SHORT COMMUNICATION

Social play in wild brown bears of varying age-sex class

Melanie Clapham[1,2]* and John Kitchin[2,3]

[1] *Department of Geography, University of Victoria, British Columbia, Canada.*

[2] *Brown Bear Research Network, Sooke, British Columbia, Canada.*

[3] *Centre for Wildlife Conservation, University of Cumbria, Ambleside, United Kingdom.*

*Corresponding author: M Clapham, Applied Conservation Science Lab, Department of Geography, University of Victoria, PO Box 1700 STN CSC, Victoria, British Columbia, Canada, V8W 2Y2.

Email: mclapham@uvic.ca Tel: +1 (250) 472-5938

Acknowledgements

Research was funded by a Mitacs Elevate Fellowship and the Brown Bear Research Network. We would like to thank Dean and Kathy Wyatt for continued financial and logistical support and all the staff at Knight Inlet Lodge for field support and assistance. Thanks to Edward Savage and Hayley Shephard for providing additional visual documentation of play observations. Special thanks to Chris Darimont and three anonymous reviewers for their comments and suggestions regarding this manuscript.

Abstract

Social play behaviour is a well described phenomenon, almost ubiquitous among mammals. Despite its prevalence, social play takes several forms and may vary in function across species. For solitary 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 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 different age and sex class. We used a previously described behavioural ethogram to recognise play. Play followed typical motor patterns and postures expressed by bears during play-fighting: relaxed face, puckered-lip, ears partially flattened to crescent, wrestling, jaw gaping, play-biting, paw-swatting and lunging. No vocalisations were conducted during play bouts. Older bears displayed ‘self-handicapping’ and ‘role-reversal’ in the play postures they selected when playing with younger bears, suggesting that tactics vary according to age class and dominance ranking. Playing likely allows for the evaluation of conspecifics in a non-aggressive way during times of reduced competition and could also relieve stress in complex social situations.

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

Introduction

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 otherwise be 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).

Assessing play behaviour can be structured in an adaptive framework; the behaviour bears immediate costs but likely carries fitness benefits. Costs incurred may include time investment, 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 success, play behaviour should have net fitness benefits or experience serious constraints (Fagen and Fagen 2004). Comparing the contexts in which social play occurs at a high or low frequency may indicate when it becomes too costly and therefore aid the interpretation of function (see Sharpe et al. 2002).

Social play has been reported primarily for gregarious species (e.g. meerkats *Suricata suricatta*, Sharpe et al 2002; lemurs *Propithecus verreauxi*, Antonacci et al 2010; macaques *Macaca* spp., Thierry et al. 2000, Ciani et al. 2012; canids *Canis* spp. Bekoff 1995), with more solitary species receiving less attention. Several studies have assessed the importance of the level of gregariousness between species for its relevance to social play frequency (see Pellis and Iwaniuk 2000; Ciani et al. 2012). As social play appears to be influenced by “socio-ecological” factors (Pellis and Iwaniuk 1999, 2000), solitary-living species which display a dominance hierarchical social structure could equally indulge in play behaviour, due to home range overlap increasing the likelihood for individuals to 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 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 primarily solitary, but also form aggregations at abundant food resources, feeding within meters of conspecifics (Craighead et al. 1995; Ben-David et al. 2004; M Clapham and J Kitchin pers. obs.).

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 described for juvenile black bears *U. americanus* (Burghardt and Burghardt 1972; Henry and Herrero 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*. Most studies that report sightings of play in wild bears do not provide a systematic description of behaviours and have an alternative subject focus (e.g. Herrero & Hamer 1977; Murie 1981; Stelmock & Dean 1986). Here, we describe the motor patterns of social play in non-littermate wild brown bears of different age-sex class. We explore exhibited behaviours under three different scenarios, not systematically reported in the current literature.

Methodology

All observations were conducted between August and October 2014 in Glendale Cove, an estuarine inter-tidal zone of Knight Inlet, British Columbia, Canada (N50°41’ W125°44’). Bears are protected within Glendale Cove by a 15km^2 ‘no-hunt zone’ established in 1989 by the Ministry of Environment (BC provincial government). As a result of commercial bear-viewing activities at the site since 1997, bears have become tolerant to being viewed and show little behavioural response to human presence, 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 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 this river system (Fisheries and Ocean Canada 2014). In 2014 the drainage experienced a high return 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.

