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1 Tool-use in the brown bear (Ursus arctos)

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11 Abstract

12 This is the first report of tool-using behaviour in a wild brown bear (Ursus arctos). Whereas the 13 use of tools is comparatively common among primates and has also been documented in several 14 species of birds, fishes and invertebrates, tool-using behaviours have so far been observed in only 15 four species of non-primate mammal. The observation was made and photographed while studying 16 the behaviour of a subadult brown bear in southeastern Alaska. The animal repeatedly picked up 17 barnacle-encrusted rocks in shallow water, manipulated and re-oriented them in its forepaws, and 18 used them to rub its neck and muzzle. The behaviour probably served to relieve irritated skin or to 19 remove food-remains from the fur. Bears habitually rub against stationary objects and overturn 20 rocks and boulders during foraging and such rubbing behaviour could have been transferred to a 21 freely movable object to classify as tool-use. The bear exhibited considerable motor skills when 22 23 manipulating the rocks, which clearly shows that these animals possess the advanced motorlearning necessary for tool-use. Advanced spatial cognition and motor skills for object 24 manipulation during feeding and tool-use provides a possible explanation for why bears have the 25 largest brains relative to body size of all carnivores. Systematic research into the cognitive abilities 26 of bears, both in captivity and the wild is clearly warranted to fully understand their motor learning 27 skills and physical intelligence related to tool-use and other object manipulation tasks.

28 **KEYWORDS:** tool-use, cognition, motor learning, brown bear

29 **SHORT TITLE:** Tool-use in the brown bear

30 Introduction

31 The use of tools by non-human animals to solve tasks not easily achieved using 32 the body alone has received much attention in comparative cognition research 33 (reviewed by Alcock 1972; Beck 1980; Bentley-Condit and Smith 2010; Seed and 34 Byrne 2010), because it can teach us about their physical intelligence, motor 35 learning skills and behavioural flexibility. While the cognitive foundations underlying the use of tools are probably diverse and differ between species and 36 37 tasks performed, tool-using has been used as evidence for cognitive faculties such 38 as goal-directedness (e.g., Bird and Emery 2009; Sanz and Morgan 2009; Sanz et 39 al. 2009), forward planning (e.g., Osvath and Osvath 2008), or the presence of culturally transmitted norms (Call and Tennie 2009; Whiten et al. 2005). 40

41 While there is on-going debate about appropriate definitions of tool-use, 42 most researchers agree that tool-use constitutes the use of a freely manipulable 43 object to modify the physical properties of a target object through a complex 44 mechanical interaction (e.g., Alcock 1972; Beck 1980; Bentley-Condit and Smith 45 2010; St Amant and Horton 2008). Possible target objects may include other 46 organisms (e.g., conspecifics; Nishida 2003, or prey; Levey et al. 2004; McGrew 47 et al. 1979) or even the tool-user's own body (Beck 1980; Seed and Byrne 2010; 48 St Amant and Horton 2008). St Amant and Horton (2008) argued that tool-use 49 does not need to be directed at an object, but additionally can also have the effect 50 of modifying the information flow in the environment. Animals may therefore use 51 tools to obtain sensory information (e.g. a gorilla apparently using a stick to test 52 water depth; Breuer et al. 2005), to avoid painful stimuli (e.g., dolphins covering 53 their rostrums with sponges during benthic foraging; Krützen et al. 2005) or 54 detection (e.g., an orang-utan hiding behind a detached branch; van Schaik et al. 55 2003), or for communicative purposes (e.g. using branches in gestures or displays; Nishida 2003; Pika et al. 2003; van Schaik et al. 2003). 56

