *Anthidium manicatum*	F	SI-use	Gawleta *et al.* (2005)	Avoidance of flowers marked by con- and heterospecific bees. Possible that this response arises from learned association between volatile cue and depleted nectary, but this remains to be confirmed.
Hermit crab *Coenobita compressus*	F	SI-use	Laidre (2010)	Foraging for shells, not food. Evidence for local enhancement. Plausible that hermit crabs learn to associate aggregations with resources but this remains to be tested.
Fruit fly *Drosophila melanogaster*	O/N	SL	Sarin & Dukas (2009)	Socially enhanced preference for novel oviposition substrate.
Fruit fly *D. melanogaster*	O/N	SL	Battesti *et al.* (2012)	Socially enhanced preference for novel oviposition substrate.
Fruit fly *D. melanogaster*	C/MC	SL	Mery *et al.* (2009)	Socially enhanced preference for mate phenotype.
Fruit fly *D. melanogaster*	C/MC	SL	Danchin *et al.* (2018)	Socially enhanced preference for mate phenotype.
Fruit fly *D. melanogaster*	C/MC	SL	Nöbel *et al.* (2018)	Potential socially enhanced preference for mate phenotype, but see Gilman *et al.* (2018, 2020) and Table S1 for further discussion.
Fruit fly *D. melanogaster*	A-P	SL	Kacsoh *et al.* (2015)	Interaction with parasitoid-exposed demonstrators causes female fruit flies to reduce the number of eggs they lay.
Fruit flies:			Kacsoh *et al.* (2018)	Interaction with parasitoid-exposed demonstrators causes female fruit flies to reduce the number of eggs they lay. Different demonstrator–observer pairings were examined. *D. melanogaster* and *D. simulans* learned from each other, as did *D. melanogaster* and *D. ananassae*, *D. melanogaster* and *D. kikkawai* and *D. virilis* and *D. mojavensis*. *D. melanogaster* and *D. virilis*, *D. melanogaster* and *D. equinoxialis*, and *D. melanogaster* and *D. willistoni* did not learn from each other.
D. melanogaster	A-P	SL		
D. simulans	A-P	SL		
D. ananassae	A-P	SL		
D. kikkawai	A-P	No learning		
D. willistoni	A-P	No learning		
D. equinoxialis	A-P	SL		
D. virilis	A-P	SL		
D. mojavensis	A-P	SL		
Wolf spider *Schizocosa* sp.	C/MC	SL	Fowler-Finn *et al.* (2015)	Socially enhanced preference for mate phenotype.
Blue-vented mason bee *Osmia caerulescens*	O/N	SL	Loukola *et al.* (2020)	Learned association between arbitrary symbol and cues of heterospecific nest success or failure.
Orange-vented mason bee *O. leaiana*	O/N	SL		
Cephalopods				
Common octopus *Octopus vulgaris*	M/D	SL	Fiorito & Scotto (1992)	Stimulus enhancement, socially learned to attack novel object for food reward.
Sharks and rays, and bony fishes				
Freshwater stingray *Potamotrygon castexi*	M/D	SL	Thonhauser *et al.* (2013)	Observers learned how to extract food from feeding devices significantly faster following social demonstration compared to individual, trial-and-error learning.