Observations were conducted from either permanent viewing stands (≤7 people occupying) or small aluminium skiff boats (≤7 people). Direct visual observations of bears were conducted as part of ongoing research at the study site by the field team (MC and JK; see Clapham et al. 2012, 2014), 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 field observation for the study period. All observations were conducted during daylight hours, between 0730 and 1800. However, as brown bears also forage nocturnally (Klinka and Reimchen 2002; Nevin and Gilbert 2005), social interactions may have occurred also outside of these viewing times. Observations were recorded using a combination of field notes and photographs and/or video using DSLR cameras (Canon and Nikon) with lenses ranging between 200-400mm. All observations conducted adhered to ethical standards involving wild animals in accordance with the University of 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).

Results

Scenario 1. Play among non-littermates - independent subadults

On 18 August 2014 six brown bears were observed from a viewing platform feeding at Glendale spawning channel. At 0848 DST a 4-year-old subadult male (M009.01) began feeding while partially submerged in water, he remained fairly stationary whilst feeding for 30 minutes. Approximately 75m away upstream two 3-year-old subadult male siblings (M014.03 and M015.03) were also feeding and 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 within 20m of each other; the siblings upstream in the middle of the flow, the female with cubs downstream (south-west), and the subadult male roughly central to the other bears.

At 0918 the older subadult moved across the river and began to head upstream, past the sibling males. In response to this, one of the sibling males (M015.03) moved towards the older male 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; the lunge terminated with a slight gape of the jaws (*relaxed open-mouth face*, less than 30°). The older subadult moved his head to avoid any contact, holding the younger male with his paws. During the first minute of play-fighting, the older bear maintained a puckered-lip expression, his ears were 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 older bear kept his face and body clear of the lunges, moving his head in anticipation of the younger 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 sibling turned slightly towards the older subadult, but showed no other behavioural response and 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 occasionally opened his mouth to a gape of 45°. Then followed a repetitive sequence of relaxed open-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 play bout was terminated when the older male relaxed his ears, closed his mouth, stood broadside (flank facing) and moved away (Fig. 1f).

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

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

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

At 1150, another female with two yearlings (F010) moved west across the estuary from where she had been feeding, towards F001 and M014.03; they did not appear to notice F010 moving closer and continued to play. At 1152 M014.03 lead F001 over to a nearby log, which he climbed up onto and used as leverage to lunge on top of F001 while exhibiting an inhibited neck bite (Fig. 3c). She responded with an inhibited bite to his throat as she rolled over. The cubs of F001 then began to separately move away from the approaching female with cubs (F010). F001 and M014.03 ceased playing at 1155 and the subadult began to feed <5m away, while F001 remained in a siting posture with *frontal alert ears* and closed mouth. At 1159 F010 approached the subadult male with crescent ears, to which he responded with crescent ears and an open mouth of 20-30° (Fig. 3d). They then engaged in a mixture of jaw-gaping, biting intention movements, and occasionally bipedal wrestling, with crescent and partially flattened ears throughout. During this play bout, the yearling male of the original female (F001) approached the playing pair and appeared to stand and observe at a distance of <2m away (Fig. 3e). At this point the bears were all turned away from the observing researcher making it difficult to accurately record this section of the interaction, but the playing pair did not appear to engage the yearling in their play bout. F001 then moved away (~10m) to feed near her 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 when the playing bears came close (<3m). At 1202 as F010 began feeding, the subadult male 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 postures, indicating they did not accept his advances to play. F010 continued to feed throughout this 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 its mother and displayed head-low and stiff-legs (low intensity threat, see Stonorov and Stokes 1972) with frontal alert ears towards the male (Fig. 3g).

Discussion

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 availability. High food availability is known to positively correlate with an increase in non-agonistic 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 immature brown bears during periods of high salmon abundance and Rogers (1987) noted that non-littermate black bears >7 months of age were only seen to play when near abundant food resources. Likewise, in other mammals an increase in long-term food availability has been shown to more than double the rate of social play under captive conditions (Sharpe et al. 2002). When food is concentrated and dense, aggregations of bears form to individually exploit the resource (Stonorov and 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-dispersed subadults (Fagen and Fagen 2004, 2009), perhaps due to reduced socially-induced stress with physiological consequences (Fagen and Fagen 2009). Such immediate benefits challenge the more traditional view of juvenile play, as a training exercise with benefits derived during adulthood (as in Fagen 1981; Pellis and Pellis 1998; Špinka et al. 2001). Here, we documented two sets of yearling cubs playing together in a nursery-like manner. Playing between non-littermates of the same age may indicate a lack of social awareness, or a selection for variation in playmate ability. Irrespective of the function behind selecting a playmate, juveniles likely learn social codes of conduct during play bouts, termed ‘social morality’ by Bekoff (2001). Likewise ‘eavesdropping’ (see McGregor 1993) on the play behaviour of older bears (scenario 3), would allow cubs to observe and learn the social conduct of play without incurring the costs involved.

