

Clapham, Melanie and Kitchin, John (2016) Social play in wild brown bears of varying age-sex class. Acta Ethologica, 19 (3). pp. 181-188.

Downloaded from: http://insight.cumbria.ac.uk/id/eprint/2586/

Usage of any items from the University of Cumbria's institutional repository 'Insight' must conform to the following fair usage guidelines.

Any item and its associated metadata held in the University of Cumbria's institutional repository Insight (unless stated otherwise on the metadata record) may be copied, displayed or performed, and stored in line with the JISC fair dealing guidelines (available <u>here</u>) for educational and not-for-profit activities

# provided that

- the authors, title and full bibliographic details of the item are cited clearly when any part of the work is referred to verbally or in the written form
  - a hyperlink/URL to the original Insight record of that item is included in any citations of the work
- the content is not changed in any way
- all files required for usage of the item are kept together with the main item file.

# You may not

- sell any part of an item
- refer to any part of an item without citation
- amend any item or contextualise it in a way that will impugn the creator's reputation
- remove or alter the copyright statement on an item.

The full policy can be found here.

Alternatively contact the University of Cumbria Repository Editor by emailing insight@cumbria.ac.uk.

# 1 SHORT COMMUNICATION

2	
3	Social play in wild brown bears of varying age-sex class
4	
5	Melanie Clapham <sup>1,2*</sup> and John Kitchin <sup>2,3</sup>
6	<sup>1</sup> Department of Geography, University of Victoria, British Columbia, Canada.
7	<sup>2</sup> Brown Bear Research Network, Sooke, British Columbia, Canada.
8	<sup>3</sup> Centre for Wildlife Conservation, University of Cumbria, Ambleside, United Kingdom.
9	
10	*Corresponding author: M Clapham, Applied Conservation Science Lab, Department of Geography,
11	University of Victoria, PO Box 1700 STN CSC, Victoria, British Columbia, Canada, V8W 2Y2.
12	Email: mclapham@uvic.ca Tel: +1 (250) 472-5938
13	
14	Acknowledgements
15	Research was funded by a Mitacs Elevate Fellowship and the Brown Bear Research Network. We
16	would like to thank Dean and Kathy Wyatt for continued financial and logistical support and all the
17	staff at Knight Inlet Lodge for field support and assistance. Thanks to Edward Savage and Hayley
18	Shephard for providing additional visual documentation of play observations. Special thanks to Chris
19	Darimont and three anonymous reviewers for their comments and suggestions regarding this
20	manuscript.
21	
22	
23	
24	
25	
26	
27	

28 Abstract

29

30 Social play behaviour is a well described phenomenon, almost ubiquitous among mammals. Despite 31 its prevalence, social play takes several forms and may vary in function across species. For solitary 32 species, the function of play outside of the family group remains unclear. Here we describe the motor patterns of play among non-littermate wild brown bears Ursus arctos of different age-sex class. Play 33 34 was documented during a time of abundant food availability in three different scenarios: play among non-littermate subadults, play among non-littermate cubs, and play among a 'group' of bears of 35 different age and sex class. We used a previously described behavioural ethogram to recognise play. 36 Play followed typical motor patterns and postures expressed by bears during play-fighting: relaxed 37 face, puckered-lip, ears partially flattened to crescent, wrestling, jaw gaping, play-biting, paw-38 39 swatting and lunging. No vocalisations were conducted during play bouts. Older bears displayed 'self-40 handicapping' and 'role-reversal' in the play postures they selected when playing with younger bears, 41 suggesting that tactics vary according to age class and dominance ranking. Playing likely allows for 42 the evaluation of conspecifics in a non-aggressive way during times of reduced competition and could 43 also relieve stress in complex social situations. 44

45 *Keywords*: behaviour, learning, play-fighting, social play, *Ursus arctos*.

46

#### 47 Introduction

48

Social play is difficult to define broadly as it takes various behavioural forms and appears to vary in function across species (Held & Špinka 2011). Although one universal definition may not be possible, play can loosely be categorised as the adaptation of a typical stress or emergency-type response (i.e attack, defend, escape, or chase) to a situation which occurs outside of its usual context (Barber 1991). Play-fighting is a form of social play which usually involves non-agonistic physical contact between individuals and appears, to some extent, to replicate agonistic contact-bouts, in a 'non-serious' manner (Barber 1991). For example, in multiple canid species, a bow posture is used to indicate

playful intent in between actions such as biting and side to side head shaking, which could otherwisebe interpreted as acts of aggression (Bekoff 1995).

