BEHAVIOURAL EFFECTS OF VIEWING AND SOCIAL DYNAMICS OF GRIZZLY BEARS ALONG THE FISHING BRANCH RIVER, YUKON

by

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RESEARCH PROJECT SUBMITTED IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF RESOURCE MANAGEMENT

In the School of
Resource and Environmental Management

Project No. 444

SIMON FRASER UNIVERSITY

Spring 2008

APPROVAL

Name: **Shelley M. Marshall**

Degree: **Master of Resource Management**

Title of Research Project: **Behavioural effects of viewing and social dynamics of grizzly bears along the Fishing Branch River, Yukon**

Project No.: **444**

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ABSTRACT

Wildlife-based ecotourism has rapidly increased in popularity, especially when featuring large mammals in their natural environment. Researchers have questioned the sustainability of wildlife-based ecotourism because it may compromise the survival and reproduction of focal animals. I investigated the potential spatio-temporal effects of bear viewers on grizzly bears at a proposed bear viewing site along the Fishing Branch River, Yukon. Spatial river use of grizzly bears was largely explained by habituation status. Bears consumed 24 % less salmon when viewers were present, posing serious energetic consequences if spatio-temporal compensation does not occur. Dominance status had no measurable effect on bears' fishing behaviour presumably because abundant salmon and few conspecifics minimized resource-driven competition. However, dominance status could influence feeding behaviour in years with reduced salmon abundance, which would compound viewer-induced reductions in fish consumption. I recommend further investigation into potential spatio-temporal compensatory behaviours of grizzly bears along the Fishing Branch River.

Keywords: grizzly bear; *Ursus arctos*; ecotourism; behaviour; Yukon; social dominance
Subject Terms: animal behaviour; animal ecology; grizzly bear; grizzly bear-behaviour; mammals-Yukon Territory; wildlife watching

ACKNOWLEDGEMENTS

I am indebted to my committee, Drs. Kristina Rothley and Alton Harestad, whose insights and advice nurtured this research to completion. I am grateful for their patience and support with my choice to balance full-time employment with the final stages of this project. Although an informal committee member, Dr. Ramona Maraj contributed an immense amount of persistence, expertise, and encouragement that shaped this project.

This research was financially supported by Yukon Department of Environment; Northern Scientific Training Program, Indian and Northern Affairs Canada; Northern Research Institute, Yukon College; Grant-in-aid Program, Arctic Institute of North America; and Simon Fraser University. Yukon Parks Branch and Fish and Wildlife Branch provided invaluable in-kind support making this research possible, with particular thanks to Erik Val, Gordon MacRae, and Ramona Maraj. Fuji Film Canada Inc. provided additional in-kind support.

Phil Timpany provided extensive knowledge of bear behaviour and bears using the Fishing Branch River. I thank Phil for his assistance in the field, particularly with set-up and camera maintenance, collection of hair samples, and camp life. Dr. G. Mori and J. Wawerla from School of Computing Science at SFU developed, purchased, and assembled the remote camera system. William Josie, Vuntut Gwitchin First Nation, provided suggestions, support, and helpful background on the research site.

I extend a huge thank you to my REM colleagues. My Applied Wildlife Ecology Lab group contributed immensely to my academic and non-academic experience at SFU.

Last, but in no way the least, I am indebted to Sean Taylor for his patience and willingness to uproot his life while I pursued my education. He suffered through my inability to go outside for extended periods of time, demand for quiet times while working from home, and cooked countless meals allowing me to continue working.

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Chapter 1: Introduction

BACKGROUND

Tourism is the largest industry in the global economy, employing an estimated 200 million people and creating approximately $3.5 trillion in economic activity (The International Ecotourism Society 2005). In the Yukon, tourism is the largest private employer with approximately 80 % of all employed Yukon residents working for businesses that reported some amount of tourism revenue (Yukon Government Department of Tourism and Culture 2007). Non-resident tourism in the Yukon created an estimated $164 million in 2000 (Yukon Government Department of Tourism and Culture 2007). In 2005, nearly 325,000 tourists visited the Yukon, up almost 3 % from 2004 (Yukon Government Department of Tourism and Culture 2007).

Ecotourism activities are continually rising world-wide, growing at three times the rate of general tourism activities in 2004 (World Tourism Organization 2004). Ecotourism is defined ideally as responsible travel to natural areas that conserve the environment and improve the well-being of local people (The International Ecotourism Society 2005). In particular, wildlife-based ecotourism featuring large mammals in their natural environment has grown in popularity (Jelinski et al. 2002, Dyck and Baydack 2004, Nevin and Gilbert 2005). Wildlife-based ecotourism can boost local economies by increasing demand for local guides and service industry workers (e.g., accommodation and food services). Social benefits of wildlife-based ecotourism include educating ecotourists about biological systems and raising awareness of conservation issues. Wildlife-based ecotourism often raises funds supporting habitat and species conservation (Goodwin 1996, Kruger 2005).

Bear viewing is overwhelmingly popular with ecotourists, prompting managers to limit viewer numbers at many sites to minimize human impacts on bears and their habitat (U.S. Forest Service 1989, Aumiller and Matt 1994). Many bear viewing sites in Alaska do not limit viewer numbers, including the Chilkoot River, Brooks River, and Fish Creek. The Chilkoot River, in Haines, had an estimated 83,000 visitor use days during the bear viewing season in 2004, 74 % of which were bear viewers and 22 % were anglers whom often fish within meters of the bears (Crupi 2005). A visitor use day was any portion of a day that one visitor spent at a viewing site. Brooks River, in Katmai National Park and Preserve, had a 10-yr average of 9500 visitor use days during the bear viewing season (Olson et al. 2002). Fish Creek, in Hyder, typically has 200-500 visitors daily over the 6-week viewing season (Sheldon 2003). Even with permit systems limiting viewer numbers, Alaskan bear viewing sites like McNeil River and Pack Creek still receive approximately 1000 visitor use days during a viewing season (Meehan 2006, J. Neary, U.S. Forest Service, unpublished data).

Researchers have questioned the sustainability of wildlife-based ecotourism (Goodwin 1996, Kruger 2005). Wildlife viewing and tourist activity compromised focal animals' survival and reproduction by reducing feeding in caribou (*Rangifer tarandus*; Duchesne et al. 2000), decreasing feeding time in breeding Alaskan Bald Eagles and their nestlings (*Haliaeetus leucocephalus*; Steidl and Anthony 2000), increasing stress hormone release in Magellanic Penguins (*Spheniscus magellanicus*; Walker et al. 2006), and reducing body weights of fledgling Yellow-eyed Penguins (*Megadyptes antipodes*; McClung et al. 2004). Wildlife viewing has shifted bears' behaviour and activity patterns spatially and/or temporally, in some cases reducing their energetic intake. Olson and Gilbert (1994) found grizzly bears (*Ursus arctos*) wary of human activity fed in suboptimal fishing areas of Brooks River where human activity was lowest. In contrast, habituated bears (habituation is defined as a diminution of responses to humans after several non-negative interactions; McCullough 1982, Gilbert 1989) exploited highly efficient fishing sites regardless of their proximity to human activity (Olson and Gilbert 1994). At Anan Creek, Alaska, almost half of the black bears (*U. americanus*) were spatially displaced by bear viewers and moved to viewer prohibited areas where they could fish undisturbed (Chi and Gilbert 1999). Along the Chilkoot River, grizzly bears captured almost three times more fish and caught higher proportions of live fish, which contain more energy than dead fish, when humans were absent or more than 100 m from the bears (Crupi 2003).

Given the popularity of bear viewing and negative effects of viewers at other bear viewing sites, the managing agencies for the Yukon's Ni'iinlii Njik (Fishing Branch) protected area complex required an investigation into the potential effects of a bear viewing program on grizzly bears at the Fishing Branch River (N 66° 30' W 139° 20') prior to the onset of commercial bear viewing. Bear viewing at the Fishing Branch River occurs during the fall chum salmon (*Oncorhynchus keta*) run because bears congregate along the river to exploit this high energy resource. Sufficient fat accumulation is essential for grizzly bears' overwinter survival and reproduction, particularly because females' physiological state influences their reproductive rate (Hilderbrand et al. 1999). This northern interior region of the Yukon has very few areas where bears can access salmon. As such, spawning salmon at the Fishing Branch River are a critical resource to these grizzly bears. Northern interior grizzly bears have the lowest reproductive rate of any North American terrestrial mammal (Stringham 1990, Wielgus and Bunnell 1994, Wielgus and Bunnell 2000, McLoughlin et al. 2003, Wakkinen and Kasworm 2004). Based on the importance of this salmon run and low reproductive rate of these bears, it was critical to determine the potential effects of viewing on these Fishing Branch River bears prior to the onset of commercial viewing.

PROJECT OVERVIEW

My research goals were to investigate the potential effects of bear viewing on these grizzly bears at the Fishing Branch River and provide area managers with recommendations for further research, management of the viewing program, and measures to mitigate negative viewer effects on bears. To this end in Chapter 2, I evaluated spatial river use by grizzly bears in response to different levels of human activity, temporal viewer effects on fish consumption by bears, effects of uncontrollable between-year factors (e.g., salmon availability and summer forage quality) on fish consumption by bears, temporal viewer effects on fishing behaviour, and daily and seasonal bear use patterns to identify high use periods. Prohibiting viewers during periods of high bear use can be an effective measure to mitigate negative viewer effects on these bears. Salmon spawning streams provide unique opportunities to study the social dynamics of these normally solitary bears (Chi 1999, Gende and Quinn 2004, Nevin and Gilbert 2005). A social hierarchy usually emerges as these bears congregate along the river, which can influence individual bears' access to fish and their feeding efficiency

(Egbert and Stokes 1976, Chi 1999, Gende and Quinn 2004). In Chapter 3, I assessed whether a dominance hierarchy existed among these bears at the Fishing Branch River, the nature of their intraspecific social interactions, and the influence of social dominance on fishing behaviour. My primary interest was to characterize any dominance effect on fish consumption by grizzly bears because these dominance-dependent effects could compound any viewer-induced changes to fish consumption. I provide a research summary and recommendations for further research, management of bear viewing, and measures to mitigate viewing effects on bears in Chapter 4.

