Systematic data are the best way forward in studies of teaching

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Abstract: Functionalist approaches to teaching can be used to great effect in the study of teaching in both human societies and nonhuman species.

Integrating disparate areas of science is a noble and often productive cause, and Kline's plea in the target article - to combine the three approaches to teaching, namely functionalist, mentalistic, and culture-based-needs serious consideration. That said, the functionalist approach proposed 22 years ago (Caro & Hauser 1992) in part grew out of an attempt to break away from the burden of having to show that nonhumans could attribute mental states to conspecifics (Pearson 1989). Mental state attribution requires establishing intent to facilitate learning in another subject, and a theory of mind, and it thereby severely constrains searches for different types of teaching in nonhumans. The focus of culture-based teaching that centers on what happens in Western classrooms is, by definition, of little help in explaining how knowledge is transmitted within the huge diversity of human societies or nonhuman species. Therefore, blending approaches and hoping that something interesting will emerge, as outlined at the start of Kline's article (see also Byrne & Rapaport 2011) is unlikely to be productive.

If one is interested, as I am, in the ecology and evolution of behavior, including teaching, one needs to establish a comparative data-base of different forms of teaching, rather than focusing on a single high-bar definition. Then, these need to be related to different ecological and social variables, and examined taxonomically. Using three criteria for demonstrating teaching - namely, teachers modify their behavior only in the presence of a naïve observer; the behavior incurs costs or no immediate benefit; and, as a result, pupils acquire knowledge or skills more rapidly or efficiently than they would otherwise, or that they would not have learned at all (Caro & Hauser 1992) - enormous progress has been made in documenting the incidence of different forms of teaching (Hoppitt et al. 2008; Thornton & Raihani 2008) and its taxonomic distribution (Thornton & Raihani 2008). For example, we now know that teaching must have evolved multiple times and in several different forms (Franks & Richardson 2006; Raihani & Ridley 2008; Thornton & McAuliffe 2006). Furthermore, some progress has also been made in trying to understand the environmental conditions under which teaching is likely to be observed in nature (Richardson et al. 2007; Thornton 2008; Thornton & Raihani 2010).

I do not believe that these advances could have occurred if teaching was shackled by mentalistic or culture-based definitions, because many phenomena that are interesting (to a biologist) would have been dismissed as being unworthy of study. Kline concurs in her closing section that "researchers should not limit the study of teaching to species with forms of mind-reading or theory of mind, because it is not an *a priori* necessity for behavior that functions as teaching to evolve" (sect. 7, para. 3).

Can the study of teaching in different human cultures benefit from the functionalist paradigm in nonhumans? The second part of Kline's target article suggests that it can, and she supplies many empirical examples from humans in support of this proposal. Anthropologists might indeed benefit from systematically documenting the extent to which different forms of social learning are seen in various societies, and then relate these to patterns of kinship, subsistence activities, and ecological variables (e.g., Hewlett et al. 2011; Tehrani & Riede 2008).

Caro and Hauser (1992) wrote "we are convinced that the only way to make progress in this area is to first provide a definition of teaching which can, and undoubtedly will, be modified as empirical data accumulate" (p. 152). Others have indeed expanded on the functionalist definition of teaching (see Hoppitt et al. 2008; Thornton & Raihani 2008), but these departures never reverted to definitions centering on intent or Western-style classroom teaching. In the target article, Kline is similarly advocating a broader approach to teaching in humans by including opportunity provisioning, stimulus or local enhancement, evaluative feedback, and direct active teaching. Once systematic qualitative, semiquantitative, and quantitative data on these and other forms of social transmission in humans accumulate, anthropologists may be able to uncover the ecological and social drivers of various forms of teaching in the same way as their biological colleagues are currently doing (e.g., Whiten 2011), and even relate different forms of social transmission, including teaching, to cultural phylogenies (Steele et al. 2010).

