The individual and social drivers of primate innovation

How does nonhuman primate innovation compare to our own? Many primates innovate, for example to get otherwise inaccessible food or to increase their social standing, and nonhuman primate innovation can be broken into three component steps. It begins with the initial invention, which is then transmitted to other members of the inventor's group, and is then adopted by other individuals and maintained within the society. These three steps – invention, transmission, and maintenance – are all required for innovation and in this review, I discuss the factors (social, environmental, and cognitive) that influence each step. I also highlight the comparable and contrasting features between human and nonhuman primate innovation. In contrast to human innovations, primate innovations are relatively simple and are typically self-serving. Nonhuman primates do not invent new products explicitly for the use of others (although group members certainly copy others' innovations) and nor are their inventions artistic or abstract in nature. Intriguingly, although chimpanzees and other nonhuman primates appear to be expert at copying others' inventions, there is far less evidence of their ability to build upon others' inventions (i.e., to show cumulative culture). At the core of our complex cultural world is the fidelity with which we copy others and our specialism at building upon the ideas of others. Thus, it is the cumulative nature of our innovative process that has created our complex material cultural world and is a key difference between how we innovate, learn and transmit knowledge, and how our chimpanzee cousins copy one another. Another difference is our ability to work collaboratively in teams to innovate and develop new technologies, as well as our potential to cooperate in an altruistic way that allows for planning for future generations. In conclusion, perhaps primate innovation can be most usefully likened to human 'user innovators' who typically innovate products or techniques to fill a personal need, rather than by being driven to create a product to go to market.

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The Individual and Social Drivers of Primate Innovation

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WHAT IS (NONHUMAN PRIMATE) INNOVATION?

Innovation is not a solitary pursuit. Inventors are shaped by their social environment and rely on their community to adopt their inventions. Furthermore, innovation is not a one-way process in which users only adopt others' innovations, but users themselves may also be active in product development and modification (von Hippel, 2005). In turn, discoveries are amended, improved upon, or discarded, streamlining and refining innovations in an iterative fashion. This ratcheting creates an accumulation of cultural complexity (Tomasello et al., 1993), a process which Matt Ridley famously crystalized and popularized as "ideas having sex" (Ridley, 2010). There is a feedback loop within the social environment as individuals innovate through trial-and-error and also by copying and improving upon the ideas of others. The importance of social information for how we learn and innovation has long been recognized. For example, in her book *Openness, Secrecy, Authorship*, Pamela Long (2001) noted that Vitruvius believed that humans discovered the art of building in part by imitating the nests of swallows[1]. Thus, innovations can arise both through personal discovery and also by adapting the ideas and behavior of others (in this case, replicating and expanding upon the nest making of birds[2]), but what drives our need to innovate?

We can innovate in a methodical planned way, in an attempt to address a current need, or we might innovate spontaneously, without forethought or clear understanding of our goal. The former relies on spotting gaps in the market or in our needs, and potentially the ability for mental time travel: future planning that allows us to predict and prepare for future events or needs (Vale et al., 2012). The latter arises from simple trial-and-error problem solving – such inventions are serendipitous and do not rely on cognitive planning or forethought. How much intentionality and active learning is involved in innovation has been much debated and some scholars divide innovation into active *versus* passive innovation (also referred to as Type I *versus* Type II innovation) (Reader et al., 2016). Simply put, active innovation requires learning and insight, while passive innovation can arise more serendipitously. Beyond our underlying understanding and motivation to innovate, the process of innovation has been subcategorized as (1) invention, (2) refinement, (3) recombination, and (4) exaptation (Mesoudi et al., 2013). In this way, an invention can be more than a new product or solution, it can also be the application of an already-existing invention repurposed in a new way, the combination of new existing

[1] The parallels between birds' nests and our abodes was also a topic of interest for Vincent van Gogh who noted in in text accompanying a sketch he drew of a bird's nest that he sent to his brother Theo "The nestlings and the nests, I feel deeply for them – especially people's nests, those huts on the heath and their inhabitants." Text from a letter written by van Gogh on September 4th 1885 translated by Johanna van Gogh-Bonger and reproduced by WebExhibits: http://www.webexhibits.org/vangogh/letter/15/425.htm

[2] Pamela Long (2001) also reported "the atomist Democritus of Abdera articulated… [that] humans discovered arts such as weaving and building houses by imitating the animals; they invented weaving, for example, after observing how spiders create their webs" (Long, p. 19)

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technologies to create a novel product, or the refinement of an existing product in a way that creates a novel innovation[3].