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Chapter 2: Behavioural responses of grizzly bears to human activity along a salmon river in the northern Yukon

INTRODUCTION

Ecotourism activities are continually rising world-wide, growing at three times the rate of general tourism activities in 2004 (World Tourism Organization 2004). Ecotourism is defined ideally as responsible travel to natural areas that conserve the environment and improve the well-being of local people (The International Ecotourism Society 2005). In particular, wildlife-based ecotourism has rapidly increased in popularity, especially when featuring large mammals in their natural environment (Jelinski et al. 2002, Dyck and Baydack 2004, Nevin and Gilbert 2005). Wildlife-based ecotourism can boost local economies by increasing demand for local guides and service industry workers (e.g., accommodation and food services). An estimated 420,000 U.S. residents participated in wildlife watching activities in Alaska in 2001, generating total trip and equipment expenditures of $499 million (U.S. Department of the Interior, Fish and Wildlife Service, and U.S. Department of Commerce, U.S. Census Bureau 2001). Social benefits of wildlife-based ecotourism include educating ecotourists about biological systems and raising awareness of conservation issues. Wildlife-based ecotourism often raises funds supporting habitat and species conservation (Goodwin 1996, Kruger 2005). Thus, wildlife-based ecotourism generates increasing conservation support for focal species and increasing socio-economic benefits for ecotourists and local communities as these activities expand globally.

Despite its socio-economic benefits, researchers have questioned the sustainability of wildlife-based ecotourism (Goodwin 1996, Kruger 2005). Kruger's (2005) multivariate analysis of 188 ecotourism studies found that 37 % were unsustainable, largely because of overwhelming tourist volume and inadequate tourist control that negatively affected the focal animals. Wildlife viewing and tourist activity compromised focal animals' survival and reproduction by reducing feeding in caribou (*Rangifer tarandus*; Duchesne et al. 2000), decreasing feeding time in breeding Alaskan Bald Eagles and their nestlings (*Haliaeetus leucocephalus*; Steidl and Anthony 2000), increasing stress hormone release in Magellanic Penguins (*Spheniscus magellanicus*; Walker et al. 2006), and reducing body weights of fledgling Yellow-eyed Penguins (*Megadyptes antipodes*; McClung et al. 2004). Wildlife viewing activities have also caused behavioural alterations in focal animals that potentially reduce their survival. For example, experimentally introduced SCUBA-diving tourists altered blackeye goby (*Coryphopterus nicholsi*) behaviours, placing them in greater risk of predation (Chuchman 2006). Ecotourism resort and transportation development often alters habitat in ways that negatively affect focal animals. Such development decreased the hatching and fledgling success of Malaysian Plovers (*Charadrius peronii*) in Thailand (Yasue and Dearden 2006). An economic trade-off framework helps describe the mechanism behind wildlife viewing's negative effects on its focal animals (Frid and Dill 2002). If wildlife respond to viewers as another type of predation risk, this anti-predator response reduces animals' time spent in fitness-enhancing activities, such as foraging, vigilance, and caring for young (Frid and Dill 2002). In light of such studies, wildlife viewing can be a consumptive, potentially unsustainable human activity contrary to traditional views.

Wildlife viewing has shifted bears' behaviour and activity patterns spatially and/or temporally, in some cases reducing their energetic intake. Olson and Gilbert (1994) found grizzly bears (*Ursus arctos*) wary of human activity fed in suboptimal fishing areas of Brooks River, Alaska, where human activity was lowest. In contrast, habituated bears (habituation is defined as a diminution of responses to humans after several non-negative interactions; McCullough 1982, Gilbert 1989) exploited highly efficient fishing sites regardless of their proximity to human activity (Olson and Gilbert 1994). At Anan Creek, Alaska, almost half of the black bears (*U. americanus*) were spatially displaced by bear viewers and moved to viewer prohibited areas where they could fish undisturbed (Chi and Gilbert 1999). Along Alaska's Chilkoot River, grizzly bears captured almost three times more fish and caught higher proportions of live fish when humans were absent or more than 100 m from the bears (Crupi 2003). Bear viewers negatively influenced the fishing success of many bears using these three Alaskan salmon (*Oncorhynchus* sp.) streams, potentially reducing their fitness.

Not all bear-viewing research found negative effects on bears. Nevin and Gilbert (2005) found that bear viewer presence created a temporal refuge for subordinate age/sex classes of grizzly bears, giving them access to optimal foraging sites at Glendale Cove, British Columbia (B.C.). This occurred because the activity of dominant male grizzly bears, who normally exclude subordinates, declined drastically in viewers' presence (Nevin and Gilbert 2005). In the Khutzeymateen Grizzly Bear Sanctuary, B.C., bear viewers increased vigilance activities of grizzly bears by moderate amounts but did not significantly influence their feeding time (Pitts 2001). Rode et al. (2006, 2007) found that a particular age/sex class of bears altered their foraging strategies to compensate for experimentally introduced bear viewers at Douglas River, Alaska. These bears maximized their feeding efficiency by consuming more of each captured fish to minimize their required fishing time in viewers' presence. The end result was no significant reduction in energetic intake when viewers were present (Rode et al. 2006, 2007). Research has found varied responses in bears to viewer activity with energetically negative, positive, and neutral responses.

Bear responses to viewers can be both site-specific and individual-specific. Individual-specific responses arise from each bear's unique individual characteristics including habituation status, age/sex class, dominance status, and reproductive status. Site-specific responses arise from differing resource (salmon) distribution, resource availability, and viewer management regimes, such as guidelines regarding viewer numbers, viewing hours, and areas of permissible viewing. This site-specificity demands investigation into the potential spatio-temporal effects of bear viewers on grizzly bears at a proposed bear viewing site along the Fishing Branch River in the northern Yukon.

Bear viewing at the Fishing Branch River occurs during the fall chum salmon (*O. keta*) run as bears congregate along the river to exploit this high energy resource. Sufficient fat accumulation is essential for grizzly bears' overwinter survival and reproduction, particularly because females' physiological state influences their reproductive rate (Hilderbrand et al. 1999). Female bears will not reproduce if they cannot accumulate sufficient fat reserves in the fall. As a result, bear viewing's potential influence on fish consumption by bears at the Fishing Branch River could be detrimental to this subpopulation's productivity. Northern interior grizzly bears, including these Fishing Branch River bears, have the lowest reproductive rate of any North American terrestrial mammal (Stringham 1990, Wielgus and Bunnell 1994, Wielgus and Bunnell 2000, McLoughlin et al. 2003, Wakkinen and Kasworm 2004). The critical nature of the salmon run and low reproductive rate of these bears emphasizes the importance of determining the potential effects of viewers on bears at the Fishing Branch River prior to the onset of commercial bear viewing. If I can quantify the negative spatio-temporal effects of bear viewing on these grizzly bears, the proposed viewing program can be modified in an effort to minimize these effects.

I investigated the potential effects of bear viewing on the feeding behaviour of grizzly bears along the Fishing Branch River in the two years prior to commercial bear viewing, 2004 and 2005. My research timing created a unique study opportunity where I could control periods with and without bear viewers, in contrast to many studies at existing bear viewing sites. My research objectives were to assess:

- spatial river use by bears in relation to human activity,
- temporal viewer effects and the effect of uncontrollable, between-year factors (e.g., summer forage quality, salmon availability) on fish consumption by bears,
- temporal viewer effects on bears' fishing behaviour, and
- daily and seasonal bear use to identify high-use periods.

I predicted that the spatial river use of bears would correspond to their level of tolerance for human activity. Tolerant bears should fish around higher human activity and when viewers were present, whereas wary bears should avoid higher human use areas except when viewers were absent. I hypothesized that viewer presence would reduce bears' fish consumption relative to times without viewers because of increased time spent reacting to viewers. I expected that uncontrollable between-year factors (i.e., factors that vary between years and were beyond my control) would influence fish consumption by bears at the Fishing Branch River. For example, years with high berry productivity would result in bears arriving at the river in good body condition. As such, these bears may consume fewer salmon compared to years when they arrive in poor body condition. I predicted that viewer presence would negatively affect the fishing behaviour of these bears. For example, bears would minimize their time spent on the river and increase their vigilance towards viewers. Lastly, I hypothesized that daily and seasonal use patterns of grizzly bears exist at the Fishing Branch River. As such, limiting viewer activity in the highest seasonal or daily use periods of these bears could effectively mitigate any negative viewer effects on these bears.

STUDY AREA

The study portion of the Fishing Branch River (N 66° 30' W 139° 20') was located within the Ni'iinlii Njik (Fishing Branch) protected area complex. This area protects the chum salmon run, grizzly bears that congregate to consume the salmon, and their habitats (Yukon Government Department of Environment and Vuntut Gwitchin Government Department of Natural Resources 2000). The 7000 km^2 protected area was established in 1999 as part of the Vuntut Gwitchin First Nation Final Agreement and under the Yukon Protected Areas Strategy. Ni'iinlii Njik protected area complex protects a representative portion of the Northern Ogilvie Mountains Eco-region in the northern Yukon Territory. This protected area complex encompasses the Fishing Branch River watershed and parts of adjacent headwaters and is comprised of four components (Fig. 2-1): 5400 km^2 Wilderness Preserve, 1000 km^2 Habitat Protection Area, 165 km^2 Ecological Reserve, and 143 km^2 Vuntut Gwitchin Settlement Lands. My study site was at the newly created commercial bear viewing area in the Ecological Reserve and Settlement Lands immediately west of Bear Cave Mountain at the centre of the protected area complex (Fig. 2-1).

Unique characteristics of Ni'iinlii Njik protected area complex include limestone caves, year-round open water, and grizzly bear densities greater than any other place at this northern latitude (Yukon Government Department of Environment and Vuntut Gwitchin Government Department of Natural Resources 2000). Dissolving limestone creates nutrient-rich ecosystems, including calcium-enriched water from underwater limestone caverns. Thermal energy from summer waters is stored in underground reservoirs. This warm ground water resurfaces through upwellings, which creates permafrost-free areas around the river and maintains the river's non-frozen state during the severe northern winters. Permafrost-free conditions around the Fishing Branch River near Bear Cave Mountain create an opportunity for relatively dense white spruce (*Picea glauca*) forests to grow, with willow (*Salix* spp.) thickets that dominate riparian areas.

Understory vegetation at the site contains many grizzly bear foods, including blueberry (*Vaccinium* spp.), soapberry (*Sheperdia canadensis*), bearberry (*Arctostaphylos rubra*), kinnickinnick (*A. uva-ursi*), rose (*Rosa* spp.), and high-bush cranberry (*Viburnum edule*). The bear viewing area at the Fishing Branch River is located in an interior region, in contrast to the coastal habitats of most bear viewing sites.

