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EDITORIAL

## Cognitive demands of sociality: from simple mechanisms to complex behaviour

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Individual learning and behaviour are often shaped by the actions of others. For example, individuals might acquire information from others about their environment (Rendell *et al.*, 2010; Leadbeater, ••) while experienced individuals might teach naïve counterparts how to behave in a given context (Thornton & Raihani, 2008). Furthermore, individuals might cooperate with others to achieve personal or common goals, or compete with them over limiting resources (McAuliffe & Thornton, ••; Thornton & McAuliffe, ••). Despite the vast and fruitful body of research into these topics, a key outstanding question is whether social learning and behaviour rely on specialized, higher-order cognitive adaptations, either for social learning or for social behaviour more generally. It was with this broad question in mind that this mini-series of reviews was commissioned. The three contributions ask, respectively, whether social learning is an adaptation to social living (Leadbeater, ••), whether cooperative breeding selects for advanced socio-cognitive abilities (Thornton & McAuliffe, ••), and more generally, how considering both psychology and ecology is essential to understand the mechanisms underpinning social learning and behaviour (McAuliffe & Thornton, ••). A key take-home message from all three contributions is that seemingly complex behavioural and learning outcomes can often arise through relatively simple psychological mechanisms and, relatedly, that similar behavioural outcomes can often be achieved via different cognitive means.

The tendency to attribute higher-order cognitive abilities to animals that learn and behave socially has, in part, stemmed from comparisons with humans, who are thought to possess and use advanced social cognition to navigate their social world. For example, some forms of human teaching require the teacher to 'know what the pupil knows' (i.e. possess theory of mind) which is a putatively uniquely human capacity (Thornton & Raihani, 2008; Thornton & McAuliffe, 2012). Similarly, the human willingness to voluntarily share resources with others (see Engel, 2011) or to punish cheats (Raihani & McAuliffe, 2012) are both thought to stem from intrinsic fairness preferences (Fehr & Schmidt, 1999), which

rely on the ability to compare own payoffs with those of a social partner. It is perhaps natural, therefore, to ask whether apparently related behaviours in other species might also rely on similar cognitive mechanisms. A key emphasized by the commissioned reviews, however, is that behaviours that serve similar functions need not all rely on the same cognitive mechanisms. For example, although human punishment is thought to be motivated, at least in part, by inequity aversion (Raihani & McAuliffe, 2012), the bluestreak cleaner wrasse *Labroides dimidiatus* shows no evidence for fairness preferences (Raihani *et al.*, 2012a,b) despite being known to punish social cheats (e.g. Raihani, Grutter & Bshary, 2010; Raihani *et al.*, 2012a,b). Similarly, although some forms of human teaching might use – or even rely on – theory of mind, examples of teaching in both humans and non-humans exist that do not necessitate such complex cognition (e.g. Thornton & McAuliffe, 2012). For example, a meerkat helper can teach a pup by provisioning it with increasingly live prey items, giving the pup opportunities to learn handling skills. However, this behaviour need not rely on the helper 'knowing what the pup knows'. Instead, experimental evidence indicates that helpers adjust provisioning behaviour according to the pup's begging calls which serve as a reliable proxy for age and therefore prey-handling expertise (Thornton & McAuliffe, 2006). These examples highlight the importance of distinguishing between behavioural function, on the one hand, and proximate mechanism on the other (Scott-Phillips, Dickins & West, 2011; Thornton & Raihani, in press). Behaviour with similar evolutionary functions (e.g. promoting learning or cooperation) might occur via markedly different mechanisms – and functions should therefore not be defined according to mechanisms (Thornton & Raihani, in press). Instead, it may be more helpful to ask why – from an ultimate perspective – some species use cognitively complex psychological mechanisms to achieve outcomes where simpler and less demanding mechanisms might often suffice.