The information available to bears about their own size and dominance status during development is unknown (Clapham et al. 2012). We observed play between non-littermate subadults of differing age (scenario 1), and between two different adult females and a subadult male (scenario 3). Social play could be a method for subadult bears to self-assess physical ability during 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 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-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 submissively to their younger playmate by either passively turning their face or body away in 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.

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 recognise other individuals, and Craighead et al. (1995) describe individual recognition of conspecifics by all members of an aggregation, and retention of such information over successive seasons (“stored knowledge”). They also hypothesize that this knowledge of other individuals reduces conflict and stress, and benefits the individuals which learn this information the fastest (Craighead et al. 1995). Individual recognition appears to be an important factor in dominance communication at aggregations and the social awareness of an individual (Craighead et al. 1995). Social play could facilitate this information transfer in a non-agonistic way, which reduces risk to those involved regardless of rank in the social order. Indeed, social play between adult polar bears is thought to function in competitor assessment during periods of low competition, with a derived benefit when competition is high (Latour 1981). This supports the theory that play-fighting functions in social 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.

References

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

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.

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.

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.

Clapham M, Nevin OT, Ramsey AD, Rosell F (2014) Scent-marking investment and motor patterns 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.

Fisheries and Oceans Canada (2014) Area 12 Mainland Inlet Pink Salmon Update Bulletin #7. 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 crowding. Anim Behav 54: 643–662.

Klinka DR, Reimchen TE (2002) Nocturnal and diurnal foraging behaviour of brown bears (*Ursus arctos*) on a salmon stream in coastal British Columbia. Can J Zool 80:1317–1322.

Latour PB (1981) Interactions between free-ranging, adult male polar bears (*Ursus maritimus 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.

McLellan BN, Hovey FW (2001) Natal dispersal of grizzly bears. Can J Zool 79: 838-844.

Murie A (1981) The grizzlies of Mount McKinley. University of Washington Press, Seattle.

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.

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.

Pellis SM, Pellis VC (1998) The structure-function interface in the analysis of play fighting. In: Bekoff M, Byers JA (eds) Animal Play: Evolutionary, Comparative, and Ecological Perspectives. Cambridge Univ. Press, Cambridge, pp 115-140.

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.

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.

Stelmock JJ, Dean, FC (1986) Brown bear activity and habitat use, Denali National Park -1980. Int C 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.

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.

Thompson KV (1996) Play-partner preferences and the function of social play in infant sable antelope, *Hippotragus niger*. Anim Behav 52: 1143-1155.

Thompson KV (1998) Self assessment in juvenile play. In: Bekoff M, Byers JA (eds) Animal Play. Cambridge University Press, Cambridge, pp183-204.

de Waal FBM (1989) The myth of a simple relationship between space and aggression in captive primates. Zoo Biol (Supplement 1): 141–148.

Wilson EO (1975) Sociobiology: The New Synthesis. Belknap Press, Cambridge.

Figure Captions

Fig. 1 Depiction of play between non-littermate subadult male brown bears (scenario 1); **a** M015.03 (left) with *flattened ears* and *open-mouth face* wrestles with M009.01 (right) who displays *puckered-lip* and *partially crescent ears*; **b** M009.01 approaching M014.03 with *neck extension*, slight *puckered-lip* and *partially flattened ears*; **c** M015.03 and M009.01 *jawing* and *pawing* with *partially flattened ears*; **d** M009.01 conducts an *inhibited bite* while *pawing*, M015.03 displays *open-mouth face* and *partially flattened ears*; **e** M015.03 conducts a *neck-bite-hold*, M009.01 moves lower and turns his body towards the other bear; **f** M009.01 ends the bout with relaxed ears (*laterad*) and closed mouth. Italics indicate terms taken from the ethogram in Henry & Herrero (1974).