The Ni'iinlii Njik protected area complex has limited human influence because of its isolation. Old Crow is the closest community to the study site at 120 km due north. Dawson City is the next closest community and is almost 280 km south. The study site and commercial bear viewing area were only accessible by helicopter, foot, or snowmobile. With the exception of commercial bear viewers, area visitors were largely limited to Yukon Government staff, Vuntut Gwitchin First Nation members, researchers, and Fisheries and Oceans Canada staff who maintain a live fish weir approximately 8 km downstream from the study site. Fisheries and Oceans Canada maintain the weir from mid-August to mid-October counting salmon daily. The chum run lasts from mid-August to early November, with escapement numbers as low as 5,000 (in 2000) and reaching highs of 301,000 (in 1975; Fisheries and Oceans Canada, unpublished data). Grizzly bears can be viewed at the study site from early September to early November.

My study site was the commercial viewing area along the Fishing Branch River, whose three bear viewing sites (A, B, C) provided approximately 500 m of continuous river viewing along chum salmon spawning grounds (Fig. 2-2). Site A was adjacent to the viewing camp and will be the primary viewing site. That is, Site A will have the most viewing hours by visitors. Sites B and C will be the secondary and tertiary sites for bear viewers, respectively. Bears displaced from the high human activity around camp and Site A may use the lower human activity area around Sites B and C as a refuge from human activity.

I based my research at the commercial bear viewing camp situated 20 m from the river in the forest adjacent to Site A. Camp infrastructure consisted of a main 5 m x 5 m cabin for cooking, two 3 m x 4 m sleeping cabins, a high cache, and outhouse. Bears were not deterred from camp unless they threatened property damage or physical harm. An electric fence protected the cabins during the non-viewing months. The commercial bear viewing program will not use viewing infrastructure (e.g., elevated platforms); rather, viewing will occur from natural river banks.

Habituation of bears is paramount to the success of commercial viewing operations because it creates safer and subsequently more optimal viewing opportunities (Aumiller and Matt 1994). Habituation efforts have been underway for over 10 years at the Fishing Branch River, with up to two months of active habituation annually (P. Timpany, personal communication). As a result, my research characterizes the behaviour and river use of bears with previous exposure to human activity at the Fishing Branch River.

METHODS

Bear Behaviour

I recorded grizzly bear behaviour in person from Site A and with a remote video camera at Site B. The remote camera system had a battery, heater, remote on-off switch, and video transmitter that sent the video signal to the receiver located in the cabin (see Appendix 1 for technical details). I placed the video camera in a tree approximately 20 m downstream of Site B, where it captured an additional 60 m of shoreline and river around Site C that were not visible during my direct observations from Site A (Fig. 2-2). By using the camera, I increased the sampling area without requiring additional observers or reducing the frequency of sampling sessions at each observation site. Decreasing sample size challenges analyses, while additional observers raise the overall human activity level, potentially confounding viewer effects on bears. With the camera, I could record bear behaviour in the area of lower human activity without altering the human activity level. A human observer would increase the human activity in what was originally a low human activity area.

I conducted direct observations from a tree stand erected 4 m up a tree at Site A. During direct observations, I was approximately 20 m from the river's edge and 10 m from the common travel paths of bears along the river shore. The tree stand masked my presence as much as possible creating a situation close to 'people absent' and elevated me above bears' travel paths giving them unimpeded movement through the observation area. I had an unobstructed view of 230 m downstream and a 50 % obstructed view of

160 m upstream from the tree stand; two spruce trees obstructed the upstream view. I selected the tree-stand location based on tree diameter, proximity to viewing Site A, level of safety while entering/exiting the stand, and view provided. Only the branches necessary to accommodate myself and the stand were removed from the tree. Branches were left to partially obscure the tree stand from bears. I conducted 142.5 hours of direct observations from Site A between September 18 and October 25, 2005. I recorded 64 hours of data with the remote video camera at Site B from October 10 to October 25, 2005. Technical difficulties delayed the commencement of camera recordings until October 10, 2005.

I collected behaviour data for randomly chosen focal bears during one 4-hour sampling session per day (Altmann 1974). I conducted direct observations and recorded video observations simultaneously, except when the camera was inoperable. Throughout September and mid-October, I used three 4-hour sampling sessions: morning, midday and evening sessions. I scheduled these daily sessions based on the length of sufficient daylight to identify individual bears. I used two sampling sessions per day starting in mid-October as available daylight declined. One 4-hour session was randomly chosen for sampling each day while ensuring equal coverage for all portions of the day throughout the bear viewing season. For each focal bear I observed from Site A, I recorded the following information (detailed in the subsequent paragraphs):

1) identity,
2) age/sex class (adult (>5 years old), subadult (3-5 years old), 2-yr old, young-of-last-year, young-of-year),
3) viewer treatment (present or absent),
4) fishing bout length (from arrival and departure times)
5) habituation status (highly wary, wary, tolerant, highly tolerant),
6) fishing behaviours, and
7) frequency of short-duration, feeding-related events.

Video quality was poor; therefore, I only recorded bear identity, age/sex class, and fishing bout duration for focal bears in the video recordings. All video recordings were in the viewer absent treatment. I collected behaviour information for independent bears only because behaviour of young is largely influenced by their mother's behaviour (Chi 1999).

I identified individual bears by natural markings and morphological characteristics including coat colouration and scars. I used binoculars to facilitate bear identification. Individuals were photographed and distinctive characteristics sketched onto identification sheets. Identification sheets were updated as new defining characteristics became apparent (e.g., new scars, coat colouration changes, loss of young). I determined sex through direct observation of genitals, urination posture, or presence of cubs. Age class was determined through prior knowledge of known bears, presence of cubs, and general body size.

I randomly assigned the viewer present treatment to eight sampling sessions throughout the season. During the viewer present treatment, human activity along the Fishing Branch River involved one to three people at Site A and myself in the tree stand. Human activity during the viewer absent treatment was only myself in the tree stand. No sampling was done with viewers present at Site B or C.

I determined fishing bout lengths as the difference between each focal bear's fishing bout start and end time. I recorded fishing bout start times as the time each focal bear became visible unless it was on the river prior to commencing the sampling session. When the bear was on the river prior to the start of the session, I recorded the sampling session start time as the focal bear's fishing bout start time because I had no knowledge of the bear's true fishing bout start time. I terminated focal observations if the focal bear became unobservable for more than 20 consecutive minutes but recorded the fishing bout end time as the time the focal bear left my field of view. This termination time was based on averaging the two longest fish consumption activities in 2004 (15 min) plus 33 % extra time (5 min) to account for any variation in fish consumption between years. I used a termination time to allow continuous fishing bouts for those bears that consumed a fish in vegetated cover and then resumed fishing. For bears still fishing on the river when a sampling session ended, I recorded the sampling session end time as their fishing bout end time because I did not know their actual fishing bout end time. Some fishing bout lengths were underestimated because of truncating fishing bouts that continued outside of sampling sessions. However, fishing bouts rarely began or continued beyond the sampling session.

I classified bear habituation status based on responses to viewers and myself on the river outside of sampling sessions. Highly wary bears were those who consistently left the river near Site A and camp (high human activity area) upon overtly recognizing human presence and were never observed entering the camp area during daylight hours. I classified bears as wary if they fished in the high human activity area but consistently avoided fishing on the shore immediately adjacent to Site A, overtly displayed vigilance directed at camp, and were never observed entering camp during daylight hours. I classified bears as tolerant if they fished the shore immediately adjacent to Site A (high human activity area), overtly displayed some vigilance directed towards camp, and/or entered camp during daylight hours. I classified bears as highly tolerant if they frequently fished for extended periods from the shore immediately adjacent to Site A, showed minimal overt vigilance towards camp, and/or frequently entered camp during daylight hours.

I determined focal bear behaviours by measuring the time (to the nearest second) the focal bear spent performing each of these eight activities:

1) fishing: searching for fish, consuming fish (live, carcass, or unknown),
2) other feeding: searching for other food, consuming other food (vegetation, terrestrial meat),
3) vigilance: scan, stare,
4) locomotion: walking, running, human avoidance walking, human avoidance running, lying, sitting, standing, standing on back legs only,
5) social behaviour: passive deferral, non-aggressive physical contact, non-aggressive vocalization,
6) aggressive behaviour: human approach walking, human approach running, overt threat, lesser threat, injure,
7) unobservable, and
8) other (Table 2-1).

I recorded the frequency of the following short duration, feeding-related events during focal observations: lunges (while searching for fish), fish captures, releases of captured fish, and vigilance (head-up) events while consuming fish. Vigilance (head-up) events differed from vigilance activities (scan or stare) because the bear continues consuming fish, usually chewing, during vigilance (head-up) events. In contrast, the bear must cease all other activities and scan or stare to be classified as a vigilance activity. I scan sampled every 10 min during focal observations to count the number of observable bears, describe their age and sex composition, and distance to the focal bear (Altmann 1974); however, no bears other than the focal bear were ever present in scan samples. These methods are based on research design from Olson and Gilbert (1994), Chi (1999), Gende and Quinn (2004), and Nevin and Gilbert (2005).

I recorded all social interactions observed throughout the field season, not only those occurring in sampling sessions. I excluded interactions captured by the remote video camera from analyses because of the difficulty distinguishing the type and outcome of interactions. I defined social interactions as any overt reaction to a conspecific (Chi 1999), including passive deferrals and aggressive interactions. Passive deferrals were when one bear, usually the subordinate, diverts around or away from the other bear to avoid an interaction. Aggressive interactions included physical contact, chases, bites, and jaw pops (Chi 1999, Gende and Quinn 2004). For all social interactions, I recorded individuals involved, interaction type (passive deferral, aggressive interaction, unknown), outcome (winner, loser, or tie), and minimum distance between individuals involved in passive deferrals.

I collected grizzly bear behaviour data during a pilot season from September 19 to 26, 2004. I conducted opportunistic focal observations directly from viewing Site A in 2004 and recorded the bear behaviour data described above, except I did not collect social interaction data. My upstream view was unobstructed when observing directly from Site A in contrast to my view from the tree stand. All 2004 focal observations were in the viewer present treatment because my presence on the viewing site elicited bear responses identical to actual viewers. I compared limited data between 2004 and 2005 because of these discrepancies in data collection techniques (described in Analyses section).

I was accompanied by the commercial bear viewing guide during my field seasons for safety reasons. The guide remained out of view of the river during daily sampling sessions in 2005, usually staying in the cabin. In the 2004 pilot season, I conducted focal observations with the guide and one additional person present as they assisted in refining the sampling techniques. Two people affiliated with the commercial viewing operation were on-site from September 18 to 26, 2005. I used these extra people and solely the guide later in the season for the viewer present treatment in 2005. Despite the viewers present and absent treatment, I could not eliminate the influence of human activity at camp or the camp infrastructure on bear activity during sampling sessions.