A related point is that ignoring ecology may lead to dubious inferences about mechanisms underpinning behaviour. For example, as pointed out by McAuliffe & Thornton (••), the

tendency for rats to release trapped conspecifics in laboratory settings has been argued as being motivated by psychological empathy (e.g. Bartal, Decety & Mason, 2011), but this inference appears problematic when considering that, in the wild, rats routinely attack and kill unfamiliar individuals (Blanchard *et al.*, 1975). Similar points have been raised regarding the interpretation of active food sharing in non-human primates in laboratory studies as indicative of other-regarding or fairness preferences (e.g. Burkart *et al.*, 2007; Horner, Carter & Suchak, 2011). As McAuliffe & Thornton (••) argue, these behaviours are often rare under natural circumstances and, when they occur, often reflect self-interested responses to harassment rather than psychologically altruistic motives to help others (Gilby, 2006). These examples underline the importance of considering whether the ecology of the animal in question is likely to have selected for prosociality before inferring that animals have cognitive mechanisms that are adapted to helping others.

Meanwhile, others have also asked whether possession of common cognitive abilities might result in similar outcomes. For example, the tendency to observe and copy the behaviour of others (social learning) underpins the emergence of group-typical norms of behaviour or culture (Boyd & Richerson, 1985). Given that several non-human species learn socially, it is perhaps unsurprising that there is also strong evidence for culture in many non-human species (Levebre & Palameta, 1988; Whiten *et al.*, 1999; Rendell & Whitehead, 2001; Laland & Hoppitt, 2003). Nevertheless, as Leadbeater (••) points out, culture is not an inevitable outcome of the ability to learn socially. Indeed, cumulative culture [where cultural modifications accumulate over time and build on previous advances (Tomasello, Kruger & Ratner, 1993)] is thought to be unique to humans (Tennie, Call & Tomasello, 2009 but see [4] Yamamoto, Humle & Tanaka, 2013). Given that several non-human species have the cognitive machinery to facilitate the emergence of culture and even, arguably, cumulative culture (Dean *et al.*, 2012; Leadbeater, ••), why are these phenomena not more widespread? Only approaches that consider both ecology and psychology in tandem are likely to be able to answer these sorts of questions.

## References

Bartal, L.B.-A., Decety, J. & Mason, P. (2011). Empathy and pro-social behavior in rats. *Science* **334**, 1427–1430.

Blanchard, R.J., Fukunaga, K., Blanchard, D.C. & Kelley, M.J. (1975). Conspecific aggression in the laboratory rat. *J. Comp. Physiol. Psychol.* **89**, 1204–1209.

Boyd, R. & Richerson, P. (1985). *Culture and the evolutionary process*. Chicago: University of Chicago Press.

Burkart, J.M., Fehr, E., Efferson, C. & van Schaik, C. (2007). Other-regarding preferences in a non-human primate: common marmosets provision food altruistically. *Proc. Natl. Acad. Sci. USA* **104**, 19762–19766.

Dean, L.G., Kendal, R.L., Schapiro, S.J., Thierry, B. & Laland, K.N. (2012). Identification of the social and

cognitive processes underlying human cumulative culture. *Science* **335**, 1114–1118.

Engel, C. (2011). Dictator games: a meta study. *Exp. Econ.* **14**, 583–610.

Fehr, E. & Schmidt, K.M. (1999). A theory of fairness, competition, and cooperation. *Quart. J. Econ.* **114**, 817–868.

Gilby, I. (2006). Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange. *Anim. Behav.* **71**, 953–963.

Horner, V., Carter, J. & Suchak, M. (2011). Spontaneous prosocial choice by chimpanzees. *Proc. Natl. Acad. Sci. USA* **108**, 13847–13851.

Laland, K.N. & Hoppitt, W. (2003). Do animals have culture? *Evol. Anthropol.* **12**, 150–159.

Leadbeater, •• (••). What evolves in the evolution of social learning? *J. Zool. (Lond.)* ••, ••–••.

Levebre, L. & Palameta, B. (1988). Mechanisms, ecology, and population diffusion of socially-learned, food-finding behavior in feral pigeons. In *Social learning, psychological and biological perspectives*: 141–165. Zentall, T. & Galef, B.G. Jr. (Eds). Hillsdale: Lawrence Erlbaum Associates, Inc.

