Identifying social learning through peering: predictions and recommendations

Elisa Bandini[1], T Revathe[2], Elliot Howard-Spink[2,3,4] & Caroline Schuppli[2]

[1]*The Interdisciplinary Center for Archaeology and the Evolution of Human Behaviour (ICArEHB), Universidade do Algarve, 8005-139 Faro, Portugal*
[2]*Development and Evolution of Cognition Research Group, Max Planck Institute of Animal Behavior, Konstanz, Germany*
[3]*School for Biological and Behavioural Sciences, Queen Mary University of London, London, UK*
[4]*Evolutionary Cognition Group, Department of Evolutionary Anthropology, The University of Zürich, Switzerland*

Abstract

Many species exhibit the capacity for social learning. However, the importance of social learning for wild individuals' daily lives and its role in the emergence of animal culture remains to be uncovered. As observing conspecifics may provide a relatively safe and efficient means of learning, visual species may use observational learning to acquire various types of information from others. However, identifying precisely when social observation leads to information transmission can be challenging. A behaviour known as "peering" (i.e., "close-range and sustained observation of the activities of conspecifics") is being studied increasingly frequently across primate species in the wild as a potential indicator of social learning. Growing individual-level observational datasets of peering behaviour and its contexts present unique opportunities to study if and how peering leads to learning. However, to determine whether peering leads to observational social learning, researchers must systematically and carefully validate whether peering events facilitate information transmission between individuals, and do not solely serve social functions unrelated to learning. In this piece, we outline key predictions and limitations associated with identifying learning through peering, and provide concrete recommendations for the collection and analysis of data to evaluate our predictions. Despite focusing primarily on primates, our predictions and recommendations can be applied to any visual species that acquires parts of their cultural repertoire via observational social learning.

Key Words: Animal Culture, Observational Social Learning, Individual learning, Primate Behaviour, Animal learning, Animal skill, Animal knowledge repertoires, Visual learning

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1. Introduction

Over half a century of research has revealed that non-human animals (henceforth animals) create and maintain their own local cultures in the wild. Whilst there are several definitions of culture in the literature, one of the most common and inclusive definitions classifies culture as: "*all behaviours and knowledge that are acquired and passed on within and between generations through social learning*" (Boyd & Richerson, 1985). Despite decades of research, the importance of culturally transmitted skills and knowledge to wild animals' survival and evolution continues to be an open question (Whiten, 2021; Boyd & Richardson 2024). Furthermore, the dynamics through which these cultures emerge at the proximate and ultimate levels remain debated.

To identify culture in wild animal populations, researchers have classically focused on cultural elements that are conspicuous and often elaborate, such as technical foraging behaviours, including tool use (e.g., Mann et al., 2012; Biro et al., 2003), animal songs and/or vocalisations (e.g., Slater & Ince, 1979; Garland & McGregor, 2020), migratory and large-scale movement patterns (e.g., Sasaki & Biro, 2017; Jesmer et al., 2018), and social behaviours (e.g., van Leeuwen & Hoppit, 2023). However, a large proportion of the skill and knowledge repertoires that animals acquire during their lives consists of "simpler" behaviours across different contexts, as well as basic information on ecological and social resources (Whiten & van Der Waal, 2018; Whiten et al., 2021; Schuppli & van Schaik 2019). How these behaviours are acquired remains largely understudied. Given that many species are capable of social learning under experimental conditions, and the adaptive benefits of social learning (Harrison et al., 2024: Kendal et al., 2025; van Schaik et al., 2011: Rendell et al., 2010 but see Feldman et al., 1996; Laland and Williams, 1998; Nocera et al., 2006 for discussions on the costs of social learning), the next step is understanding to what extent species use social learning to acquire aspects of their behavioural repertoires (see Box 1 and Heyes, 1994; Galef & Laland, 2005, van Schaik 2010). So far, animal culture research has focused a lot on supposed ***know-how*** elements of culture (see Tennie, 2023 and Box 1) even though, just as in human culture, animal culture is likely composed of socially learned elements containing different information types (e.g., *know-when*, *know-where*, etc. see Box 1). Grasping the true extent of naturally-occurring animal cultures (i.e., those which spontaneously emerge as part of habitual behaviours of wild individuals, rather than due to experiments in captive or wild settings) requires mapping *all* socially transmitted behavioural elements in wild populations, irrespective of their salience, complexity, or type of transmitted information. Only then can researchers evaluate the true extent to which culture shapes wild animals' daily lives.

Detecting naturally-occurring cultures in wild populations is challenging. One of the most commonly adopted methods to study animal culture so far has been "the method of exclusion", which infers social learning via observed variation in behavioural repertoires between populations (also called the ethnographic method; Whiten et al., 1999; Whiten & Boesch, 2001; Krützen et al., 2011; Santorelli et al., 2011; Robbins et al., 2016). As such, the method of exclusion attempts to identify the results of social transmission and thus i) utilizes indirect evidence of social learning and ii) can only capture social learning if it results in group-level variation.

However, it is becoming increasingly clear that this method cannot robustly rule out confounding factors that may also lead to the emergence of behavioural variations (e.g., genetic and environmental differences, which are often not systematically controlled for because of feasibility constraints; see Humle, 2006). As a consequence, the method of exclusion can lead to inferring social learning when it is not present (i.e., false positive inferences, see Galef, 1992; Laland & Janik, 2006; Laland & Galef, 2009; Motes-Rodrigo & Tennie, 2021; Acerbi et al., 2022). Equally, not all social learning results in population-level behavioural variations, and social learning itself often has genetic and ecological correlates (van Schaik & Burkart, 2011; Acerbi et al., 2012). In other words, the method of exclusion may overlook some socially transmitted behaviours as well (i.e., leading to false negative inferences). Therefore, whilst a valuable proof of principle, the method of exclusion can both over- and underestimate the size of cultural repertoires (Schuppli & van Schaik 2019). Furthermore, because the method of exclusion assesses culture at the population level, it offers only limited insight into the factors that facilitate or hinder individuals from social learning, and cannot distinguish between types of social learning, and thus provides only limited understanding of cultural dynamics.

To gain a comprehensive understanding of animal culture, including the breadth of culturally transmitted information and the dynamics that underlie social transmission, we need to systematically study direct incidences of naturally occurring social learning at the individual level. Incidents of social learning have previously been studied from the spread of new behaviours through social groups (e.g., Biro et al., 2003; Mann et al., 2012; Hobaiter et al., 2014; Lamon et al., 2017). However, this requires witnessing the origin(s) of innovation and its subsequent spread (or at least the early phases thereof), which is bound to be rare in wild settings. Social learning can also be detected through linking behavioural indicators of this type of learning—i.e., identifiable behaviours suggesting that an individual is obtaining information through social interactions or observations—with contexts in which learning is predicted supported by evidence of behavioural change (e.g., Schuppli et al., 2016a; Musgrave et al., 2016; Estienne et al., 2019a,b). Among the currently available methods used to assess animal culture, studying social learning via its behavioural indicators has the potential to yield comprehensive catalogues of candidate socially-learned behaviours (regardless of the form of social learning being adopted; Schuppli & van Schaik, 2019).

