Celebrating the Continued Importance of "Machiavellian Intelligence" Thirty Years On

Lydia M. Hopper[1], Erica van de Waal[2], & Christine A. Caldwell[3]

1. Lester E. Fisher Center for the Study and Conservation of Apes, Lincoln Park Zoo, Chicago, IL 60622, USA
2. Department of Ecology and Evolution, University of Lausanne, 1015 Lausanne, Switzerland
3. Division of Psychology, University of Stirling, Stirling, FK9 4LA, UK

Corresponding authors: L.M. Hopper (lhopper@lpzoo.org); E. van de Waal (erica.vandewaal@unil.ch); C.A. Caldwell (c.a.caldwell@stir.ac.uk)

Abstract

The question of what has shaped primates' (and other species') cognitive capacities, whether technical or social demands remains a hot topic of inquiry. Indeed, a key area of study within the field of comparative psychology in the last few decades has been the focus on social life as a driving force behind the evolution of cognition, studied from behavioral and neurological perspectives, and from theoretical and empirical perspectives. Reflecting on contemporary studies of primate social cognition specifically one cannot ignore the book, *Machiavellian Intelligence,* co-edited by Richard Byrne and Andrew Whiten (Byrne & Whiten, 1988a). It is a keystone for the field: the volume as a whole has been cited over 3,000 times, without even including citations to individual chapters. This year, 2018, is the 30th anniversary of the first publication of *Machiavellian Intelligence*, and with this special issue of the *Journal of Comparative Psychology* we mark that milestone. The key concept put forth in *Machiavellian Intelligence* was that primates' socio-cognitive abilities were shaped by the complex social worlds that they inhabited, rather than the technical or foraging challenges that they faced, as had previously been posited. In this issue, we consider the strength of the Machiavellian intelligence hypothesis 30 years on to explain primate social cognition, and we consider its applicability to non-primate species and to other cognitive domains.

Keywords: Machiavellian intelligence hypothesis; social intelligence hypothesis; social cognition; brain size; encephalization quotient

Introduction

"The idea of social intelligence is one whose time has come, but such ideas have been struggling to the surface for some time, in interestingly different forms" (Whiten & Byrne, 1988a, p.1)

From reading Humphrey's (1976) essay, *The Social Function of Intellect*, Whiten and Byrne (1988a) identified three hypotheses regarding the interplay between social complexity and intelligence (Whiten, this issue). These were that species, such as primates, that live in complex social systems have evolved cognitive adaptations to negotiate their social environment; that social complexity selects for greater general intelligence; and that social complexity selects for more sophisticated *social* cognition specifically. And so were born the nascent ideas that ultimately formed the Machiavellian intelligence hypothesis (MIH). Importantly, MIH directed focus on primates' cognitive skills in the social realm, rather than in the technical realm and, more specifically, how the challenges that socially-living primates face have shaped their intelligence. To create a cohesive discussion around this topic, which had been contemplated contemporaneously by a number of scholars, including Humphrey (1976), Jolly (1966), and Kummer and Goodall (1985), and often using different terminology, Byrne and Whiten (1998a) published the edited volume *Machiavellian Intelligence.*

With *Machiavellian Intelligence*, Byrne and Whiten (1998a) brought together a collection of chapters, some which represented previously-published works (e.g., Humphrey, 1988; Jolly, 1988; Cheney & Seyfarth, 1988) and some that were novel contributions (e.g., Harcourt, 1988; Premack, 1988; Wynn, 1988). The chapters in *Machiavellian Intelligence* discussed topics related to social behavior and collective action (Chance & Mead, 1988; Menzel, 1988), primates' understanding of social relationships (Dasser, 1988; Seyfarth & Cheney, 1988), and how primates use that understanding to manipulate the actions of others for their own benefit (so-called tactical deception, Byrne & Whiten, 1988b; Whiten &

Byrne 1988b) and to form alliances (e.g., de Waal, 1988; Kummer, 1988). The book also contained contributions from authors who considered these topics in relation to human behavior (LaFrenière, 1988; Smith, 1988), thus providing a comparative perspective with our own species.