Despite no current consensus in the literature on the ultimate cause of play fighting, functional
explanations usually relate to refining skills needed during combat (the practice hypothesis; Fagen
1981, Pellis and Pellis 1998), preparing for the unexpected (Špinka et al. 2001), self-assessment
(Thompson 1998), increasing physical stamina (Smith 1982), learning social skills (Bekoff 2001) and
expelling surplus energy (Spencer 1898 in Barber 1991). Play can be multifunctional and influenced
within a species by age, sex, dominance, and both social and environmental context (Brueggeman
1978; Tacconi and Palagi 2009).

65 Assessing play behaviour can be structured in an adaptive framework; the behaviour bears 66 immediate costs but likely carries fitness benefits. Costs incurred may include time investment, 67 energetic expenditure, increased risk of predation (increased conspicuousness), direct injury, or escalation into an agonistic encounter (Smith 1982). As these costs can affect future reproductive 68 69 success, play behaviour should have net fitness benefits or experience serious constraints (Fagen and 70 Fagen 2004). Comparing the contexts in which social play occurs at a high or low frequency may 71 indicate when it becomes too costly and therefore aid the interpretation of function (see Sharpe et al. 2002). 72

73 Social play has been reported primarily for gregarious species (e.g. meerkats Suricata suricatta, 74 Sharpe et al 2002; lemurs Propithecus verreauxi, Antonacci et al 2010; macaques Macaca spp., 75 Thierry et al. 2000, Ciani et al. 2012; canids *Canis* spp. Bekoff 1995), with more solitary species 76 receiving less attention. Several studies have assessed the importance of the level of gregariousness 77 between species for its relevance to social play frequency (see Pellis and Iwaniuk 2000; Ciani et al. 78 2012). As social play appears to be influenced by "socio-ecological" factors (Pellis and Iwaniuk 1999, 79 2000), solitary-living species which display a dominance hierarchical social structure could equally 80 indulge in play behaviour, due to home range overlap increasing the likelihood for individuals to 81 interact.

Brown bears *Ursus arctos* display a dominance hierarchy social system with overlapping home
ranges across sexes (Stirling and Derocher 1990; McLellan and Hovey 2001) and are a species that

84 traditionally have been classed as asocial, other than during courtship or when raising young (Stonorov and Stokes 1972). However, brown bears also display variation in sociality as they are 85 primarily solitary, but also form aggregations at abundant food resources, feeding within meters of 86 conspecifics (Craighead et al. 1995; Ben-David et al. 2004; M Clapham and J Kitchin pers. obs.). 87 88 Anecdotal observations of social play among bear cub littermates are abundant, but systematic descriptions of the motor patterns and sequences of play are rare and have only sufficiently been 89 90 described for juvenile black bears U. americanus (Burghardt and Burghardt 1972; Henry and Herrero 91 1974; Pruitt 1976; Rogers 1987) and wild brown bear littermate cubs (Fagen 1981; Fagen and Fagen 2004). Latour (1981) also describes the motor patterns of play in adult male polar bears U. maritimus. 92 Most studies that report sightings of play in wild bears do not provide a systematic description of 93 94 behaviours and have an alternative subject focus (e.g. Herrero & Hamer 1977; Murie 1981; Stelmock 95 & Dean 1986). Here, we describe the motor patterns of social play in non-littermate wild brown bears 96 of different age-sex class. We explore exhibited behaviours under three different scenarios, not 97 systematically reported in the current literature.

98

# 99 Methodology

100

101 All observations were conducted between August and October 2014 in Glendale Cove, an estuarine 102 inter-tidal zone of Knight Inlet, British Columbia, Canada (N50°41' W125°44'). Bears are protected 103 within Glendale Cove by a 15km<sup>2</sup> 'no-hunt zone' established in 1989 by the Ministry of Environment 104 (BC provincial government). As a result of commercial bear-viewing activities at the site since 1997, 105 bears have become tolerant to being viewed and show little behavioural response to human presence, 106 unless approached too closely. Brown bears are attracted to the tidal marshes (e.g. Carex spp.) in the south of the estuary to feed during spring, and the river mouth and Glendale Creek from August 107 108 onwards for the annual return of Pacific pink salmon Oncorhynchus gorbuscha (see Clapham et al. 2012 for more information on the study site). The abundance of returning fish fluctuates annually to 109 this river system (Fisheries and Ocean Canada 2014). In 2014 the drainage experienced a high return 110 111 of pink salmon (n = 334,021, mean over 10 years = 210,559 [estimates from Fisheries and Oceans

Canada 2014; Fisheries and Oceans Canada, unpublished data]). In mid-September, high tides
combined with high pre-spawn mortality of pink salmon, followed by high rainfall, caused carcasses
to be washed downstream and ultimately deposited across the marshes during ebb tide, leaving them
exposed and creating a feeding opportunity for bears which lasted 5-7 days.

