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Leveraging Social Learning to Enhance Captive Animal Care and Welfare

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Abstract: From ants to zebras, animals are influenced by the behavior of others. At the simplest level, social support can reduce neophobia, increasing animals' exploration of novel spaces, foods, and other environmental stimuli. Animals can also learn new skills more quickly and more readily after observing others perform them. How then can we apply animals' proclivity to socially learn to enhance their care and welfare in captive settings? Here, I review the ways in which animals (selectively) use social information, and propose tactics for leveraging that to refine the behavioral management of captive animals: to enhance socialization techniques, enrichment strategies, and training outcomes. It is also important to consider, however, that social learning does not always promote the uniform expression of new behaviors. There are differences in animals' likelihood to seek out or use socially provided information, driven by characteristics such as species, rank, age, and personality. Additionally, social learning can result in inexact transmission or the transmission of undesirable behaviors. Thus, understanding when, how, and why animals use social information is key to developing effective strategies to improve how we care for animals across settings and, ultimately, enhance captive animal welfare.

Keywords: behavioral management; do-as-I-do; emotional contagion; enrichment; personality; positive reinforcement training; socialization; refinement; welfare

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1. Introduction

The ability to learn allows animals to respond to their (changing) environment, increasing their chances of survival and their fitness outcomes [1,2]. While learning clearly confers benefits to wild animals, what about for captive animals whose environments are less variable and more predictable? Animals do not stop learning or responding to their environment simply because they are housed in captive settings [3], and animals' proclivity to learn can be leveraged to enhance behavioral management practices [4]. Moreover, individual animals' learning is often influenced by their social environment, and such social learning can be co-opted to refine behavioral management practices and enhance captive animal welfare. These are ideas that I have explored previously in relation to the care and management of captive primates [5], but my aim with this article is to expand upon these ideas to encompass applications for animal learning across taxa and settings and to provide reference to new work that has emerged since I first wrote about this topic.

In the first half of this article, I provide an overview of what we know about how animals learn, both individually and socially, to offer a theoretical foundation for the applications to captive animal management that I propose. After this introduction I offer suggestions as to how behavioral managers, trainers, and care staff might harness animals' social environment to improve their care and welfare in captivity, focusing on ways in which social learning may be applied to enhance socialization techniques, enrichment strategies, and training outcomes. Finally, I end with some caveats and notes of caution that must be considered when applying such techniques across different species.

What an animal can learn depends on their species, rearing history, individual traits, morphology, and social environment, among other things. While I consider how intrinsic and extrinsic factors may influence animals' ability to learn a new skill, or the rate at which they learn it, it is beyond the scope of this article to fully discuss all the things that animals can learn, although I discuss a variety of examples throughout the article. Additionally, most of the examples I provide in this article relate to zoo and laboratory settings, where most of this work has been conducted. However, where appropriate, I also provide examples from agricultural settings and with domestic pets. Indeed, some of the earliest work on social learning was run with cats (e.g., [6,7]) and dogs (e.g., [8,9]), and recently researchers have returned to studying their social learning capacities in more depth (e.g., [10–13]).

2. Animal Learning

2.1. Research History and Theory

In the mid-to-late 19th Century, researchers began to methodically and experimentally study how animals learn [14–16]. The standard way to test for learning in animals is to measure changes in behavior over time, often in response to a novel challenge or stimulus. Later work by researchers including Thorndike, Pavlov, and Skinner provided more detailed accounts on the mechanisms that explain how animals learn, both via individual learning and from watching conspecifics (reviewed in [14]). In particular, Skinner's work showed that when animals make a connection between their behavior and a positive outcome the rate of that behavior will increase, and it is these principles of operant conditioning that are applied when training animals [17,18], which I discuss further in Section 3.3.

A common finding of early work exploring animal learning was that individuals had different rates of learning [15]; a finding that continues to be borne out in the data [19]. Indeed, a recent meta-analysis of research on animal's innovative behavior across taxa revealed some consistent patterns that predicted animals' likelihood to innovate [20], including that larger and older, exploratory, or neophilic animals are typically more likely to innovate than juveniles or more neophobic individuals. Such individual differences are important to consider when planning ways in which learning theory can be applied to setting training goals (e.g., [21,22]) as well as refining behavioral management practices more generally [23].

Importantly, what, when, and how animals learn depends on both intrinsic and extrinsic factors, and a series of elegant experiments with captive populations of rock pool prawns (*Palaemon* spp.) highlights how these factors may interact. Duffield et al. [24] tested prawns' problem-solving abilities across two novel tasks in two social contexts: singly or in groups of four. Additionally, the prawns were either large or small, with half of each group fed continuously while the other half were not fed the day before testing. Thus, there were four categories of test subjects: small and hungry, small and satiated, large and hungry, and large and satiated prawns. Duffield and colleagues [24] found that, when the prawns were tested by themselves, the small prawns performed better than did the large prawns, but there was no difference according to the hunger state of the individuals. However, when the prawns were tested in small social groups, size no longer predicted learning success; instead, the prawns' state of hunger mediated their proficiency, likely due to increased motivation to outcompete group mates. Such patterns are not isolated, but they underscore that, when studying animal learning, we must take into account a number of different factors about the animal and their environment, and in this article I focus on the social environment. Accordingly, I next discuss how the social landscape mediates animals' learning.