In the 30 years since the publication of *Machiavellian Intelligence* it has been well established that conspecifics influence the daily decision making of individual primates, and these interactions may be mediated further by the primates' relative rank (e.g., Kendal et al., 2015; Lee & Cowlishaw, 2017), age, (e.g., Biro et al., 2003) or sex (e.g., Lonsdorf et al., 2004; van de Waal et al., 2010), to name a few factors. More specifically, much work has investigated primates', and other species', cognitive abilities in the social domain (e.g., de Waal & Ferrari, 2012; Seyfarth & Cheney, 2017), as well as what mechanisms might be homologous to those of humans (e.g., Banaji & Gelman, 2013; Tremblay et al., 2017). However, there has been remarkably limited investigation formally testing the hypotheses laid out by Whiten and Byrne (1988a). In particular, little work has tested the relationship between species' cognitive skills *specific to* the social domain, with the complexity of their social structure or the average group size in which they live. In spite of this, the theories discussed by Byrne and Whiten (1988a) continue be to cited in contemporary empirical and theoretical work regarding a variety of species (e.g., Bshary, 2011; Plotnik & Clayton, 2015; Farris, 2016; Hall & Brosnan, 2016; Reichert & Quinn, 2017; Bereczkei, 2018), even inspiring book titles such as *Macachiavellian Intelligence* (Maestripieri, 2007). In recognition of the importance of *Machiavellian Intelligence*, and to highlight what advances have been made in the last 30 years in testing the MIH, in this special issue we include invited essays by both Byrne (this issue) and Whiten (this issue). In their essays Byrne and Whiten outline the foundations of the MIH while reflecting on contemporary considerations of primate social intelligence. In addition to Byrne and Whiten's retrospective essays, we also showcase two empirical studies (Schweinfurth et al., this issue; Borgeaud

& Bshary, this issue) and a review by Lucas et al. (this issue) that considers how animals' communicative abilities might interface with the MIH.

In their review, Lucas et al. (this issue) stretch the previous focus of Machiavellian Intelligence on behavioral interactions to communicative interactions. They consider the interplay between social complexity and communicative complexity, providing examples from an array of species to support their arguments, beyond the primate-centered focus of *Machiavellian Intelligence* (Byrne & Whiten, 1988a). In the way that social complexity has been proposed to generate cognitive complexity (i.e. MIH), Lucas and colleagues outline how social complexity is also associated with more complex vocal communication. Lucas et al. also highlight how communicative strategies exemplify both the competitive and cooperative aspects of Machiavellian intelligence. They cite, for example, reports of low-ranking wild capuchins (*Cebus apella nigritus*) who deceptively use alarm calls to disperse group mates and gain access to food resources (Wheeler, 2010; Wheeler & Hammerschmidt, 2012; Kean et al. 2017) and, conversely, how chimpanzees (*Pan troglodytes*) produce rough grunt vocalizations to inform group mates about the presence and availability of food (Slocombe & Zuberbühler, 2006; Schel et al., 2013).

In their empirical study, Borgeaud and Bshary (this issue) used an elegant approach to test social cognition in primates. Borgeaud and Bshary trained wild vervet monkeys (*Chlorocebus pygerythrus*), living at the Inkawu Vervet Project, South Africa, to obtain food from personalized boxes, which the researchers opened by remote control when specific monkeys approached. They attracted pairs of adult females to the experimental setup, with their two personal boxes placed in close proximity to one another, thus potentially creating conflict over the monopolizable food resources. The authors used this set up to investigate if monkeys anticipate partners' reciprocity decision rules. Specifically, they

presented the boxes to dyads of monkeys for which the subordinate monkey had recently been seen to groom the more-dominant individual or for which no such grooming interaction had occurred. The questions Borgeaud and Bshary addressed included whether subordinates were less likely to approach their box when dominants were already present, how this was mediated by their previous grooming interactions, and how the two monkeys' interactions at the box were influenced by audience effects (i.e. which other group members were in the vicinity of the boxes). Their results showed some effects of audience composition on the monkeys' decisions to approach their boxes, however they did not find any evidence that monkeys took in account their previous grooming-partner in their decisions.

Cooperation and competition are now well recognized as potential aspects of Machiavellian intelligence. However, in their contribution to this volume, Schweinfurth et al. (this issue) focus on a potentially neglected facet of social intelligence, which is the ability to engage in coercion. They report observations of "social tool" use by chimpanzees at the Chimfunshi Wildlife Orphanage in Zambia. The chimpanzees were presented with a novel drinking fountain that required the chimpanzees to press buttons to release juice from the fountain. However, the fountain was located 3m away from the buttons and so individuals could not simultaneously operate the mechanism and benefit from the juice produced. The authors report multiple instances in which a 24-year-old male chimpanzee, Bobby, coerced two young chimpanzees, Kenny (aged six) and Jewel (aged four), to press the buttons while he drank the juice. By recruiting the two juveniles, and using them as social tools, Bobby was able to increase the rate at which he drank juice. Schweinfurth et al. liken this behavior to that of previous reports of Japanese macaque (*Macaca fuscata,* Tokida et al., 1994) and orangutan (*Pongo pygmaeus,* Völter et al. 2015) mothers recruiting their infants to obtain out-of-reach food before taking it from the infants to eat themselves. Thus, the use of social tools by primates (and other species - Schweinfurth et al. also provide examples from birds) speaks to the "exploitative dimensions" of Machiavellian Intelligence.