It has been proposed that imagination, which is linked to our ability to remember and predict events, is a key component of creativity, itself a potential driver of innovation. Creativity is an intriguing and somewhat elusive property, and there is much individual variation in peoples' creativity, although current research is helping to elucidate the neural underpinnings of creativity (Bashwiner et al., 2016; Jung et al., 2016). Creativity is inherently playful, and innovations driven by creativity arise from curiosity, not need (van Schaik et al., 2016). Yet the adage states that necessity is the mother of invention (not creativity). I reality, it is likely that, for humans, both need and creativity can drive innovation, although there is likely to be individual and situational variation. Determining whether an individual's tinkering is driven by curiosity, rather than need, may be difficult, especially for nonverbal nonhuman primates. Considering primates, 'environmental opportunity' actually appears to be a better predictor of when monkeys and apes make and use tools (Koops et al., 2014). Essentially, a chimpanzee cannot invent a new kind of stone tool if there are no stones lying around, however badly she needs to crack open a nut, or how curious she is. Furthermore, captive primates are thought to be more innovative than their wild counterparts because they have more 'spare time' in which to explore. Kathelijne Koops and colleagues (2014) concluded that when and how wild chimpanzees, orangutans and capuchin monkeys make tools can be explained by a combination of environmental opportunity, cognitive ability, and sociality, all of which differentially influence when and if individuals innovate and when and if others adopt their innovations. It is likely that creativity is not a pre-requisite for innovation, especially if we consider the innovations of nonhuman primates.

INNOVATION BY NONHUMAN PRIMATES

A classic case of primate innovation is that of Imo, the Japanese macaque, who discovered that if she washed sand-covered potatoes left on the beaches of Koshima Island, Japan, by researchers trying to study her group's behavior, they would be more palatable (Yamagiwa, 2010). Primatologists in the late 1940s and early 1950s studying the Japanese macaques that lived on Koshima Island placed potatoes on the sea shore to lure the monkeys out of the forests where they lived, making it easier for the researchers to observe the monkeys' behavior[4]. Imo (whose name means potato in Japanese) was the first to wash her potatoes in a nearby freshwater stream. Later, she innovated for a second time and carried the potatoes to the sea to wash off the sand before eating them; not only did washing the potato in the sea remove the sand, but this latter variant added a salty seasoning to the food. Imo was quickly copied by offspring, and soon the behavior spread throughout the troop (de Waal & Bonnie, 2009). Such socially-mediated learning has been dubbed the 'second inheritance system' (Whiten, 2005): a behavior is spread throughout a group of individuals via observational learning rather than by genetic inheritance.

[3] The adaptation of previously-made inventions for new markets or cultures is a process that is alive and well in current day China. As Clive Thompson (2015) noted in his article about Chinese "copy cat" firms, local firms in China had an edge over the established giants from abroad because they had local cultural understanding and so were able to adapt existing technologies to better suit the local market. The examples Thompson provides demonstrate that not only can replications be considered innovations when applied in a new setting, but that they also spawned future (novel) innovations.

[4] The Japanese primatologists studying Imo and her troop were also innovative, as unlike many behaviorists before them who studied animals at the population or species level, Kinji Imanishi, Shunzo Kawamura, and Jun'ichiro Itani were interested in studying animal societies at the level of unique and identifiable individuals (Hirata et al., 2001).

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Imo's potato-washing innovation is a perfect example of what is considered as innovation by primatologists: a novel behavior, invented by a single individual, is adopted by others in the innovator's group (Laland & Reader, 2003). Of note too, and in contrast to human innovations, Imo's innovation was relatively simple and was very self-serving. She was not inventing a new product for the use of others in her group (although they certainly exploited her innovation by copying her) and nor was her invention artistic or abstract in nature. We are unique in the scale and scope of our innovations, even as compared to our closest living cousins, the chimpanzees. Chimpanzees are renowned for their cognitive prowess, and are both expert innovators and keen observers of their group mates' behavior allowing them to copy the innovations of others. They have been documented to create and use a variety of tools, which appear to vary culturally across different societies, and to develop novel behavioral and gestural cultures (Whiten et al., 1999). Despite this, they do not have the complexity of material culture that we do; they do not live in cities, communicate over long distances using technologies designed for that purpose, nor do they use symbolic representation (Hill, 2009).