McAuliffe, •• & Thornton, •• (••). The psychology of cooperation in animals: an ecological approach. *J. Zool. (Lond.)* ••, ••–••.

Raihani, N.J. & McAuliffe, K. (2012). Human punishment is motivated by inequity aversion, not a desire for reciprocity. *Biol. Lett.* **8**, 802–804.

Raihani, N.J., Grutter, A.S. & Bshary, R. (2010). Punishers benefit from third-party punishment in fish. *Science* **327**, 171.

Raihani, N.J., McAuliffe, K., Brosnan, S.F. & Bshary, R. (2012a). Are cleaner fish, *Labroides dimidiatus*, inequity averse? *Anim. Behav.* **84**, 665–674.

Raihani, N.J., Pinto, A.I., Grutter, A.S., Wismer, S. & Bshary, R. (2012b). Male cleaner wrasses adjust punishment of female partners according to the stakes. *Proc. Roy. Soc. Lond. Ser. B.* **279**, 365–370.

Rendell, L. & Whitehead, H. (2001). Culture in whales and dolphins. *Behav. Brain Sci.* **24**, 309–324.

Rendell, L., Laland, K.N., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M.W., Fogarty, L., Ghirlanda, S. & Lillicrap, T. (2010). Why copy others? Insights from the social learning strategies tournament. *Science* **328**, 208–213.

Scott-Phillips, T.C., Dickins, T.E. & West, S.A. (2011). Evolutionary theory and the ultimate-proximate distinction in the human behavioral sciences. *Perspect. Psychol. Sci.* **6**, 38–47.

Tennie, C., Call, J. & Tomasello, M. (2009). Ratcheting up the ratchet: on the evolution of cumulative culture. *Philos. Trans. Roy. Soc. B.* **364**, 2405–2415.

Thornton, A. & McAuliffe, K. (••). Cognitive consequences of cooperative breeding? A critical appraisal. *J. Zool. (Lond.)* ••, ••–••.