A common misconception about the MIH is that it *only* pertains to primates' skill at competitive or agonistic interactions, likely as a consequence of the impact of Byrne and Whiten's early work on tactical deception among baboons (Whiten & Byrne, 1988b), as well as the adoption of the term "machiavelliansim" in modern psychology to refer to a manipulative personality trait (Sloan Wilson et al., 1996). Indeed, Byrne and Whiten, in reference to their observations of baboons, asserted that deception was "a particularly sensitive yardstick for the depth of Machiavellian intelligence a species can display" (Byrne & Whiten, 1988b, p.205). However, as both Byrne (this issue) and Whiten (this issue) point out, the MIH refers to both cooperative as well as competitive aspects of social cognition, as highlighted by the articles included in this special issue. Theoretical modelling has also demonstrated how the competitive challenges that group living creates, can also generate cooperative capacities (Orbell et al. 2004). Indeed, from their recent study of group-movement decision making in wild baboons (*Papio anubis*), Strandburg-Peshkin et al. (2015) concluded "democratic collective action emerging from simple rules is widespread, even in complex, socially stratified societies" (p. 1358). Due in part to the misinterpretation of the term Machiavellian intelligence, or its limited pertinence to certain (non-primate) species, some researchers have adopted the term 'social intelligence hypothesis' or 'social brain hypothesis' (Barton & Dunbar, 1997; Dunbar, 1998) in favor of MIH. However, the social intelligence hypothesis is often used to describe the relationship between social complexity and domain-general cognitive abilities, which is just one of the three potential relationships between social lives and cognition which are encompassed under the umbrella of the MIH (Whiten, this issue).

However, it is almost certainly this particular aspect of the MIH that has most captured the imagination of the scientific community. There has been a heavy emphasis on work investigating domain-general cognitive ability and its relationship with the skills required to navigate social living. Commonly, in an

attempt to discern relationships between social complexity and cognitive skill, researchers have investigated the correlation between a species' relative brain size, or their encephalization quotient, and the size of the social groups in which they typically live (reviewed in Reader & Laland, 2002; Byrne, this issue), as well as neocortex ratio and a species' network efficiency (important when considering information transmission among group members for example, Pasquaretta et al., 2014). Such research offers an opportunity for a nuanced perspective, important because, as Barton and Dunbar (1997) noted "group size may be confounded with other ecological variables, such as diet, home range size and activity timing, so it is also important to make sure that none of these is the 'real' correlate of neocortex size" (p. 247, see also Reader & Laland, 2002). In his essay, Byrne (this issue) provides an overview of this line of investigation while also highlighting recent work that has challenged previously-published findings that brain size and encephalization quotient are positively correlated with group size. Specifically, last year DeCasien et al. (2017) reported that diet was a better predictor of primates' encephalization quotient than was sociality, while Powell et al. (2017) questioned the relationship between primates' brain size and group size, instead finding a relationship between brain size and home range size, diet, and activity. Furthermore, Fedorova et al. (2017) compared the relative brain size of 61 woodpecker (*Picidae*) species and found that group-living species had smaller relative brain sizes compared to those that were solitary. There are, of course, limitations to this approach, not least the limited picture that can be gained from substituting brain size for cognition, as noted by Barrett (2018). Addressing this, both Byrne (this issue) and Whiten (this issue) showcase a study, published earlier this year by Ashton et al. (2018), that empirically tested the role between cognitive skill (problem solving) and group size with Australian magpies (*Cracticus tibicen dorsalis*). In their intra-species study, Ashton and colleagues reported that the birds' ability when presented with a battery of cognitive tasks was related to the group size in which they lived, providing support for the social intelligence hypothesis. This recent study paves the way for a new generation of empirical investigations of not only the mental

hardware supporting Machiavellian intelligence, but also the mechanistic outcomes that have promoted primates socio-cognitive expertise.