116 Observations were conducted from either permanent viewing stands ( $\leq 7$  people occupying) or small aluminium skiff boats ( $\leq$ 7 people). Direct visual observations of bears were conducted as part 117 118 of ongoing research at the study site by the field team (MC and JK; see Clapham et al. 2012, 2014), 119 and by accredited (by the Commercial Bear Viewing Association of British Columbia) bear viewing guides (Knight Inlet Lodge), taken during daily tours of the study site; this amounted to ~224 hours of 120 field observation for the study period. All observations were conducted during daylight hours, 121 between 0730 and 1800. However, as brown bears also forage nocturnally (Klinka and Reimchen 122 123 2002; Nevin and Gilbert 2005), social interactions may have occurred also outside of these viewing 124 times. Observations were recorded using a combination of field notes and photographs and/or video 125 using DSLR cameras (Canon and Nikon) with lenses ranging between 200-400mm. All observations 126 conducted adhered to ethical standards involving wild animals in accordance with the University of 127 Victoria Animal Care Committee (#2014-031(1)).

We used previously established definitions (indicated in italics) to recognise when social play behaviour in brown bears was occurring (black bears: Henry and Herrero 1974; Pruitt 1976, brown bears: Fagen 1981; Fagen and Fagen 2004, 2009). Namely, these included: a complete lack of any vocalisation during direct interaction, specific facial expressions, and specific body postures during contact. Similarly, we used previously described postures to recognise when an initiation to play was not accepted by a potential playmate, such as signals of anxiety through scratching and low intensity threat through head position and stiffening of the front legs (see Stonorov and Stokes 1972).

All individuals involved in play bouts (n = 9) have individual reference numbers [ongoing field
records kept at the site since 1999 (see Nevin 2003; Nevin and Gilbert 2005; Clapham et al. 2012,
2014)]. No interactions prior to 2014 have been observed between the cubs of female F001 and
female F025, or between themselves. F025 is only observed at the study site in the fall, whereas F001
is usually present throughout the whole non-denning period each year. The possibility that they are

- siblings cannot be discounted. Female F001 was 13 years old and female F010 ~10 years old during
- the study period. Subadult male M014.03 is not the offspring of F001 or F010. Cubs refers to bears
- that were 1.5 years old during the study period (yearlings).
- 143
- 144 **Results**
- 145
- 146 Scenario 1. Play among non-littermates independent subadults

On 18 August 2014 six brown bears were observed from a viewing platform feeding at Glendale 147 spawning channel. At 0848 DST a 4-year-old subadult male (M009.01) began feeding while partially 148 submerged in water, he remained fairly stationary whilst feeding for 30 minutes. Approximately 75m 149 150 away upstream two 3-year-old subadult male siblings (M014.03 and M015.03) were also feeding and 151 slowly moving downstream exploiting different feeding patches. A female with two first year cubs (F034) entered the pool downstream (west) at 0902. At around 0915 all bears were feeding in the pool 152 153 within 20m of each other; the siblings upstream in the middle of the flow, the female with cubs 154 downstream (south-west), and the subadult male roughly central to the other bears.

155 At 0918 the older subadult moved across the river and began to head upstream, past the 156 sibling males. In response to this, one of the sibling males (M015.03) moved towards the older male 157 with *partially flattened ears* and *puckered-lip face*. The older subadult paused and reciprocated the approach. The younger subadult then initiated play by making a slow *lunge* towards the older male; 158 159 the lunge terminated with a slight gape of the jaws (*relaxed open-mouth face*, less than  $30^\circ$ ). The 160 older subadult moved his head to avoid any contact, holding the younger male with his paws. During 161 the first minute of play-fighting, the older bear maintained a puckered-lip expression, his ears were 162 partially flattened to partially crescent. The younger bear's ears were maintained partially flattened and his jaws were open to a maximum of 45°, as he made various lunges at the older subadult. The 163 older bear kept his face and body clear of the lunges, moving his head in anticipation of the younger 164 165 bear's advances (Fig. 1a).