- 1 Thornton, A. & McAuliffe, K. (2006). Teaching in wild  
2 meerkats. *Science* **313**, 227–229.
- 3 Thornton, A. & McAuliffe, K. (2012). Teaching can teach us  
4 a lot. *Anim. Behav.* **83**, e6–e9.
- 5 Thornton, A. & Raihani, N.J. (2008). The evolution of teach-  
6 ing. *Anim. Behav.* **75**, 1823–1836.
- 7 Thornton, A. & Raihani, N.J. (in press). The proximate-  
8 ultimate confusion in teaching and cooperation. *Behav.*  
9 *Brain Sci.* ••, ••–••.
- 10 [12] Tomasello, M., Kruger, A.C. & Ratner, H.H. (1993). Cultural  
11 learning. *Behav. Brain Sci.* **16**, 495–511.
- Tomasello, ••. (1994). ••. [13] 12
- Whiten, A., Goodall, J., McGrew, W.C., Nishida, T.,  
13 Reynolds, V., Sugiyama, Y., Tutin, C.E.G., Wangan,  
14 R.W. & Boesch, C. (1999). Cultures in chimpanzees. *Nature*  
15 **399**, 682–685.
- 16 Yamamoto, S., Humle, T. & Tanaka, M. (2013). Basis for  
17 cumulative cultural evolution in chimpanzees: social learn-  
18 ing of a more efficient tool-use technique. *PLoS ONE* **8**,  
19 e55768.
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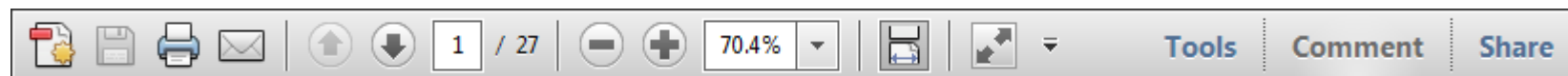
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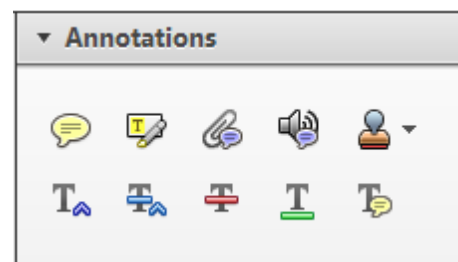
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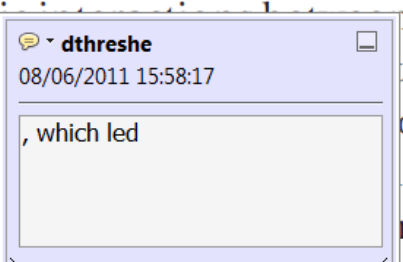
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
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
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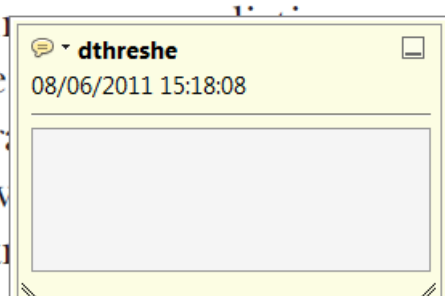
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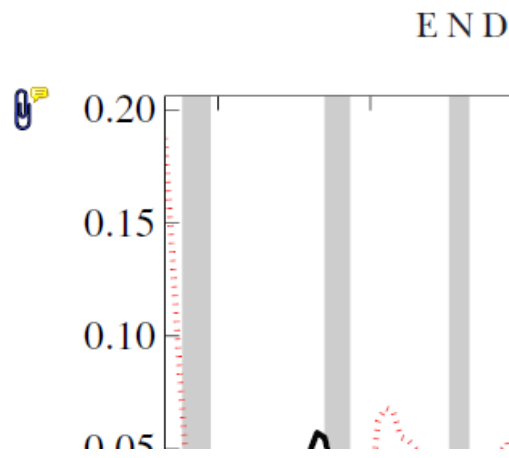
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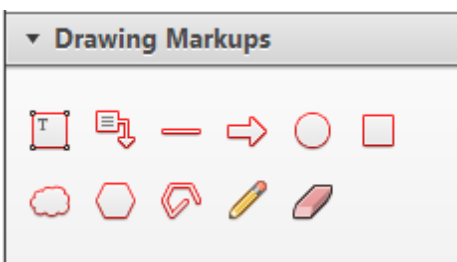


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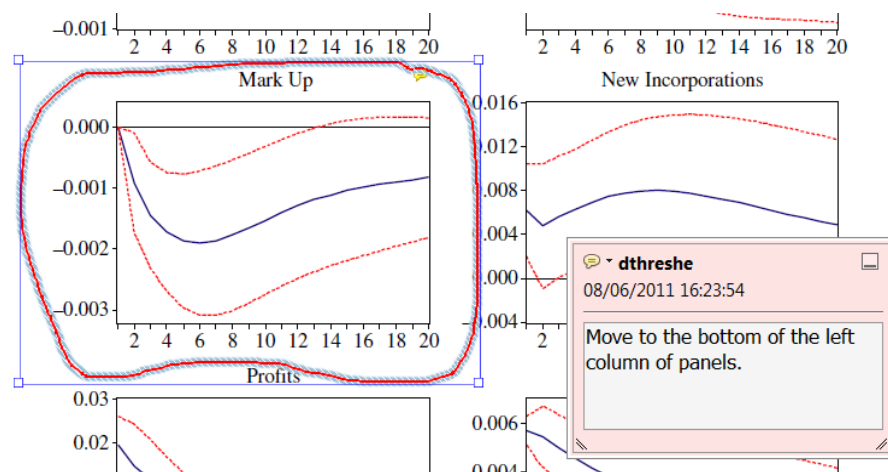


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