Analyses

All analyses pertain to 2005 data only unless otherwise stated. I used the 2004 data only to examine the effect of uncontrollable, between-year factors on fish consumption. Differences in data collection techniques between 2004 and 2005 limited inter-year analyses.

Spatial River Use

I evaluated bears' spatial river use in response to human activity by separating focal observation data based on site (A or C) and the presence or absence of bear viewers. I compared individual bear activity around the area of higher human use (Site A) to the area of lower human use (Site C) using a metric called Site Use Index (SUI). SUI evaluated small-scale fishing location preferences (i.e., within the 500 m viewing area) at the individual bear level by comparing individual bear use, from focal sampling, at each site relative to the total bear use at each site. I formulated SUI this way to account for any differences in fish availability or linear fishing opportunities between sites that would alter absolute fishing times regardless of any human-induced site preference. Thus, a SUI with preference for Site C does not indicate the bear spent more absolute time fishing at Site C than Site A. Rather, relative to total bear use at either site, this bear spent more time foraging around Site C than Site A. I calculated SUI for individual bears using the following equation:

$$SUI_{yz} = \frac{P_{ayz} + 1}{P_{cy} + 1}$$

where P = percent of total use, a = Site A, c = Site C, y = individual bear, and z = viewer state (present or absent at Site A). Fishing time at Site C was always in the viewer absent state. I calculated percent of total use using the following equations:

$$P_{ayz} = \frac{T_{ayz}}{\sum T_{ayz}} * 100\ \%$$

$$P_{cy} = \frac{T_{cy}}{\sum T_{cy}} * 100\ \%$$

where T = total use (min). Bears with disproportionately higher use of Site A have a SUI >1, those with relatively equivalent site use have a SUI $\approx$ 1, whereas those with disproportionately higher use of Site C have a SUI < 1. I classified SUI between 0.8 and 1.2 as being $\approx$ 1; therefore, the true classification was SUI >1.2 for higher use of Site A, 0.8< SUI <1.2 for equivalent use, and SUI <0.8 for higher use of Site C. I calculated two SUIs for each bear to evaluate fishing location preferences in response to viewer state: SUI with viewers present and SUI with viewers absent. To assess changes in bears' spatial river use dependent on the timeframe of data used, I calculated two additional SUIs for each bear: SUI with viewers present and absent using only Site A data from the period when remote video camera was operating. I compared these additional SUIs to the original SUIs calculated with Site A data from the entire season. Sample size at Site C was 15. For Site A, sample size was 50 for the entire season and nine for data collected when the remote camera was operating.

Viewer Effects on Fish Consumption

I used Akaike's Information Criterion, adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002), to assess the importance of viewer presence on bears' fish consumption. I investigated the potential temporal effects of viewers on consumption using data collected from Site A during times with viewers present and absent (n = 50). Fish consumption for each fishing bout was estimated using the following equation:

$$F_x = \frac{C_x}{c}$$

where F = fish consumption, x = fishing bout, C = total length of consumption activities (min), and c = maximum overall consumption activity (min). A consumption activity was a period of time within a fishing bout in which a bear continuously consumed fish, including behaviours such as biting, chewing, or manipulating fish position. I defined maximum overall consumption activity (c) as the longest single consumption activity within all fishing bouts that was not 50 % greater than the next longest consumption activity. I used this 50 % rule to ensure that the maximum overall consumption activity was not uncharacteristically long as can occur when a bear's focus deviates from consumption activities, such as concentrating on nearby conspecifics that slowed their chewing. I standardized consumption activities such that fish consumption per fishing bout (F_x) was a proportion of the maximum fish consumption activity. I did not create fish consumption values based on individual-specific maximum consumption lengths, which would have accounted for any individual-specific variation in consumption rates. Use of individual-specific maximum consumption activities required the invalid assumption that each bear consumed approximately equal proportions of salmon in their maximum consumption activity.

I used presence/absence of viewers, fishing bout length, dominance score, daily bear use, and cumulative salmon as explanatory variables for fish consumption. I excluded other relevant variables because of sample size constraints. Presence/absence of viewers was a binary variable (0 = viewers absent, 1 = viewers present) and represented viewer effects on bears' consumption. Fishing bout length was a continuous variable representing the effect of fishing effort on consumption. I used dominance score (continuous variable) as a potential explanatory variable for fish consumption because social dominance has influenced feeding behaviours of bears. Dominant bears at salmon streams secured prime fishing locations, consumed more salmon, and reduced their energetic expenditures by consuming salmon at the capture location (Egbert and Stokes 1976, Chi 1999, Ben-David et al. 2004, Gende and Quinn 2004). I calculated dominance score (DS) using the following equation:

$$DS_y = \frac{W_y + 0.5 * T_y}{N_y}$$

where y = individual bear, W = number of interactions where the individual displaced another bear (wins), T = number of interactions where neither bear was supplanted by the other (ties), and N = total number of interactions the individual was involved in (Lehner 1996, Chi 1999, Koene et al. 2002). I selected daily bear use, expressed as the number of minutes that any bear was present during a sampling session relative to the length of the sampling session (continuous variable), to represent the effect of conspecific activity on fish consumption. High bear use may reduce consumption by the focal bear because extra time was spent avoiding interactions or interacting with conspecifics. I chose cumulative salmon in the river (ordinal variable) to account for the effects of resource availability on bears' consumption. Cumulative salmon was the total number of salmon to date that passed through the counting weir downstream of my study area. Daily salmon counts were obtained from Fisheries and Oceans Canada.

I excluded one fishing bout from this analysis because I was unable to distinguish between searching and consuming behaviours due to the substantial distance between the bear's fishing location and my observation site. Based on prior experience, I assumed bears require >5 seconds to bite, chew, and swallow a single bite of fish. As such, I excluded any consumption events within fishing bouts that were ≤5 seconds because these largely represented bears carrying captured fish or examining captured fish only to discard them without any consumption.

I used variance inflation factor (VIF), tolerance, and Pearson's correlation (*r*) as diagnostic tests to assess collinearity between explanatory variables. I considered all correlations >0.7, or tolerance scores ≤0.1, or individual VIF scores of >10 as collinear and excluded one of the collinear variables from the models. I excluded the collinear variable with the least predictive power as determined through Pearson's correlation with the dependent variable (fish consumption).

I calculated AIC_c for the global linear regression model (all explanatory variables: viewers, fishing bout length, dominance score, daily bear use, and cumulative salmon) and all nested subsets of this model (Burnham and Anderson 2002). I ranked all models based on their AIC_c score. ΔAIC_c was calculated as the difference between individual model AIC_c scores and the minimum overall AIC_c score (Anderson et al. 2000, Burnham and Anderson 2002). I followed the suggested classification, where models with ΔAIC_c <2 have strong support, ΔAIC_c 2-10 have less support, and ΔAIC_c >10 have no support (Burnham and Anderson 2002). Individual model Akaike weights (w) were calculated to assess the strength of each model in predicting fish consumption (Anderson et al. 2000, Burnham and Anderson 2002). Variable importance was calculated by summing the Akaike weight of all models containing the variable (Burnham and Anderson 2002). Using multimodel inference, I created model-averaged regression coefficients by multiplying the model regression coefficient by the model's Akaike weight (w) and summing these values separately for each variable (Burnham and Anderson 2002). I assessed the statistical significance of each linear model through Pearson's correlation to determine the fit of the model to the data (r; Zydelis et al. 2006). A significance level of 0.05 was used. I used SAS 9.1 to calculate root mean square error and regression coefficients for each model (SAS Institute 2006).

Year Effects on Fish Consumption

I used AIC_c, as described above, to assess the importance of uncontrollable factors that vary between years (e.g., summer forage quality, salmon availability) on fish consumption by bears (F_x; n = 67). These uncontrollable factors could influence fish consumption regardless of any viewer effects or they could compound viewer effects. I was unable to include the year effect in the previous analysis because sampling differences in 2004 left me unable to create daily bear use values and dominance scores. Thinking that bear use and dominance scores were important variables affecting fish consumption by bears, I evaluated the 2005 data separately so I could include these two variables.

I used the following explanatory variables to examine year effects on fish consumption by bears: year (binary variable; 1= 2004, 0 = 2005), viewer presence/absence (binary variable), fishing bout length (continuous variable), and cumulative salmon (ordinal variable). I calculated 2004 fish consumptions using a maximum overall consumption activity specific to 2004.

Viewer Effects on Fishing Behaviour

I assessed whether bears' fishing behaviour at Site A differed temporally with viewers present or absent (n = 38). I calculated one value for each of the 12 fishing behaviours for each individual bear during each sampling session in which they were a focal bear (i.e., one value of each fishing behaviour per bear per day; Table 2-2). Therefore, if an individual was a focal bear more than once during a single sampling session, I summed his observed behaviours and used these summed behaviours to create his respective fishing behaviour values for that sampling session. For example, suppose I observed Bear A as the focal bear twice in one day. To create one lunge rate value for Bear A on that day, I would divide the summed lunges from both fishing bouts by the summed fishing bout lengths. The exception to this technique was the only non-rate behaviour, fishing bout length, for which I averaged the bout lengths. Creating one value for each fishing behaviour per bear per day reduced pseudoreplication in the data (Hurlbert 1984). I coded each set of fishing behaviours (1 set per bear per day) with presence or absence of viewers and bear identification. Although viewer numbers varied from zero to three, I simply classified fishing bouts as either occurring with viewers present or absent because my sample size was too small to investigate behaviour differences based on the number of viewers.

I compared each fishing behaviour between times with viewers present and absent using a blocked analysis of variance (ANOVA). Individual bear behaviour can vary substantially even when conducting the same activities under the identical conditions. To account for this individuality in behaviour, I treated the analysis as a block design; more specifically, as random incomplete block design (Lehner 1996, Zar 1996). I accounted for individuality by blocking each fishing behaviour by individual bear, and thereby decreased this experimental error that could otherwise mask or amplify any measured response (Lehner 1996, Newman et al. 1997). The technique of blocking data further reduces pseudoreplication in the data (Hurlbert 1984). The 'random' (in random incomplete block design) was because I randomly chose a sampling session each day as well as observed randomly chosen focal bears. The 'incomplete' (in random incomplete block design) was because I did not observe every bear during each sampling session.