Fig. 2 Depiction of play between non-littermate brown bear cubs (scenario 2); **a** F yearling of F001 (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 yearling of F025 following *locomotion*; **c** M yearling of F001 (left) *jaws* with M yearling of F025 (right); **d** M yearling of F025 *lunges* on top of F yearling of F001, who displays *partially flattened 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 ethogram in Henry & Herrero (1974).

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

male, UNK = unknown sex. Italics indicate terms taken from the ethogram in Henry & Herrero (1974).

All figures to be printed in black and white, colour online only

Figure 1

Figure 2

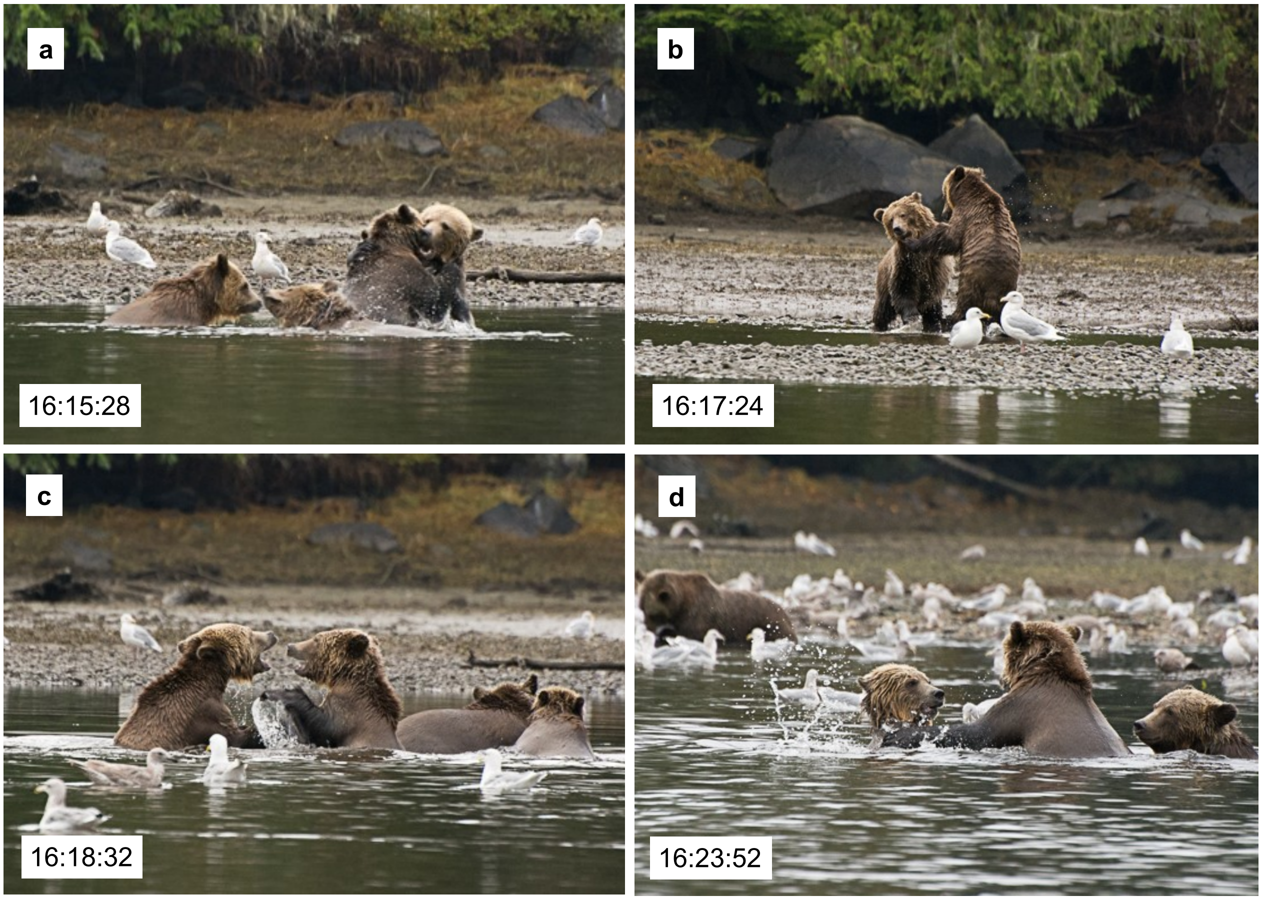

Figure 3