2.2. Social Learning

Reportedly, one of Oscar Wilde's many pithy quotes was "Imitation is the sincerest form of flattery that mediocrity can pay to greatness." Here, Wilde insinuates that copying others is not as noteworthy as original creativity. Of course, it is through innovation that novel ideas, customs, and technologies are born [25–28]. However, innovation can be time consuming and risky, so watching others can allow individuals to save time and to avoid potentially fatal missteps, such as eating a poisonous food. Therefore, it often pays to observe what others are doing, and to take a lead from them. However, indiscriminately copying others is also not beneficial as information may be outdated or inefficient. Furthermore, at a population level, not all animals can rely on social learning as no new behaviors or skills would enter the population. Thus, a balance is needed between individual and social learning, and individuals should be selective about who they copy, and when [29].

Heyes [30] defined social learning as learning that arises from observation of, or interaction with, another individual. Heyes [30] went on to note that social learning can also occur indirectly, from artifacts created by others. For example, a chimpanzee could, in theory, learn to crack nuts with a stone hammer either by observing a conspecific performing the behavior or by discovering nut shells and hammer tools discarded by a group mate. Hayes' definition [30] is broad and, in the 25 years since its publication, a mass of work has been conducted to further understand and define how animals socially learn [31]. Specifically, social learning is an umbrella term that describes a variety of ways in which an individual's learning is influenced by the presence or actions of others, whether via direct observation or not (Table 1) (see [31] for a detailed description of different social learning mechanisms and how they can be distinguished). For the purposes of this article, I want to consider all the ways in which an individual animal's choices and behavior may be influenced by others (i.e., socially influenced learning), not just cases of direct observational learning in which a new skill is acquired (i.e., imitation). Indeed, some have argued that much purported imitation by nonhuman animals is actually individual learning spurred by social influence ("reinnovation"), that leads to group-level consistency in behavioral forms [32,33].

Table 1. Social learning mechanisms.

Mechanism *	Description
Stimulus enhancement	When an individual's attention is drawn to a specific stimulus by the presence or actions of another individual.
Local enhancement	When an individual is more likely to approach and engage with objects at a particular location following another individual's presence at that location.
Observational conditioning	When an individual learns the relationship between two stimuli from the observation of another's interactions with them.
Response facilitation	When the probability of an individual performing an action is increased by the presence of another individual also performing that action.
Social facilitation	The process by which an individual's behavior is influenced by the mere presence of another individual. Depending on the relationship between the individuals, the social influence may promote or suppress exploration and learning.
Affordance learning	When observing the behavior of another allows an individual to learn about the physical properties of various objects, in turn allowing them to individually learn a behavior performed by the other individual.
Emulation	When observing the behavior of another allows an individual to reach the same goal but via their own means (also called goal emulation or end-state emulation).
Imitation	When an individual copies a novel (to them) action or sequence of actions after observing another individual perform those actions. For imitation to be inferred, these actions cannot have been a part of the observing individual's repertoire previously (i.e., the novelty of the copied action is what distinguishes imitation from response facilitation).

* This list of mechanisms is not exhaustive, with other texts suggesting additional forms (e.g., [31,34,35]), but for the purposes of this review, these examples provide sufficient representation of the scope of mechanisms by which social learning can occur.

Across the mechanisms outlined in Table 1, the transmission of information is passive on the part of the 'demonstrator' who is observed. This is distinct from cases of teaching, in which an individual modifies their actions with the aim of facilitating learning by the observer. In comparison to humans, examples of teaching are rare for nonhuman animals, although examples are found across taxa (for reviews see [36,37]). For the purposes of this article, and in seeking applications for social learning to the behavioral management of captive animals, I focus on the flow of information leading to behavior change without reflecting on the goals of the demonstrator or observer (i.e., whether teaching is determined or not). (Of course, in cases when a human trains an animal (see Section 3.3), the aim of the trainer is to change the animal's behavior and so this case is distinct from animal-to-animal transmission.) Moreover, for this article, I am not concerned with whether the socially influenced behavior expressed by the observer is novel to them (i.e., imitation), but rather if social influence leads to a change in the behavioral expression of observer animals, and what that change is. Thus, throughout this article, I discuss social learning in general terms, without differentiating the form of that learning, except where appropriate to considering applications and outcomes for training and management.