At 0919 the older bear then stretched (*neck extension*) towards the other sibling (M014.03),
who was then feeding ~3m away, with a slight puckered expression and partially flattened ears. The

168 sibling turned slightly towards the older subadult, but showed no other behavioural response and 169 continued to feed (Fig. 1b). The original bears then continued to play for two minutes. This bout displayed increased intensity; there was less restraint showed by the older subadult and he 170 occasionally opened his mouth to a gape of  $45^{\circ}$ . Then followed a repetitive sequence of relaxed open-171 172 mouth face, pawing, face-pawing, lunging, jawing, play-biting (biting intention movements and inhibited biting), rearing, and attempts at neck-bite-hold (not necessarily in that order; Fig 1c-e). The 173 174 play bout was terminated when the older male relaxed his ears, closed his mouth, stood broadside 175 (flank facing) and moved away (Fig. 1f).

176

## 177 Scenario 2. Play among non-littermates – dependent cubs

On 4 October 2014 at 1557 DST two family groups were observed feeding close to one another 178 179 (within 50m) on salmon carcasses in the estuary; F001 with two yearlings (male and female), and 180 F025 with two yearlings (male and unknown sex). Play was initiated by F001's male cub 181 approaching the cubs in the other family group. Play followed typical motor patterns and postures 182 expressed by bears when play-fighting: relaxed face, puckered-lips and ears partially flattened to 183 crescent, jaw gaping of typically no more than 20-45°, biting intention movements and inhibited 184 biting, and some face-pawing (Fig. 2a-c). Play took place while the bears were in water <1m deep and 185 also moved to land for some short bouts of wrestling and locomotion (chasing). Playmates were 186 interchanged between the two sets of siblings, occasionally both of F025's cubs played with F001's 187 female cub (Fig 2d). Play was occasionally paused for feeding and was not reinitiated after 1637. 188 Neither F001 nor F025 played, but frequently came in close proximity to one another's cubs (< 3m) as 189 they moved around feeding in the shallow water, to which the mother of the cubs showed no 190 behavioural response. Play was observed between the cubs of these two family groups on four occasions during September/October 2014. 191

192

193 Scenario 3. 'Group' play among different age and sex classes

194 On 19 September 2014 at 1140 DST we observed a female bear (F001) feeding on salmon carcasses

in the estuary with her two yearling cubs nearby. At 1148 a 3-year-old subadult male (MO14.03)

196 approached from the surrounding forest-edge and walked towards the adult female. Play was initiated 197 by the subadult male as he approached with crescent ears and sniffed the lateral side of her face with his face adjacent to hers. F001 responded with partially flattened ears and reciprocated by smelling 198 the lateral side of his face (Fig. 3a). She then rolled on the ground next to him and began face-pawing 199 200 (Fig. 3b) as the subadult male displayed biting intention movements towards her face with his jaws 201 open no more than 40°. F001 then resumed a quadrupedal stance and avoided the subadult male's 202 movements by turning her face away from his advances. The yearling cubs of F001 did not attempt to 203 approach during the play bout, but continued feeding nearby.

At 1150, another female with two yearlings (F010) moved west across the estuary from where 204 she had been feeding, towards F001 and M014.03; they did not appear to notice F010 moving closer 205 206 and continued to play. At 1152 M014.03 lead F001 over to a nearby log, which he climbed up onto 207 and used as leverage to lunge on top of F001 while exhibiting an inhibited neck bite (Fig. 3c). She 208 responded with an inhibited bite to his throat as she rolled over. The cubs of F001 then began to 209 separately move away from the approaching female with cubs (F010). F001 and M014.03 ceased 210 playing at 1155 and the subadult began to feed <5m away, while F001 remained in a siting posture 211 with frontal alert ears and closed mouth. At 1159 F010 approached the subadult male with crescent 212 ears, to which he responded with crescent ears and an open mouth of  $20-30^{\circ}$  (Fig. 3d). They then 213 engaged in a mixture of jaw-gaping, biting intention movements, and occasionally bipedal wrestling, 214 with crescent and partially flattened ears throughout. During this play bout, the yearling male of the 215 original female (F001) approached the playing pair and appeared to stand and observe at a distance of 216 <2m away (Fig. 3e). At this point the bears were all turned away from the observing researcher 217 making it difficult to accurately record this section of the interaction, but the playing pair did not 218 appear to engage the yearling in their play bout. F001 then moved away (~10m) to feed near her 219 female yearling; her male yearling also moved away from the playing bears.