When we consider primate innovation, creativity and intention are not always inferred, while when we discuss human innovation, we often consider innovation to be insightful – entrepreneurs aim to spot gaps in the market and launch the product to market. Primates, by contrast, are typically not trying to innovate to create a product, tool, or skill that others will adopt. They do not teach, and any transmission of information is passive (Matsuzawa et al., 2001). Given this, perhaps primate innovation can be more usefully likened to 'user innovators.' Eric von Hippel (2005) provides a comprehensive overview of the current activity and importance of user innovators who typically innovate products or techniques to fill a personal need, rather than by being driven to create a product to go to market. For example, in addition to innovating and creating products for sale, manufacturing companies invent and develop tools for their own use, that enhance the fabrication process of their products. These user innovations can be in the form of modifications to existing tools or the invention of a completely novel tool. Primates, like user innovators, typically create tools for their own needs or adapt the tools used by others. In both cases, their inventions are for use by them personally, rather than to distribute within their community. Any distribution that is observed, would be unintentional on the part of the inventor, and happen passively by social learning as shown experimentally in a number of experiments (Hopper, in press, provides a review).

THE PROCESS OF INNOVATION

As highlighted through the example of Japanese monkey Imo's potato washing described above, innovation is process that can be broken in three component steps. It begins with the initial invention, which is then transmitted to other members of the inventor's group, and is then adopted by other individuals and maintained within the society. These three steps – invention, transmission, and maintenance – are all required for innovation and yet the factors that influence each step vary (Brosnan & Hopper, 2014 provide a review of the mechanisms that can inhibit each of these three steps when animals innovate).

Inventive Inventors

"In order to educate and support innovative leaders, we should first identify what characterizes them" Rebecca Bagley wrote in a 2014 *Forbes* article entitled *The 10 Traits of Great Innovators*, before going on

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to list ten characteristics of innovative personalities. Such an approach is not uncommon and highlights both our desire to pinpoint the specific characteristics of innovators and also the inherent difficulties in doing so. It is clear that there is no single trait associated with 'innovativeness' in humans, and the same appears to be true for nonhuman primates and other animals.

In a recent study run with a group of chimpanzees housed at Chicago's Lincoln Park Zoo, the chimpanzees were provided with plastic tokens that they could exchange with researchers who stood at the perimeter of their enclosure (Hopper, Kurtycz et al., 2015). The experiment was designed such that if the chimpanzees took their tokens to the experimenter who was standing furthest away and exchanged it with them, they received a highly-desirable food reward (for them, this was a grape). Contrastingly, if the chimpanzees choose to carry their tokens to the nearer researcher they received a less-desirable piece of carrot for each token exchanged. Importantly, the chimpanzees were not trained how to exchange tokens with the researchers, and nor were they trained about the relative value of the food rewards available at each location. The beta-ranking male chimpanzee, Optimus Prime, was the first member of the group to ever exchange a token for a food reward and he did so with the researcher standing closest by, gaining a piece of carrot. The rest of his group then quickly learned his new skill, all exchanging their tokens for the readily-accessible, but less-desirable, carrot pieces. The seventh time that the chimpanzees were presented with tokens, the lowest-ranked member of the group, a 13-year old female named Chuckie innovated. She was the first in her group to discover that if she carried her tokens a little further, she could exchange them for better rewards. She was also the first to do so again in a later phase of the study when the locations where the researchers stood to exchange tokens changed. What was it about Chuckie and Optimus Prime that encouraged them to innovate how and where to exchange the otherwise seemingly-useless plastic tokens? A review of innovations by wild primates revealed that chimpanzees' innovative tendencies are influenced by their age, rank and sex, with juvenile, low-ranking, or male chimpanzees being more likely to innovate, most likely to enable them to secure otherwise inaccessible resources (Reader & Laland, 2001). This pattern mirrors that seen among the chimpanzees at Lincoln Park Zoo. The first to innovate, Optimus Prime, was lower-ranking and male and, Chuckie was very low ranking young member of the group.