We find evidence for socially influenced learning across taxa [38]. Through observational, experimental, and theoretical research, we have also gained a deeper understanding as to who individuals are more likely to copy and when it pays animals to use to social information—so-called social learning strategies [29,31,39]. In many species, animals are more likely to rely on social information when they are 'uncertain' and do not have a solution for a novel problem they face (e.g., *Bombus terrestris* [40]; *Lasius niger* [41]; *Rattus norvegicus* [42]; *Pan troglodytes* [43]) and when they are young and/or of low rank (e.g., *Cyanistes caeruleus* [44]). Moreover, animals appear more likely to copy older and/or dominant individuals (e.g., *Corvus monedula* [45]; *Chlorocebus pygerythrus* [46]; *Sapajus* spp. [47]; *Pan troglodytes* [43]), their kin (e.g., *Chlorocebus pygerythrus* [48]), familiar individuals (e.g., *Sus* spp. [49]; *Taeniopygia guttata* [50]), or what the majority of their group mates are doing (e.g., *Pungitius pungitius* [51]; *Pan troglodytes* [52]). Of course, there is variation across species, with some showing no clear biases in their social learning, likely mediated by their socioecology. For example, ringdoves (*Stroptopelia risoria*) appear equally likely to copy familiar non-kin as they are to copy kin [53], while a study with Norway rats (*Rattus norvegiucus*) revealed that they preferentially copied the choices of unfamiliar, over familiar, conspecifics [54]. Furthermore, and reflecting patterns seen in individual learning, there also appear to be individual differences in different animals' propensity to seek out and/or use social information (e.g., *Parus major* [55]; *Equus caballus* [56]; *Lutrogale perspicillata* [57]; *Papio ursinus* [58]; *Pan troglodytes* [59]).

When social learning does occur in animals, the 'copying' is often inexact as imitation is rare, or even nonexistent, in nonhuman animals [32,33]. Animals do not tend to faithfully replicate every detail of an action, or sequence of actions, they observe (this is in contrast to humans, who often copy even seemingly redundant behaviors [60,61]). Rather, animals typically recreate the outcome of another's actions, but via their own method (i.e., emulation), or they simply may be drawn to a certain location by others and be 'encouraged' to individually learn due the presence of others nearby (i.e., local and stimulus enhancement), while in other cases the actions of group members may elicit the expression of an already known behavior (i.e., response facilitation) (Table 1). The fidelity of information transmission is not only of theoretical interest, but is also important to recognize if social learning is being applied to encourage captive animals to perform a new behavior or to seed a new behavioral tradition within a group (discussed in [5]). Similarly, the aforementioned biases, which describe who and when animals copy, may also impact management applications. For example, seeding a novel behavior in a group of animals that are a matrilineal species may create uniformity within matrilines but not consistency at the group level [62]. Given the variation in how, what, and who animals copy, understanding how different species obtain information and learn new skills allows us to best enhance their welfare in captivity [63]. Furthermore, it can allow us to determine how such cognitive capacities can be leveraged to aid training outcomes and other elements of behavioral management strategies [5].

3. Potential Applications of Social Learning for Captive Management

In this section I discuss the potential ways we may leverage captive animals' social environments as part of a behavioral management program. I focus on three key components of behavioral management—socialization, enrichment, and training—but I also discuss how animals' social interactions with people may interact with strategies for husbandry and training.

3.1. Socialization and Seeding New Cultural Traditions

A key priority for the behavioral management of many species is housing animals in social groups, which requires the integration of individuals and the maintenance of groups with ever-changing social dynamics, due to births, deaths, and changes in dominance structures [64]. Once socially housed, animals can be influenced by their social environment in a number of ways. For example, an individual's social group might influence their movement patterns [65], how they weigh the relative importance or value of things [66], or even their affect [67]. Moreover, an animal's social environment can impact their health and mortality [68], which not only has welfare ramifications but may also affect animals' responses to research protocols and the validity of research outcomes [69]. In captive environments, animals are exposed to a number of social influences including conspecific (and potentially heterospecific) cage mates, familiar and unfamiliar humans, and animals in neighboring enclosures. For example, Watson and Caldwell [70] found that affiliative "chirp" calls made by captive marmosets (*Callithrix jacchus*) resulted in spontaneous increases in affiliative behaviors among marmosets housed in nearby cages. Experimental work with captive chimpanzees has even demonstrated the transmission of novel problem-solving skills between groups of neighboring chimpanzees (*Pan troglodytes*) [71]. However, social influences do not have to arise from direct observation. In an experiment testing innate predator responses, Caine and Weldon [72] showed that captive red-bellied tamarins (*Saguinus labiatus*) exhibited increased fear and anxiety responses to odor cues of predators their wild counterparts naturally experience, despite the test subjects being captive born and having no direct experience with such predators. Therefore, when considering the 'social world' of a captive animal, it is important to think in broad terms about all the ways in which animals may receive socially provided information, whether directly or indirectly, both from conspecifics and heterospecifics, and also whether that is likely to be received positively or negatively.