57 The vast majority of animal species do not use tools, and those that do come 58 from a diverse taxonomic background (Alcock 1972; Beck 1980; Bentley-Condit 59 and Smith 2010). Tool-using behaviours are often highly stereotyped, but some 60 species exhibit the ability to modify tools and their use depending on the task at 61 hand (e.g., Hunt and Gray 2004; Sanz and Morgan 2009; Tebbich and Bshary 62 2004). Such behavioural flexibility may be a better indicator of physical 63 intelligence than the use of tools alone (Emery and Clayton 2009). Several species 64 that do not use tools in the wild can be taught their use in captivity and show 65 comparable aptitude at tool-using tasks as tool-using species (e.g., Bird and Emery 2009; Tebbich et al. 2010). Among the invertebrates, antlions 66 67 (Myrmeleontidae; Alcock 1972) and veined octopus (Amphioctopus marginatus; 68 Finn et al. 2009) are known to use tools. Fishes known to use tools include archer 69 fishes (Toxotes spp.; Alcock 1972; Bentley-Condit and Smith 2010) that use a jet 70 of water to dislodge insects from vegetation and show surprising behavioural 71 flexibility related to tool-use (Schuster et al. 2006). Tool-use has been documented in a few tens of species of birds including buzzards and old-world 72 73 vultures (Accipitridae), owls (Strigidae), herons (Ardeidae), Galápagos finches 74 (Thraupidae) and corvids (Corvidae; summarised by Alcock 1972; Beck 1980; 75 Levey et al. 2004; Emery and Clayton 2009). Particularly corvids and Galápagos 76 finches show significant levels of behavioural flexibility when using tools (e.g., 77 Bird and Emery 2009; Hunt & Gray 2004; Tebbich and Bshary 2004; Tebbich et 78 al. 2010).

79 Among mammals tool-use is comparatively common in primates and has 80 been documented in the wild for chimpanzees (Pan troglodytes; e.g., Boesch and 81 Boesch 1990; McGrew et al. 1979; Sanz and Morgan 2009; Whiten et al. 2005), 82 bonobos (Pan paniscus; e.g., Ingmanson 1996), gorillas (Gorilla gorilla; Breuer 83 et al. 2005), orang-utans (Pongo spp.; van Schaik et al. 2003), capuchin monkeys 84 (Cebus spp.; e.g., Ottoni and Izar 2008), as well as humans. Some great apes 85 exhibit the ability to use tools flexibly depending on the task at hand (e.g., Hall 86 1963; Sanz and Morgan 2009; Sanz et al. 2009) and show evidence for imitation and cultural transmission (Call and Tennie 2009; Whiten et al. 2005; Whiten et al. 87 88 2009). However, there is little evidence that any non-human primates understand 89 causal relationships underlying complex tool-use tasks (Emery and Clayton 2009; 90 Visalberghi and Limongelli 1994).

Interestingly, for mammalian taxa other than primates evidence for tool-use in the wild is surprisingly rare – to date true tool use has only been described for four species. Sea otters (*Enhydra lutris*) habitually use rocks to break the shells of sea urchins and clams (e.g.: Kenyon 1959). Some Asian elephants (*Elephas maximus*) modify tree branches and use them to repel flies (Hart et al. 2001). A small number of bottlenose dolphins (*Tursiops sp.*) in Shark Bay, Australia cover their rostrums with sponges while foraging, presumably to protect themselves
from stingrays (Krützen et al. 2005). Finally, humpback whales (*Megaptera novaeangliae*) in several areas exhale curtains of bubbles and use them to trap
schools of fish (e.g., Jurasz and Jurasz 1979).

101 In this paper I report an incident of tool-use by a wild North American 102 brown bear (Ursus arctos). Although brown bears have been studied extensively 103 in the wild (e.g., Gilbert 1999; Green and Mattson 2003; Fagen and Fagen 2004) 104 and are commonly kept in captivity, little is known about their cognitive abilities. 105 While there has been limited cognitive research on other species of bears (family 106 Ursidae) investigating basic aspects of colour perception, learning, and spatial 107 memory (e.g., Bacon and Burghardt 1973; Mazur and Seher 2008; Perdue et al. 108 2011) no studies have investigated cognitive aspects in brown bears to date.

109 Brown bears show many ecological and life-history traits that have been 110 used to explain the evolution of advanced cognitive abilities in other species. 111 They have a long life span, and an extended period of maternal dependency (Pasitschniak-Arts 1993) providing opportunities for both individual and social 112 113 learning (Gittleman 1986). Brown bears are omnivorous with a high metabolic 114 demand and live in highly seasonal environments requiring them to exploit a 115 variety of food sources effectively. Brown bear diets vary regionally and some 116 feeding strategies exhibit considerable complexity and may be learned (Gilbert 117 1999). Environmental variability has been implicated as a force selecting for 118 behavioural innovations and increased brain size (Lefebvre et al. 2004).