Conclusion

Investigations of primates', and other species', socio-cognitive abilities have ammassed since the publication of *Machiavellian Intelligence* (Byrne & Whiten, 1988a), providing many novel insights into animals' social intelligence. However, evaluations of the mechanisms driving these skills are still lacking. As we reflect on the impact of Byrne and Whiten's seminal volume, it is clear that it has had a profound impact on how we consider animals socio-cognitive abilities, even changing the vernacular we use to describe it. Highlighting the importance and impact of Byrne and Whiten's MIH, their work has spawned empiricial research in both the lab and field, addressing topics discussed in *Machiavellian Intelligence,* including deception, theory of mind, and alliance formation cooperation, as well as other areas of social cognition, such as inequity aversion, communication, and the nuances of social learning mechanisms and strategies. While contemporary research continues to challenge our notions of what the key drivers for social intelligence might be, our interest in this topic shows no signs of abating.

It has been our great pleasure to edit this volume, celebrating this seminal scientific work. All three of our research careers have been directly influenced by the work of Whiten and Byrne, including the ideas put forth in *Machiavellian Intelligence.* We have each studied aspects of primate social cognition, and have taken a comparative approach in doing so, studying multiple species including humans. We are proud to present the novel contributions it contains, which extend and relfect upon the central themes of *Machiavellian Intelligence*.

References

Ashton B.J., Ridley A.R., Edwards, E.K., & Thornton, A. 2018 Cognitive performance is linked to group size and affects fitness in Australian magpies. *Nature* 554, 364-367.

Banaji, M. & Gelman, S. (2013). *Navigating the Social World: What Infants, Children, and Other Species Can Teach Us.* (pp. 371-376). New York, NY: Oxford University Press.

Barrett, L. (2018). Picturing primates and looking at monkeys: why 21st Century primatology needs Wittgenstein. *Philosophical Investigations, 41*(2), 161-187.

Barton R. A., & Dunbar, R.I.M. 1997 Evolution of the social brain. In A. Whiten & R.W. Byrne (Eds.) *Machiavellian Intelligence II: Extensions and Evaluations* (pp. 240-263). New York, NY, US: Cambridge University Press.

Bereczkei, T. (2018). Machiavellian intelligence hypothesis revisited: what evolved cognitive and social skills may underlie human manipulation. *Evolutionary Behavioral Sciences, 12*(1), 32-51.

Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C. & Matsuzawa, T. (2003). Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Animal Cognition, 6*(4), 213-223.

Bshary, R. (2011). Machiavellian intelligence in fishes. In C. Brown, K. Laland, & J. Krause (Eds.) *Fish Cognition and Behavior*. Oxford, UK: Wiley Blackwell.

Byrne R. & Whiten, A. (1988a). *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans*. Oxford, UK: Oxford University Press.

Byrne, R. & Whiten, A. (1988b). Tactical deception of familiar individuals in baboons. In R. Byrne & A. Whiten (Eds.) *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans* (pp. 205-201). Oxford, UK: Oxford University Press.

Chance, M.R.A. & Mead, A.P. (1988). Social behaviour and primate evolution. In R. Byrne & A. Whiten (Eds.) *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans* (pp. 34-49). Oxford, UK: Oxford University Press.

225 Cheney, D.L. & Seyfarth, R.M. (1988). Social and non-social knowledge in vervet monkeys. In R. Byrne &
226 A. Whiten (Eds.) *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in*
227 *Monkeys, Apes, and Humans* (pp. 255-270). Oxford, UK: Oxford University Press.
228 Dasser, V. (1988). Mapping social concepts in monkeys. In R. Byrne & A. Whiten (Eds.) *Machiavellian*
229 *Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans* (pp.
230 85-93). Oxford, UK: Oxford University Press.
231 DeCasien, A.R., Williams, S.A. & Higham, J.P. (2017). Primate brain size is predicted by diet but not
232 sociality. *Nature Ecology & Evolution, 1,* 0112.
233 de Waal, F. (1988). Chimpanzee politics. In R. Byrne & A. Whiten (Eds.) *Machiavellian Intelligence: Social*
234 *Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans* (pp. 122-131). Oxford,
235 UK: Oxford University Press.
236 de Waal, F.B.M. & Ferrari, P.F. (2012) *The Primate Mind: Built to Connect with Other Minds.* Cambridge,
237 MA: Harvard University Press.
238 Dunbar, R.I.M. 1998 The social brain hypothesis. *Evolutionary Anthropology,* 6(5), 178-190.
239 Farris, S.M. (2016). Insect societies and the social brain. *Current Opinion in Insect Science*, *15,* 1-8.
240 Fedorova, N., Evans, C.L. & Byrne, R.W. (2017). Living in stable groups is associated with reduced brain
241 size in woodpeckers (*Picidae*). *Biology Letters, 14*(3), 20170008.
242 Hall, K. & Brosnan, S.F. (2016). Cooperation and deception in primates. *Infant Behavior and*
243 *Development, 48*(A), 38-44.
244 Harcourt, A.H. (1988). Alliances in contests and social intelligence. In R. Byrne & A. Whiten (Eds.)
245 *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and*
246 *Humans* (pp. 132-152). Oxford, UK: Oxford University Press.
247 Humphrey, N.K. (1976). The social function of intellect. In P.P.G. Bateson & R.A. Hinde (Eds.) *Growing*
248 *Points in Ethology* (pp. 303-317). Cambridge, UK: Cambridge University Press.