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Table 1. *(Cont.)*

Species	Context	SL or SI-use	Reference	Notes
Port Jackson shark *Heterodontus portusjacksoni*	N	SL	Vila Pouca *et al.* (2020)	Juvenile Port Jackson sharks socially learned to navigate a barrier through observing and interacting with conspecifics.
Fifteenspine stickleback *Spinachia spinachia*	F	SL	Webster & Laland (2017)	Test subjects socially learned the location of a feeding patch after watching heterospecific demonstrators feed there.
Bullhead sculpin *Cottus gobio*	F	SL		
Stone loach *Barbatula barbatula*	F	SL		
European flounder (juvenile) *Platichthys flesus*	F	SL		
Amphibians				
Wood frog (larvae) *Rana sylvatica*	A-P	SL	Ferrari *et al.* (2007)	Conditioning of conspecific injury cue and predator chemical cue.
Wood frog (embryos) *R. sylvatica*	A-P	SL	Mathis *et al.* (2008)	Conditioning of conspecific injury cue and predator chemical cue.
Ringed salamander (larvae) *Ambystoma annulatum*	A-P	SI-use	Crane *et al.* (2012)	Social facilitation of anti-predator behaviour plausibly may lead to social learning but yet to be demonstrated.
Ringed salamander (larvae) *A. annulatum*	F	SL	Crane *et al.* (2018)	Social learning of a novel food preference.
Wood frog (larvae) *R. sylvatica*	N	SL	Chapman *et al.* (2015)	Socially learned local enhancement using visual cues.
Spotted salamander (larvae) *A. maculatum*	N	No learning	Chapman *et al.* (2015)	No evidence for socially learned local enhancement using visual cues, same assay as wood frog tadpole example, above.
Luschan's salamanders *Mertensiella luschani*	S	SI-use	Gautier *et al.* (2006)	Salamanders use conspecific chemical cues when selecting shelters.
Snakes and lizards				
Flat lizard *Platysaurus broadleyi*	F	SI-use	Whiting & Greeff (1997)	Local enhancement. Lizards approached foraging conspecifics when feeding on fruit.
Flat lizard *P. broadleyi*	F	SI-use	Whiting & Greeff (1999)	Local enhancement. Lizards approached birds in fruit trees and on the ground. Associative learning of bird presence and fruit availability plausible but unconfirmed.
Timber rattlesnake *Crotalus horridus*	F	SI-use	Clark (2007)	Rattlesnakes used conspecific chemical cues to select ambush sites.
Skink *Eulamprus quoyii*	M/D	SL	Noble *et al.* (2014)	Skinks socially learned how to access a covered dish for a food reward following social demonstration.
Bearded dragon *Pogona vitticeps*	M/D	SL	Kis *et al.* (2015)	Bearded dragons learned how to open a sliding door (and copied opening direction) from videos of demonstrators.
Bearded dragon *P. vitticeps*	M/D	SL	Siviter *et al.* (2017)	Using the same protocol as Kis *et al.* (2015) (see above), this experiment found that bearded dragons incubated at lower temperatures learned more effectively than those incubated at warmer temperatures.
Italian wall lizard *Podarcis sicula*	M/D	SL	Damas-Moreira *et al.* (2018)	Wall lizards learned how to access a covered dish for a food reward following social demonstration from both con- and heterospecifics.
Turtles and tortoises				
Florida red-bellied cooter *Pseudemys nelson*	M/D	SL/No learning	Davis (2009); Davis & Burghardt (2011)	Demonstrators were trained to knock over coloured bottles for a food reward. Observers socially learned to approach the rewarded bottle colour but did not socially learn how to knock the bottles over.

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Table 1. *(Cont.)*

Species	Context	SL or SI-use	Reference	Notes
Red-footed tortoise *Geochelone carbonaria*	N	SL	Wilkinson *et al.* (2010)	Tortoises socially learned to navigate around an obstacle though observing conspecifics.
Birds				
Zenaida dove *Zenaida aurita*	M/D	SL	Lefebvre *et al.* (1996)	Both zenaida doves and the flocking feral pigeon (*Columba livia*) socially learned a motor task, with no species differences once species-level factors affecting learning were controlled for.
Mammals				
Collared pikas *Ochotona collaris*	A-P	SI-use	Trefry & Hik (2009)	Pikas responded to con- and heterospecific alarm calls in absence of predators. Social learning (associating alarm calls and predator presence) plausible but to be confirmed.

nutcrackers, while no species difference in learning rates was seen for the discrimination task. This study is noted here as it has been widely discussed as a test of the idea that social learning is an adaptive specialisation for group living. As mentioned in Section I.1, ascribing differences in cognitive performance between pairs of species to particular traits without controlling for other confounds can be problematic (Giraldeau & Lefebvre, 1996; Lefebvre, Palameta & Hatch, 1996). In fairness, Templeton *et al.* (1999) do emphasise that further work should consider a greater variety of tasks in a broader range of species, which could allow further insight into the generality of their findings.

III. DISCUSSION

Section II illustrates how social learning has been documented in a variety of non-grouping species, and in a range of contexts. This body of work is almost certainly
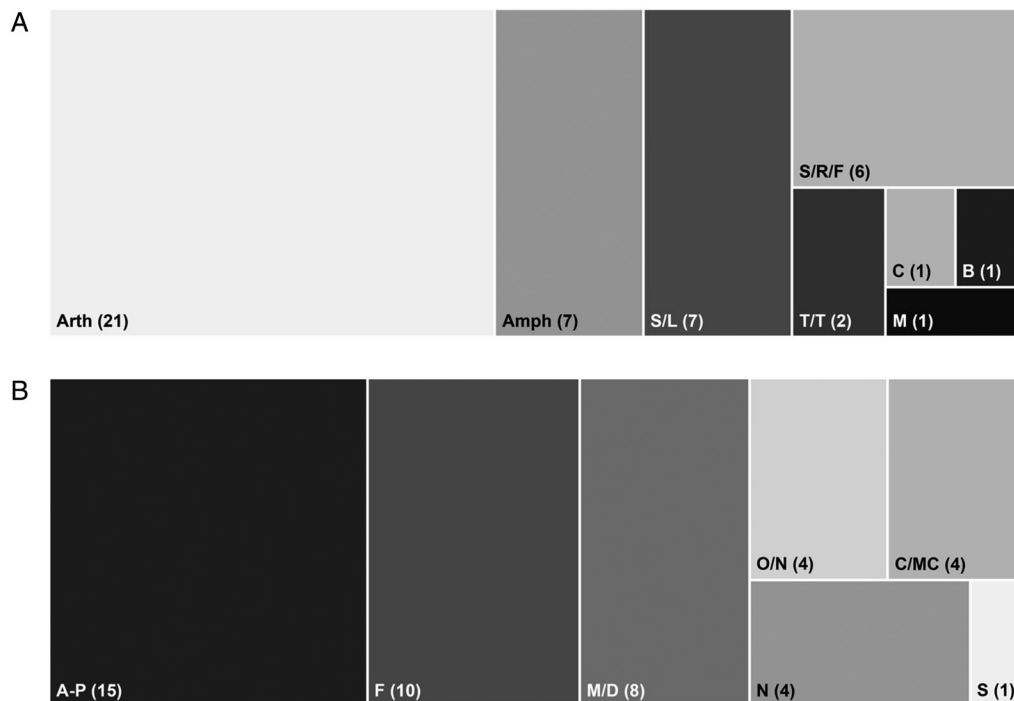