Studying behavioural indicators of social learning requires knowledge of how information is transferred between individuals. In visual species, close-range visual observation of conspecifics provides opportunities for social learning (of various *know-x* types; see also Zentall, 2012; Carcea & Froemke, 2019). Learning through observing conspecifics (henceforth called "observational social learning") allows animals to focus on relevant information whilst largely circumventing some of the risks of unguided individual exploration (e.g., injury, poisoning, or predation; van Schaik & Burkart 2011, Forss et al., 2017, Montrey & Shultz 2020). Learning through observation also avoids potentially risky direct physical contact with conspecifics, which is required in interactive forms of social learning (e.g., food sharing) but can elicit aggression or facilitate disease transmission (Lohele, 1995, Craft, 2015). Furthermore, through observing social partners, animals may acquire various types of information, including *know-where*, *know-when*, *know-what*, and *know-why* information (see Box 1). Thus, the ability to learn through social observation may hold various fitness benefits (Shier and Owings, 2007, Sheppard et al., 2018; Harrison et al., 2024; Kendal et al., 2025; but see Feldman et al., 1996; Laland and Williams, 1998; Nocera et al., 2006). Therefore, it is possible that observational social learning underlies the acquisition of important parts of visual species' behavioural repertoires. However, this prediction remains to be tested.

Behavioural indicators of observational social learning have, until recently, been understudied in animals, primarily because such behaviours are generally rare. Moreover, observing a conspecific's behaviour does not always result in learning. In the wild, many animals rely on social observation for a myriad of other functions such as collective vigilance, assessing the condition of conspecifics, or anticipating the behaviours of association partners (Hare et al., 2000, Fernández-Juricic et al., 2005, Watts 1998, Blois-Heulin 1999, Blois-Heulin & Girona 1999). It is also very difficult, without conducting controlled targeted experiments, to confidently determine what types of information wild animals acquire during social observation (e.g., what *know-x* information), nor track how this information is processed in the brain. These challenges highlight the need for tools and predictive frameworks that allow researchers to parsimoniously infer learning via the contexts social observations take place in and/or the behavioural changes that follow them. Emerging long-term data from the wild can help researchers overcome these barriers by enabling quantitative analyses of how and when animals engage in social observations across contexts, including if and when instances of social observation are indicative of learning.

Insert Table 1 here

Table 1. Example studies of peering in wild primates. Bold words across the findings of these studies highlight the diverse ways in which peering behaviours are reported in the existing literature (e.g., Peering, Visual attention, Social attention, Visual monitoring, (Social) Staring). The supported function describes the suggested function of peering in the context of each study (as discussed by the authors); however, hardly any studies have examined whether peering fulfils similar or different function across behavioural contexts.

Many long-term studies of wild animal social learning focus on the behaviours of primates, perhaps due to humans' close phylogenetic relationship with other primates (e.g., chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*)), and their resultant behavioural similarities providing a unique window through which we can study the evolution of humans' cultural capacities (Kalan et al., 2020). In the following sections, we discuss how to validate an increasingly frequently studied behavioural indicator of observational social learning in wild primates, called *peering* (Matsuzawa et al., 2001, Schuppli et al., 2016a, van Schaik et al., 2016, Berdugo et al., 2024; Nodés-Langlois et al., 2025, Revathe et al., 2025, see Box 1). We aim to generate testable predictions that can be broadly used to link instances of peering and learning across primates, thus offering a toolkit to researchers for identifying observational social learning. Studies on peering in primates are rapidly increasing, as reflected in the growing number of recently published peer-reviewed papers and preprints (Table 1). Our recommendations aim to help streamline this emerging field and facilitate future comparisons across study systems. We anticipate that from this case study of primate peering, many predictions can be translated and adapted to other visually-learning species (see below).

Box 1: Glossary

Knowledge: Any and all information possessed by an individual (regardless of whether it influences an individual's behaviour), including all cases of *know-x* information.

Skill: Any behaviour where learnt information shapes how the behaviour is performed (regardless of whether this information is learnt socially or individually).

Social Learning: "The learning about other agents, or the inanimate world, that is influenced by the observation of, or interaction with, another individual or its products" (Heyes, 2012).

Observational Learning: Learning that involves visual observation of an individual and/or the materials of a behaviour (both those involved in the process of the behaviour, and artefacts) and leads to the transmission of any type of information. Below we list different types of knowledge and how it can be socially acquired. However, note that these knowledge types can also be individually acquired by wild animals.

Know-how: Information about the actions and/or steps of a behaviour, and how they should be organized in time and/or space (Tennie, 2023). This type of information may be socially acquired through processes such as certain types of "imitation", "copying", or "program-level imitation"," (Heyes, 1994; Byrne & Russon, 1998; Byrne, 2005; Tennie, 2023. Note that this differs from processes such as social contagion).
Know-what: Information about the objects associated with a behaviour (e.g., which materials are required for the behaviour: Tennie, 2023). This type of information is often argued to be socially acquired through processes such as "stimulus enhancement" (Heyes, 1994).
Know-when: Information about the temporal relations of a behaviour (e.g., when certain fruit is available; Tennie, 2023). This type of information can also be socially acquired via "broad-scale emulation" (Heyes, 1994).
Know-where: Information about where a behaviour should be performed (e.g., where productive fruit trees are located; Tennie 2023). This type of information can be socially acquired through forms of "local enhancement" (Heyes, 1994).
Know-who: Information about the subjects involved in a behaviour (e.g., which individuals to attend to; Heyes, 1994; see also literature on "social learning biases", e.g., Kendal et al., 2009).
Know-why: Information about the goals or intentions behind a behaviour (e.g., which may be acquired socially through processes such as "goal emulation"; Tennie, 2023) and/or understanding of the world (e.g., causal understanding; *Tennie, personal communication*).

Peering: "Attentive and sustained close-range [observation] of the behaviours of a conspecific from a close enough distance to see the details of the behaviour" (Schuppli et al., 2016a). Note however that the definition of close-range will depend on the species under observation (as some species are more socially tolerant or live in environments more suitable for close interactions).

Peerer: The individual that is performing close-range observation of a conspecific's behaviour (sometimes also referred to as "pupil" or "apprentice" when described in the context of learning, see Matsuzawa et al., 2001).

Peering target(s): The individual(s) whose behaviour is the focus of the peerer's observation (when in assumed learning contexts, sometimes also referred to as "role model", "master" or "demonstrator": see also Matsuzawa et al., 2001).

1.1 Studying peering to infer social learning

Whilst peering (see Table 1 and Fig. 1) has been studied in several primate species over many decades, it is becoming increasingly common for researchers to use peering as a behavioural indicator of observational social learning in wild primate research. Peering (or any sustained, close-range social observations which meet the criteria for peering) has, so far, been studied in chimpanzees (Matsuzawa et al., 2001, Biro et al., 2003, Humle et al., 2009, Lonsdorf 2005, Peter et al., 2022, Berdugo et al. 2024, Nodés-Langlois et al., 2025, Slania et al., 2025 in review); bonobos (Furuichi 1989; Idani 1995; Stevens et al., 2005), capuchins (*Sapajus spp.*; Ottoni et al., 2005, Coelho et al. 2015, 2024); mountain gorillas (*Gorilla beringei beringei*; Watts 1991, 1998, Yamagiwa 1992); vervet monkeys (*Chlorocebus spp.*; van de Waal et al., 2010, Grammp et al. 2019); moustached guenons (*Cercopithecus cephus cephus*), Campbell's monkeys (*Cercopithecus campbelli*), and red-capped mangabeys (*Cercocebus torquatus torquatus*; Querouil & Blois-Heulin 1998, Blois-Heulin 1999, Blois-Heulin & Girona 1999), long-tailed macaques (*Macaca fascicularis;* Tan et al., 2018) and, perhaps most extensively, in wild orangutans (*Pongo spp.*; Kaplan & Rogers 2002, Jaeggi et al., 2010, Schuppli et al., 2016a, Schuppli et al., 2017, Schuppli & van Schaik, 2017, Ehmann et al., 2021, Mörchen et al., 2023; 2024, Kukofka et al., 2025, Permana et al., 2025, Howard-Spink et al. 2025, Revathe et al., 2025).