I used JMP 6.0.0s Fit Model option to incorporate the block design into these ANOVAs (SAS Institute 2005). I used bear identification and viewers present or absent as model effects for each comparison. Tukey's HSD test was used post hoc to determine which means differed when the ANOVA returned a significant result (Zar 1996, Haroldson et al. 2002). I used a significance level of 0.05 and report 95 % confidence intervals. I tested all fishing behaviours for normality using the Shapiro-Wilk (W) goodness of fit test (Zar 1996). Fishing behaviour outliers were those data points that were outliers from the fitted model, not necessarily the highest or lowest raw values of each fishing behaviour. I reported fishing behaviours as their least square means rather than their actual means. Least square mean values are common with unequal observations in each comparison category, that is, unbalanced data (Milliken and Johnson 1984). Least square mean values are adjustments of the actual mean values to represent balanced data (Milliken and Johnson 1984). If the data were balanced, the actual mean and least squares mean would be equal (Milliken and Johnson 1984).

Bear Use

I examined bear use around Site A looking for daily and seasonal patterns ($n = 50$). I used a metric of bear minutes per observer minute (bm/om) to standardize bear use by observer effort (Olson and Gilbert 1994, Olson et al. 1997, Chi 1999). To examine seasonal patterns in bear use, I divided the summed minutes present for all bears on a given day by the total observation minutes on the same day. This created a measure of bear use (bm/om) for each day. For daily patterns of bear use, I categorized sampling hours relative to the start of each morning, midday, and evening sampling session (e.g., categories of 0-1 hour after start of morning session, 1-2 hours after start of morning session, 2-3 hours after start of morning session, etc.) because absolute sampling session times varied throughout the season with changing daylight availability. I divided the summed minutes present for all bears in each hour category throughout the season by the total number of observation minutes in the same hour category throughout the season. This created a measure of bear use (bm/om) for each hour.

Study Limitations

Several factors limited my ability to evaluate potential viewer effects on bear fishing activities. The remote camera system provided only limited support for my investigation into the spatial effects of human activity on bear behaviour. While the remote video camera recorded bear use and minimized researcher activity in the area with lower human activity, the trade-off was marginal video quality that only permitted bear identification and calculation of fishing bout lengths. Consequently, I was unable to evaluate whether bears compensated for higher human activity around Site A by maximizing their fish consumption in this area of lower human activity. Furthermore, I was unable to fully examine bear spatial river use because of the technical difficulties that limited camera recordings to the latter portion of the season.

My investigation into the temporal effects of viewers on bear behaviour was limited by the inherent need to have an observer present. Bears were inevitably aware of my presence in the tree stand despite attempts to conceal myself. As a result, behavioural observations collected in viewer absent states were potentially influenced by my presence in the tree stand. I intended to quantify the effect my presence in the tree stand had on bear behaviour around Site A by comparing video recording of bear behaviour around Site A in my absence to bear behaviour observed while in my tree stand. Marginal video quality left me unable to compare bear behaviour under these conditions. However, any influence of myself in the tree stand would be constant throughout all observations in the viewer absent state. Small sample sizes limited my ability to analyze some data and interpret the results. Despite these limitations, I was able to assess viewer effects on these fishing bears and recommend further research that would overcome these limitations.

RESULTS

Bear Identification

The number of grizzly bears I observed in 2004 and 2005 appeared independent of salmon abundance and length of the sampling season each year. I identified eight independent bears during the eight-day pilot season in 2004: a tolerant female (F0403) with three 2-year-olds who exhibited increasing tolerance to human presence over the eight days, two highly tolerant adult females (F0401 and F0402), one highly tolerant adult male (M0401), and four highly wary adult males (M0402, M0403, M0404, and M0405; Table 2-3). Over 47 days in 2005, I observed seven independent bears: one highly tolerant adult female (F0502), one highly tolerant adult male (M0401), three wary adult males (M0502, M0402, and M0501; M0501 became highly tolerant of human presence throughout the season), one highly tolerant female (F0501) with a wary female yearling, and one highly wary female subadult (S0503; Table 2-4). M0401 and M0402 were the only bears observed in both 2004 and 2005. I observed fewer independent bears using the Fishing Branch River in the year with five times more salmon (121,000 and 19,700 in 2005 and 2004, respectively; Fisheries and Oceans Canada, unpublished data).

Spatial River Use

Incorporating Site A bear use from the entire season, I found that three bears preferred fishing around Site A regardless of viewer presence or absence: M0401, F0502, and M0402 (Fig. 2-3). Two bears preferred fishing around Site C regardless of viewer presence at Site A: F0501 and S0503. M0501 preferred to fish around Site A when viewers were present but displayed no site preference in their absence. M0502 showed no site preference when viewers were at Site A, but preferred to fish around Site A in their absence.

Incorporating Site A bear use collected during the period of remote camera operation, I found that only F0502 showed preference for fishing around Site A regardless of viewer presence or absence (Fig. 2-4). Two bears displayed preference for fishing around Site C regardless of viewer presence at Site A: M0401 and S0503. M0501 preferred to fish around Site A in viewer presence but preferred Site C in viewer absence.

F0501 preferred fishing around Site C in viewer presence but had no preference in their absence. M0402 and M0502 had no river use at either site during this period, giving them a SUI of 1.0, or in this case, SUI of equal non-preference.

Viewer Effects on Fish Consumption

The maximum consumption activity I observed in 2005 was 17.0 min; however, this was >50 % longer than the next longest consumption activity (11.0 min). I excluded this absolute longest consumption activity and used 11.0 min as the maximum overall consumption activity for 2005. Dominance scores for individual bears varied from zero to one, where zero was the completely subordinate individual, M0401, and one was the completely dominant individual, M0501 (Fig. 2-5). Sixteen linear regression models had $\Delta AIC_c < 10$, while only three had $\Delta AIC_c < 2$ (Table 2-5). Fishing bout length was the common variable in the top 16 models. The top ranking model did not have considerably more weight ($w = 0.2468$) than its next closest model ($w = 0.1424$; Table 2-5). I calculated the ratio of the first to second ranked model at 1.73, meaning that the top ranking model (bout, viewers) was only 1.73 times better at describing the data than the second ranking model (bout only; Burnham and Anderson 2002). The top ranking model had an r^2 of 0.6432 ($P < 0.0001$), which showed the statistical significance of this model for predicting fish consumption. I also found strong statistical significance for the second and third (bout, viewers, dominance) ranking models with r^2 values of 0.6163 ($P < 0.0001$) and 0.6501 ($P < 0.0001$), respectively. Based on the top ranking model, and confirmed by the model-averaged regression coefficients, fish consumption was positively correlated with fishing bout length and negatively correlated with viewer presence when all other independent variables were held constant (Tables 2-5 and 2-6). Viewer presence reduced fish consumption, a proportion of maximum fish consumption activity, in any given fishing bout by 0.2383, or almost 24 % based on multimodel inference. Viewer presence was the second-most important variable in predicting fish consumption. Based on variable importance, daily bear use, cumulative salmon, and dominance scores were the least important variables for predicting fish consumption (Table 2-6).

Year Effects on Fish Consumption

I created the 2004 fish consumption values using the second longest consuming activity (10.7 min) because the maximum overall consumption activity (25.1 min) was >50 % greater than this second longest consumption activity. Using diagnostic tests for collinearity among explanatory variables (VIF, tolerance, and Pearson's correlation), I found that year and cumulative salmon were highly collinear ($r = 0.939$). I excluded cumulative salmon as an explanatory variable because it was less predictive of fish consumption than year ($r = 0.032$ and $r = 0.100$, respectively). Because of this collinearity, results from the year variable also incorporate the effects of resource availability that cumulative salmon represented.

Four linear regression models had $\Delta AIC_c < 10$, while only three had $\Delta AIC_c < 2$ (Table 2-7). Fishing bout length was the common variable in the top four models. The top ranking model (bout, viewers) did not have considerably more weight ($w = 0.3865$) than its next closest model (bout; $w = 0.3271$) and therefore was only 1.18 times better at describing the data than the second ranking model (Table 2-7). The top ranking model had an r^2 of 0.6107 ($P < 0.0001$), which showed the statistical significance of this model for predicting fish consumption. I also found that the second and third ranking models (bout, viewers, year) had strong statistical significance with r^2 values of 0.5948 ($P < 0.0001$) and 0.6152 ($P < 0.0001$), respectively. Based on the top ranking model and confirmed by the model-averaged regression coefficients, fish consumption was positively correlated with fishing bout length and negatively correlated with the presence of viewers when all other independent variables are held constant (Tables 2-7 and 2-8). Based on variable importance, year was the least important for predicting fish consumption and multimodel inference showed a mere 2.67 % reduction in fish consumption in 2005 relative to 2004. Models without fishing bout length were no better than the null model (random variation) at explaining fish consumption (Table 2-7).

Viewer Effects on Fishing Behaviour

Of the 12 fishing behaviours, only the percent of time grizzly bears spent fishing significantly differed between periods with viewers present and absent (Table 2-9). With viewers present, percent of time spent fishing dropped from 75.4 % to 58.8 % despite no significant increase in any other activity.

Bear Use

Grizzly bear use varied widely from day to day throughout the 38 sampling days and became increasingly sporadic towards the season's end (Fig. 2-6). Twelve sampling sessions were entirely without bears present: three in the first half of the season (sampling days 1-19) and nine in the latter half of the season (sampling days 20-38). Bears were present for almost 60 % of one sampling session, although the average bear use throughout the season was 0.195 bm/om or 19.5 %. With respect to daily bear use, I found that bear use was highest during midday sampling sessions, followed closely by evening sessions (Fig. 2-7). Bears had the lowest river use in morning sampling sessions. Within sampling sessions, I found reduced bear use during the first hour of the midday and evening sampling sessions relative to the remainder of each session. Bear use in the first hour of the morning session did not differ from use in the third and fourth hours.

DISCUSSION

Spatial River Use

Habituated bears characteristically show little response to human presence and are commonly observed fishing near human activity when it coincides with high salmon availability or minimal conspecific competition (Olson and Gilbert 1994, Chi and Gilbert 1999, Nevin and Gilbert 2005, Tollefson et al. 2005). Grizzly bears wary of human activity fed in suboptimal fishing areas of Brooks River where human activity was lowest, whereas habituated bears exploited highly efficient fishing sites regardless of their proximity to human activity (Olson and Gilbert 1994). The almost complete absence of male grizzly bears at Wolverine Creek, Alaska, was attributed to the high level of human activity at this site (Tollefson et al. 2005). The habituation status of bears at the Fishing Branch River largely explained their fishing site preferences, regardless of the analysis timeframe I used. Viewer presence and the camp (e.g., infrastructure and human odors) appeared to influence bears' spatial use of the Fishing Branch River. I do not think that fishing opportunities substantially differed between Site A and C because different bears displayed fishing preferences for each location independent of viewer activity.