Fig. 1. Tree maps showing the proportion of studies of social learning in non-grouping animals arranged by (A) taxonomic group and (B) behavioural context. In A, Amph, amphibians; Arth, arthropods; B, birds; C, cephalopods; M, mammals; S/L, snakes and lizards; S/R/F, sharks, rays, and bony fishes; T/T, turtles and tortoises. In B, A-P, anti-predator; C/MC, courtship/mate choice; F, foraging; M/D, motor/discrimination; N, navigation; O/N, oviposition/nest-site selection; S, shelter selection. Numbers in parentheses show number of studies.
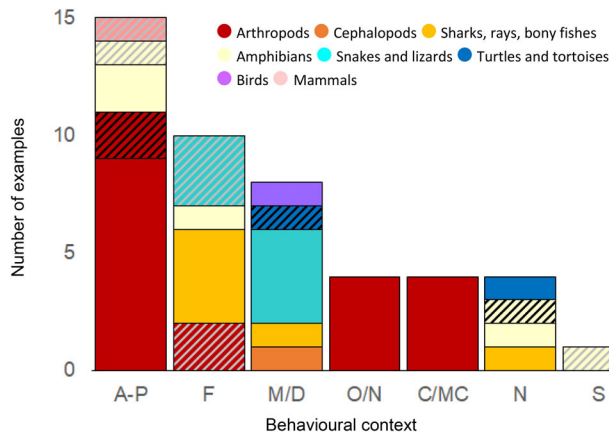
Fig. 2. Stacked chart showing the number of examples of social learning in non-grouping animals arranged by taxonomic group and behavioural context. Solid colours show studies where evidence was found for social learning. Grey hatching shows studies where evidence for social information use was provided, but not specifically for social learning. Black hatching indicates studies where no evidence for social learning or social information use was found. Behavioural contexts: A-P, anti-predator; C/MC, courtship/mate choice; F, foraging; M/D, motor/discrimination; N, navigation; O/N, oviposition/nest-site selection; S, shelter selection.

skewed by publication biases and file-drawer effects, where negative findings are harder to publish or are not submitted for publication at all, but, based on the existing evidence, it is clear that among non-grouping animals social learning is widespread. This section outlines what we can learn from this body of work. Can this tell us anything about how social learning works? And how can non-grouping species be used to provide insight into the evolution and development of social learning?

(1) What non-grouping animals can(not) tell us about social learning

The idea that social learning might be linked to group living has largely been abandoned, owing in part to a lack of evidence linking sociality to social learning ability, as well as observations that social and asocial learning performances are connected and likely measure the same process (Giraldeau & Lefebvre, 1996; Reader & Lefebvre, 2001). In fact, we should not be surprised to see widespread evidence for social learning in non-grouping species. Non-grouping does not equate to non-social, and animals that do not actively group with others are still exposed to social information and can benefit by responding to it. For non-grouping species, social information may come from conspecifics in neighbouring territories, who may be encountered, directly or indirectly, on a regular basis. They might share their range with heterospecifics with whom they have common predators or with which they compete for food. They could also aggregate with con- or heterospecifics around patchily distributed resources, such as shelters, food

or water sources. Individuals must come together to mate, and to compete with rivals for mates. Furthermore, many animals may form groups at key points during their lives, even if they spend the majority of their time alone. This applies most obviously to young born in broods or litters, who will be exposed to cues from their siblings before they disperse. Social learning has been documented in some species even during embryonic development (Mathis *et al.*, 2008), meaning that even in species where juveniles disperse immediately after hatching there may still be opportunities for social learning. In species with parental care, juveniles also have the opportunity to learn from one or both parents (and parents from young). Animals do not need to be socially attracted to others in order to gain adaptive advantage from responding to and learning from social information. Non-grouping animals may, under natural conditions, receive fewer opportunities to learn socially compared to group-living species, discussed in Section III.4, but most do not live in a social vacuum.