Figure 1. Examples of peering in foraging contexts across different primate species. Examples of peering at foraging using tools: (a) West African chimpanzees (*Pan troglodytes verus*; photo: T. Matsuzawa). An immature female (left) and an immature male (right) peer at their mother (center) cracking oil-palm nuts (*Elaeis guineensis*) using stone tools during a long-term naturalistic field experiment at Bossou, Guinea. **(b)** Sumatran orangutans (*Pongo abelii*; photo: G. Duvot). An immature orangutan peers at their mother performing extractive foraging using a stick tool. **Examples of peering at foraging without tools: (c)** Bonobos (*Pan paniscus*; photo: B. Fruth). **(d)** Chacma baboons (*Papio ursinus*; photo: E. Fernàndez-Fueyo). **(e)** Vervet monkeys (*Chlorocebus pygerythrus*; photo: L. Schad). **(f)** Panamanian white-faced capuchin monkeys (*Cebus imitator*; photo: B Barrett).

Whilst peering seems to constitute some form of attendance to social information, it is challenging to confidently demonstrate that peering is being used for learning. Indeed, for some species—such as in bonobos and gorillas—empirical data suggest that peering can be used for a number of functions unrelated to learning (see Table 1 & Box 2). These findings highlight the importance of more precisely establishing whether peering is indeed associated with learning, as opposed to, for example, facilitating social behaviours.

Orangutans are the species in which peering has been most extensively studied in relation to learning. Long-term data collected on wild orangutans support the role of peering in guiding learning by examining (1) the situations in which peering occurs and (2) how it influences individuals' subsequent behaviours. Wild orangutans have been estimated to peer up to 40,000 times during their lifetimes (based on observed and extrapolated peering rates across individuals' lives; Schuppli & van Schaik 2019), with the highest rates occurring during developmental stages associated with skill and knowledge acquisition (Schuppli et al., 2016a, Kukofka et al., 2025). Young orangutans primarily peer at their mothers, but as they age, they not only have greater access to other individuals (non-maternal adults and immatures) but also preferentially peer at them rather than at their mothers. (Schuppli et al., 2016a). This shift is accompanied by sex differences in peering target selection, which may help individuals learn sex-specific behavioural strategies for success in adulthood (Ehmann et al., 2021). Peering has significant effects on immatures' long-term diet development (Howard-spink et al., 2025, Revathe et al., 2025). Moreover, peering is selectively used by adult males following migration to new areas, and males selectively peer at resident individuals who are likely more knowledgeable about available foods (Mörchen et al. 2024). Both immatures and migrant males peer more frequently when their association partners are eating food items that require more processing steps or are rarely encountered, compared to when association partners are eating items that require fewer processing steps or are more commonly encountered (Schuppli et al., 2016a, Mörchen et al., 2024). Despite extensive research on peering in orangutans, attempts to identify the specific types of information transmitted through peering are only just beginning (Permana et al., 2025).

Notably, several of these aspects of peering have also been identified in studies of other primate species, suggesting that peering may be used for learning across species (see Table 1). Yet, to date, a systematic predictive framework of how peering data should be analysed to test whether it is associated with learning is missing. Growing long-term data sets on peering—which include the contexts in which peering is performed—therefore offer important opportunities to systematically assess the contribution of peering to learning across primate species. To leverage the opportunities provided by these growing data sources, we offer predictions and recommendations for studying whether and how peering is used by wild primates for learning.

Box 2: The motivations to peer: learning and other potential drivers.

Even in instances in which peering leads to learning, the performance of peering is has been argued to be motivated by a generalized interest in the activities of conspecifics, the objects they manipulate, or the desire to perform similar behaviours to specific individuals (Matsuzawa et al., 2001; de Waal 2001). These instances of peering can be scaffolded by dyadic dynamics such as through the peering target expressing tolerance towards the peerer. The motivation to attend to others is presumably shared across primates, particularly great apes, in which associations with mothers and other social partners are common throughout extended immature periods, potentially serving functions including the acquisition of survival-relevant information; Ross et al., 1998; Schuppli et al., 2016b). Indeed, in human children, it is not necessary for any learner to hold a conscious desire to learn, rather information can be acquired through being drawn to role models and attending to their behaviours (Bandura et al. 1977; Ledford et al. 2008).

This generalized motivation for peering opens the door to several additional, adaptive functions. In many primate species, peering is most frequently performed by younger or subordinate individuals, and is performed while approaching older, or higher-ranking conspecifics (Biro et al., 2003, Furuichi, 1989, Grampp et al., 2019, Yamagiwa, 1992, Idani, 1995, Schuppli et al., 2016a, Coelho et al., 2015, 2024, Querouil & Blois-Heulin 1998, Ottoni et al. 2005). Thus, in some species, peering may be a useful behavioural mechanism for inducing tolerance in association partners during approach. Indeed, this alternative use of peering is supported by studies of bonobos (Idani, 1995; Vervaecke et al., 2000), where once in close proximity, peerers may either continue to engage in sustained close observation of the target's behaviour (thus leading to the acquisition of visual information, and perhaps learning), or begin to engage in alternative social interactions, such as soliciting food or social services (e.g., grooming), sexual behaviours, or scrounging of items in close proximity (Furuichi, 1989; Idani, 1995; Stevens et al., 2005; also see Coelho et al., 2015 for scrounging behaviours associated with peering at tool-users in capuchin monkeys). Taken together, in addition to processes of information acquisition, peering may serve as a generalized cue of submission to dominant, target individuals.

These additional possible functions of peering further intensify the need to identify the circumstances (if any) in which peering is being used as a means of observational social learning. Thus, it is paramount that researchers are equipped with a toolkit of predictions that identify these specific cases. These additional functions of peering may also confound our predictions about the interplay of peering and learning. Therefore, it is likely necessary that analyses of peering include control variables for these other potential functions when aiming to demonstrate learning. Including control variables may be challenging, especially when they have non-linear effects on peering. Furthermore, the additional utility of peering as a potential cue of submission, or method of inducing social tolerance in conspecifics, opens up questions surrounding how peering is perceived by target individuals and employed by peerers. This includes the extent to which peering is an indirectly informative behaviour (offering a cue to targets about the likely intentions of peerers) or if peering meets the criteria to be considered an additional gestural signal employed by primates, and perhaps other species (Stevens et al., 2005).

2. Preconditions for inferring social learning of any know-x information through peering

Whether learning occurs during or after peering, and whether such learning can be detected by human observers, depends on three main factors:

2.1. **How the observed information relates to what the peerer already knows.** If the peerer is observing a conspecific performing a behaviour that is, in its *exact* form, already in the peerer's behavioural repertoire, the act of peering will not transmit any new information and thus cannot lead to observational social learning. In these cases, we would hypothesise that peering is either serving an alternative purpose (e.g., an individual could be soliciting food or social services from the peering target, Kano 1980, Idani 1995, Stevens et al. 2005, Watts 1991), or that the peerer may simply be ascertaining that they already have knowledge of the behaviour (see Discussion and Box 2). Alternatively, if the peerer can perform the observed behaviour, but does so with lower proficiency, peering may assist in acquiring information needed to perfect the behaviour. Additionally, an individual could be peering at a novel variant of a behaviour that is already within its repertoire (e.g., distinct tool-using techniques, such as using two instead of one tool to reach the same end goal when harvesting underground honey, Gunasekaram et al., 2024). Understanding what the peerer already knows requires an *a priori* comprehensive knowledge of an individual's behavioural repertoire (see Box 3).