Materials and Methods

120 Observations were made from an 11m diesel-powered vessel in Glacier Bay National Park and Preserve, Alaska, during July 19-26 2011. Bears are protected 121 122 inside the National Park, habituated to the presence of vessels and showed little or 123 no behavioural response to the boat. Bears were photographed using a digital SLR 124 camera (Nikon D700) with a telephoto zoom lens (Nikkor 28-300mm F5.6 AF-S) 125 and detailed notes on behaviour were taken. Observations were made in 126 compliance with the National Park's wildlife viewing guidelines and under a valid boating permit (Permit # 9152). 127

128 **Results**

129 On 22 July 2010 at 14:30 ADT, we encountered a single brown bear in the West 130 Arm of Glacier Bay (58°50.7'N 136°37.8'W). The bear, a subadult estimated to be 131 between 3 and 5 years old, was feeding on the carcass of a humpback whale, 132 which had washed ashore at least 2 months earlier. At 14:53 a second bear, also a 133 subadult, emerged onto the beach some 300m distant. After some initial posturing, 134 the two bears joined up at 15:04 approximately 200m from the carcass and spent 135 the next 45min play-fighting interrupted by one short bout of feeding (on the 136 whale carcass, as well as on intertidal barnacles; *Balanus sp.*). Play-fighting 137 showed the characteristics of brown bear play (lack of vocal behaviour, frequent 138 open-mouth grin or play-face; Fagen and Fagen 2004). The behaviour was 139 initiated on shore, but the animals quickly moved into shallow water. The animals 140 remained largely stationary and we observed little running or chasing.

141 At 15:20 the second bear temporarily returned to the carcass to feed, while 142 the animal first observed on the beach remained in water estimated to be 1.5m 143 deep close to shore. The animal picked up a small (approximately 25cm x 25cm x 144 15cm) rock in its forepaws (Fig 1A and B). It used both forepaws to re-orient the 145 rock and dropped it one minute later. It immediately picked up another rock of 146 similar size, and, after re-orienting it, rubbed the rock against its muzzle and face 147 for one minute (Fig 1C-E) before dropping it (Fig 1F). During the rubbing, the 148 bear used its left paw to press the rock against its face and muzzle and supported it 149 from below using the claws of the right paw. The bear repeated the action with a 150 third rock, rubbing its muzzle, face and neck for another two minutes. Close 151 examination of the photographs taken during the encounter showed that all three 152 rocks had barnacles growing on them (presumably Balanus sp., see Fig. 1B-C). 153 The animal then spent two minutes cleaning/grooming its right forepaw using its 154 teeth before joining the other bear at the whale carcass.

155 **Discussion**

The stone-rubbing behaviour fulfils all commonly accepted criteria for animal tool-use (e.g., Alcock 1972; Beck 1980; St Amant and Horton 2008): the bear used freely manipulable objects (barnacle-encrusted rocks) in a complex mechanical interaction (rubbing behaviour) to effect a physical change in a target 160 object (in this case the tool-user itself). The behaviour is analogous to non-human 161 primates using sticks to scratch parts of their bodies (e.g., van Schaik et al. 2003) 162 or Asian elephants using branches as fly switches (Hart et al. 2001). While the 163 precise nature of the physical change remains unclear, it is likely that the bear was 164 using the rock and rough carapaces of the attached barnacles to relieve itching 165 skin. Brown bears moult during the summer (Green and Mattson 2003; 166 Pasitschniak-Arts 1993) and both individuals showed clear signs of moulting. Moulting brown bears commonly rub against trees or rocks (Green and Mattson 167 168 2003), but the use of unattached objects for rubbing and scratching has not 169 previously been reported. Alternatively, the bear may have been attempting to 170 remove bits of whale blubber and oil from its fur using the rock. A similar use of 171 an object for body maintenance has been described for giant pandas (Ailuropoda 172 *melanoleuca*): a captive individual apparently rubbed its belly using a clod of soil (Eisenberg and Kleiman 1977). 173

174 Because bears habitually rub against stationary objects and also use their 175 claws to scratch themselves it is easy to see how these behaviours could have been 176 transferred to a freely manipulable object and thus fulfil the criteria for tool-use. 177 In the case of stone-rubbing, sensory feedback from the use of the tool is 178 instantaneous if the intended function of the behaviour is the relief of itchy skin. 179 Such immediate feedback could have facilitated the transfer of rubbing or 180 scratching behaviour from claws or attached objects to a freely manipulable rock. 181 Using intermediate steps towards tool-use such as displacement behaviours 182 (Alcock 1972) is therefore not necessary to explain the evolution of stone-rubbing 183 in brown bears.