Forming and managing social groups requires an understanding of the species' behavior, as well as that of the specific individuals in question [64]. The process of group formation can be enhanced by managing the social information that individuals receive, potentially by controlling which individuals they can observe and engage with before and during the introduction process. This can include both direct observation or the provision of video footage of the animals that are to be introduced into the group [73]. Furthermore, it is important to recognize that, in addition to monitoring their own, direct interactions with others, for some species there is evidence that individuals recognize and respond to third-party relationship dynamics (e.g., *Crocuta crocuta* [74]; *Callithrix jacchus* [75]; *Macaca arctoides* [76]; *Pan troglodytes* [77]). Thus, hearing or seeing others not only allows for the transmission of information about skills and behaviors (as discussed above), but it also allows animals to learn about the rank, status, and relationships of other group members. Moreover, animals can gain information about the wellbeing and affect of group mates by observing their behavior posture, and, potentially, facial expressions; information that behavioral managers can also use to evaluate animal welfare (e.g., [78–80]). Such social information about individual identity and wellbeing can also be transmitted via non-visual pathways in the form of vocalizations [81].

The social contagion of fear among animals has long been recognized [82], but emerging work suggests that animals are also influenced by positive states experienced by conspecifics (e.g., [83,84]), both of which have important ramifications for the care and management of socially housed animals (Düpjan et al. [85] provide a review). This is true for socially housed animals, but also for singly housed animals that have visual or auditory contact with other individuals. Thus, it is worth thinking in very broad terms about an animal's social world and how social cues—both from conspecifics and human care takers—can and will influence animals' decision making, behavior, and welfare [86,87]. Importantly, emotional contagion can be leveraged in beneficial ways. For example, and reflecting a report of a more pacific culture emerging in a wild baboon (*Papio anubis*) troop when despotic dominant males died [88], Watson and colleagues [89] played affiliative vocalizations to groups of captive marmosets (*Callithrix jacchus*) that then exhibited increased rates of affiliative behaviors, although the effects were not long lasting. While Watson et al. [89] ran their study with socially stable groups, future work could explore how such interventions may help stabilize group dynamics or aid the integration of new group members during an introduction process. Shedding more light on monkeys' responses to conspecific vocalizations, more recent work with a different population of common marmosets used thermal imaging to measure changings in monkeys' nasal temperature, as a proxy for changes in arousal, in response to playbacks of different conspecific calls. While Ermatinger et al. [90] reported that the marmosets showed increased arousal (a decrease in nasal temperature) to negative calls (aggressive vocalizations), only males showed an increase in nasal temperature after hearing positive (food) calls. This highlights the marmosets' differential response to different vocalizations, but also suggests that such playbacks may be received differently by male and female monkeys. In a more direct test of social influence on behavior, Claidière et al. [91] tested chimpanzees' (*Pan troglodytes*) proclivity to share food with others. They then created an intervention in which the subjects were partnered with a chimpanzee that shared food with them. After this experience, the chimpanzees were found to be more likely to then share food with other chimpanzees. Thus, experiencing food sharing primed the chimpanzees to share more themselves (i.e., downstream reciprocity).

Social learning can also be applied to enable animals to learn species-typical behaviors, which may aid their social integration into captive groups or prepare them for reintroduction into the wild. Individuals that experience atypical rearing histories (e.g., being human raised) may be less able to assimilate into social groups later in life due to their lack of exposure to species-typical behaviors during development (e.g., [92,93]). While hand-rearing is not ideal, in some cases it is necessary (e.g., in cases of maternal rejection) and so research has explored ways in which the long-term effects of such practices can be ameliorated. Much work studying the long-term impacts of hand-rearing and subsequent socialization strategies has focused on primates (e.g., [94,95]) and fewer published reports exist for non-primates. However, a documented case of the hand-rearing of a Sumatran tiger cub (*Panthera tigris sumatrae*) demonstrated the importance of regular socialization with conspecifics during rearing that aided later reintroduction to the social group and the expression of species-typical behaviors [96]. While this was a case study, a more controlled experimental study with black-tailed prairie dogs (*Cynomys ludovicianus*) demonstrated how social learning may help ameliorate the impacts of nursery rearing. Captive-born black-tailed prairie dogs were trained in antipredator behaviors in response to three animals (a ferret, a rattlesnake, and a hawk) either in the presence of an adult demonstrator or alone [97]. Prairie dogs trained with an experienced adult were more wary of the predator animals, than those trained alone, and had greater survivorship a year after reintroduction to the wild. The authors [97] concluded that "social transmission of antipredator behaviour during training can enhance long-term survival following release and that as long as a social training regime is used, predator avoidance training can emulate experience acquired in the wild" (p. 567). Socially acquired predator recognition has been demonstrated in a number of species and this study demonstrated how social learning can be leveraged to aid with the management and care of captive animals (see also [98]).