Questions that include whether progressive teaching (where teachers adjust their behavior as pupils' skills improve) occurs with a small number of pupils who can be monitored, whether teaching is principally found in solitary activities where there are few opportunities to learn by imitation, or whether teaching usually occurs where the costs of teaching are low in terms of lost opportunities for teachers, or where the costs of mistakes are high in terms of injury for pupils, can all be asked by anthropologists just as they can by field biologists (Thornton & Raihani 2010). Maybe commonalities about the ecology and even evolution of teaching in human societies and nonhuman species will emerge, maybe not. These are empirical issues. Kumbaya-style cross-disciplinary harmonizing will not yield progress, but systematic documentation of behavior based on cost-benefit analyses without explicit recourse to intent or classroom teaching just might.

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Does all teaching rest on evolved traits?

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Abstract: Classification schemes are useful when they elucidate common underlying mechanisms, bring together diverse examples, or illustrate gaps in knowledge for empirical investigation. Kline's scheme merges different approaches, but is orthogonal to existing schemes and overemphasizes evolved specializations, potentially at the detriment of clarifying teaching processes. Focus on underlying mechanisms, what is learned, and consequences for information transfer may provide additional utility.

Kline provides a new and adaptationist taxonomy of different types of teaching that aims to unite fields of research. Kline bases this categorization not on underlying processes or on consequences for cultural transmission, but instead on the adaptive problem that each type of teaching is proposed to solve. There is clear utility in combining knowledge from different approaches to teaching, and the new taxonomy usefully explores how teaching can result from both simple and complex processes. It also clarifies what precise knowledge or opportunities pupils lack. However, over-categorization without appropriate support risks suggesting that we understand more about underlying processes than we do, stifling investigation: a criticism already leveled at social learning taxonomies (Heyes 1994).

Multiple mechanisms may solve the same adaptive problem and multiple adaptive problems may be solved by a single mechanism (de Kort & Clayton 2006); therefore, adaptive-problem-based categorizations will not necessarily match underlying mechanisms. However, Kline often links adaptive problems (themselves notoriously awkward to define) to underlying mechanisms, and her categories are not mutually exclusive, meaning that the new and existing schemes overlap uncomfortably. Rather than adding new categories of teaching, we may do better by incorporating classifications into existing schemes (see e.g., Hoppitt et al. 2008). For example, bringing together individual learning and social learning classifications suggested the possibility of undiscovered social learning processes (Heyes 1994).

Evolved specializations are core to Kline's definition of teaching ("behavior that evolved to facilitate learning in others"; target article, sect. 3, para. 1). We feel that this definition is overly restrictive, more restrictive than definitions used by scholars of the evolution of teaching (Caro & Hauser 1992; Thornton & Raihani 2008), and potentially unappealing to researchers whose focus is not on evolutionary processes. We prefer simply "specialization" (see our Table 1), which emphasizes that teaching processes, like other social learning processes (Heyes 2012a; Reader 2014), could be the result of genetic evolution, cultural evolution, changes within the lifetime of an individual, or interactions between these processes. For example, it is plausible that adult humans may independently develop behavior patterns that fit current functionalist criteria of at least simple modes of teaching. Much teaching may involve a mixture of evolved adaptations for teaching, evolved exaptations that facilitate the development of teaching, and experiential and culturally transmitted effects.

Table 1 also emphasizes that all social learning, including teaching, could be subdivided according to observer specialization. In tandem-running ants, for example, the learners do not appear to be specialized to promote their own learning, whereas children appear to manifest multiple specializations that promote their learning during teaching (Csibra & Gergely 2009; Franks & Richardson 2006). Similarly, learners may or may not show specializations to take advantage of inadvertent social information. Ninespine but not threespine sticklebacks use public information to learn from others, data consistent with a specialized ability having evolved in ninespine sticklebacks (Coolen et al. 2003). In contrast, growing disquiet questions the idea that all social information use rests on adaptive specializations (Heyes 2012b). Recent data show that bees can be trained to approach or avoid conspecific-marked flowers through simple associative learning, just as they might learn the value of an asocial cue (Dawson et al. 2013). Thus, at least prior to training, the bees are not specialized to utilize this social information. These data are consistent with the idea that social learning tendencies may emerge as the result of within-lifetime experience rather than adaptive specializations (Lindeyer et al. 2013).