F010 continued to play with the subadult, with her yearling cubs (unknown sex) now
observing the interaction ~10m away. At 1200 the female yearling of F001 looped behind the playing
bears to join the two yearlings from the other family group in observing the play bout. She displayed
frontal alert ears, while the other yearling's ears were relaxed (*laterad*; Fig. 3f), and moved away

224 when the playing bears came close (<3m). At 1202 as F010 began feeding, the subadult male 225 attempted to play with her two yearlings, approaching them without hesitation with crescent ears and a slightly puckered-lip. However, they displayed frontal alert ear posturing, scratching, and head-low 226 postures, indicating they did not accept his advances to play. F010 continued to feed throughout this 227 228 interaction and showed no behavioural response to the subadult male pursuing her cubs. The subadult male moved away and the play bout ended at 1202 when one cub of F010 moved directly adjacent to 229 230 its mother and displayed head-low and stiff-legs (low intensity threat, see Stonorov and Stokes 1972) 231 with frontal alert ears towards the male (Fig. 3g).

232

#### 233 Discussion

234

Social play in brown bears is a fairly common phenomenon within family groups, particularly
between sibling cubs (e.g. Fagen and Fagen 2004, 2009) and as such, is frequently observed in the
field by researchers and commercial bear-viewing operators (M Clapham pers. obs.). However, play
between non-littermates of varying age-sex class and play between the cubs of different family groups
has not been adequately described in the literature. By using a descriptive ethogram for social play in
black bears (Henry and Herrero 1974), previously supported for brown bears (Fagen and Fagen 2004,
2009), we were able to confirm that bears were conducting play behaviour in these scenarios.

We observed play behaviour between non-littermates during a time of abundant food 242 availability. High food availability is known to positively correlate with an increase in non-agonistic 243 244 bear interactions (Egbert and Stokes 1976) and even reduces cortisol levels in coastal brown bears (Bryan et al. 2013). Fagen & Fagen (1990) also documented a higher frequency of play between 245 246 immature brown bears during periods of high salmon abundance and Rogers (1987) noted that nonlittermate black bears >7 months of age were only seen to play when near abundant food resources. 247 Likewise, in other mammals an increase in long-term food availability has been shown to more than 248 double the rate of social play under captive conditions (Sharpe et al. 2002). When food is 249 concentrated and dense, aggregations of bears form to individually exploit the resource (Stonorov and 250 251 Stokes 1972; Craighead et al. 1995; Ben-David et al. 2004). Bears are then faced with the dilemma of

increased feeding opportunity but also increased risk of injury due to close proximity to conspecifics.
Behavioural plasticity would therefore be a useful coping mechanism to avoid increased tension
during space reduction (de Waal 1989; Judge and de Waal 1993; Tacconi and Palagi 2009). Playing
could aid in familiarising individuals with each other in a non-aggressive way, therefore reducing
xenophobia (Antonacci et al. 2010).

Social play has been found to increase survival of brown bear dependant cubs and newly-257 dispersed subadults (Fagen and Fagen 2004, 2009), perhaps due to reduced socially-induced stress 258 with physiological consequences (Fagen and Fagen 2009). Such immediate benefits challenge the 259 more traditional view of juvenile play, as a training exercise with benefits derived during adulthood 260 (as in Fagen 1981; Pellis and Pellis 1998; Špinka et al. 2001). Here, we documented two sets of 261 262 yearling cubs playing together in a nursery-like manner. Playing between non-littermates of the same 263 age may indicate a lack of social awareness, or a selection for variation in playmate ability. 264 Irrespective of the function behind selecting a playmate, juveniles likely learn social codes of conduct 265 during play bouts, termed 'social morality' by Bekoff (2001). Likewise 'eavesdropping' (see 266 McGregor 1993) on the play behaviour of older bears (scenario 3), would allow cubs to observe and 267 learn the social conduct of play without incurring the costs involved.

268 The information available to bears about their own size and dominance status during 269 development is unknown (Clapham et al. 2012). We observed play between non-littermate subadults 270 of differing age (scenario 1), and between two different adult females and a subadult male (scenario 271 3). Social play could be a method for subadult bears to self-assess physical ability during 272 development, as shown in infant sable antelopes Hippotragus niger (Thompson 1996). When play is observed in adult mammals, it usually involves a partner of contrasting age and between them, one 273 274 individual will be dominant and one subordinate (Pellis and Iwaniuk 2000). Play is usually initiated by the subordinate (Fagen 1981; Pellis and Iwaniuk 2000). In both scenarios, we documented 'role-275 276 reversing' and 'self-handicapping' (see Bekoff and Allen 1998) by the older, presumably more dominant bears. Both subadult male M009.01 (scenario 1) and adult female F001 (scenario 3) acted 277 submissively to their younger playmate by either passively turning their face or body away in 278 279 response to play advances without any resistance, or actively orientating their body lower to the

ground than the younger bear, increasing their vulnerability. Bekoff (2001) suggests that this type of
role reversal serves to provide a more 'level playing field' and to signal play intent by the dominant,
which may elongate the play bout. Play tactics appear to vary according to age class and dominance
ranking in brown bears.