Examples illustrating the point that non-grouping animals are exposed to social stimuli can be drawn from some of the studies discussed in Section II. In a navigation task, red-footed tortoises (*Geochelone carbonaria*) were shown to copy the direction taken around an obstacle by a demonstrator (Wilkinson *et al.*, 2010). While these tortoises may not form social groups, in parts of their range they do sometimes aggregate when sheltering in armadillo burrows during the dry season (Noss *et al.*, 2013). Armadillo burrows are not especially complex, typically consisting of a single main tunnel, but they can sometimes have multiple exits (Clark, 1951), and the ability to learn to follow the movements of others may be useful to tortoises when moving through these burrows. Webster & Laland (2017) described social information use and social learning by several species of non-grouping fishes foraging in the presence of heterospecific demonstrators. These fishes do not form shoals as adults, but some, such as bullhead sculpin (*Cottus gobio*) and fifteen-spine sticklebacks (*Spinachia spinachia*), do exhibit parental care, with males defending broods of young post-hatching (Bisazza & Marconato, 1988; Östlund & Ahnesjö, 1998). Under these conditions, young have ready exposure to social cues from each other and their father and could benefit adaptively by responding to these.

Can the examples of social learning reviewed in Section II tell us anything about how social learning works? By themselves, probably not. It has been argued that social learning can be explained through associative mechanisms, where the stimulus is provided through the presence or actions of another animal (Heyes, 2012). In making this case some have drawn on instances of social learning in non-grouping animals, arguing that if social learning is an adaptive specialisation for making use of cues provided by other animals, then it should not be seen in non-grouping species, where infrequent exposure to social information would limit the fitness advantages necessary for social learning mechanisms to evolve (Heyes, 2012). This line of argument is problematic, however, because it fails to consider the ecology and phylogeny

of non-grouping species. If, hypothetically, social learning is an adaptive specialisation, evolutionarily distinct from learning based on asocial stimuli, then the conditions favouring its selection should apply to group-living and non-grouping animals alike, because group-living and non-grouping animals are all exposed to social information and can benefit adaptively by responding to it. It should be made clear that this review does not take the position that social learning is an adaptive specialisation. Rather, for the reasons discussed above, instances of social learning in non-grouping species cannot by themselves be mustered as evidence against this idea.

Are there other lessons to be learned about social learning from non-grouping animals? Heyes (2012) proposes that even if social learning relies on the same cognitive mechanisms as associative learning more generally, selection may operate on input mechanisms associated with the acquisition of and response to social information. These may evolve, potentially in response to the social environment animals are exposed to, and may provide a basis for selection for social learning.

(2) Phylogeny

If asocial and social learning make use of the same learning mechanisms, then selection can only act on learning generally and we should not expect to see selection for social learning specifically. However, if selection acts upon the input mechanisms that affect how animals perceive, attend to, and respond to social cues (Heyes, 2012), then we might see evidence of adaptive specialisation in these. While non-grouping animals are expected to be exposed to social information, they may differ from those that live in groups in terms of the type and frequency of social information that they are exposed to. Many kinds of social information likely have a limited range. Visual, auditory or chemical cues decay with distance from the producer and may attenuate further in cluttered or turbulent environments, so that the information content that can be gleaned from particular cues might be different for group-living species that are close to one another than for solitary animals that are physically distant. Signals may be more common among grouping than non-grouping species. Signals are evolved communications that alter the behaviour of a receiver, whose response has coevolved with the signal (Smith & Harper, 2003). In other words, selection on perception and motivation to respond to a signal on the part of the receiver is implicit in the definition. Signals are transmitted between non-grouping species too (and may be eavesdropped by non-grouping species) but might reasonably be expected to occur more frequently among animals that are in close proximity for extended periods of time. The nature of interactions between grouping animals may also differ from those experienced by non-grouping species when they meet. Social settings provide the opportunity for individual recognition, prolonged observation of complex behaviours that can be copied, the formation of dominance hierarchies and the potential for alliances,

cooperation and deceit, for example. Indeed, the demands of living in a complex social environment have previously been suggested to be major drivers of brain size and complexity and the emergence of intelligence (Byrne & Whiten, 1988; Dunbar, 1998) (although other factors, such as diet are perhaps better predictors of brain size in primates; DeCasien, Williams & Higham, 2017). While social complexity may not necessarily drive the evolution of intelligence as previously supposed, it may nevertheless shape selection on input channels associated with social learning (Heyes, 2012). This idea echoes earlier predictions about the relationship between social learning and group-living (Klopfer, 1959, 1961; discussed by Giraldeau & Lefebvre, 1996), but recasts input channels rather than the outcome – social learning itself – as being under selection.