Present classification schemes do not stress distinctions on the basis of observer specializations (i.e., dividing case 1 from 3 or 2 from 4 in our Table 1). Observer specializations are important, not least because specializations may allow inferences to be made on the costs and benefits relevant to a particular learning process. Moreover, some teaching may require observer specializations, that is, demonstrator–observer co-adaptation. However, specialized observers may be more open to exploitation and deceit (Kline's "pupil as skeptic"), potentially prompting the development of countermeasures.

Estimating the costs and benefits of teaching and social learning is complicated by the numerous direct and indirect payoffs potentially involved. For example, learning from others may carry competitive costs (Seppänen et al. 2007), but provide benefits from joint action, group cohesion, or safety-in-numbers when all perform the same act. As Grüter and Leadbeater (2014) note, high relatedness does not necessarily favor the development of high-efficacy social learning, since highly related groups may benefit from sharing the rewards of individual, independent exploration. Direct benefits may be also diverse and unexpected. In humans, for example, graduate students who teach improve their research skills (Feldon et al. 2011), thus gaining a delayed benefit rather like the superior parenting skills some cooperative helpers can acquire (Komdeur 1996). Sensitivity to the costs and benefits of teaching is expected, particularly when payoffs are variable, and evidence from several taxa suggests that teachers are indeed sensitive to costs. For example, ants abandon tandem running more quickly when teaching costs increase (Richardson et al. 2007) and superb fairy wrens trade calling at the nest against predation risk (Kleindorfer et al. 2014).

Much theory from the study of social learning, cooperation, and communication applies to teaching, although teaching also has distinctive qualities and therefore "teaching" is a useful category (Hoppitt et al. 2008). Subdividing teaching is more challenging.

		Specialization in demonstrator?	
		Yes	No
Specialization in learner?	Yes	 Teaching with specialization in learner E.g.: children's sensitivity to ostensive signals¹ 	 ISI with specialization in learner E.g.: prior public information use in ninespine sticklebacks choosing feeding locations²
	No	3. Teaching without specialization in learner E.g.: route learning in tandem- running ants ³	 ISI without specialization in learner E.g.: observational learning of flowers in bumblebees⁴

 Table 1. (Chouinard-Thuly & Reader). Classification of social learning instances according to whether the individual learned from (the "demonstrator") or the learner (the "observer") show specializations in behavior.

Note: Teaching occurs in cases 1 and 3, inadvertent social information use (ISI; (Danchin et al. 2004) in cases 2 and 4. We use the term "specialization" to underscore that teaching could result from both evolutionary and developmental processes, or from interactions between these processes. In italics we include possible examples, categorizing them according to current evidence. Future work may reveal specialization in learners, for example, bumblebees may preferentially learn about social cues over asocial ones. (1: Csibra & Gergely 2009; 2: Coolen et al. 2003; 3: Franks & Richardson 2006; 4: Dawson et al. 2013.)

Commentary/Kline: How to learn about teaching

Ideally we would determine the correspondence between different categories of teaching, their underlying mechanisms, and their consequences for information transmission. For example, we might demarcate teaching processes based on the neurocognitive mechanisms involved, and determine whether these mechanisms differ in the fidelity of social transmission achieved and the kind and generalizability of the information transmitted. Definitions and distinctions are important, but require concrete grounding to maximize productive debate.

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Learning about teaching requires thinking about the learner

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Abstract: Kline argues for an expanded taxonomy of teaching focusing on the adaptive behaviors needed to solve learning problems. Absent from her analysis is an explicit definition of learning, or a discussion of the iterative nature of the relationship between teaching and learning. Including the learner in the discussion may help to distinguish among the adaptive values of different teaching behaviors.

In an ambitious review, Kline aims to integrate literature across multiple species and theoretical perspectives. She develops a comprehensive taxonomy of teaching behaviors, arguing for distinctions to be made based on the adaptive value of the teaching behavior. I am sympathetic to her goal of developing a framework that can be used across sub-disciplines. However, focusing solely on the teacher – or on the first act of teaching between the teacher and learner – defines teaching as a rather one-sided process. I argue that a broader inspection of teaching requires a more thoughtful discussion of learning, for three reasons.