2.2. **Whether the peerer acts upon what they observed.** Even though not all learning results in behavioural change, and not all behavioural change is reflective of learning, in observational studies, learning can currently only be detected through such changes (Kieffer and Coglan 1992, Alcock 2009, van Schaik 2010). If there is a noticeable and consistent change in an individual's behavioural repertoire after a peering event, it is possible, though not certain, that observational learning occurred (see predictions IV & V below). A large body of literature on 'social learning biases' reports that individuals preferably attend to and utilize social information from specific types of peering targets (e.g., high-ranking individuals, knowledgeable individuals and/or kin., etc; Coelho et al., 2015, 2024, Ottoni et al. 2005, Luncz et al., 2014; Watson et al., 2018, Ehmann et al., 2021, Botting et al., 2018, van de Waal et al. 2010). Whether an individual decides to act upon observed information may depend on the skill difference between the peerer and the peering target, their relatedness, their age difference, the peerer's absolute age (Watson et al., 2018), the difference in dominance status between the peerer and the peering target (which may change with age). Additionally, whether an individual changes its behaviour following a peering event may be influenced by characteristics specific to that individual. For example, an individual's motivation can affect whether they are willing to modify its behavioural repertoire upon peering, particularly when the behaviour observed does not markedly improve the efficiency of existing behaviours or does not solve a novel problem for the peerer (Harrison & Whiten, 2018). Lastly, individual experiences (Bandini et al., 2025; Bohn et al., 2023), and personality traits (such as neophobia and curiosity, Forss et al., 2017; Forss & Willems, 2022) may also affect whether a newly observed behaviour will be adopted or not.

2.3. **How feasibly the peerer can act upon the acquired information.** Lastly, there are limiting factors on an individual's ability to learn through peering and subsequently adapt their behaviour. This includes whether the species has the capacity to process certain information, and/or the need for further development of cognition, physical strength, and dexterity before acquired information can be successfully incorporated into performed behaviours (Bründl et al., 2019, Malherbe et al., 2024). In terms of cognitive abilities, an individual's behavioural flexibility may affect their ability to act upon acquired information (Claidière & Whiten 2012, Gruber, 2016). Furthermore, whether an individual adapts their behaviour based upon the observed information also depends on whether environmental and social factors limit the performance of a behaviour recently after peering (e.g., van de Waal et al., 2013). For example, whether a peerer has access to the resources or objects needed to perform a behaviour, within a reasonable timeframe following peering, determines whether the peerer can explore the behaviour using relevant resources (*know-what* information) and then practice implementing the *know-how* via individual attempts at producing similarly-formed behaviours.

In sum, peering can only lead to detectable learning (1) if the peerers were naive to the peered at behaviour (or its exact form), (2) if the peering individuals incorporate the peered at behaviour (or elements/substrates of it) into their behavioural repertoire and, (3) if the peering individuals have the cognitive and physical prerequisites to act upon the information they obtained via peering.

3. Predictions for inferring Social Learning through Peering

The points discussed above highlight that not all peering leads to learning, and not all learning through peering can be detected with the methods that we have currently available. As a result, instances in which peering leads to learning are difficult to identify in the wild. In particular, inferring the type(s) of information that are transmitted (if any) during peering events is bound to be even more difficult (if not impossible, at times). Nonetheless, to equip researchers with a practical toolkit to address whether peering leads to learning or not, we propose a series of *a priori* predictions about peering patterns to test whether these events **involve observational learning (of any *know-x* type of transmitted information)** and highlight the necessary data to do so**.** These predictions can be translated into analyses of observational data to make more robust inferences surrounding primate observational learning through peering.

I. Contexts: We predict peering to be most frequent in learning-intense contexts. These contexts should be predicted based on the demands of the ecological and social environments of the study species. For example, in species that engage in limited social interactions but occupy cognitively demanding foraging niches—characterized by rare and/or ephemeral foods and those requiring dexterous or multi-step processing—we predict that individuals will peer more frequently in feeding contexts than in social ones (e.g., orangutans; Schuppli et al., 2016). Furthermore, we predict peering to occur most frequently in social settings that allow for knowledge transfer, particularly when there is a difference in knowledge between the peering target and the peerer. For example, we predict that individuals peer more frequently at those who are more experienced or who possess different behavioural repertoires than themselves (e.g., in vervet monkeys (van de Waal et al., 2010), capuchin monkeys (Coelho et al., 2015), orangutans (Schuppli et al., 2016a, Mörchen et al., 2023, Kukofka et al., 2025), and chimpanzees (Biro et al., 2003; Lonsdorf et al., 2005; Humle et al., 2009; Nodés-Langlois et al. 2025; Péter et al. 2022; see also prediction III).

II. Effects of complexity and rarity of information: if learning of underlies a peering event, we predict peering to be most frequent for behaviours that are difficult to learn, as information about a behaviour becomes increasingly difficult to discover independently. For example, we would predict higher rates of peering for feeding techniques that require more intensive pre-ingestive processing (such as multi-step food processing behaviours including tool-use) compared to feeding techniques that require fewer steps (such as pick and eat techniques). This effect of complexity on peering has been reported in capuchin monkeys (feeding context: Perry and Ordonez Jiménez, 2006), orangutans (feeding context: Jaeggi et al., 2010, Schuppli et al., 2016a, Kukofka et al., 2025; nest building context: Permana et al., 2025), and chimpanzees (feeding context: Slania et al., (in review); Nodé-Langlois et al., 2025). Similarly, we predict rare behaviours to also elicit proportionately higher levels of peering compared to frequent ones because these behaviours are more salient due to their rarity, and individuals may have a higher incentive to utilize rarer learning opportunities. Thus, when encountering rare behaviours, immatures may engage in higher relative rates of peering than when encountering common behaviours once differences in overall exposure time are controlled for. For example, we would predict relatively more peering at individuals eating a fruit species that is available during short periods compared to a fruit species that is available all year around as it has been reported in capuchin monkeys (Perry and Ordonez Jiménez, 2006), orangutans (Schuppli et al., 2016a, Kukofka et al., 2025), and chimpanzees (Slania et al., in review). Lastly, there may be some cases in which a behaviour is both rare and complex (e.g., orangutans use multi-step stick tools use to feed on honey from bees' nests which constitutes less than 0.02 percent of their diet (Fox et al., 2004). It may be possible to study the interactive effect between complexity and rarity on peering, provided that sufficient data are available.

III. Age/own competence: We predict peering to be most frequent at the age in which individuals are acquiring the majority of their skills and knowledge. For example, we predict peak peering rates to coincide with phases of pronounced behavioural repertoire expansion, increasing skill competence, and/or sensitive learning windows for specific behaviours (Biro et al., 2003, Schuppli et al., 2016a, Kukofka et al., 2025, Permana et al. 2025). As the competence of the peerer increases, we predict peering to become more selective, targeting only behaviours that the individual does not yet know or cannot perform efficiently, such as learning-intensive skills (e.g., multi-step feeding techniques) or rarely encountered behaviours (e.g., eating a fruit species that is available during short periods). The effects of the complexity and rarity of observed behaviours on peering frequencies and/or durations may therefore depend on the peerer's own behavioural competence. Note also that during skill learning ontogeny, focus on different aspects of the behaviour may change based on the peerer's developmental stage (Inoue & Matsuzawa, 1997).