Comparative phylogenetic analysis provides a means to understanding how input channels related to social learning might be shaped by selection. Such approaches that attempt to understand the relationship between the distribution of traits between species in relation to their phylogenetic relationships and adaptation to ecological pressures, are well established, although they do not appear to have been applied to social learning input channels before. A set of studies presenting phylogenetic analyses of the relationships between brain size, life history, group size and learning (including social learning) in primates provide insight into how researchers might proceed (Reader & Laland, 2002; Reader, Hager & Laland, 2011; Street et al., 2017). Reader & Laland, (2002) found that innovation and social learning were linked and were related to measures of brain size, but that group size and social learning frequency were unrelated. Similarly, Reader et al. (2011) showed that measures of social learning, innovation and tool use were closely related and could be explained by a single factor of general intelligence, which also did not covary with group size. The findings that different measures of learning were positively related and could be explained by a single factor are consistent with the idea that social and asocial learning rely on the same cognitive mechanisms. In a later comparative analysis of an expanded primate data set, Street et al. (2017) tested the idea that measures of brain size, longevity, social learning and group size had co-evolved. Extent of social learning was calculated using the number of reported instances of social learning for each species, corrected for estimates of research effort. Street et al. (2017) found that there was a positive relationship between the group size of primate species and reported instances of social learning. This relationship was independent of positive relationships between social learning and measured life-history traits and was not confounded by measures of brain size. The authors attribute the relationship between group size and social learning to larger or more stable groups generating more social information and relying more upon it. Street et al. (2017) noted that the earlier studies by Reader & Laland (2002) and Reader et al. (2011) did not find the same relationship between group size and (social) learning and attributed this to their more powerful phylogenetic analyses which benefitted from a greater sample size and more advanced statistical models.

These primate examples (Reader & Laland, 2002; Reader *et al.*, 2011; Street *et al.*, 2017) used recorded instances of social learning, corrected for research effort, to produce continuous measures of 'richness' of social learning for the species in their analyses, and social learning was only one component of interest among many in their studies. It should be noted that while general intelligence factors have been described for primates (Reader & Laland, 2002) and some other mammals and some bird species (Poirier *et al.*, 2020), their existence has not been widely investigated across taxa, and where researchers have tested for general intelligence, they have not always found evidence for it (Poirier *et al.*, 2020; Aellen, Burkart & Bshary, 2022). Similar approaches to those used by Reader & Laland (2002), Reader *et al.* (2011) and Street *et al.* (2017) will be necessary for properly investigating the role, if any, that living in groups plays in the evolution of input mechanisms associated with social learning. To address this question, we will require data sets for clades of species where phylogenetic relationships are known, which contain non-grouping and group living species and ideally data on measures of social complexity beyond mean group size, such as on the nature and frequency of interactions between members. We would need estimates of the frequency of social learning, ideally categorised by task, and with estimates of how proficiently individuals socially learn, and comparable data for asocial learning performance. We would also require detailed data on the input channels of interest, which may include relative size and responsiveness to stimuli of specific brain regions, and measure of attention and motivation to respond to different types of social and non-social stimulus. Studies of gene expression by gross brain region in response to different information sources can be used to identify input channels associated with perception and response to social information. For example, zebrafish (*Danio rerio*) can learn to associate social and asocial stimuli with a food reward equally effectively, however the gene of interest, *c-fos*, was expressed in different brain regions when presented with social stimuli compared to an asocial stimulus. Learning from social and asocial cues involved the same learning module, but with differences in localised activation (Pinho *et al.*, 2021). Assembling such a data set may be too tall an order for a survey of existing literature, although partial data sets could perhaps be assembled for well-studied fish or bird clades. More likely we would require further primary research to generate these data. It would be a substantial undertaking but could provide valuable insight into if and how selection shapes perception and response to social cues, how this translates into social learning, and whether species' social systems, from living alone, to living in groups with different levels of complexity of social interaction, provide a selective environment for this.

(3) Development

Social learning can be shaped by developmental factors. These include phenotypic plasticity, changes in physiology and behaviour in response to environmental cues, and more broadly, learning, which can shape how animals learn to associate social information cues with particular outcomes or resources. Phenotypic plasticity in response to the social environment experienced during ontogeny can shape the development of brain regions involved in perception of and response towards social information. Exposure to social cues in conjunction with rewarding or aversive stimuli might be necessary for animals to learn associations between these. An animal might use the posture of foraging conspecifics to learn that there is food at a particular location, but the ability to make use of this social information might depend upon the animal having previously learned that approaching group mates that adopt these postures is reliably associated with the reward of finding food. Both phenotypic plasticity and learning are likely important in the development of social learning.

Restricting test subjects' access to certain social stimuli at certain stages of their development, or even rearing them in the absence of conspecifics, is a potentially powerful way of understanding the role that the social environment plays in shaping how animals process and make use of social information. For test subjects that are habitually group living however, restriction or deprivation of social exposure may be problematic. Social deprivation may lead to developmental abnormalities, meaning that socially deprived species do not behave naturally, which complicates researchers' efforts to understand how social exposure affects social learning, and raises ethical and welfare implications (Fone & Porkess, 2008; Lihoreau, Brepson & Rivault, 2009; Ballen, Shine & Olsson, 2014; Hesse & Thünken, 2014; Schausberger, Gratzer & Strodl, 2017). Adopting non-grouping species as research subjects could potentially sidestep some of these issues, and this point is revisited at the end of this section.