Using Site A data from the entire season, four bears' spatial river use appeared dictated by the proximity of camp to Site A rather than direct viewer presence; their spatial river use did not change when viewers were present and absent. Two highly habituated bears preferred to fish around the camp, while a highly wary subadult and a female whose yearling was highly wary preferred to fish away from the camp regardless of viewer presence or absence. Habituation status also explained the spatial river use of a bear that responded to viewer presence or absence rather than the indirect influence of camp. The wary individual, M0502, appeared to be influenced negatively by viewer presence because he preferred to fish around Site A only when viewers were absent. Habituation status did not explain the spatial river use of two bears. One wary bear, M0402, preferred to fish around Site A regardless of viewer presence. I do not know why this occurred but perhaps the activity of dominant bears forced this individual to fish near high human use despite his wariness of people. In addition, a highly tolerant individual (M0501) appeared positively influenced by viewer presence but given his high level of dominance and tolerance, I think this bear selected fishing sites based on his true site preferences rather than by human or conspecific activity.

Habituation status explained the spatial river use of most bears when I examined data only from the latter portion of the season. One of the exceptions was M0401 whose river use remained independent of viewer presence but changed from preferring Site A to Site C for the seasons' latter half. I think M0401's altered site preference was individual-specific and not in response to changing resource availability or activity of dominant individuals. A spatial change in resource availability in the latter part of the season should be reflected in multiple bears' spatial river use, which I did not observe. Nor did I observe any changes in dominant bear activity coinciding with M0401's changed river use. In fact, the dominant bear, M0501, still exhibited fishing preference for Site A with viewers present, but now preferred fishing around Site C in viewer absence. If M0501 was a less dominant bear, I would suggest viewers created a temporal feeding refuge by excluding dominant bears from feeding in their presence (Nevin and Gilbert 2005). Because M0501 was the most dominant bear on the river, a temporal refuge effect is highly unlikely and I think his observed spatial river use simply reflected his preferred fishing times and locations independent of viewer activity. The remaining bear whose spatial river use was not easily explained by habituation status was the highly tolerant female with her highly wary yearling. This female changed her site preference in viewer absence from Site C to no preference in the season's latter portion. I think her yearling became less wary of camp in general as the season progressed, enabling them to fish around both sites when viewers were absent. Regardless of the timeframe of data used, habituation status largely explained the spatial river use of grizzly bears around the commercial viewing area. Bears wary of human activity preferred to fish away from high human activity or away from sites when viewers were present.

The delayed camera operation resulted in a small sample size for the spatial river use comparison incorporating data from only the latter part of the season. Based on sample size alone, spatial river use results were more reliable using Site A data from the entire season. However, the comparison from the latter part of the season may more accurately reflect bears' spatial river use because it captured bear activity at both sites over a comparable timeframe. Regardless of the timeframe, grizzly bears at the Fishing Branch River showed individual-specific spatial river use in response to viewer presence and general camp presence with wary bears being negatively influenced by human activity. The spatial river use of these Fishing Branch River bears was largely explained by their habituation status, which was similar to other bear viewing sites (Olson and Gilbert 1994, Chi and Gilbert 1999, Nevin and Gilbert 2005, Tollefson et al. 2005). Although some bears showed negative spatial responses to human activity, I did not quantify how this influenced their fish consumption. I discuss this further in the following section.

Viewer Effects on Fish Consumption

In evaluating effects of viewers on fish consumption by bears, I found that viewer presence or absence was the second-most important variable, next to fishing bout length, for predicting fish consumption. Viewer presence reduced fish consumption by almost 24 % based on multimodel inference when all other variables were held constant. I do not think this negative relationship between viewers and consumption was an artifact of the seasonal timing of fishing bouts with viewers present because they largely occurred early in the season. For this to be the case, I would expect a higher variable importance for cumulative salmon because cumulative salmon increased as the season progressed. Although I could not control for the general influence of camp on fish consumption, it consistently influenced bears' fish consumption regardless of viewer presence or absence.

A 24 % reduction in fish consumption could have drastic fitness consequences for Fishing Branch River bears; however, I did not incorporate any potential spatio-temporal compensatory fishing activities into my study design. Bear behaviour, including foraging strategies, is very adaptable giving bears the ability to compensate for factors that alter their natural behaviours (Gilbert 1989). Spatio-temporal compensation for human activity at bear viewing areas has been documented on numerous occasions (e.g., Klinka and Reimchen 2002, Smith 2002, Crupi 2003, Rode et al. 2006). Similarly, bears along the Fishing Branch River may have adapted spatial or temporal compensatory behaviours for viewer presence, such as increasing their nocturnal foraging or maximizing their foraging in lower human activity areas. Despite not directly examining potential spatio-temporal compensation, I found some bears used the area with lower human activity more frequently or the high human use area as long as viewers were absent (discussed in the previous section). Furthermore, I consistently heard bears in the river overnight. These observations suggest that bears may be spatially compensating for viewer presence by increasing their feeding elsewhere or temporally compensating by feeding at times without human activity. However, spatio-temporal compensatory feeding can only occur if sufficient feeding opportunities exist. Other bears may occupy these potential compensatory times and locations leaving limited opportunity for bears displaced by viewer activity. I strongly recommend further investigation into potential spatio-temporal compensations for the negative effects of viewers on bears' fish consumption around Site A. Spatio-temporal compensations must be assessed by monitoring fish consumption under a well designed sampling regime that includes the presence/absence of viewers and fish consumption in areas of higher and lower viewer activity within a single viewing season.

The remaining explanatory variables, dominance status, resource availability, and daily conspecific use, were the least important variables for predicting bears' fish consumption at the Fishing Branch River. I found that fishing bout length was the most important variable for predicting consumption and was positively related with fish consumption. I expected this positive relationship because bears should consume more salmon the longer they fish until limited by gut capacity (Klinka and Reimchen 2002). Dominance scores were positively related to fish consumption but likely biologically unimportant given their low variable importance. I suspect the above-average salmon abundance and increased fishing opportunities created by low water levels precluded any resource-driven intraspecific competition that creates dominance-dependent resource access (Egbert and Stokes 1976, Chi 1999, Gende and Quinn 2004). Cumulative salmon was negatively related to fish consumption. However counterintuitive, bears along the Chilkoot River also consumed fewer salmon towards the end of the season when cumulative salmon was highest (Crupi 2003). Daily conspecific use was positively related to fish consumption but with its small model-averaged regression coefficient, conspecific use negligibly affected individuals' consumption. I suspect the above-average abundance of salmon, low number of conspecifics, and increased availability of fishing sites contributed to the low importance of conspecific use on fish consumption. Based on the importance of fishing bout length and viewer presence in predicting bears' fish consumption, I recommend any required mitigation measures provide bears with ample fishing time in viewer absence to compensate for reduced consumption in viewer presence.

I limited my explanatory variables to those I deemed most critical because of small sample size and an inability to measure certain variables within my study design. I recommend investigating the influence of three additional variables on bears' fish consumption: index of body condition upon arrival at river, time spent in vigilant activities, and an index of bear use by bears more dominant than the focal bear in the 24 hours preceding the focal bear's fishing bout. First, bears' fish consumption likely depends on the frequency of more dominant bears using the river because of time spent avoiding interactions with dominant bears (e.g., increased vigilance or increased time spent in locomotive activities). This index of bear use would account for the frequency of those more dominant bears on the river in the preceding 24 hours. I think this dynamic approach to incorporate the influence of social structure on bears' fish consumption is more informative than the static approach I used with dominance scores. Second, bears' fish consumption probably declines as vigilance activities increase, particularly if those vigilance activities were directed at unnatural activities such as bear viewers.

Lastly, body condition of these bears upon arrival at the river can substantially influence their fish consumption and responses to viewer presence. Bears using the Fishing Branch River enter hyperphagia well prior to the availability of salmon (Nielson et al. 2004). As a result, their initial hyperphagia is supported largely by berry crops. In years with low berry productivity, bears may arrive at the river in poor body condition, which increases the importance of these salmon to their overwinter survival. Conversely, in years of high berry productivity, bears may arrive at the river with substantial fat accumulation, such that fish consumption is less critical. I used the year variable as a proxy for factors such as forage quality prior to the salmon run; however, indexing body condition of each bear would allow for specific conclusions to be drawn about the effects of body condition on fish consumption rather than the numerous factors that were encapsulated in the year variable. These additional three variables could alter the importance and magnitude of viewer effects on bears' fish consumption. As such, I recommend evaluating these three variables and including them in a new AIC_c analysis to assess how important viewer presence remains on fish consumption by bears at the Fishing Branch River.

Year Effects on Fish Consumption

In evaluating the effect of uncontrollable, between-year factors on fish consumption by bears, I found that year was the least important variable for predicting consumption. Identical to the previous analysis, fishing bout length and viewer presence were the most important variables for predicting fish consumption. Because cumulative salmon was collinear to the year variable, resource availability changes throughout a season were also less important at determining fish consumption than bout length and viewer presence. The model-averaged regression coefficient for year was biologically negligible; bears consumed 2.67 % more salmon per fishing bout in 2004 compared to 2005 when all other variables were held constant. Thus, uncontrollable between-year factors (e.g., salmon availability, summer forage quality), as measured by the year variable, had little influence on bears' fish consumption at the Fishing Branch River given these data. My findings that show strong viewer effects on fish consumption by bears are consistent with this lack of evidence for uncontrollable between-year factors influencing bears' fish consumption. In addition, I think that the negligible influence of uncontrollable year factors means that the viewer effects I found on fish consumption were not an artifact of the state of these uncontrollable year effects that particular year.

The behavioural plasticity in consumption strategies of these Fishing Branch River bears is highlighted by the lack of importance of year in dictating fish consumption. Bears alter the proportions of each fish consumed depending on salmon availability (Gende et al. 2001). Bears selectively consume only the most energy-rich portions of each fish in years of high salmon availability (e.g., roe), whereas they consume more of each fish, including the less energy-rich portions, in years of low salmon availability (Gende et al. 2001). Therefore, bears capture more fish but consume lower proportions of each fish in years of high salmon availability and capture fewer fish but consumer higher proportions of each fish in years of low salmon availability. This adaptability in consumption strategies allows bears to acquire relatively equal energy regardless of differences in salmon availability among years and has been observed at other bear viewing sites (e.g., Crupi 2003). Bears at the Fishing Branch River appeared to modify their consumption strategies based on resource availability because of the minimal influence of the year variable on their fish consumption, particularly in light of the large disparity in salmon availability between years.