More recent studies with captive chimpanzees investigating how chimpanzee personality traits correlate with their problem-solving prowess have reported that chimpanzees rated highly on personality factors related to curiosity, exploration, and persistence are more dogged in their efforts to solve the puzzles presented to them and are ultimately more successful in solving them (Massen et al., 2013; Hopper et al., 2014). Ultimately, it is most likely that an individual's innovative tendencies arise from a combination of factors. Therefore, 'innovativeness' can likely be considered as an emergent property comprising of internal states and predispositions as well as external environmental factors (Reader et al., 2016). Beyond simply considering cognitive skills, it is also important to consider motor flexibility, learning and physiology, all of which influence the different ways in which animals can interact with their physical environment and, therefore, what and how they innovate (Griffin, 2016).

Transmission and Adoption

We can all call to mind specific inventors, individual's whose tireless work or genius insight resulted in the creation of a novel creation: Henry Ford who founded the Ford Motor Company, Sir Timothy John Berners-Lee who invented the World Wide Web, and Ada Lovelace who is recognized as the first computer programmer when she wrote her notes on algorithms to be computed by machines (Isaacson, 2014). However, even the most highly inventive individuals are inspired by those around them (whether directly or not). So, beyond the intrinsic factors that some individuals have that drive them to innovate, it is absurd to think that individuals are not influenced by the society around them. As Muthukrishna and Henrich (2016) noted "innovations arise as an emergent consequence of our species' psychology applied within our societies and social networks" and there is a swathe of research showing how, just like us, nonhuman primate decision making is also influenced by their social environment (Cronin & Hopper, in press; Hopper & Cronin, in press). Beyond this, the social environment in which an innovator lives is key as it is what allows the innovation to be propagated and distributed (Rogers, 2003).

Nonhuman primates are more explorative and less fearful to approach new things (neophobic) when they have social support. Studies with captive New World monkeys, including capuchin monkeys and squirrel monkeys, have shown that they are much more likely to solve novel puzzles when they are tested with their group mates present, than when tested alone (Dindo et al., 2009). For example, squirrel monkeys that were given a box that contained a meal worm (a tasty treat for a squirrel monkey!) were only able to learn how to slide open a door on the box to retrieve the meal worm if they had a companion in the testing booth with them, whereas those monkeys tested by themselves never solved the task despite its relative simplicity (Hopper et al., 2013).

Beyond providing social support and encouraging exploration, being in the presence of group mates allows primates to exploit the behavior of others and replicate their actions and innovations, which saves them the potential costs associated with trial-and-error learning (Hopper, in press). For example, experimental research with captive and wild primates has shown that they can socially learn how to assemble and use tools from observing others (Price et al., 2009), how to solve problems presented on touchscreen computers (Subiaul et al., 2004), and which foods to eat or avoid, even if that contradicts their own personal experiences (van de Waal et al., 2013). Social learning is important because it is the key mechanism that facilitates transmission of innovations within social groups – primates are experts at gaining new skills this way – and it is the first step of cultural diversification. Via social learning, primates learn skills that will sustain them, such as how to capture and process prey or how to make and use tools, as well as social gestures and customs, which are important for maintaining social bonds (Hopper et al., 2011). Interestingly, just as certain individual characteristics are associated with greater innovativeness, certain primates are more likely to copy the behavior of others, which is influenced by factors including an individual's personality (Carter et al., 2011) and rank (Kendal et al., 2015), as well as their species (Pasquaretta et al., 2014) (Hopper, in press, provides a review).

Imitating and Improving Others' Inventions

Perhaps more importantly than simply 'blindly' copying the behaviors of others, is the ability to build upon the ideas of others. This 'ratcheting' effect (Tomasello et al., 1993) is a keystone of human culture. A key characteristic of cumulative cultural artifacts is that contemporary inventions could not be invented by a single individual; they are the creation of multiple generations' tinkering and modifying. Cumulative culture further emphasizes the idea that innovators are not uninfluenced by their social environment, whether their current social group or previous generations. We are all standing on the shoulders of giants. Intriguingly, although chimpanzees and other nonhuman primates appear to be expert imitators (apes really do ape), there is far less evidence of their ability to build upon others' inventions (i.e., to show cumulative culture, Mashall-Pescini & Whiten, 2008). While some groups of wild chimpanzees have an array of over 20 different tools in their tool kit, in only a few circumstances do they use different tools in combination (so-called 'tool sets,' e.g., Sanz, Schoning & Morgan 2009). Furthermore, chimpanzees have never been observed to combine tools, to add on elements to tools (such as adding a handle), or to create tools to make other tools. Thus, although chimpanzees use tools that are differentiated, and show forethought in their creation and use of tools (Sanz, Call & Morgan, 2009; Hopper, Tennie et al., 2015), all their tools could likely be invented by a single individual, and cannot be considered as the result of an accumulation of techniques (Tennie et al., 2009).