3.2. Enrichment

In addition to socialization, a cornerstone of behavioral management programs is the provision of enrichment for captive animals. Environmental enrichment is designed to foster the expression of species typical behaviors and create dynamic environments for captive animals, which in turn enhances their welfare [64,99,100]. Enrichment is typically classified into different categories according to the stimulation it provides and the behaviors it is designed to elicit [99], although the specific forms of enrichment will vary depending on the target species [100]. In very broad terms, enrichment is either social (fosters social interaction among animals), physical (requires some kind of manipulation or encourages physical movement), cognitive (promotes problem solving), food-based (food of different flavors, textures, or colors), or sensory (typically olfactory or auditory stimuli are presented), although there may be overlap across these categories and more fine-grained delineations have also been offered [99]. How then does the provision of enrichment interface with captive animals' social environment?

Perhaps the clearest link between an animal's social environment and the provision of enrichment is in the form of social enrichment [99]. Social enrichment can be provided via direct socialization, as discussed in Section 3.1, or enrichment devices can be offered that facilitate or mimic social interactions. For example, animals can be given mirrors to allow them to view and engage with animals in neighboring enclosures [101,102] or they may be shown video footage of conspecifics [103,104]. However, the efficacy of such enrichment as a substitute for social housing has been questioned [105,106] and animals' likelihood of engaging with such enrichment may differ across species or based on their experience with such stimuli [107].

Beyond social enrichment, animals' engagement with other forms of (non-social) enrichment can be enhanced via social learning. Even early work studying social influences on animal behavior demonstrated the importance of social support for exploration and learning. For example, in 1955, Davitz and Mason [108] reported that fearful rats showed less freezing behavior and more exploration when tested with conspecifics. When with a social cohort, animals are more likely to explore novel spaces, eat novel foods, and engage with novel stimuli, and this social information can also shape individuals' preferences. For example, vervet monkeys (*Chlorocebus aethiops*) develop food preferences from observing the choices of others [109], and zebra finches (*Taeniopygia guttata*) are more likely to use the same color nesting material as used by familiar individuals as compared to the color chosen by unfamiliar individuals [50]. Thus, observing others engaging with novel enrichment devices can encourage interaction by naïve group members [110]. In this way, social support can be leveraged to encourage animals to engage with novel enrichment, but also with other novel stimuli, such as unfamiliar husbandry and veterinary equipment or newly introduced foods, by introducing them to a group of animals rather than to isolated individuals.

As noted above, there are consistent individual differences in animal's exploration rates [111] and so bolder individuals may be more likely to engage with enrichment devices sooner, in turn encouraging other group members to do so themselves (e.g., via stimulus enhancement). This process could be augmented by preemptively training a (more bold or dominant) group member to engage with the novel stimulus and to act as a 'demonstrator' for their group (e.g., [112]) (see also Section 3.3).

Social learning can facilitate animals' use of novel enrichment, but can enrichment promote social learning? By offering novel and/or complex stimuli, environmental enrichment encourages informal learning by animals. While much work has presented the ways in which enrichment can stimulate individual learning in animals (reviewed in [113]), less attention has been given to the interplay between environmental enrichment and social learning. However, a study with fish (*Gadus morhua*) revealed that young fish reared in enriched habitats later showed better success in a social learning task than did fish raised without enrichment [114]. Furthermore, recent work has also focused on investigating how captive animals' social dynamics may be influenced by the provision of enrichment (e.g., [115,116]). For example, an experimental evaluation of the provision of enrichment to mice in a laboratory setting revealed that mice housed with environmental enrichment devoted more time to social behaviors than their counterparts housed in standard caging [117], although rates of agonistic behavior were also higher in the enriched groups. This research highlights the interplay between social learning, which may encourage engagement with novel enrichment, and the role enrichment may play in fostering socialization and social learning.

3.3. Training

Learning new skills and solving problems is enriching to captive animals [4] and training confers benefits to both animals and staff [118–120]. Fundamentally, training allows people to have a dialogue with animals. Moreover, training creates greater choice and control for captive animals and the training process can be cognitively stimulating for animals, offering enrichment benefits in of itself. A key benefit of training animals is that it allows them to voluntarily participate in various husbandry or research procedures, which can reduce or eliminate the need for restraint, further enhancing the animals' welfare [121,122]. Given the benefits that training confers, how can we facilitate the training process further via the application of social learning? As many excellent reviews on learning theory and animal training have been published (e.g., [17,123,124]), the aim of this next section is not to provide a training 'how to' but rather an overview of how social information might be leveraged to aid training (see also [5]).

Social support encourages exploration and learning in animals, as discussed in Section 3.2. For example, research has shown that the number of guppies (*Poecilia reticulata*) in a shoal is negatively correlated with their latency to solve novel mazes [125], while juvenile marmosets (*Callithrix jacchus*) are more likely to eat a novel food when with their family group as opposed to when tested alone [126]. Accordingly, Prescott and Buchanan-Smith [127] noted that " ... individual primates often are more relaxed when in groups than when isolated and can learn socially through observation of their conspecifics" (p. 159), and experimental data have supported this (e.g., [128]). Therefore, can social facilitation and other forms of social learning be leveraged to encourage participation in training sessions and learning of novel behaviors during training sessions?