I was unable to incorporate the year variable into the previous analysis of viewer effects on fish consumption because of inconsistencies in data collection between 2004 and 2005. I recommend any future research be designed with consistent between-year sampling to accommodate all variables into one analysis.

Viewer Effects on Fishing Behaviour

I found that percent of time spent fishing (searching and consuming fish) was the only behaviour that significantly differed between grizzly bears fishing in the presence and absence of bear viewers. With viewers present, bears spent on average 16.6 % less time fishing, which is consistent with the viewer-induced reduction in fish consumption I found (see Viewer Effects on Fish Consumption section). Bears can adapt their fishing strategies to compensate for viewer presence. Rode et al. (2006) found that bears increased the proportion of each captured salmon they consumed and reduced their vigilance activities to compensate for shortened fishing bouts in viewers' presence. These adaptations allowed bears to maintain fish consumption levels while spending less time around viewers. I did not observe any behavioural adaptation in bears at the Fishing Branch River to accommodate their reduced time spent fishing. This could result from small sample size, and subsequent high variation in each behaviour, that limited my ability to detect any viewer-induced adaptations or because all bears did not adapt their behaviour in the same manner. I recommend further investigation into behavioural adaptability of these bears in response to viewer activity with emphasis on increased sample size to help reduce variation in individual behaviours.

Bear Use

Grizzly bear use varied greatly throughout the season, ranging from 0 – 60 % during sampling sessions. Inter-day fluctuations in bear use were common at other bear viewing sites (Olson and Gilbert 1994, Crupi 2003). Many potential factors contributed to this variable use at the Fishing Branch River including bear numbers, salmon abundance, and abundance of fishing locations. Abnormally low water levels opened up new spawning areas and consequently new fishing areas for bears. Many of these new fishing opportunities were upstream from my observation area. As a result, I may have observed low bear use during some sampling sessions simply because bears were fishing out of my view. In addition, low water levels and above-average salmon numbers made fish readily available to bears. This readily accessible food source meant minimal time was required to reach satiation, resulting in a hit-and-miss situation of bear use during sampling sessions. I think bear use was highly variable because of increased fishing locations, above-average salmon abundance, and low number of bears using the river.

The predominant seasonal trend in bear use was the increasing prevalence of sampling sessions without bear use towards the season's end. This trend was consistent with the seasonal use patterns found along the Chilkoot River (Crupi 2003). Bears appeared more lethargic in the latter part of the season. Perhaps this lethargy resulted in reduced fishing time. More likely, the increasing availability of live salmon and carcasses throughout the season reduced the fishing effort required to reach satiation, which translated into decreased bear use near the end of the season. I also observed bears increasing their travel between the river and denning caves on the adjacent, and aptly named, Bear Cave Mountain later in the season. As a result of this increased travel time, bears may have reduced their river use towards the season's end. Regardless of the cause, bears had substantially lower river use near the end of the season. Grizzly bear use at other viewing areas varied throughout the spawning season but was often dictated more by seasonal human activity levels than salmon abundance (Olson et al. 1997, Smith 2002, Crupi 2003). Perhaps this seasonal trend will not change once viewing commences at the Fishing Branch River because viewer numbers will be largely constant throughout the viewing season. As a result, creating non-viewing days in the first half of the viewing season would be an effective measure to mitigate any negative viewer effects on bears because it coincides with the highest bear use.

Two trends dominated the daily bear use at the Fishing Branch River: 1) bear use was lowest in the first hour of each session relative to the remainder of the sampling session and 2) bear use was lowest during morning sessions. Bear use at other salmon streams with minimal human activity varied from predominately crepuscular to largely uniform throughout the day (Warner 1987, Olson et al. 1998). With this variability in bear use at other salmon streams, it was not surprising that hourly bear use at the Fishing Branch River had its own pattern. I think low bear use during morning sampling sessions was an artifact of preferential fishing during the twilight hours prior to the morning sampling session. I was unable to sample these twilight periods because of insufficient light conditions, although I consistently heard bears fishing in the river during morning twilight. High bear use at this time is common at other fishing sites (Warner 1987, Olson et al. 1998, Smith 2002, Crupi 2003, Nevin and Gilbert 2005). Thus, many bears probably reached satiation prior to my morning sampling sessions and consequently were off the river, likely resting, for a large part of the morning sessions. Given the daily pattern of bear use at the Fishing Branch River, bears would benefit most from human-free periods in either the midday or evening when bear use was highest.

I found reduced bear use in the first hour of the midday and evening sampling sessions. Rode et al. (2006) attributed the low bear use in the hour following tour group arrival to the movement of these groups to the viewing site. Because viewers were rarely present at the Fishing Branch River, viewer movement was an unlikely cause of the observed pattern. Although I travelled to the tree-stand for each sampling session, the travel distance was less than 15 m and largely concealed from fishing bears by vegetation. My entrance into the tree-stand created unnatural noise, potentially deterring bears from fishing nearby. However, I think this noise was not responsible for the reduced bear use during the first hour of each sampling session because bear use was not consistently lower in the first hour of all sessions; the morning session's first hour of use was not reduced relative to its last two hours. With human activity an unlikely cause of the seasonal and daily patterns of bear use, I anticipate these patterns largely reflect the natural activity patterns of these bears along the Fishing Branch River. I recommend assessing seasonal and daily use patterns of these bears during a commercial viewing season to evaluate whether consistent viewer activity alters their pre-viewing use patterns.

CONCLUSIONS AND RECOMMENDATIONS

I found that grizzly bear spatial river use along the Fishing Branch River was largely explained by their habituation status. Bears wary of human activity predominantly fished away from high human activity or at sites when viewers were absent. Bears reduced their time spent fishing by almost 17 % around Site A when viewers were present corresponding to a 24 % decline in salmon consumption. This reduced consumption has energetic consequences for these bears, particularly if they do not temporally or spatially compensate for this reduction. I recommend further investigation into potential spatio-temporal compensatory behaviours of these Fishing Branch River grizzly bears. Spatio-temporal compensations must be assessed by monitoring fish consumption under a well designed sampling regime that includes the presence/absence of viewers and fish consumption in areas of higher and lower human activity within a single viewing season. Observation of nocturnal fishing activities would be ideal to assess whether bears increased their nocturnal fish consumption to compensate for reduced daytime consumption. However, nocturnal observations may not be possible due to safety concerns.

I recommend investigating the influence of three additional variables on bears' fish consumption: index of body condition upon arrival at river, time spent in vigilant activities, and an index of bear use by bears more dominant than the focal bear in the 24 hours preceding the focal bear's fishing bout. My study design and sample size did not permit inclusion of these variables into the analysis of viewer effects on fish consumption despite their potential to alter the importance and magnitude of viewer effects on bears' fish consumption. I was unable to incorporate the year variable into the analysis of viewer effects on fish consumption because of inconsistent data collection techniques between 2004 and 2005. Any future research should be designed with consistent between-year sampling to accommodate all variables in one analysis. Small sample size may have influenced my assessment of bear behavioural changes in response to viewer presence. I recommend further investigation into the behavioural adaptability of these Fishing Branch River bears in response to viewer activity with emphasis on increased sample size to help reduce variation in individual behaviours.

With human activity an unlikely cause of the seasonal and daily patterns of bear use, I anticipate these patterns largely reflect the natural use patterns of Fishing Branch River bears. I recommend assessing seasonal and daily use patterns of these bears during a commercial viewing season to evaluate whether consistent viewer activity alters their pre-viewing patterns of use. Based on the patterns of bear use at the Fishing Branch River, designating non-viewing days in the first half of the viewing season or creating consistent midday or evening human-free times would be an effective means to mitigate any negative viewer effects on bears because they coincide with highest bear use periods.

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TABLES

Table 2-1. Behaviour descriptions used for grizzly bear observations along the Fishing Branch River, Yukon, 2005.

Coarse-level Behaviour	Fine-level Behaviour	Descriptors
Fishing	Searching for fish	
	Consuming fish	Live or carcass
Other feeding	Searching for other food	
	Consuming other food	Vegetation, terrestrial meat
Vigilance	Scan	Cease other behaviour, no focal point
	Stare	Cease other behaviour, focal point
Locomotion	Walking	
	Running	
	Human avoidance walking	Walking from possible encounter
	Human avoidance running	Running from possible encounter
	Lying	Prostrate
	Sitting	On haunches
	Standing	On four feet
	Investigative standing	On two feet
Social behaviour	Passive deferral	Alter path or posture to avoid conflict
	Non-aggressive physical contact	“Play” behaviour
	Non-aggressive vocalization	
Aggressive behaviour	Human approach walking	
	Human approach running	Charge
	Overt threat	Charging, biting, or physical contact with another bear
	Lesser threat	Ground slaps, aggressive vocalization directed at human or bear
	Injure	Injure bear or human
Other		
Unobservable		

Table 2-2. Fishing behaviours, and their equations, compared between times with viewers present or absent at the Fishing Branch River, Yukon, 2005.

Fishing Behaviour	**Equation**
Daily bear use	$= \frac{bear\ present\ minutes\ during\ sampling\ session}{length\ of\ sampling\ session}$
Fishing bout length	$= departure\ time - arrival\ time$
Lunge rate	$= \frac{number\ of\ lunges}{fishing\ bout\ length}$
Success rate	$= \frac{number\ of\ fish\ captures}{number\ of\ lunges}$
Selectivity rate	$= \frac{number\ of\ fish\ releases\ (without\ consuming)}{number\ of\ fish\ captures}$
Vigilance rate	$= \frac{number\ of\ headup\ events}{consuming\ minutes}$
Proportion of each fish state consumed (live or carcass)	$= \frac{number\ of\ fish\ consumed\ in\ each\ state}{total\ number\ of\ fish\ consumed}$
Percent of time spent in vigilance	$= \frac{minutes\ spent\ in\ vigilance}{fishing\ bout\ length}$
Percent of time spent fishing	$= \frac{minutes\ spent\ fishing}{fishing\ bout\ length}$
Percent of time spent other	$= \frac{minutes\ spent\ in\ other\ activities}{fishing\ bout\ length}$
Percent of time spent unobservable	$= \frac{minutes\ spent\ unobservable}{fishing\ bout\ length}$

Table 2-3. Independent grizzly bears and their sex, age, age class, reproductive status, and habituation status at the end of the season observed using the Fishing Branch River, Yukon, 2004.