What is it about our ability not just to copy others, but to extend upon their inventions, that chimpanzees lack? Lewis Dean and colleagues (2014) reviewed characteristics that might be unique to us and explain why we, but not chimpanzees, evidence complex cumulative culture. They cited cognitive skills including our ability to innovate and to faithfully imitate the behavior of others; our propensity to work collaboratively and to share; and that we actively teach one another and can communicate complex instructions and descriptions. As the idea of a single innovative trait seems too reductionist, so does the idea that a single characteristic is what differentiates our social learning skills from our chimpanzee cousins. It is likely that multiple cognitive, social and ecological factors inhibit chimpanzees' ability or drive to develop complex cultural artifacts, tools and customs. Contemporary experimental research (e.g., Dean et al., 2012) and theoretical research (e.g., Lewis & Laland, 2012) is now just beginning to tap into the mechanisms that promote and hinder cumulative cultural transmission in us and other species (Caldwell et al., 2012).

SOCIAL NETWORKS, DOMINANCE, AND FRIENDSHIPS

Although chimpanzees appear less likely than us to (intentionally) modify and improve upon previous generations' innovations, they are certainly skilled at copying the actions of others and replicating their inventions. In this way, inventions can become spread within a community. However, the likelihood that an invention will be adopted by the innovator's social group and spread widely within their community is dependent on the place of the innovator in their social network, and the dynamics of their network. From 40 years of observing wild chimpanzees living in Tanzania, Toshisada Nishida and colleagues (2009) concluded that "innovation was not rare, but the emergence of fashion or establishment of traditions seems to occur rarely in chimpanzee society." This nicely highlights the important interplay between the individual innovator and their society with regard to the adoption and transmission of inventions. When considering the inventions of human entrepreneurs, we often merit the success of an invention as to whether it reached commercialization, which may be related to the relevance or 'excellence' of the invention itself (Scott et al., 2015) or how well connected the entrepreneur is (Lee, 2015). While it may be a complex exercise to evaluate the merit of chimpanzees' innovations, through the use of social network analysis, combined with observational and experimental research focused on the transmission of inventions, it is possible to dissect how the social dynamics of a social group might influence the likely transmission of an invention (Hobaiter et al., 2014) and the stability of the social system (Fushing et al., 2014).

In her study of human innovation transmission and the characteristics of communities that foster entrepreneurship, Minha Lee (2015) identified three key aspects of human societies that would promote knowledge dissemination and the transfer of inventions. The first two related to defining how interconnected the social group is; the number of individuals who engage positively with one another ('density') and the number of connections that key individuals have ('central connectors'). The third component was the relative knowledge that individuals within a group have, with those individuals with key knowledge ('knowledge bases') and their connectivity with central connectors being key to enable innovation. Similarly, experimental work with captive primates (e.g., squirrel monkeys: Claidière et al., 2013) and observations of wild groups (e.g., chimpanzees: Hobaiter et al., 2014) have revealed that an

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individual's social relationship with an inventor predicts their likelihood of copying that inventor and adopting their invention; birds of a feather flock together, and then go on to copy one another. Nicolas Claidière and colleagues (2013) also found that more centrally-connected squirrel monkeys were more likely to learn new innovations and would also adopt the innovation more quickly than other members of the group, as has also been shown within wild communities of birds (Alpin et al., 2015).

Beyond the number of social connections a primate has, the quality of those relationships is also important, something that varies both within, as well as across, species (Cronin et al., 2014; Pasquaretta et al., 2014). Many primate societies are governed by strong dominance hierarchies, and, as discussed above, low-ranking chimpanzees are more likely to innovate than dominants, but they are also more likely to copy the behavior of others than are dominants (Kendall et al., 2015). The role of subordinate chimpanzees in the innovative process (i.e. their propensity to innovate and also to copy others) may also explain Nishida and colleagues' (2009) report that many wild chimpanzee inventions were not adopted by their group mates[5]. Chimpanzees typically only look to older and more dominant individuals for information, and are less likely to copy individuals that are subordinate or younger individuals (Biro et al., 2003). This applies to low-ranking individuals and juveniles within a group, and also chimpanzees that are low-ranking because they immigrated into a new group. The low rank of immigrant (typically female[6]) chimpanzees also inhibits transmission of information between chimpanzee communities, as well as within them, as residents are less likely to copy to the behavior of immigrants, even if they arrive with novel skills (Matsuzawa & Yamakoshi, 1996; Biro et al., 2003).