284 Støen et al. (2005) report that brown bears are able to distinguish kin from non-kin, facilitating the spatial structure of individuals. Egbert and Stokes (1976) suggest that bears learn to 285 recognise other individuals, and Craighead et al. (1995) describe individual recognition of 286 conspecifics by all members of an aggregation, and retention of such information over successive 287 seasons ("stored knowledge"). They also hypothesize that this knowledge of other individuals reduces 288 conflict and stress, and benefits the individuals which learn this information the fastest (Craighead et 289 al. 1995). Individual recognition appears to be an important factor in dominance communication at 290 291 aggregations and the social awareness of an individual (Craighead et al. 1995). Social play could 292 facilitate this information transfer in a non-agonistic way, which reduces risk to those involved 293 regardless of rank in the social order. Indeed, social play between adult polar bears is thought to 294 function in competitor assessment during periods of low competition, with a derived benefit when 295 competition is high (Latour 1981). This supports the theory that play-fighting functions in social 296 evaluation and manipulation (Brueggeman 1978; Pellis and Iwaniuk 2000).

Across the animal kingdom, there is increasing evidence that socio-ecological factors influence social play. Food availability appears to dictate both the ecological and social landscape for many species, including brown bears. Under complex social situations, such as dense aggregations, even 'asocial' animals can demonstrate behavioural flexibility and could use tactics such as social play to evaluate conspecifics and reduce xenophobia.

302

### 303 References

304 Antonacci D, Norscia I, Palagi E (2010) Stranger to familiar: wild strepsirhines manage xenophobia

305 by playing. PLoS ONE 5(10): e13218. doi:10.1371/journal.pone.0013218.

Barber N (1991) Play and energy regulation in mammals. Q Rev Biol 66 (2): 129-147.

- Bekoff M (1995) Play signals as punctuation: the structure of social play in canids. Behaviour 132
  (5/6): 419-429.
- Bekoff M (2001) Social play behaviour. Cooperation, fairness, trust, and the evolution of morality. J
  Conciousness Stud 8 (2): 81-90.
- Bekoff M, Allen C (1998) Intentional communication and social play: how and why animals negotiate
- and agree to play. In: Bekoff M, Byers JA (eds) Animal Play: Evolutionary, Comparative, and
   Ecological Perspectives. Cambridge University Press, Cambridge, pp 97-114.
- Ben-David M, Titus K, Beier LVR (2004) Consumption of salmon by Alaskan brown bears: a trade-
- off between nutritional requirements and the risk of infanticide? Oecologia 138: 465-474.
- Brueggeman JA (1978) The function of adult play in free-living *Macaca mulatta*. In: Smith EO (ed)
  Social Play in Primates. Academic Press, New York, pp 169-192.
- 318 Bryan HM, Darimont CT, Paquet PC, Wynne-Edwards KE, Smits JEG (2013) Stress and reproductive
- hormones in grizzly bears reflect nutritional benefits and social consequences of a salmon
  foraging niche. PLoS ONE 8(11): e80537. doi:10.1371/journal.pone.0080537.
- Burghardt GM, Burghardt LS (1972) Notes on the behavioral development of two female black bear
  cubs: the first eight months. Int C Bear 2: 207-220.
- 323 Ciani F, Dall'Olio S, Stanyon R, Palagi E (2012) Social tolerance and adult play in macaque
- societies: a comparison with different human cultures. Anim Behav 84: 1313-1322.
- 325 Clapham M, Nevin OT, Ramsey AD, Rosell F (2012) A hypothetico-deductive approach to assessing
- the social function of chemical signalling in a non-territorial solitary carnivore. PLoS ONE
  7(4): e35404. doi:10.1371/journal.pone.0035404.
- 328 Clapham M, Nevin OT, Ramsey AD, Rosell F (2014) Scent-marking investment and motor patterns
  329 are affected by the age and sex of wild brown bears. Anim Behav 94:107-116.
- Craighead JJ, Sumner JS, Mitchell JA (1995) The Grizzly Bears of Yellowstone: Their Ecology in the
  Yellowstone Ecosystem, 1959-1992. Island Press, Washington DC.
- Egbert AL, Stokes AW (1976) The social behaviour of brown bears on an Alaskan salmon stream. Int
  C Bear 3: 41-56.
- Fagen R (1981) Animal Play Behavior. Oxford University Press, New York.