While the predictions outlined in I-III do not provide direct evidence of learning, they suggest that the peerer is selectively attending to information. A parsimonious explanation for this targeted information seeking is that it serves some form of learning. This claim can be further strengthened by analyzing data describing potential behavioural indicators of learning:

IV. Performance or practice after peering: We predict peering individuals to engage in/with the observed activity and/or objects/substrates relevant to an activity (or attempt to do so) more frequently after peering compared to before (leading to so-called "peering practice cycles", Schuppli et al., 2016a). For example, peerers may interact more frequently with objects (e.g., specific fruit, tools), or stimuli relevant to a behaviour (e.g., tree holes) *after* compared to *before* peering—an effect observed in both orangutans and chimpanzees (Schuppli et al., 2016a, Mörchen et al., 2023, Berdugo et al., 2024, Permana et al. 2025). Whilst there are various factors that may limit whether peerers can engage in an observed behaviour or the objects/substrates involved in the behaviour following peering (see previous section *3. How feasibly the peerer can act upon the acquired information*), augmented rates of behavioural practice (including exploration, individual learning, and successful behavioural performance) following peering strengthen the confidence with which peering can be linked to processes of learning (Revathe et al., 2025). The key difficulty in testing this prediction is defining the time frame in which performance and practice after peering are predicted (see section V below).

In addition to potentially providing information on various aspects of new behaviours and the objects involved in them, learning through peering may also entail adapting an existing behaviour to be more similar to certain observed variants, or to become more goal-directed. Importantly, however, a peerer may require multiple peering and/or individual learning events before they can implement a new behaviour in its exact form. The degree of 'matching' between the behaviours and the frequency with which the new behaviour is practised can all provide additional evidence on whether learning occurred and, potentially, what type of information was transmitted. For example, if a peerer is reported to manipulate the same (or a similar) object that the demonstrator was using during a peering event, but they do not go on to use the object in the same way (e.g., as a tool), then the peerer may have acquired *know-what* information on the behaviour (but not *know-how* information).

In contrast to I-III, prediction IV (performance after peering) would suggest that some form of learning occurred during peering, and that the peerer was motivated and able to act upon the information that they observed. However, whilst socially induced practice can be a key indicator of learning in action, learning should ultimately entail a long-term change in the peerers' behaviour, such as the incorporation of new behaviours in the peerer's repertoire and/or a lasting increase in competence in performance (e.g., suitable know-what, know-where, know-when etc):

V. Increase in behavioural diversity and competence: If peering leads to long-term learning, we predict an individual's own behavioural diversity and competence to increase following peering (even gradually over long time periods following successive instances of peering). This may manifest as an increase in the size of an individual's behavioural repertoire—for example, by incorporating a new food item observed during peering into its diet (Visalberghi & Addessi, 2000, Howard-Spink et al., 2025, Revathe et al., 2025), or by adding a new item or tree species to its repertoire of nest construction materials (Guillette et al., 2016; Vistalli et al., 2023); or improved efficiency in performing specific tasks, for example faster food processing. These long-term behavioural changes might be more straightforward to assess for some behaviours than others and require competing explanations to be accounted for (see below). However, if a species' peering dynamics have been observed to fulfil the requirements set by predictions I to IV, and instances of peering are also generally followed by tangible increases in behavioural diversity and competence, this can be taken as evidence that individuals of that species learn some information on a behaviour through peering. Finally, entire knowledge repertoires can be quantified (e.g., diet-repertoire size) to test whether an individual attains a broader repertoire with the increasing use of peering opportunities (e.g., Revathe et al., 2025; see Fig. 2).

For Predictions IV and V, a key challenge lies in defining the time frame within which performance, practice, or increases in behavioural diversity and competence are predicted to occur following peering. If learning indeed occurs during a peering event, successful performance may not occur immediately after, as learning triggered by peering often requires a period of socially induced individual practice—particularly for skills that are difficult to acquire (see also Whiten 2015; Schuppli et al., 2016a; Bandini & Tennie, 2017; Galef & Whiten 2017). If a behaviour is practiced, performed, or appears in a peerer's repertoire following an extended period after it was last peered at, it is also possible that the behaviour predominantly emerged via gradual individual learning or as a result of the individual's advancing overall physical and cognitive development rather than via observational social learning alone. Probabilistic modelling may allow for identifying the contributions of social learning through peering relative to non-socially induced individual learning, as well as baseline developmentally-induced behavioural changes (see Box 3).

An increase in behavioural diversity and competence after peering constitutes more direct evidence of learning compared to I-IV. It also paves the way to pin down the types of information that are acquired during learning. In particular, understanding whether primates are able to acquire '*know-how*' during social observation is a long-standing point of debate (Tomasello, 1996; Whiten et al., 2004; Byrne & Russon 1998, Byrne, 2005; 2007; Tennie et al., 2009; Tennie, 2021). We provide a further prediction for identifying potential *know-how* learning through peering:

VI. **Duration of peering**: If individuals peer to learn how to do things (*know-how*; as opposed to *know-what* or where or why, etc.), we predict peering events to be longer when they are directed at multistep behaviours that require specific actions and objects used in an exact sequence. Multistep behaviours involve more actions (Whalen et al., 2015) and often the manipulation of a greater number of objects (Sanz & Morgan 2010), all of which must be understood, processed, and redeployed as functional behavioural sequences. Crucially, this prediction relies on controlling for the total duration of demonstrated behaviours as shorter behaviours are naturally limited in the total time over which they can be peered at. Additionally, the number of objects should also be controlled for, as more objects may elicit longer bouts of peering to obtain *know-what* information. An increase of peering per performance time could be indicative of potential *know-how* learning (but see considerations section). However, note that peering to obtain *know-why* information may also correlate with duration of peering, because peerers are waiting to observe end-states. This makes disentangling peering for *know-how* and *know-why* information particularly difficult in the wild.

If peering was used to acquire information on *know-what* and *know-where* only, we would predict behaviours consisting of single and multiple steps to be peered at for comparable proportions of their performance time. However, robust inferences about specific types of *know-x* learning likely require targeted experimental approaches, making controlled research in both captive and wild settings essential for understanding what information primates acquire through observational social learning (see *Considerations* section below).

Box 3. Statistical approaches to analyse predictions on whether peering results in learning.

Standard modelling approaches (e.g. (G)LM(M)s, GAMMs) can be used to investigate the above proposed predictions on whether peering leads to learning. These include hierarchical modelling at the population-level (Perry and Jimenez, 2006; Schuppli et al., 2016; Slania et al., 2025; see Fig 2A) or the individual-level (Revathe et al., 2025; see Fig 2B). However, for several of these predictions, standard approaches typically require setting specific thresholds to define the time window within which a behavioural change is predicted to emerge following peering, and for which a causal relationship can be assumed (i.e., what we subjectively refer to as "after peering" in predictions IV and V). These thresholds are inherently arbitrary and, therefore, would require sensitivity analyses which have their own limitations. An alternative approach to determining whether learning takes place during peering is through studying the time series of related actions across development (e.g. "peered at a behaviour", "performed the behaviour", "attempted the behaviour", "did nothing"; Lind et al., 2019, see Fig 2C). Using probabilistic associative reinforcement models (Rescorla and Wagner 1972), or hidden Markov models (Glennie et al., 2023), baseline rates of behavioural development can be estimated independently of any form of learning. These models can consider probabilities *conditional* on past events and disentangle the contributions of baseline developmental change and individual and social learning to behavioural change. This conditionality can, for example, be tackled using classical exponential decay functions (Ranc et al., 2021; Ye et al., 2024). By doing so, arbitrary thresholds are avoided, thus providing a more standardised and possibly comparable quantification of the dynamics of behavioural ontogeny across species.