184 Using tools as an extension of the body changes the periphery between body 185 and environment and thus has consequences for psychological processes such as 186 perception, motor learning, attention, and cognition (Seed and Byrne 2010). 187 Because tool-use requires advanced cognitive and perceptual faculties, it is 188 commonly used as an indicator for advanced physical intelligence (Emery and 189 Clayton 2009; Seed and Byrne 2010), and has been linked to increased brain size 190 in several taxa (e.g., Reader and Laland 2002; Lefebvre et al. 2004). Bears are largely solitary, but have the largest brain weight and size in relation to their 191 192 bodies of all carnivores, larger than far more sociable canids, felids and hyenids 193 (Gittleman 1986). This appears to contradict theories about sociality as an 194 evolutionary force promoting increased brain size and advanced cognition (e.g., 195 Reader and Laland 2002). A possible explanation for the large brain size of bears 196 in the light of their apparent lack of sociality may be that their high metabolic 197 demand, especially during the months before hibernation selects for particularly 198 efficient feeding strategies. The selective advantage of being able to track a 199 variety of high-calorie food sources in space and time could have led to the 200 evolution of advanced spatial and temporal cognition (Gilbert 1999) and 201 manipulative and extractive foraging tasks may promote the evolution of physical 202 cognition and motor learning skills. A comparative analysis of the brain anatomy 203 of bears and other carnivores would be helpful to identify which brain regions 204 have undergone evolutionary change.

205 But the asociality of bears itself may be something of a red herring: brown 206 bears have an extended period of maternal dependency with cubs remaining with 207 the mother for 2-4 years (Pasitschniak-Arts 1993; Gilbert 1999). Even after 208 independence, siblings often remain together for several additional years and adult 209 individuals are often found associated at sites of high food abundance (Gilbert 210 1999). Such prolonged social interactions could provide ample opportunity for 211 social transmission of complex feeding strategies and other behaviours - vertical 212 transmission from mother to offspring and horizontal transmission between 213 siblings. However, social learning may not be necessary to explain the spread of 214 stone-rubbing even if this form of tool-use was found to be common: brown bears 215 frequently turn over rocks in search of food and feed on intertidal barnacles 216 (Balanus spp.; Smith and Partridge 2004) both of which would provide ample 217 opportunity for the acquisition of stone-rubbing behaviour through individual 218 learning alone.

219 Creative behaviours such as tool-use are likely to be missed in systematic 220 assessments of behaviour because they occur spontaneously only at low 221 frequencies and may be limited to a few individuals. Anecdotes of such 222 behaviours can therefore provide valuable information about the cognitive 223 abilities of a species, so long as the observations were made by an experienced 224 observer and were recorded immediately afterwards (Bates and Byrne 2007). 225 While this observation of tool-use in a brown bear was documented with 226 photographs and detailed behavioural notes as it occurred, to date it remains an 227 isolated incident. Dedicated research is therefore ultimately required to determine

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how wide-spread stone-rubbing and other tool-using behaviours are in thisspecies.

230 The observation establishes brown bears as the fifth non-primate mammal 231 known to exhibit true tool-use. The fact that brown bears are able to use external 232 objects as an extension of their bodies could suggest that the cognitive and 233 perceptive faculties for tool-use have evolved earlier during the mammalian 234 radiation than previously thought. Alternatively, and more likely perhaps, they 235 may have evolved independently and convergently in several mammalian clades. 236 Cognitive research in mammals has focussed disproportionately on primates while 237 other taxa have received comparatively little attention. Data on the behaviour of wild brown bears is limited and their cognitive abilities have not yet been studied 238 239 systematically. Discovery of tool-use in brown bears illustrates that dedicated 240 research into the behaviour and cognition of bears is clearly warranted so that we 241 can determine how these animals use the largest carnivore brains to make sense of 242 their environment and to interact with it and with each other.