- Fagen R, Fagen J (1990) Play behavior of brown bears (*Ursus arctos*) and human presence at Pack
  Creek, Admiralty Island, Alaska. Int C Bear 8: 315-319.
- Fagen R, Fagen J (2004) Juvenile survival and benefits of play behaviour in brown bears, *Ursus arctos*. Evol Ecol Res 6:89-102.
- Fagen R, Fagen J (2009) Play behaviour and multi-year juvenile survival in free-ranging brown bears,
   *Ursus arctos*. Evol Ecol Res 11:1053-1067.
- 341 Fisheries and Oceans Canada (2014) Area 12 Mainland Inlet Pink Salmon Update Bulletin #7.

342 Internal Report, Fisheries and Ocean Canada, British Columbia.

- Held SDE, Špinka M (2011) Animal play and animal welfare. Anim Behav 81:891-899.
- Henry JD, Herrero SM (1974) Social play in the American black bear: its similarity to canid social
  play and an examination of its identifying characteristics. Amer Zool 14 (1): 371-389.
- Herrero S, Hamer D (1977) Courtship and copulation of a pair of grizzly bears, with comments on
   reproductive plasticity and strategy. J Mammal 58: 441-444.
- Judge PG, de Waal FBM (1993) Conflict avoidance among rhesus monkeys: coping with short term

349 crowding. Anim Behav 54: 643–662.

- 350 Klinka DR, Reimchen TE (2002) Nocturnal and diurnal foraging behaviour of brown bears (Ursus
- 351 *arctos*) on a salmon stream in coastal British Columbia. Can J Zool 80:1317–1322.
- 352 Latour PB (1981) Interactions between free-ranging, adult male polar bears (Ursus maritimus
- 353 *Phipps*): a case of adult social play. Can J Zool 59:1775-1783.
- McGregor PK (1993) Signalling in territorial systems: a context for individual identification, ranging
  and eavesdropping. Phil Trans R Soc B 340: 237-244.
- 356 McLellan BN, Hovey FW (2001) Natal dispersal of grizzly bears. Can J Zool 79: 838-844.
- 357 Murie A (1981) The grizzlies of Mount McKinley. University of Washington Press, Seattle.
- 358 Nevin OT (2003) The Influence of Prey Abundance and Risk-Sensitive Behavioral Change on
- Individual Access to High-Energy Food (Salmon): Impacts on the Density and Viability of
  Bear Populations. Dissertation, Utah State University.
- 361 Nevin OT, Gilbert BK (2005) Perceived risk, displacement and refuging in brown bears: positive
- impacts of ecotourism? Biol Conserv 121: 611-622.

- Pellis SM, Iwaniuk AN (1999) The problem of adult play fighting: a comparative analysis of play and
  courtship in primates. Ethology 105: 783-806.
- Pellis SM, Iwaniuk AN (2000) Adult-adult play in primates: comparative analyses of its origin,
  distribution and evolution. Ethology 106: 1083-1104.
- 367 Pellis SM, Pellis VC (1998) The structure-function interface in the analysis of play fighting. In:
- 368 Bekoff M, Byers JA (eds) Animal Play: Evolutionary, Comparative, and Ecological
- 369 Perspectives. Cambridge Univ. Press, Cambridge, pp 115-140.
- 370 Pruitt CH (1976) Play and agonistic behavior in young captive black bears. Int C Bear 3: 79-85.
- Rogers LL (1987) Effects of food supply and kinship on social behavior, movements, and population
  growth of black bears in Northeastern Minnesota. Wildlife Monogr 97:3-72.
- 373 Sharpe LL, Clutton-Brock TH, Brotherton PNM, Cameron EZ, Cherry MI (2002) Experimental
- provisioning increases play in free-ranging meerkats. Anim Behav 64: 113-121.
- Smith PK (1982) Does play matter? Functional and evolutionary aspects of animal and human play.
  Behav Brain Sci 5: 139-184.
- Špinka M, Newberry RC, Bekoff M (2001) Mammalian play: training for the unexpected. Q Rev Biol
  76 (2): 141-168.
- 379 Stelmock JJ, Dean, FC (1986) Brown bear activity and habitat use, Denali National Park -1980. Int C
  380 Bear 6: 155-167.
- Stirling I, Derocher AE (1990) Factors affecting the evolution and behavioural ecology of the modern
  bears. Int C Bear 8:189-204.
- Støen OG, Bellemain E, Sæbø S, Swenson JE (2005) Kin-related spatial structure in brown bears
   *Ursus arctos*. Behav Ecol Sociobiol 59: 191-197.
- 385 Stonorov D, Stokes AW (1972) Social behavior of the Alaska brown bear.Int C Bear 2:232-242.
- Tacconi G, Palagi E (2009) Play behavioural tactics under space reduction: social challenges in
  bonobos, *Pan paniscus*. Anim Behav 78: 469-476.
- Thierry B, Iwaniuk AN, Pellis SM (2000) The influence of phylogeny on the social behaviour of
   macaques (Primates: Cercopithecidae, genus *Macaca*). Ethology 106: 713-728.