(a) Developmental plasticity

The following examples demonstrate how social experience during ontogeny can shape brain region development, with implications for social learning. Note that these case studies are all concerned with group-living species. Guppies (*Poecilia reticulata*) reared at lower densities shoaled more and learned to find food faster in a socially demonstrated foraging task than did those reared at higher densities (Chapman, Ward & Krause, 2008). It is not clear whether this difference in social learning performance arose from experience alone (perhaps guppies learn to avoid foraging with others at higher densities to reduce competition, for example) or as a result of induced plasticity in brain regions affecting learning performance. The social environment experienced during development is known to affect development in brain regions such as the optic tectum in guppies (Kotrschal *et al.*, 2012) and the cerebellum (involved in cognition and locomotion) in Atlantic salmon (*Salmo salar*) (Näslund, Rosengren & Johnsson, 2019). In ninespine sticklebacks (*Pungitius pungitius*) from multiple populations raised either alone but with access to conspecific chemical cues, or in groups where chemical, visual and tactile cues were all available, fish that were reared with

access only to conspecific chemical cues developed larger olfactory bulbs, the brain region involved in receiving and processing odour, than those reared in groups. Fish raised in groups, with access to visual social stimulation, developed larger optic tecta, where visual information is processed, than those reared alone (Gonda, Herczeg & Merilä, 2009).

Similar developmental effects in relation to social environment occur in other taxa. In honeybees (*Apis melifera*), the development of mushroom bodies, brain regions involved in learning and sensory integration, is influenced by social experience early in adult life. Bees reared in isolation exhibited slower mushroom body growth compared to those reared in hives. Rearing a bee with a single dead conspecific led to increased mushroom body volumes compared to those reared alone, but this did not translate into learning differences (Maleszka *et al.*, 2009). Desert locust (*Schistocerca gregaria*) brain morphology changes as they transition from the solitarious to the gregarious, swarming phenotype. Compared to solitarious locusts, those in the gregarious phase have a greater midbrain to optic lobe ratio, a larger central complex and greater ratio of olfactory primary calyx to first olfactory neuropile. These changes may reflect the challenges of socially foraging and heightened resource competition (Ott & Rogers, 2010). Desert locusts are something of a special case, undergoing a spectacular transformation from solitary to group-living, with a range of associated changes in morphology, physiology, neurobiology and behaviour. While gregarious desert locusts exhibit local enhancement (a tendency to join others), they are not known to engage in social learning (Dukas & Simpson, 2009; Lancet & Dukas, 2012). These studies demonstrate that for some species at least, the social environment experienced during ontogeny shapes the development of brain regions that receive and process social information, potential input channels that might play a role in social learning.

(b) Experience

Simultaneous experience of social cues and resources or hazards may be necessary for animals to learn to associate the two. For example, scrounging spice finches (*Lonchura punctulate*) approach others that lower and raise their heads, a behaviour predictive of the presence of seeds on the ground (Coolen, Giraldeau & Lavoie, 2001), while minnows (*Phoxinus phoxinus*) reduced feeding rates and began to hide in response to the erratic movements of conspecifics that have detected a predator (Magurran & Higham, 1988). In both cases the previous experiences of the test subjects was unknown. If the finches had never had the experience of foraging among others, and if the minnows had never encountered a predator while in the presence of conspecifics, would they still exhibit these behaviours? This has been explicitly demonstrated for house sparrows (*Passer domesticus*). Captive-reared fledgling sparrows were allowed to join either a taxidermied demonstrator that was reliably placed in a location containing food, or a model that was situated away from food. When tested, those fledglings that had previously found food when joining

the stimulus bird were more likely to join other foragers at food patches than those that had not found food when doing so (Katsnelson *et al.*, 2008). A famous example of social learning, forming the paradigm for dozens of published experiments, is that of the social acquisition of food preferences in rats (*Rattus norvegicus*) (Galef, 1996). Rats learn preferences for novel foods after smelling the foods on the breath of conspecifics in conjunction with exhaled carbon disulphide (Galef *et al.*, 1988). This may occur in shared burrows or nests where rats interact in close proximity and groom one another, with the nests acting as information centres, providing clues about the availability and palatability of new resources. Social acquisition of food preferences may also depend on the rats' early experience. Rat mothers groom their young, but different rates. Grooming is likely rewarding to the pups, and the frequency of grooming likely determines their exposure to exhaled carbon disulphide from their mothers. As adults, rats that were groomed extensively by their mothers were shown to be capable of learning novel food preferences from conspecifics, while those that were groomed at low rates failed to learn in this way (Lindeyer, Meaney & Reader, 2013). Such experiments can provide a window into the development of social learning, and further elaborations allow insight into the degree of exposure needed for learning to occur, and the presence of sensitive phases in which learning occurs more readily.