Figure 2. Statistical approaches used to analyse whether peering results in learning. Standard modelling approaches to A) test contextual predictions at the population level and B) link levels of peering with broad-scale behavioural change at individual level, and C) mechanistic models to test if peering elicits fine-scale behavioural change during a peering event.

4. Recommendations for data collection specifically targeting whether peering results in learning:

With regards to the predictions made above, and the modelling approaches we propose in Box 3, we suggest that researchers interested in assessing the learning potential of peering events consult these general guidelines and collect the following types of data:

General guidelines:

1. *Choosing the most appropriate study species:* there is likely a trade-off between the number of individuals whose development can be studied within a given time period and the amount of socially learned behaviours those individuals are likely to acquire. Whilst shorter-lived species have developmental periods that are briefer (making data collection across the entirety of development more feasible), they also tend to have smaller and less learning-intense skill repertoires, and may thus be less reliant on social learning than longer living species like apes (van de Waal et al., 2010, Whiten, 2005; but see Deffner & McElreath 2020). In light of this trade-off, researchers will have to select species that seem most appropriate for their specific research questions.

2. *Ensure data reliability:* For many study species, testing the proposed predictions requires collecting peering data over multiple years. Such long-term efforts inevitably involve multiple observers. To ensure data reliability, inter-observer reliability testing should be conducted regularly, with any resulting observer differences accounted for in the statistical models. Furthermore, video recordings can help analysing the details of peering events in a reproducible way.

Data collection recommendations:

For all predictions

1. *Study sample.* Demographic data should be collected for every individual included in the sample (age, sex, rank, relatedness, rearing history, social network data, neophobia and social tolerance levels). Due to the volume and type of data required to make robust inferences on whether learning underlies a peering event (see Box 3), we recommend systematic data collection that is as continuous as possible, even if it leads to a lower number of sampled focal individuals.
2. *Overall frequency and duration of behaviours within the populations' repertoire.* These data will allow for estimating the opportunities that individuals have to peer at different behaviours in their population. This, in turn, enables predictions about the number of peering events and the relative length of peering required for individuals to develop a specific behaviour.

For predictions I, II & IV

3. *Existing behavioural repertoires of individuals and the population.* To understand a peerer's existing repertoire, behavioural data should be collected from birth or the youngest age possible, across the entire developmental period and into adulthood. By comprehensively tracking the development of individuals' behavioural repertoires, comparisons can be made

between the repertoires of peerers and their peering targets. Similarly, the form and efficiency of the behaviours being peered at can be compared with the existing behavioural form and skill level of the peerer (i.e. if the peerer indeed is incapable of, or naïve to, the behaviour they peered at). Data on the behaviours of adult individuals is indispensable for creating adult reference values, such as adult-like efficiency during skill performance, or adult-like breadth of particular knowledge repertoires.

For predictions III, IV, V

4. *Average behavioural development across individuals and sensitive learning periods*. This information can be used to predict when, during an individual's lifetime, peering at specific behaviours is most likely to occur—for example, when the individual has developed the cognitive and physical capacities required to perform the behaviour, but not yet the behaviour itself. Furthermore, this will allow for predictions on when targeted practice after peering should occur (rather than just peering) and when increases in competencies are feasible. These data will also allow for understanding whether individuals who peer more than average have a faster skill acquisition trajectory than those who do not, therefore allowing for stronger inferences to be made on the learning resulting from these peering events.

For prediction II and IV

5. *General food/resource availability.* These data are essential for examining opportunities to peer at, practice, or perform a behaviour, as if resources are limited or monopolised by conspecifics, opportunities to engage in peering will also be limited. Furthermore, information on the availability of certain resources will allow to further estimate the rarity of behaviours (also see point 2above).

5. Considerations

Above, we outline different conditions that should be met in order to infer that learning may be occurring during a peering event. However, even in cases in which these predictions are met, there are still some important considerations that should be taken into account.

For example, at the neural level, information processing may change throughout the individual's lifetime. Indeed, there is evidence that experience changes the forms of learning an animal can draw from, and how information acquired during learning bouts is processed. Previous experiences in human environments (e.g., training in "do-as-I-do" paradigms or enculturation) can alter the pathways of primates' brains, allowing them to process information in ways not available to their non-enculturated and/or wild conspecifics (e.g., enculturated individuals can copy behaviours, an ability not yet identified in untrained, wild primates: Buttlemann et al., 2007; Hecht et al., 2013; Pope et al., 2018). While these are examples of extreme experiences, it is likely that even less-extreme experiences also have an effect on how animals attend to and process information, even in the wild (Bandini et al., 2025). For example, habituation in wild animals affects behaviour, alongside information processing (Bandini et al., 2025; Samuni et al., 2014; Costa et al., 2024). Therefore, even when it appears that learning is occurring from a purely observational standpoint, subtle nuances in what learners observe, and how that information is being processed in the individuals' brains is still opaque, and can even change over time and contexts (Matsuzawa, 2003, Matsuzawa et al., 2006; Myowa et al., 2012).

Secondly, even when learning is identified as the most parsimonious function underlying a peering event, it will remain challenging, and in many cases impossible, to determine the *type of information* transmitted (e.g., *know-what, where*, *when* or *how*) from observational data alone. Whilst *know-how* learning is often inferred in these contexts, we argue that in most cases, the *type* of information being transferred can only be reliably determined via a combination of systematic and targeted observational (Permana et al., 2025) and experimental approaches (e.g., Tennie et al., 2009; Clay & Tennie, 2018; Neadle et al., 2021). Indeed, in captivity, it may be possible to associate increases in manipulation of novel objects of a behaviour after peering to a transfer of *know-what* and/or *know-where* information, if the naivety of the subjects is established, and their interactions with the objects before the peering event are known. Therefore, whilst peering is a promising avenue towards examining whether and when social learning of any type is happening in other species (if it meets the predictions we outline above), it is likely somewhat limited in its ability to inform on whether *know-when*, *what*, *where* or *how* information is being transferred between individuals.

Thirdly, peering is only one way to acquire information about the environment, and alternative senses (such as taste, smell and hearing) can be used to acquire information from conspecifics without the need for observation. Indeed, many of these sensory systems are implicated during social learning of foraging-relevant information in mammals (Galef & Giraldeau 2001); for example, chemical cues can provide information about the specific types of food available in the local environment (*know-what*). The relative importance of different senses for information acquisition will likely be a product of the affordances of a species' own sensory systems (e.g., visual range and acuity, olfactory sensitivity, etc.) and the types of information which animals must learn (e.g., *know-what* information about available foods may be socially-learnt through chemical cues, whereas *know-how* for food processing may require individual experimentation and/or social observation). Given these factors, studies of observational learning alone are bound to offer only a partial view of primate culture, and animal culture more broadly.