- 390 Thompson KV (1996) Play-partner preferences and the function of social play in infant sable
- antelope, *Hippotragus niger*. Anim Behav 52: 1143-1155.
- 392 Thompson KV (1998) Self assessment in juvenile play. In: Bekoff M, Byers JA (eds) Animal Play.
- 393 Cambridge University Press, Cambridge, pp183-204.
- de Waal FBM (1989) The myth of a simple relationship between space and aggression in captive
- 395 primates. Zoo Biol (Supplement 1): 141–148.
- 396 Wilson EO (1975) Sociobiology: The New Synthesis. Belknap Press, Cambridge.

### 398 Figure Captions

**Fig. 1** Depiction of play between non-littermate subadult male brown bears (scenario 1); **a** M015.03

400 (left) with *flattened ears* and *open-mouth face* wrestles with M009.01 (right) who displays *puckered*-

- 401 *lip* and *partially crescent ears*; **b** M009.01 approaching M014.03 with *neck extension*, slight
- 402 puckered-lip and partially flattened ears; c M015.03 and M009.01 jawing and pawing with partially
- 403 *flattened ears*; **d** M009.01 conducts an *inhibited bite* while *pawing*, M015.03 displays *open-mouth*
- 404 *face* and *partially flattened ears*; **e** M015.03 conducts a *neck-bite-hold*, M009.01 moves lower and
- 405 turns his body towards the other bear; **f** M009.01 ends the bout with relaxed ears (*laterad*) and closed
- 406 mouth. Italics indicate terms taken from the ethogram in Henry & Herrero (1974).

407 Fig. 2 Depiction of play between non-littermate brown bear cubs (scenario 2); a F yearling of F001 408 (far left) with puckered-lip face towards M yearling of F025, M yearling of F001 (far right) wrestles and attempts neck-bite-hold with UNK yearling of F025; b F yearling of F001 (right) face-paws M 409 410 yearling of F025 following *locomotion*; c M yearling of F001 (left) *jaws* with M yearling of F025 411 (right); d M yearling of F025 lunges on top of F yearling of F001, who displays partially flattened 412 ears and puckered-lip, UNK yearling of F025 observes the play (right) as F025 is feeding in the background. F = female, M = male, UNK = unknown sex. Italics indicate terms taken from the 413 414 ethogram in Henry & Herrero (1974).

415 Fig. 3 Depiction of a 'group' play interaction in brown bears (scenario 3); a F001 (front) sniffs the 416 lateral side of M014.03s face with *partially flattened ears*; **b** F001 lays on her back and *face paws* 417 M014.03; c M014.03 (right) lunges on top of F001 with partially flattened ears and inhibited neck 418 *bite*, F001 displays an *inhibited neck bite*; **d** F010 (right) approaches M014.03 with *crescent ears*, 419 M014.03 responds with *relaxed open-mouth face*; e M yearling of F001 (centre) approaches F010 and 420 M014.03, F010 feeds adjacent to the left, the two yearlings of F010 observe the interaction (far left) 421 and the F yearling of F010 feeds (far right);  $\mathbf{f}$  F yearling of F010 (left) observes the play bout with 422 frontal alert ears, next to the UNK yearlings of F010 who both display relaxed ears (laterad); g UNK 423 yearling of F010 (left) displays *frontal alert ears* and head down towards M014.03. F = female, M =

- 424 male, UNK = unknown sex. Italics indicate terms taken from the ethogram in Henry & Herrero
- 425 (1974).
- 426 \*All figures to be printed in black and white, colour online only\*

# Figure 1



```
Figure 2
```



# Figure 3