Social learning can be more sophisticated than simply copying others or not, and mounting evidence has shown that animals integrate social information with their own experience and with cues from the environment, using information flexibly, following social learning strategies (Laland, 2004; Rendell *et al.*, 2011; Laland, Atton & Webster, 2011; Kendal *et al.*, 2018). Animals may be more likely to copy certain individuals or groups of individuals, such as familiar group members (Swaney *et al.*, 2001), or the majority of their group (Pike & Laland, 2010). They might also rely on social information to a lesser or greater extent under certain conditions, such as when the environment is unpredictable (Smolla *et al.*, 2016), when they have not recently sampled the environment for themselves (van Bergen, Coolen & Laland, 2004) or when they perceive the environment to be risky (Webster & Laland, 2008). Social learning strategies have been documented in a wide range of species and contexts, but how these rules develop and are shaped by the animals' experience is not well understood (Heyes & Pearce, 2015; Kendal *et al.*, 2018), and further work investigating the role of experience in shaping social learning rules is needed.

Broadly speaking, researchers can tackle the question of how experience shapes social learning rules using two approaches. They can present subjects with a novel task and vary their experience with social information before allowing them to attempt to solve it. Alternatively, they can raise animals under conditions in which their exposure to social cues is strictly controlled, before quantifying the ways in which they make use of social information. There are advantages and drawbacks to both approaches. In the first approach, where subjects are confronted with an unfamiliar

challenge, the prior experience of the subjects is relatively unimportant so long as the task is truly novel. A disadvantage here is that the task may sometimes need to be contrived or unnatural to ensure that it is unfamiliar. For example, Webster & Laland (2018) presented threespine sticklebacks (*Gasterosteus aculeatus*) and ninespine sticklebacks with a novel foraging task that required them to use social information to anticipate the arrival of food at the surface of the water. Test subjects were first trained to feed from either the underside of a floating tile at the water surface or from the bed of their tank and were also exposed to conspecifics feeding from the surface or the tank bottom in a factorial design. When tested, only those subjects that had both fed from the surface themselves and which had seen others doing so were able to use conspecific behaviour to anticipate food arriving at the surface. The task presented to the test subjects was unnatural (these species do not generally feed at the surface) but because of this they were able to design an experiment in which the subjects' direct and indirect (*via* social learning) experience of the task could be precisely controlled, affording an insight into the role of experience in shaping subsequent social information use in this context. The second approach, raising subjects under conditions in which their social environment is controlled, provides a powerful system for exploring the development of social learning, but can be time consuming and logistically difficult. There are also practical and ethical concerns to be surmounted, as described above. Mathis *et al.* (2008) provide an example of this approach, albeit in an unusually tractable system, social learning of anti-predator behaviour during embryonic development in wood frogs, as discussed in Tables 1 and S1.

(*c*) A role for non-grouping model species

The examples of how social experience shapes development and social learning discussed in the preceding sections all concern cases where group-living species were used as study subjects. Since many non-grouping animals are as adept at social learning as group-living species, there is scope to adopt these as models for use in longitudinal research in the development of social learning. Ultimately, the model species should be selected based upon the demands of the experiment, but it is possible to identify attributes of species that might make them useful candidates. Appropriate species could include those that disperse after birth or hatching, and that exhibit no parental care. This would allow researchers to run no- or restricted social exposure controls without the ethical and methodological issues associated with developmental behavioural abnormalities that might affect group-raised species. For non-grouping test subject species, exposure to social cues could be rigidly controlled or allowed to vary continuously in appropriately monitored captive or mesocosm populations, and their use of social learning quantified in scheduled assays that relate their performance directly to their social experience. With the increasing availability of suitable automated tracking and tagging technologies there is potential for gathering fine-grained data on the

social interactions of freely moving or mesocosm-housed animals. This in turn could allow researchers to identify opportunities for asocial and social learning in individual animals over the duration of their early development and even into their adult lives, allowing us to map these onto the development of complex social learning rules under naturally realistic conditions. Many of the accounts of social learning in non-grouping animals are presented as interesting sidenotes in our understanding of this behaviour, but there is much to be gained from adopting carefully chosen species as models in their own right to be used in thorough investigations of how social learning is shaped by developmental experience.

(4) Functional considerations

Most of the examples discussed in Section II document social learning under experimental and/or captive conditions, sometimes after periods of training. This article has argued that we should not be surprised to see social learning in non-grouping species because they are still exposed to social information and because they can benefit by responding to it. This is true, but it may often also be the case that non-grouping species are exposed to social information and socially demonstrated outcomes less frequently than are group-living species. If repeated exposure to social information is required for an animal to learn a relationship (e.g. between a body posture and the presence of food at a location), then non-grouping animals might learn this relationship more slowly than grouping species. If two species are equally capable of learning a task, relationship or outcome, then under laboratory conditions we might not see a difference in learning rates. Under natural conditions however, where one species is exposed to social information less frequently, it might be expected to acquire socially learned behaviours less frequently too. The same logic applies to relationships that can be learned readily after only one or a few observations. If the demonstrated behaviour is relatively rare, then non-grouping species, exposed to fewer social interactions, may have fewer opportunities to learn than grouping species.