Given these considerations, it is likely that solely studying peering in wild individuals will not provide a complete characterisation of the total breadth nor potential of primate social learning and culture, nor its precise cognitive underpinnings. Accordingly, integrative insights are required from field observations, field experiments, and controlled experiments in captivity (and should target potential instances of learning that involve diverse sensory systems). Each of these approaches offers unique opportunities for studying primate social learning, and combining them will generate a more comprehensive understanding of the scope of primate culture.

Nevertheless, alongside these limitations, it is likely that studies of peering also have underutilized potential for understanding the scope of animal culture. In this piece, we focused on primate peering and culture, as primates are a visual species commonly studied long-term, with easily identifiable gaze direction due to their forward-facing eyes and highly binocular vision. However, other species also attend to–and likely learn through– visual information, especially amongst vertebrates (Galef & Giraldeau 2001). Indeed, there is evidence that other species also perform peering behaviours (see selected examples of reported social observation in experimental studies of birds, e.g., Turner 1964, Chimento et al., 2024) although peering in these species is yet to be studied as systematically in wild individuals as in primates. Our methods and predictions are thus likely applicable to these species as well. We encourage researchers to study peering (or analogous behaviours) in other species as well, as this will likely enrich our overall understanding of how social observation contributes to the maintenance of animal culture at large.

6. Conclusions

1. Peering offers a rare potential window into observational social learning in non-human animals, providing insights into what and how animals learn socially and, as such, further clarity on the extent and nature of animal culture.
2. Because peering may allow us to study social learning on the individual level, it would enable researchers to examine the immediate contextual and developmental factors that prompt individuals to engage in social learning. Understanding these individual-level dynamics of social learning is essential for uncovering the importance of social learning for individuals' development, as well as proximate and ultimate drivers of culture.
3. However, to generate robust inferences, we need to move away from *a priori* assumptions that all peering, or any other instance of individuals observing each other, necessarily constitutes learning. To this end, we have provided several key predictions (see predictions I - VI above) to help with identifying cases in which observational social learning is occurring during peering. Many of these predictions involve indirect indicators of learning (such as contextual evidence, Predictions I - II), and some indicators have alternative possible explanations which are not associated with social learning (Box 2). Therefore, claims that wild individuals learn from peering become increasingly stronger when progressively more of these predictions are supported.
4. Identifying instances in which peering leads to learning brings us one step closer to understanding the true magnitude of animal cultures across the animal kingdom—and, in turn, their evolutionary origins and consequences—which is fundamental to understanding the most complex culture of all: human culture.

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Table 1.

Common Name	Scientific Name	Context	Study	Summary of findings related to peering	Potenital supported function
Chimpanzees	*Pan troglodytes sspp.*	Foraging (tool-use)	Matsuzawa et al., 2001	A hypothesis for the development of chimpanzee tool-use behaviours, emphasizing the need for visual observation of role models, facilitated by roles models' high tolerance of learners, and driven by immatures' generalized interest in role models' behaviours (specifically, those of their mothers). Initial data for **peering** was collected during an outdoor experiment with wild chimpanzees at Bossou (see also Biro 2003).	Learning Note: there is a complementary prediction by de Waal (2001) mentioned under the term "Bonding and identification-based observational learning" (BIOL)
		Foraging (tool-use)	Biro et al., 2003	Immature chimpanzees frequently **observe** adult chimpanzees cracking open nuts with stone tools, and immatures' mothers were the most frequent targets of observation. Infants were never observed by other individuals. Adults were the least likely to observe other individuals, and when doing so, usually observed other adults.	Learning
		Foraging (tool-use)	Humle et al., 2009	Young chimpanzees exposed to higher frequencies of ant dipping (measured by frequency of mothers' ant dipping) **observed** mothers performing the behaviour more intensely from earlier ages, and developed higher tool-using efficiency faster (N=5-6). The duration of tool dips correlated between mothers and offspring on ant trails, but not nests.	Learning
		Foraging (tool-use)	Lonsdorf 2005	The time young chimpanzees spent **watching** mothers termite fish correlated with learning termite-fishing behaviours at earlier ages.	Learning
		Foraging (water)	Peter et al., 2022	A novel well-digging behaviour, introduced by an immigrant female chimpanzee, was reported in other members of the group, potentially spreading through a combination of **peering** and exploitation of produced wells.	Learning
		Foraging (tool-use)	Berdugo et al., 2024	The rate of social learning opportunities afforded to immature chimpanzees learning to crack nuts with stone tools - including through **peering** - predicted skill efficiency immediately following the skill acquisition. If peering targets were intolerant to peerers, peerers were less likely to exhibit high skill efficiency following learning.	Learning
		Foraging (including tool-use)	Nodes-Langlois et al., 2025	Throughout development, immature chimpanzees **peer** more often at tolerant individuals (often mothers, but also other role models later during development), and peer more frequently at complex food-processing tasks.	Learning
		Foraging, Social interaction	Slania et al., 2025	Chimpanzees **peer** at conspecifics in a wide range of behavioural contexts, including when peering targets were performing common,	Learning & Social Signalling

				every-day skills. Peerers generally target older conspecifics, and whilst they frequently peered at their mothers, they also leveraged opportunities to peer at unrelated conspecifics from an early age. From seven years old, peerers began to increasingly target similarly aged individuals. Peering followed predicted dynamics for learning, however may also be a means to initiate social interactions (but was not used for begging to signal submission).	
Bornean orangutans	*Pongo pygmaeus sspp.*	Social	Kaplan & Rogers 2002	Rehabilitant orangutan juveniles spend more time **gazing** at social partners than younger infants and older adults. Unlike other apes, prolonged mutual gazing does not occur in orangutans. Field and zoo studies find patterns of gazing of both humans and other orangutans via sidewards glancing. Most attention during gazing is directed at other individuals' faces, however it is also directed at limbs and objects if the target individual is feeding.	Learning & Social Monitoring
		Foraging, Nesting	Jaeggi et al., 2010	Immature bornean orangutans were considerably more likely to **watch** mothers when processing difficult to process foods, particularly embedded (difficult to extract) food items compared to non-embedded foods. Immatures also referred to their mothers' behaviours prior to consuming novel foods. Ultimately, immatures' diet repertoires overlapped heavily with those of their mother.	Learning
Bornean and Sumatran orangutans	*Pongo pygmaeus sspp. and Pongo abelii*	Foraging & Nest Building	Schuppli et al., 2016	Immature orangutans (Sumatran & Bornean) **peered** frequently in feeding contexts (particularly when foods were difficult to process) and nest-building contexts. Food peering was associated with an increased likelihood of subsequent exploration of foods, indicating that it leads to selective practice of food processing. Immatures´ food peering at their mothers was increased for food items that required a larger number of pre-ingestive processing steps or were rarer in the diet of their mothers. Nest peering was most frequently performed by immatures at the age at which immatures begin building their own nests, and was also associated with subsequent practice. Older immatures were more likely to peer at non-maternal figures, whereas younger immatures were more likely to peer at their mothers.	Learning
		Foraging	Schuppli et al., 2017	As Sumatran orangutans at Suaq Balimbing are more sociable, immatures make use of more opportunities to **peer** than same-age immatures at a less sociable population of Bornean orangutans (Tuanan), including when association time was controlled for. Suaq orangutans were also more exploratory, and had more complex and diverse diets.	Learning