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251 **References**

252	Alcock J (1972) The evolution of the use of tools by feeding animals. Evolution 26:464-473
253 254	Bacon ES, Burghardt GM (1973) Assessment of color vision and form recognition in the American black bear (<i>Ursus americanus</i>). Bull Psychonomic Soc 2 (5B):346
255 256	Bates LA, Byrne RW (2007) Creative or created: Using anecdotes to investigate animal cognition. Methods 42 (1):12-21. doi:10.1016/j.ymeth.2006.11.006
257 258	Beck BB (1980) Animal Tool Behavior: the Use and Manufacture of Tools. Garland STPM Press, New York
259 260 261	Bentley-Condit VK, Smith EO (2010) Animal tool use: current definitions and an updated comprehensive catalog. Behaviour 147 (2):185-132A. doi:10.1163/000579509X12512865686555
262 263 264	Bird CD, Emery NJ (2009) Insightful problem solving and creative tool modification by captive nontool-using rooks. Proc Natl Acad Sci USA 106 (25):10370-10375. doi:10.1073/pnas.0901008106
265 266	Boesch C, Boesch H (1990) Tool use and tool making in wild chimpanzees. Folia Primatol 54 (1-2):86-99

267 Breuer T, Ndoundou-Hockemba M, Fishlock V (2005) First observation of tool use in wild 268 gorillas. PLoS Biology 3 (11):2041-2043. doi:10.1371/journal.pbio.0030380 269 Call J, Tennie C (2009) Animal culture: Chimpanzee table manners? Curr Biol 19:R981-R983. 270 doi:10.1016/j.cub.2009.09.036 271 Emery NJ, Clayton NS (2009) Tool use and physical cognition in birds and mammals. Curr Opin 272 Neurobiol 19 (1):27-33. doi:10.1016/j.conb.2009.02.003 273 Eisenberg JF, Kleiman DG (1977) The usefulness of behaviour studies in developing captive 274 breeding programmes for mammals. Int Zoo Yearbook 17:81-89 275 Fagen R, Fagen J (2004) Juvenile survival and benefits of play behaviour in brown bears, Ursus 276 arctos. Evol Ecol Res 6 (1):89-102 277 Finn JK, Tregenza T, Norman MD (2009) Defensive tool use in a coconut-carrying octopus. Curr 278 Biol 19 (23):R1069-R1070 279 Gilbert BK (1999) Opportunities for social learning in bears. In: Box HO, Gibson KR (eds) 280 Mammalian social learning: Comparative and ecological perspectives. Symposia of the 281 Zoological Society of London. Cambridge University Press, Cambridge UK, pp 225-235 282 Gittleman JL (1986) Carnivore brain size, behavioral ecology, and phylogeny. J Mammal 67 283 (1):23-36 284 Green GI, Mattson DJ (2003) Tree rubbing by Yellowstone grizzly bears Ursus arctos. Wildl Biol 285 9(1):1-9 286 Hall KRL (1963) Tool-using performances as indicators of behavioural adaptability. Curr 287 Anthropol 4:479-487 288 Hart BL, Hart LA, McCoy M, Sarath CR (2001) Cognitive behaviour in Asian elephants: use and 289 modification of branches for fly switching. Anim Behav 62:839-847. 290 doi:10.1006/anbe.2001.1815 291 Hunt GR, Gray RD (2004) The crafting of hook tools by wild New Caledonian crows. Proc R Soc 292 Lond B: Biol Sci 271:S88-S90. doi:10.1098/rsbl.2003.0085 293 Ingmanson EJ (1996) Tool-using behavior in wild Pan paniscus: social and ecological 294 considerations. In: Russon AE, Bard KA, Parker ST (eds) Reaching into Thought: the 295 Minds of Great Apes. Cambridge University Press, Cambridge, pp 190-210 296 Jurasz CM, Jurasz VP (1979) Feeding modes of the humpback whale (Megaptera novaeangliae) in 297 southeast Alaska. Sci Rep Whales Res Inst 31:69-83 298 Kenyon KW (1959) The sea otter. Ann Rep Smithsonian Inst 1958:399-407 299 Krützen M, Mann J, Heithaus MR, Connor RC, Bejder L, Sherwin WB (2005) Cultural 300 transmission of tool use in bottlenose dolphins. Proc Natl Acad Sci USA 102 (25):8939-301 8943. doi: 1073/pnas.0500232 102 302 Lefebvre L, Reader SM, Sol D (2004) Brains, innovations and evolution in birds and primates. 303 Brain Behav Evol 63 (4):233-246. doi:10.1159/000076784 304 Levey DJ, Duncan RS, Levins CF (2004) Use of dung as a tool by burrowing owls. Nature 431 305 (7004):39-39. doi:10.1038/431039a 306 Mazur R, Seher V (2008) Socially learned foraging behaviour in wild black bears, Ursus 307 americanus. Anim Behav 75:1503-1508. doi:10.1016/j.anbehav.2007.10.027 308 McGrew WC, Tutun CEG, Baldwin PJ (1979) Chimpanzee, tools, and termites: Cross-cultural 309 comparisons of Senegal, Tanzania, and Rio Muni. Man 14:185-214 310 Nishida T (2003) Harassment of mature female chimpanzees by young males in the Mahale 311 Mountains. Int J Primatol 24 (3):503-514 312 Osvath M, Osvath H (2008) Chimpanzee (Pan troglodytes) and orangutan (Pongo abelii) 313 forethought: self-control and pre-experience in the face of future tool use. Anim Cogn 11 314 (4):661-674. doi:10.1007/s10071-008-0157-0 315 Ottoni EB, Izar P (2008) Capuchin monkey tool use: overview and implications. Evol Anthropol 316 17:171-178. doi:10.1002/evan.20185