Non-grouping animals may possess the cognitive mechanisms necessary to learn from others but socially learning some tasks, such as how to manufacture tools or nests or process difficult food items for example, might only be possible through prolonged observation at close proximity (Tóth *et al.*, 2020). These conditions may be more likely to be met in groups than in solitary settings, although it should be noted that animals can also learn socially to process novel foods (Terkel, 1996) and potentially to manufacture tools (Jelbert *et al.*, 2018) *via* artifacts left by others without direct social interaction. An extension of social learning is teaching, which, technically defined, occurs when a demonstrator modifies its behaviour in the presence of a naïve observer at cost or no immediate benefit to itself, leading the observer to learn a new behaviour or to improve its efficiency in engaging with the task (Caro & Hauser, 1992). Some of the

most compelling examples of teaching are seen within cooperatively breeding species, among groups of closely related individuals where inclusive fitness gains may offset the costs of teaching others (Hoppitt *et al.*, 2008; Thornton & Raihani, 2008). It seems unlikely that teaching will be found in non-grouping species.

Finally, differences in social learning rates arising from differences in social learning opportunities have implications for the spread of innovations – new behaviours, or new solutions to existing problems (Reader & Laland, 2003) – and the emergence of traditions and cultures in the wild (Tóth *et al.*, 2020). It is not enough simply to demonstrate potential to learn socially, under standardised or idealised conditions. A functional perspective on opportunity to learn is necessary if we are to understand how social learning is used in the wild. One approach may be to tailor social stimuli presentation in laboratory studies to reflect better the rate of interaction, observation, stimuli concentration or other opportunities to learn that the test subject species is likely to encounter under natural conditions. These could be systematically varied to map learning outcomes onto social information exposure frequency or intensity curves. By using data on interaction frequencies in the wild, along with direct measures of social transmission and diffusion of social learning in free-ranging non-grouping animals, researchers could obtain estimates of whether the exposure to social cues required to facilitate learning under idealised, captive conditions are actually realised under natural conditions, and even whether this varies among populations, as a function of population density, habitat fragmentation, or other factors. Attempting to extrapolate from laboratory experiments to the wild without accounting for opportunity to learn is problematic and may give rise to misleading assumptions about how animals rely on different sources of information. In other words, do non-grouping species socially acquire behaviours as rapidly and proficiently under natural conditions as they do under experimental conditions?

IV. CONCLUSIONS

(1) Social learning is widespread, both in taxonomic distribution and functional context, and the literature survey presented here demonstrates that this breadth applies to non-grouping species too. This pattern is consistent with the mechanism-focussed idea that social learning reflects general learning ability, i.e. that it uses the same cognitive mechanisms as other kinds of associative learning, but with stimuli provided by another animal. It is also consistent with ecological or functional explanations, i.e. that non-grouping does not equate to non-social, and that non-grouping animals may be frequently exposed to social cues under natural conditions, and that they stand to benefit from responding to these in the same ways as group-living species do.

(2) This article has used a binary grouping *versus* non-grouping classification, and it is acknowledged that this fails to capture the complexity of grouping behaviour. In nature, animals may switch facultatively from grouping to solitary, and they may change grouping behaviour with life history. The nature of interactions between group members also varies. Group membership may be ephemeral or stable, may involve no recognition, or class-level or even individual recognition, and may involve hierarchical, affiliative or cooperative relationships. All of these have the potential to shape opportunities for social learning. The dichotomous classification of grouping presented here should be taken as a first step, with the aim of incorporating more complexity into future reviews of the distribution of social learning.

(3) The survey presented herein is descriptive in nature, providing information on the species, the context in which social learning was observed, and, where relevant, details of the experimental design employed by the authors. There is scope in the future for more detailed formal investigation of how different species learn, that is with reference to input channels involved in social learning. This may include phylogenetic comparative approaches that draw on data sets for clades containing grouping and non-grouping species, where it may 1 day be possible to infer selection on social learning input channels through analyses that incorporate data on these input channels, social learning performance and group structural complexity.

(4) Non-grouping species may also prove useful in the experimental study of the role of plasticity and experience in shaping the development of social learning. Raising animals under conditions in which their social environment is strictly controlled provides powerful means of studying how social exposure shapes responses to social learning, and potentially the formation of social learning rules or strategies. However, housing group-living species in isolation is problematic both because it may have consequences for the development of social behaviour more generally and because it has negative welfare implications. Using non-grouping species as research models may allow researchers to sidestep these problems.

(5) Finally, it would also be informative to discover what kinds of things non-grouping species actually learn from others under natural conditions. Non-grouping animals may possess the cognitive mechanisms necessary to learn from others but learning some tasks might require multiple demonstrations to be socially acquired, while other tasks might only be learned through prolonged observation at close proximity – conditions that may be more likely to satisfied in groups than in solitary settings. This functional perspective has been overlooked, and for a rounded perspective on animal behaviour we need to consider not only what animals are capable of, but what they actually do in their day-to-day lives.

V. ACKNOWLEDGEMENTS

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VII. SUPPORTING INFORMATION

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

Table S1. Summary of studies that have investigated social learning and social information use in non-grouping animals.