Training animals in a social setting may expedite the training process as animals will be more exploratory given the social support of group mates, and individuals may even learn directly from observing the actions of others [5]. This idea was proposed by Prescott and Buchanan-Smith [127] who suggested that "allowing animals to be observers during training sessions may enable them to be trained more rapidly because of their familiarity with the training situation" (p. 159). However, training animals in a group setting may be seen as a challenge [129] and some tests of social learning have revealed that the presence of conspecifics creates a distraction, leading to reduced learning by observers as compared to animals tested alone [130]. Therefore, it is important to develop strategies to facilitate both training and social learning when working with groups of animals, such as through cooperative training techniques in which dominant individuals are reinforced for allowing subordinate animals to participate and to receive their own reinforcers [131].

In an early experiment of domestic cats' social learning conducted in the 1940s, the authors [6] concluded that "observation of fifteen skilled performances is much less beneficial than observation of the learning process" (p. 81). Despite this proposal that the observation of other animals being trained should expedite learning, little empirical work has subsequently validated this. However, controlled experimental work exploring this with primates is emerging, and suggests that allowing individuals to observe others being trained reduces the time needed for those observers to subsequently be trained on the same behaviors (e.g., [132–134]). This, of course, has both practical and welfare benefits, as animals are granted social support and the training process is expedited. Furthermore, some studies have suggested that social information can be provided via video footage [135], creating further refinements to the training process. However, the relative saliency of video footage, as compared to live observation, has been questioned [107] and the efficacy of using video likely varies across species, depending on their vision and experience with observing videos [136]. To date, most of the behaviors examined in these tests of social learning of training were simple (e.g., target training), and so more work is needed to validate the benefits of observing training of more complex, aversive, or multi-step behaviors and how social learning augments different forms of training and reinforcement strategies.

Another way that social learning can be leveraged to aid husbandry practices is via the introduction of novel behaviors to a group of animals [5]. For example, one individual in a group could be trained to perform a new behavior, and other individuals in the group could learn via observation of that trained individual even if they did not observe the "demonstrator" being trained (e.g., [112,128]). This may negate the need to train each individual in the group in turn. In this way, animals can learn different behaviors or skills that enhance how we manage them in captivity, such as learning to stand on a weighing scale, learning to shift from one space to another, or learning how to access food from a new feeding device. Given experimental work showing that animals can learn to solve new routes through mazes by following or observing others [137–139], a key way in which training in a social setting may aid husbandry is when teaching animals to shift from one enclosure to another or from their home cage to a transport box [140,141]. Although a relatively simple behavior, shifting animals between spaces is a key management tool for many captive species and across settings. Demonstrating the applicability of this, one study with rats showed that rats could be taught to move between cages either via direct training or from observing conspecifics who had previously been trained [142].

3.4. Learning from Humans

Captive animals' social environments also include humans, and their relationships with humans can directly impact their welfare [143]. Humans control many aspects of captive animals' lives, and animals regularly encounter both familiar and unfamiliar people. Familiar people can include care staff, veterinarians, trainers, and researchers, and, even though all may be familiar to the animals, the animals' relationships and experiences with each person will differ greatly. In zoos, most animals are also exposed to unfamiliar people on a regular basis (i.e., visitors [144]), although animals in other captive contexts may also encounter unfamiliar people [145]. Familiar people, in particular care takers and trainers, offer a considerable source of social information for captive animals, especially in the context of training. Moreover, it has been suggested that animals learn better from familiar people [146], likely due to the trust established with them, although this may also reflect a "copy familiar" social learning bias [29,39]. Despite this, in zoo settings, where animals encounter unfamiliar visitors as well as familiar and trained care staff [147], animals may learn from, and copy, visitors' behavior [148]. However, such copying is spontaneous, and may not be beneficial, which I discuss more in Section 4.3.

While there is some tentative evidence that exotic species can learn from observing the actions of humans [148–150], domesticated species, which are more attuned to human behavior, appear to be able to learn from observing people. For example, in a test of spontaneous social learning, Pongrácz et al. [151] showed that dogs (*Canis familiaris*) learned how to solve a task after first observing a human perform it, and although the dogs did not faithfully replicate all aspects of the person's behavior, they were quicker to solve the task than when they were not provided with any social information. Furthermore, this study suggested that the dogs were able to learn equally well from familiar people or strangers, due to their long domestication and cohabitation with people. Similarly, a study with horses (*Equus caballus*) showed that more horses that had observed a familiar person open a novel feeding device were then able to do so themselves as compared to horses that received no such demonstration [152]. However, only eight of the 12 horses that observed a person demonstrate the solution were successful [152]. This highlights that, while social learning can enhance learning outcomes, success is not universal and marked individual differences exist across animals in their proclivity to use social information.