- 317 Pasitschniak-Arts M (1993) Ursus arctos. Mammalian Species 439:1-10
- Perdue BM, Snyder RJ, Zhihe Z, Marr J, Maple TL (2011) Sex differences in spatial ability: a test
 of the range size hypothesis in the order Carnivora. Biol Lett 7 (3):380-383.
 doi:10.1098/rsbl.2010.1116
- Pika S, Liebal K, Tomasello M (2003) Gestural communication in young gorillas (*Gorilla gorilla*):
 Gestural repertoire, learning, and use. Am J Primatol 60 (3):95-111.
 doi:10.1002/ajp.10097
- Reader SM, Laland KN (2002) Social intelligence, innovation, and enhanced brain size in primates. Proc Natl Acad Sci USA 99 (7):4436-4441. doi:10.1073/pnas.062041299
- Sanz C, Call J, Morgan D (2009) Design complexity in termite-fishing tools of chimpanzees (*Pan troglodytes*). Biol Lett 5:293-296. doi:10.1098/rsbl.2008.0786
- Sanz CM, Morgan DB (2009) Flexible and persistent tool-using strategies in honey-gathering by
 wild chimpanzees. Int J Primatol 30 (3):411-427. doi:10.1007/s10764-009-9350-5
- Schuster S, Wöhl S, Griebsch M, Klostermeier I (2006) Animal cognition: How archer fish learn
 to down rapidly moving targets. Curr Biol 16 (4):378-383. doi:10.1016/j.cub.2005.12.037
- 332 Seed A, Byrne RW (2010) Animal tool-use. Curr Biol 20 (23):R1032-R1039.
 333 doi:10.1016/j.cub.2010.09.042
- Smith TS, Partridge ST (2004) Dynamics of intertidal foraging by coastal brown bears in southwestern Alaska. J Wildl Manage 68 (2):233-240
- St Amant R, Horton TE (2008) Revisiting the definition of animal tool use. Anim Behav 75:1199 1208. doi:10.1016/j.anbehav.2007.09.028
- Tebbich S, Bshary R (2004) Cognitive abilities related to tool use in the woodpecker finch,
 Cactospiza pallida. Anim Behav 67:689-697. doi:10.1016/j.anbehav.2003.08.003
- Tebbich S, Sterelny K, Teschke I (2010) The tale of the finch: Adaptive radiation and behavioural
 flexibility. Phil Trans R Soc B 365:1099–1109. doi:10.1098/rstb.2009.0291
- van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, Singleton I, Suzuki A, Utami SS,
 Merrill M (2003) Orangutan cultures and the evolution of material culture. Science 299:102-105
- Visalberghi E, Limongelli L (1994) Lack of comprehension of cause- effect relations in tool-using
 capuchin monkeys (*Cebus apella*). J Comp Psychol 108:15–22
- 347 Whiten A, Horner V, de Waal FBM (2005) Conformity to cultural norms of tool use in chimpanzees. Nature 437 (7059):737-740. doi:10.1038/nature04047
- Whiten A, Schick K, Toth N (2009) The evolution and cultural transmission of percussive technology: integrating evidence from palaeoanthropology and primatology. J Hum Evol 57 (4):420-435. doi:10.1016/j.jhevol.2008.12.010

352 Figure Legend

Figure 1: Photographs showing stone-rubbing behaviour in a subadult brown bear (*Ursus arctos*). The animal picked up a rock from the sea floor and manipulated it (Panels A and B). It then retrieved a second rock, manipulated it, and rubbed it repeatedly against its neck and muzzle (Panels C-E) before dropping it (Panel F). The entire sequence was repeated with another rock (not shown).