249 Humphrey, N.K. (1988). The social function of intellect. In R. Byrne & A. Whiten (Eds.) *Machiavellian*
250 *Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans* (pp.
251 13-26). Oxford, UK: Oxford University Press.
252 Jolly, A. (1966). *Lemur Behavior*. Chicago, IL: Chicago University Press.
253 Jolly, A. (1988). Lemur social behaviour and social intelligence. In R. Byrne & A. Whiten (Eds.)
254 *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and*
255 *Humans* (pp. 27-33). Oxford, UK: Oxford University Press.
256 Kean, D., Tiddi, B., Fahy, M., Heistermann, M., Schino, G. & Wheeler, B.C. (2017). Feeling anxious? The
257 mechanisms of vocal deception in tufted capuchin monkeys. *Animal Behaviour*, *130*, 37-46.
258 Kendal, R.L., Hopper, L.M., Whiten, A., Brosnan, S.F., Lambeth, S.P., Schapiro, S.J., & Hoppitt, W. (2015).
259 Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity.
260 *Evolution & Human Behavior,* 36, 65-72.
261 Kummer, H. (1988). Tripartite relations in hamadryas baboons. In R. Byrne & A. Whiten (Eds.)
262 *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and*
263 *Humans* (pp. 113-121). Oxford, UK: Oxford University Press.
264 Kummer, H. & Goodall, J. (1985). Conditions of innovative behavior in primates. In L. Weiskrantz (Ed.)
265 *Animal Intelligence* (pp. 203-214). Oxford, UK: Oxford University Press.
266 LaFrenière, P.J. (1988). The ontogeny of tactical deception in humans. In R. Byrne & A. Whiten (Eds.)
267 *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and*
268 *Humans* (pp. 238-252). Oxford, UK: Oxford University Press.
269 Lee, A.E.G., & Cowlishaw, G. (2017). Switching spatial scale reveals dominance-dependent social
270 foraging tactics in a wild primate. *PeerJ, 5,* e3462.
271 Lonsdorf, E.V., Eberly, L.E., & Pusey, A.E. (2004). Sex differences in learning in chimpanzees. *Nature*, *428,*
272 715-716.

Maestripieri, D. (2007). *Macachiavellian Intelligence: How Rhesus Macaques and Humans Have Conquered the World.* Chicago, IL: The University of Chicago Press.

Menzel, E.W. (1988). A group of young chimpanzees in a one-acre field: leadership and communication. In R. Byrne & A. Whiten (Eds.) *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans* (pp. 155-159). Oxford, UK: Oxford University Press.

Orbell J, Morikawa T., Hartwig J., Hanley J., & Allen N. (2004). "Machiavellian" intelligence as a basis for the evolution of cooperative dispositions. *American Political Science Review*, 98(1), 1-15.

Pasquaretta, C., Levé, M., Claidière, N., van de Waal, E., Whiten, A., Macintosh, A., Pelé, M., Bergstrom, M., Borgeaud, C., Brosnan, F., Crofoot, M., Fedigan, L., Fichtel, C., Hopper, L.M., Mareno, M., Petit, O., Schnoell, A.V., Polizzi di Sorrentino, E., Thierry, B., Tiddi, B., & Sueur, C. (2014). Social networks in primates: smart and tolerant species have more efficient networks. *Scientific Reports, 4,* 7600.

Plotnik, J.M. & Clayton, N.S. (2015). Convergent cognitive evolution across animal taxa: comparisons of chimpanzees, corvids, and elephants. In E. Margolis & S. Laurence (Eds.). *The Conceptual Mind: New Directions in the Study of Concepts* (pp. 29-56). Cambridge, MA: MIT Press.