A fundamental component of training protocols is that a specific behavior is elicited by a specific command or cue. Thus, a trainer can not only train an animal *what* to do, but also *when* to do it. Considerations of cueing are also important when thinking about social learning from humans' actions, both when a person intentionally or unintentionally cues an animal [153]. To that end, researchers have explored what prompts animals to copy humans [148]. For example, Range et al. [154] reported that dogs with training experience were more likely to copy humans than were less-experienced dogs. Research with dogs has also shown that they are more likely to learn from a human demonstrator who offers verbal attention-getting sounds during their demonstration [155]. In a more directed way of testing training cues and social learning, some limited research has also explored the applicability of the "do-as-I-do" test for training. In this approach, an animal is trained to copy the actions of a person, on command ("copy this!"). Typically, the animal is trained to copy a set of behaviors, then novel ones are later introduced to the animal to determine if they can spontaneously copy them when asked to do so [156], sometimes after a delay [157]. This approach has been applied to a range of exotic and domestic species (reviewed in [5]), and may offer a way to speed up the training process if animals can generalize the "copy this!" command and spontaneously replicate new behaviors without each needing to be trained. However, there has only been limited research exploring the relative efficacy of this approach as compared to more standard training methods, and with most evaluations having been run with dogs [158,159]. However, work to date suggests that this may be an efficient way to train animals, although the success of this approach is mediated by both the relationship between the animal and trainer and the complexity of the behavior being trained (reviewed in [5]).

4. Considerations and Caveats

In the previous sections, I discussed how animals can learn new skills from observing others and how social learning can be leveraged to enhance captive care more generally. Unfortunately, to date, there have not been extensive research efforts dedicated to testing the efficacy of the approaches I propose here. Thus, while animals' social learning skills have certainly been well documented, the applicability of this to management is less well known. Therefore, I outline next a number of key considerations that should be recognized by those hoping to apply these principles with the animals they care for.

4.1. Learning Modalities

It is important to remember that not all species get their social information in the same way. Humans primarily rely on visual information when learning from others, and it can be easy to be anthropocentric when thinking about how animals receive social information. However, social information can be transmitted via other modalities. For example, many insect and fish species transmit and receive social information via pheromones (e.g., [41,160]), while other taxa socially learn auditory information, such as vocalizations (e.g., [161,162]). Even within mammals there is variation in their primary sensory modalities—elephants, for example, have relatively poor vision, but can recognize individuals from their vocalizations and can use odor cues to locate group members [163]—while rats can form food preferences from the smell of others' breath after they have eaten different foodstuffs [54]. There may well also be differences in social information transmission in diurnal as compared to nocturnal species. Moreover, and likely due to the focus on visual pathways for information transmission in studies of animal social learning, most research has overlooked the importance of tactile interactions [164]. However, as Monsó and Wrage [165] note, given the universality of touch across social animals "discriminative touch thus likely constitutes the very first source of social information" (p. 9). Therefore, when applying social learning to behavioral management practices, the information should be provided in ways that are relevant and accessible to the animals themselves.

4.2. Individual and Species Differences

Not only is there variation across species in the mode through which they gain social information, but there are also differences in species' and groups' social structures that influence the availability and flow of information [5,166,167]. Thus, it is important to consider the manner with which new information is presented and how it may spread within a group. For example, socially gregarious species may be more prone to social learning than solitary species (although see [168,169]), and a species' natural ecology may also shape how they learn and what they can learn [170].

Within social groups, dominance hierarchies and kin networks will mediate which individuals get access to social information and when. For example, a study of wild birds (*Parus major*), revealed that individuals with more social connections acquired novel information more quickly than peripheral group members [171]. Additionally, because vervet monkeys (*Chlorocebus pygerythrus*) are a matrilineal species, and are more likely to copy related individuals [48,172], the transmission of information can be restricted within matrilines [62]. Furthermore, even if lower-ranked individuals within a group can access social information, they may not be able to express the newly learned behavior due to inhibition of behavior expression ([173]; not to be confused with behavioral inhibition [174]). Thus, a lack of behavior change may not necessarily indicate a lack of learning.

Lastly, and group dynamics notwithstanding, certain individuals are simply more likely to seek out and use social information than others, and certain individuals are likely better able to learn new skills than others, due to demographic, social, and personality factors (e.g., [175–177]—see [178] for a comprehensive discussion of this topic). Of course, within a captive setting, the physical environment may also constrain the transmission of social information, as discussed in Hopper [5]. For example, singly housed animals may be less able to learn from animals in neighboring enclosures than they would from a cage mate [5,179].

4.3. Spontaneous Social Learning of Unanticipated or Negative Behaviors

Given many species' natural proclivity to attend to, and be influenced by, the behavior of others, it is likely that social learning is occurring all the time. Therefore, those who care for animals and design behavioral management programs should also consider all the different ways in which animals may gain social information.