Wild chimpanzees that join new communities typical adopt the traditions of the new group; they conform to the majority. Recent observations of two communities of chimpanzees in Côte d'Ivoire revealed the perhaps surprising insight that when females left their natal group, in which they had a culture of using wooden tools to crack open nuts, and joined the neighboring troop that typically used stone tools to crack nuts, within a couple of months, the immigrant females too were predominantly using stone tools to crack nuts (Luncz & Boesch, 2014). This transition from wooden to stone tools arose despite the females already knowing an equally efficient strategy, and one which they had used all their life previously. Just as chimpanzees typically copy the majority, they also ignore the minority. This is highlighted by the example described by Matsuzawa and Yamakoshi (1996) of a female chimpanzee in Guinea, called Yo, who was an immigrant to her group. The Japanese researchers provisioned the chimpanzee group with novel coula nuts, which are hard shelled and difficult to crack open. Almost immediately Yo placed a coula nut on a stone 'anvil' and used a second stone hammer to crack open the nut. It is probable that Yo had experience cracking these nuts in her natal group and so likely did not invent this behavior. What is striking though, is that despite 'demonstrating' this neat new trick to her group, the only other chimpanzees to follow her lead and start cracking open and eating the coula nuts were two youngsters. None of the adults copied and the behavior never spread within the group.

[5] This interplay between a chimpanzee's individual status and innovation (invention and transmission) is reminiscent of the incumbent's curse, which posits that large dominant firms are less nimble than smaller companies and startups and are less likely to innovate, or, if they do, they do so slowly in small incremental steps. However, and as with innovation by dominant chimpanzees, the lore that large and old firms is not always borne out (Chandy & Tellis, 2000).

[6] Female chimpanzees typically leave their natal group around adolescence and join neighboring communities; an evolutionary strategy for avoiding inbreeding.

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CONCLUDING THOUGHTS

We are a species renowned for our innovative abilities, both to invent independently and to copy the innovations of others. At the core of our complex cultural world is the fidelity with which we copy others[7], allowing for faithful transmission and adoption of innovations within a community, and also our specialism at building upon the ideas of others. Andrea Griffin (2016) characterized this as 'connective thinking', while Matt Ridley coined the term 'ideas having sex.' Indeed, as Eric von Hippel (2005) noted, "to say an innovation is minor is not the same as saying it is trivial: minor innovations are cumulatively responsible for much or most technical progress" (p. 21). Thus, it is the cumulative nature of our innovative process that has created our complex material cultural world and is a key differentiator between how we innovate, learn and transmit knowledge, and how our chimpanzee cousins copy one another (Tennie et al., 2009; Dean et al., 2014).

Another difference is our ability to work collaboratively in teams to innovate and develop new technologies, as well as our potential to cooperate in an altruistic way that allows for planning for future generations (Stout, 2015). While chimpanzees can cooperate, for example when hunting, it does not appear that they collaborate in the process of innovating as is seen among human teams (Cronin & Hopper, in press). With our communicative skills, we can transmit ideas via written or oral instruction, whereas primates typically only learn from others via direct observation. Some primate social learning can occur indirectly, for example a chimpanzee might learn how to crack nuts by discovering the discarded hammer and anvil used by a group mate, but this appears to be a less effective and efficient transmission stream (Caldwell et al., 2012).

Although nonhuman primates have not created the diversity of material technologies that we have, nor do they build and live in complex cities, they nonetheless are expert innovators. Innovations by primates have been reported in a range of realms including tool construction (e.g., Hobaiter et al., 2014), the eating and processing of novel foods (e.g., Leca et al., 2008) and the invention of novel gestures to communicate meaning and maintain social bonds (e.g., Laidre, 2008). They are also experts in the social realm. Highly intelligent, political, and social creatures that can navigate the complexities of group living through the formation of alliances and friendships. Currently, more than half of the world's primate species are facing extinction, so perhaps their biggest challenge to date is to innovate and adapt to the changing demands of their fragmented habitat and the anthropogenic pressures they encounter.

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[7] Indeed, developmental psychologist Andy Meltzoff dubbed us *Homo imitans* (Metlzoff 1998).

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