Powell, L.E., Isler, K., & Barton, R.A. (2017). Re-evaluating the link between brain size and behavioural ecology in primates. *Proceedings of the Royal Society: B, 284*(1865) doi:10.1098/rspb.2017.1765.

Premack, D. (1988). 'Does the chimpanzee have theory of mind?' revisted. In R. Byrne & A. Whiten (Eds.) *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans* (pp. 160-179). Oxford, UK: Oxford University Press.

Reader, S.M., & Laland, K.N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences of the U.S.A., 99*(7), 4436-4441.

Reichert, M.S. & Quinn, J.L. (2017). Cognition in contests: mechanisms, ecology, and evolution. *Trends in Ecology & Evolution, 32*(10), 773-785.

297 Schel, A.M., Machanda, Z., Townsend, S.W., Zuberbühler, K. & Slocombe, K.E. (2013). Chimpanzee food
298 calls are directed at specific individuals. *Animal Behaviour, 86,* 955-965.
299 Seyfarth, R.M. & Cheney, D.L. (1988). Do monkeys understand their relations? In R. Byrne & A. Whiten
300 (Eds.) *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes,*
301 *and Humans* (pp. 69-84). Oxford, UK: Oxford University Press.
302 Seyfarth, R.M. & Cheney, D.L. (2017). Social cognition in animals. In JA Sommerville & J. Decety (Eds.)
303 *Social Cognition: Development Across the Life Span*. (pp.46-68). New York, NY: Taylor and
304 Francis.
305 Sloan Wilson, D., Near, D., & Miller, R. R. (1996). Machiavellianism: a synthesis of the evolutionary and
306 psychological literatures. *Psychological Bulletin, 119*(2), 285-299.
307 Slocombe, K.E. & Zuberbühler, K. (2006) Food-associated calls in chimpanzees: responses to food types
308 or food preferences? *Animal Behaviour, 72,* 989-999.
309 Smith, P.K. (1988). The cognitive demands of children's social interactions with peers. In R. Byrne & A.
310 Whiten (Eds.) *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in*
311 *Monkeys, Apes, and Humans* (pp. 94-109). Oxford, UK: Oxford University Press.
312 Strandburg-Peshkin, A., Farine, D.R., Couzin, I.D. & Crofoot, M.C. (2015). Shared decision-making drives
313 collective movement in wild baboons. *Science,* 348(6241), 1358-1361.
314 Tokida, E., Tanaka, I., Takefushi, H., & Hagiwara, T. (1994). Tool-using in Japanese macaques: use of
315 stones to obtain fruit from a pipe. *Animal Behaviour*, *47*(5), 1023–1030.
316 Tremblay, S., Sharika, K.M. & Platt, M.L. (2017). Social decision-making and the brain: a comparative
317 perspective. *Trends in Cognitive Sciences, 21*(4), 265-276.
318 van de Waal, E., Renevey, N., Favre, C.M., & Bshary, R. (2010). Selective attention to philopatric models
319 causes directed social learning in wild vervet monkeys. *Proceedings of the Royal Society B,*
320 *277*(1691) DOI: 10.1098/rspb.2009.2260

Völter, C.J., Rossano, F., & Call, J. (2015). From exploitation to cooperation: social tool use in orang-utan mother-offspring dyads. *Animal Behaviour, 100,* 126-134.

Wheeler, B.C. (2010). Production and perception of situationally variable alarm calls in wild tuften capuchin monkeys (*Cebus apella nigritus*). *Behavioral Ecology and Sociobiology, 64*(6), 989-1000.

Wheeler, B.C. & Hammerschmidt, K. (2012). Proximate factors underpinning receiver responses to deceptive false alarm calls in wild tufted capuchin monkeys: is it counterdeception? *American Journal of Primatology, 75*(7), 715-725.

Whiten A & Byrne RW (1988a). The Machiavellian intelligence hypotheses: editorial. In R. Byrne & A. Whiten (Eds.) *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans* (pp. 271-284). Oxford, UK: Oxford University Press.

Whiten, A. & Byrne R. W. (1988b). The manipulation of attention in primate tactical deception. In R. Byrne & A. Whiten (Eds.) *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans* (pp. 211-223). Oxford, UK: Oxford University Press.

Wynn, T. (1988). Tools and the evolution of human intelligence. In R. Byrne & A. Whiten (Eds.) *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans* (pp. 1-9). Oxford, UK: Oxford University Press.