		All contexts	Schuppli & van Schaik 2019	Orangutans **peer** many thousands of times across their lives (with populations & subspecies potentailly exhibiting considerable variation across lifetimes, on the scale of 10s of thousands of peering events). By requantifying cultural information on the basis of individual-level interactions (rather than the method of exclusion) social information & cultural inheritance in wild orangutans may be far greater than previously estimated	Learning
Sumatran orangutans	*Pongo abelii*	Foraging	Ehmann et al., 2021	Older immature orangutans begin to **peer** more frequently at same-sex role models. Female immatures continue to direct social attention towards the mother, whereas male immatures begin to direct social attention at adult males. By the end of the dependency period, female immatures' diets are more similar to their mothers than male immatures' diets.	Learning
		Foraging	Mörchen et al., 2023	After migrating to a new area, adult male orangutans would peer at local individuals, particularly when consuming food items which were not eaten in the local diet of their previous population. Migrants were more likely to interact with novel foods following peering, suggesting that peering is a mechanism for post-dispersal learning.	Learning
		Foraging	Mörchen et al., 2024	Migrant adult males orangutans were more likely to **peer** when food availability was high. Additionally, males from the more sociable Sumatran population (Suaq) peered at conspecifics more frequently than males from the less sociable Bornean population (Tuanan), even after accounting for differences in food availability. Both environmental, and either intrinsic or developmental factors, likely influence migrants' propensity to peer at conspecifics.	Learning
		All contexts	Kukofka et al., 2025	When comparing peering behaviours in wild and zoo-housed Sumatran orangutans, both groups exhibited similar age trajectories for **peering**. Immatures universally preferred to peer at older individuals and in learning-intense contexts. However, zoo-housed immatures peered more often, and more frequently at non-maternal targets (including once opportunity was controlled for).	Learning
		Foraging	Howard-Spink et al., 2025	Biologically-calibrated agent-based simulations support that **peering** is critical for long-term diet development in immature orangutans. Without the influence of peering on development, adult-like diets do not emerge by the age immatures become independent from their mothers.	Learning
		Nesting	Permana et al., 2025	Immature orangutans were more likely to practice nest building after peering at individuals who were making nests, compared to when they were within peering distance but did not peer. Peering is most often	Learning

				performed when peering targets are constructing more complex nests. Mothers and offspring overlap heavily in the types of tree species they use for nesting, and once immatures become independent, they peer at a greater diversity of individuals, and expand their tree-nesting choices to reflect new observations.	
Bonobos	*Pan paniscus*	Foraging, Social interaction	Kano 1980	**Staring** behaviour was recorded in the context of food sharing bouts, in which individuals would stare intently into conspecifics faces to ellicit food sharing.	Social signalling
			Furuichi 1989	Most **peering** is performed by younger female bonobos, and is directed at older females. Most peering behaviours were performed when target individuals were feeding; however, peering never led to food sharing or scavenging. Peering was occasionally followed by food begging, or solicitation of other social behaviours (e.g. genitogenital rubbing).	Social monitoring (potentially signalling)
			Idani 1995	**Peering** is most often performed by younger female bonobos, and directed at older females. Male bonobos rarely peered. Peering appeared to lead to tolerance of younger (subordinate) individuals by older (dominant) individuals.	Social signalling
Mountain Gorillas	*Gorilla beringei beringei*	Social Interaction	Watts 1991	Social **staring** is frequently used by female gorillas when approaching males to initiate sexual behaviours.	Social signalling
		Foraging, Social interaction	Yamagiwa, 1992	In all-male gorilla groups, social **staring** occurred during diverse social contexts, as well as when feeding. Younger males often stared at older males, and staring may function differently based on the social context. When initiating non-antagonistic interactions, males rarely stared at each other, but when doing so, males could initiate play behaviours or homosexual interactions. Staring was also likely directed from younger to older males for greeting or appeasement.	Social signalling
		Social interaction	Watts 1998	Female gorillas perform sustained **watching** of males - likely to monitor their behaviour - and may leave feeding spots following watching. Similarly, female gorillas will watch other females with whom they have more agonistic relationships.	Social monitoring
Capuchin monkeys	*Sapajus spp.*	Foraging (tool-use)	Ottoni et al., 2005	Younger capuchins who were less proficient in nut cracking using stone tools were more likely to **observe** conspecifics performing this behaviour. Observers would choose who to watch non-randomly, and exhibited preferences for more skilled tool-users.	Learning

	Cebus imitator	Foraging	Perry and Ordonez Jimenez 2006	Capuchins were **peering** more (i.e., showing more food interest) at conspecifics who were eating food items that were either rare in their diet, required more pre-intestive processing steps, or were larger.	Learning
		Foraging (tool-use)	Coelho et al., 2015	Young capuchins **watched** older, more proficient, and dominant individuals during nut-cracking bouts. Monkeys with higher productivity rates were also more frequently watched, and were tolerant to scrounging.	Learning
		Foraging (tool-use)	Coelho et al., 2024	During an open-ended diffusion task, naive capuchins were more likely to **observe** successful males than other individuals.	Learning
Guenons	*Cercopithecus spp.*	Foraging	Querouil & Blois-Heulin 1998	For Cambell's monkeys and moustached guenons, the youngest immatures spent the most time **looking** at other individuals, and the likelihood of looking at other individuals decreased with age. Immatures were more likely to look at their mothers than other individuals, particularly when mothers were feeding.	Potentially learning
Vervet monkeys	*Chlorocebus spp.*	Foraging	van de Waal et al., 2010	During a social learning experiment on six groups of wild vervet monkeys, naive individuals were more likely to copy the precise solution to an experimental task if **looking** at a female demonstrator prior to attempting the task (due to sex-biased selective attention).	Learning
		Social	Grammp et al., 2019	Younger and orphaned vervet monkeys exhibited the highest rates of **social attention**. Juveniles payed specific attention to kin. However, higher ranked individuals were also more likely to be the object of attention than lower ranked individuals. This rank effect was stronger for younger females; the authors explain this sex-biased effect as being part of females' higher demands for knowledge for socialisation, as they are the philopatric sex.	Learning
Cercocebus mangabeys	*Cercocebus spp.*	Foraging	Querouil & Blois-Heulin 1998	Immatures in the youngest age cartegory spent the most time **looking** at other individuals, and the likelihood of engaging in social observation decreased with age. Red-capped mangabeys were more likely to look at their fathers than other individuals, however payed specific attention to mothers when they were eating.	Potentially learning
		Foraging	Blois-Heulin & Girona 1999	Red-capped mangabeys **look at** other individuals for extended durations if there is not high-value foods nearby; in such an instance they swap to rapid, quick glances at other individuals. For both behaviours, **gazing** of any kind at conspecifics is hypothesized to be important for monitoring conspecifics behaviours.	Social monitoring

	Note: the grey-cheeked mangabey has now been reallocated to lophocebus.	Social interaction	Blois-Heulin 1999	Grey-cheeked mangabeys often glanced at social partners (short-duration looking), whereas red-capped magabeys **looked at often** other individuals for longer durations. This may reflect a greater need for social monitoring in red-capped mangabeys, where males exhibit higher levels of dominating behaviour than in grey-cheeked mangabeys.	Social monitoring
Long-tailed macaques	*Macaca fascicularis*	Foraging	Tan et al., 2018	Immature and juvenile macaques were more likely to interact with tool-users (including **watching**, scrounging and stealing food) than older individuals who could use tools. Infants in particular spent the most time watching tool-users and exploring objects. Younger individuals often watched conspecifics with whom they had positive social bonds. Immatures also frequently watched older individuals, and all individuals were more likely to watch tool users who were more productive.	Learning