While animals typically learn from conspecifics, they can also learn to interpret the behavior and cues of heterospecifics, such as in cases when birds and primates learn and respond to the calls of heterospecific animals in their environment (e.g., [180,181]). In captivity, animals also learn from, and copy, heterospecifics. For example, observations of a beluga whale (*Delphinapterus leucas*) housed with bottlenose dolphin (*Tursiops truncatus*), revealed that the whale could reproduce dolphin vocalizations [161]. While seemingly harmless, learning the vocalizations of a heterospecific may impact an animal's later success at socialization with conspecifics. Therefore, while social learning can facilitate faster and less costly learning, animals do not always distinguish between positive/useful behaviors and negative/harmful behaviors. Indeed, cannibalistic behavior in chickens has been shown to be transmitted via social learning [182], as has coprophagy in primates [183,184]. As noted in Section 3.1, the social contagion of fear has also been studied for a number of years [82], highlighting that negative or undesirable information may be transmitted in captive settings [185]. For example, pigs (*Sus scrofa*) that have been previously restrained show increased levels of stress when they later observe pen mates being restrained, even though they themselves are not restrained in that moment [86].

Animals in captivity interact with humans regularly, and in a variety of ways, and transmission of information can occur intentionally, as discussed in Section 3.3, or unintentionally (i.e., spontaneous copying or accidental cuing), which is also important to consider [148,153]. For example, one report documented evidence of an orangutan (*Pongo pygmaeus*) spontaneously copying whistling from humans [186]. Furthermore, captive animals often show anticipatory behavior [187] or produce specific attention-getting calls or gestures to attract people's attention [188,189]. Given this, it is important to recognize more generally that the presence and behavior of humans can influence animals' behavior and welfare [190]. Moreover, informal human–animal interactions may not always confer welfare benefits [191], although playful handling of rats has been shown to reduce the rats' fear of caretakers [192]. It has been shown that the identity and experience of the person providing care can influence an animal's welfare [193–195] and a recent study with pigs demonstrated that animals that had seen a stockperson using gentle handling techniques on pen mates were more likely to approach and make contact with the stockperson than pigs who had not received such social information [87]. From this, the authors [87] concluded that "pigs can learn to perceive humans positively through observational social learning" (p. 127). Given this, the selection and training of staff is key [196–198], although the efficacy of such training depends on how it is administered [199].

4.4. What Can Be Copied?

As I have mentioned throughout this article, while animals of many species appear able to socially learn from others, how faithfully they copy is variable and often unpredictable. The reliability of transmission is mediated by individual and species characteristics of both the observer and who they are observing, the behavior to-be copied, and the context within which learning is occurring. The fidelity with which animals copy one another (Table 1) has been a hot topic amongst academic researchers interested in studying behavioral traditions and the emergence of cultures [31,34]; but, of course, this also has ramifications for the applications of social learning in captive management settings or requirements [5].

Within the field of primate social learning, a theoretical debate has been simmering about the role of social learning in primate cultures. Specifically, there is disagreement over what skills primates are capable of copying from others and whether high-fidelity copying is required for the transmission of behaviors [200,201]. Tennie and colleagues have argued that what differentiates human culture from that of apes is that we alone can copy behaviors that we could not invent ourselves, whereas apes are restricted to copy behaviors within their "Zone of Latent Solutions" [32,33,200]. This Zone of Latent Solutions hypothesis posits that apes are influenced by the behavior and presence of others to individually discover solutions ("reinnovation"). This theory does not rule out the role of social influences in the expression of behaviors by individuals, or the emergence of traditions within groups, but does consider certain behaviors as being beyond the capacity of nonhumans to be copied [200,202].

While this debate may seem just one of theory and semantics, it may also have relevance to the proposed application of social learning to aid training and captive management. Specifically, if animals cannot copy behaviors that they could not themselves individually discover [202], this may limit what behaviors can be introduced to captive groups of animals via social learning alone. Obviously, this does not negate that social support will encourage exploration of novel stimuli, nor observation of training sessions, but that very complex behaviors cannot be expected to be spontaneously transmitted within a group. Rather, social support and social learning facilitates and speeds up the process by which individual animals learn new skills via human-directed training, and training may be required for the introduction of more complex behaviors [149]. Gaining a more detailed understanding of what can, and cannot, be socially learned without additional scaffolding from training sessions, would therefore be very beneficial for applications to captive management.

5. Conclusions

Captive animals are continually exposed to social information provided from a range of sources (e.g., their cage mates, animals in neighboring enclosures, and people), which influences their behavior and welfare. Furthermore, social information, provided intentionally or unintentionally, can lead to the transmission of both desirable and undesirable behaviors. Recognizing these different sources of information, and how animals may attend to them, is key when considering ways in which we can actively leverage social information to enhance behavioral management strategies. Furthermore, identifying the modality via which an animal primarily learns, their motivation to learn, and their receptivity to social information will further enhance the success of training outcomes that incorporate social learning into the process. More research is needed to evaluate the feasibility of the approaches I have outlined here, but with care and intentionality, animals' use of socially provided information can be leveraged to expedite training and improve the welfare of captive animals for a variety of species and in numerous contexts.

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