First, although Kline explicitly defines teaching according to the three different theoretical perspectives, and again according to the six different adaptive problems, she fails to focus on the tobe-learned behavior. Indeed, in some places, the learned behavior is situation-specific, whereas in others the information to be learned allows the learner to generalize to new contexts. For example, Kline highlights ants' ability to signal the location of food to a naïve learner through tandem running (Franks & Richardson 2006; Richardson et al. 2007). This example certainly fulfills Kline's definition of teaching, as well as the teaching definition widely used in studies of animal behavior (Caro & Hauser 1992). However, guiding a naïve learner to a food destination only helps that learner return to that specific destination - and not to other destinations in general. Such an act might be considered teaching, but it is also consistent with more general prosocial behavior directed towards conspecifics (Tomasello 2009), which often is directed towards a specific instance.

For an act to be considered teaching, learning must be present, and the information to-be-learned must be generic and representational. Such a definition of learning is consistent with how learning and teaching have been described in developmental science (e.g., Csibra & Gergely 2009; Gelman et al. 2013; Strauss et al. 2002), allowing teaching behaviors to be uniquely distinguishable from more general prosocial helping interactions (e.g., Warneken 2013), as well as learning behaviors to be distinguishable from imitation (Lyons et al. 2007). Based on this framework, several of the adaptive behaviors mentioned in Kline's review might not be classified as teaching (or for that matter, learning).

Second, Kline's model of teaching focuses solely on instances in which the teacher motivates the exchange of information – through ostensive cues (Csibra & Gergely 2006; 2011) or stimulus enhancement. What may distinguish human teaching from other species is the *learner's* ability to signal to the teacher that an intervention is necessary – either through nonverbal signals such as joint attention (e.g., Butterworth & Jarrett 1991; Tomasello 1995; Tomasello et al. 1993), motoric gestures such as pointing (e.g., Bates 1976), or early question-asking abilities (e.g., Chouinard 2007). Such requests for intervention have implications for cultural and interspecies variation, as well as for the speed of the transmission of information. Indeed, it is plausible that learner-motivated teaching may look very different from a teacher-directed interaction.

Moreover, the interaction between the teacher and learner does not end after the first exchange. Kline's taxonomy certainly allows for this possibility, but I would argue that the follow-up exchanges are the most interesting when exploring the relationship between teaching and learning. Kline rightly notes that even after a teaching exchange, there is likely to be a wide range of possible inferences available to the learner (e.g., Boyer 1998; Sperber 1996). True teaching is contingent teaching – that is, teaching that is adaptive to the learner's changing knowledge state.

Finally, although Kline touches on this somewhat in her discussion of the psychology of teaching, a large body of developmental research suggests that the *type* of teacher matters for learning (e.g., Harris 2012; Harris & Corriveau 2011; Sobel & Kushnir 2013). A consideration of teacher qualities should go beyond questions of honesty, to focusing on the learners' understanding of the knowledge or expertise of the teacher (Keil et al. 2008; Mills & Keil 2004) as well as their recognition that the teacher is a member of their cultural group (Corriveau et al. 2014; Richerson & Boyd 2005). Moreover, most of the examples presented by Kline involve a more senior member teaching a naïve learner, although knowledge is also transmitted horizontally, as well as vertically (e.g., Flynn & Whiten 2008, 2012). More research is needed to determine how children's learning from and teaching to peers might be different from their interacting with adults (Wood et al. 2012).

Overall, although Kline has done a commendable job in integrating literature from animal behavior and developmental science, more thought is needed in placing teaching behaviors in the context of learning.

Subjectivity may hinder the application of Kline's teaching framework in comparative contexts

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Abstract: We welcome Kline's attempt to develop an overarching framework to allow much needed collaboration between fields in the study of teaching. While we see much utility in this enterprise, we are concerned that there is too much focus on the behavior of the teacher, without examining results or costs, and the categories within the framework are not sufficiently distinct.

Kline provides us with a comprehensive and thought-provoking review of our current understanding of teaching. We particularly