Name	Sex	Age in 2004	Age Class	Reproductive Status	Habituation Status at Season End
M0401	male	7	adult	n/a	highly tolerant
F0401	female	8	adult	n/a	highly tolerant
M0402	male	unknown	adult	n/a	highly wary
F0402	female	13	adult	n/a	highly tolerant
F0403	female	unknown	adult	three 2-year-olds	tolerant
M0403	male	unknown	adult	n/a	highly wary
M0404	male	unknown	adult	n/a	highly wary
M0405	male	unknown	adult	n/a	highly wary

Table 2-4. Independent grizzly bears and their sex, age, age class, reproductive status, and habituation status at the end of the season observed using the Fishing Branch River, Yukon, 2005.

Name	Sex	Age in 2005	Age Class	Reproductive Status	Habituation Status at Season End
M0501	male	unknown	adult	n/a	highly tolerant
M0401	male	8	adult	n/a	highly tolerant
F0501	female	18	adult	1 yearling	highly tolerant
M0502	male	unknown	adult	n/a	wary
F0502	female	13	adult	n/a	highly tolerant
M0402	male	unknown	adult	n/a	wary
S0503	female	unknown	subadult	n/a	highly wary

Table 2-5. Top 10 linear regression models for predicting fish consumption by grizzly bears along the Fishing Branch River, Yukon, 2005. Number of parameters (*k*), root mean square error (*RMSE*), AIC_c, ΔAIC_c, and Akaike weight (*w*) are shown for each model.

Model	***k***	***RMSE***	AIC_c	ΔAIC_c	*w*
bout - viewers	4	0.6280	-36.7375	0.0000	0.2468
bout	3	0.6444	-35.6376	1.0998	0.1424
bout - viewers + dominance	5	0.6287	-35.1755	1.5620	0.1130
bout - viewers - salmon	5	0.6329	-34.5334	2.2041	0.0820
bout - viewers + use	5	0.6347	-34.2555	2.4820	0.0714
bout - salmon	4	0.6457	-34.0755	2.6620	0.0652
bout + dominance	4	0.6467	-33.9187	2.8188	0.0603
bout + use	4	0.6512	-33.2601	3.4774	0.0434
bout - viewers + dominance - salmon	6	0.6326	-33.0124	3.7251	0.0383
bout - viewers + dominance + use	6	0.6355	-32.5735	4.1640	0.0308

Table 2-6. Variable rank, variable importance (*I*), and model-averaged regression coefficient for each explanatory variable used to predict fish consumption for grizzly bears along the Fishing Branch River, Yukon, 2005.

Variable	**Rank**	***I***	**Model-Averaged Regression Coefficient**
bout	1	1.0000	0.0340
viewers	2	0.6142	-0.2383
dominance	3	0.3074	0.0728
salmon	4	0.2745	-1.123×10^{-6}
use	5	0.2223	0.0053

Table 2-7. All linear regression models for predicting fish consumption of grizzly bears along the Fishing Branch River, Yukon, 2004 and 2005. Number of parameters (*k*), root mean square error (*RMSE*), AIC_c, ΔAIC_c, and Akaike weight (*w*) are shown for each model.

Model	***k***	***RMSE***	AIC_c	ΔAIC_c	***w***
bout - viewers	4	0.6313	-52.1386	0.0000	0.3865
Bout	3	0.6391	-51.8048	0.3338	0.3271
bout - viewers + 2004year	5	0.6326	-50.5357	1.6029	0.1734
bout - 2004year	4	0.6434	-49.6784	2.4602	0.1130
Null	2	0.9889	4.7164	56.8550	1.74×10^{-13}
- 2004year	3	0.9986	6.2138	58.3524	8.24×10^{-14}
Viewers	3	1.0037	6.8672	59.0058	5.95×10^{-14}
viewers - 2004year	4	0.9997	7.6206	59.7592	4.08×10^{-14}

Table 2-8. Variable rank, variable importance (*I*), and model-averaged regression coefficient for each explanatory variable used to predict fish consumption for grizzly bears along the Fishing Branch River, Yukon, 2004 and 2005.

Variable	**Rank**	***I***	**Model-Average Regression Coefficient**
bout	1	1.0000	0.0329
viewers	2	0.5599	-0.1623
2004year	3	0.2864	0.0267

Table 2-9. ANOVA results for the blocked comparisons of grizzly bear fishing behaviours in the presence and absence of bear viewers along the Fishing Branch River, Yukon, 2005. Least square (LS) means and 95 % confidence intervals (CI) are shown for each behaviour in each viewer state.

Fishing Behaviour	***P* value**	***F* statistic**	***n***	**LS Mean No Viewers (± 95%CI)**	**LS Mean with Viewers (± 95%CI)**
Daily bear use	0.1024	2.8326	38	0.281 ± 0.075 bm/om	0.375 ± 0.101 bm/om
Fishing bout length	0.2212	1.5659	35	21.635 ± 6.655 min	28.149 ± 9.413 min
Lunge rate	0.5388	0.3866	36	0.0995 ± 0.067 bout min^{-1}	0.129 ± 0.081 bout min^{-1}
Success rate	0.2708	1.2909	24	0.243 ± 0.118 lunge^{-1}	0.340 ± 0.152 lunge^{-1}
Selectivity rate	0.5878	0.3049	23	0.221 ± 0.197 capture^{-1}	0.151 ± 0.189 capture^{-1}
Vigilance rate	0.4770	0.5191	35	0.507 ± 0.220 consuming min^{-1}	0.620 ± 0.265 consuming min^{-1}
Proportion live fish	0.2746	1.2384	36	0.232 ± 0.173	0.370 ± 0.211
Proportion carcasses	0.4434	0.6033	36	0.656 ± 0.186	0.551 ± 0.227
Percent vigilance	0.3285	1.0060	26	0.422 ± 0.068 %	0.476 ± 0.104 %
Percent fishing	0.0457	4.3321	38	75.438 ± 10.700 %	58.806 ± 14.412 %
Percent other	0.3638	0.8544	33	0.739 ± 0.570 %	1.163 ± 0.836 %
Percent unobservable	0.7711	0.0861	38	21.134 ± 10.032 %	23.333 ± 13.512 %

FIGURES

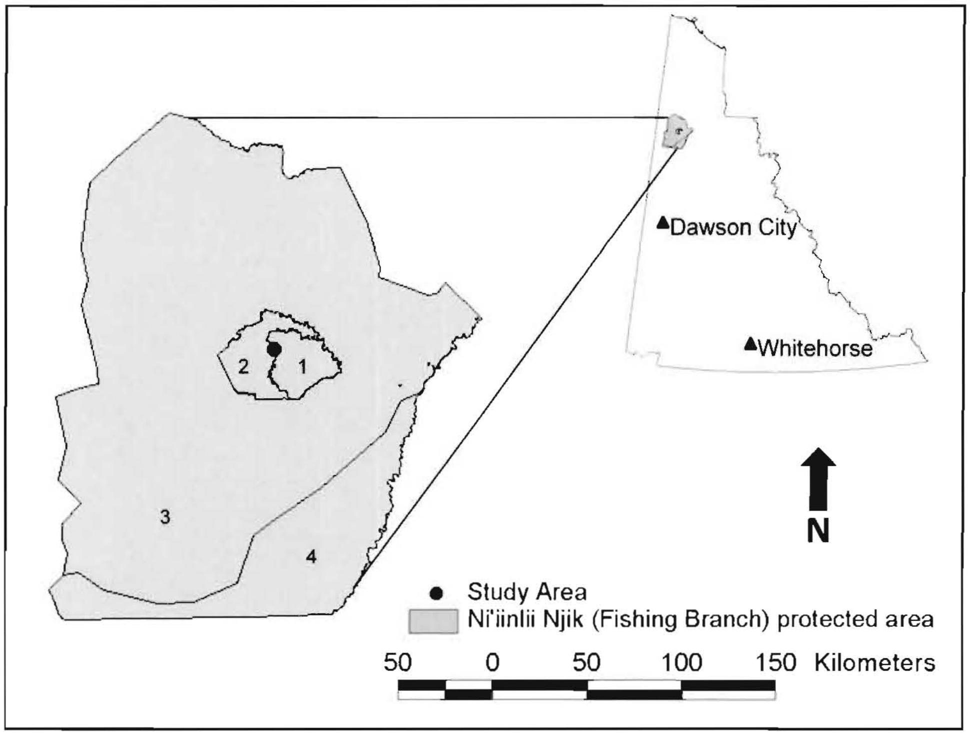

Figure 2-1. Study area in the Ni'iinlii Njik (Fishing Branch) protected area complex, Yukon. Divisions within the protected area represent the Vuntut Gwitchin Settlement Lands (1), Ecological Reserve (2), Wilderness Preserve (3), and Habitat Protection Area (4).

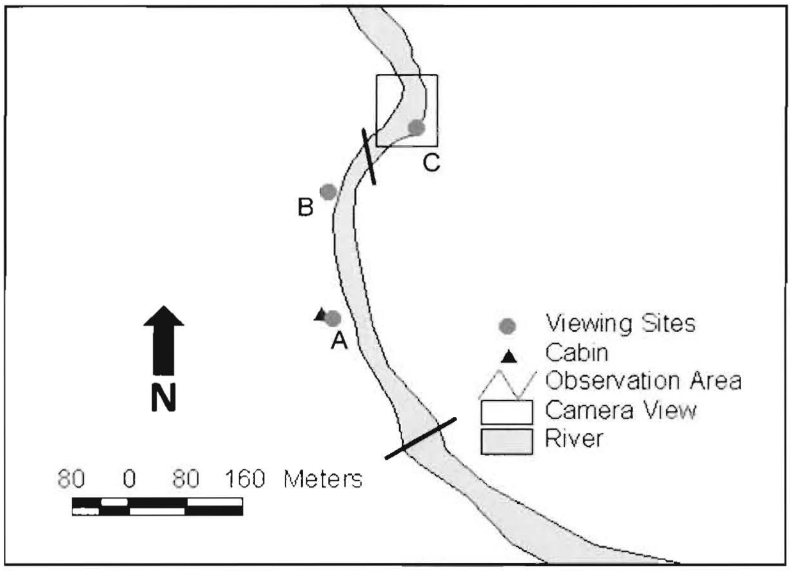

Figure 2-2. Commercial bear viewing area and research site along the Fishing Branch River, Yukon, 2005. A camera erected near Site B was used to record grizzly bear activity around the area of lower human activity (Site C). I directly observed bear activity in the area of higher human use from a tree stand at Site A.

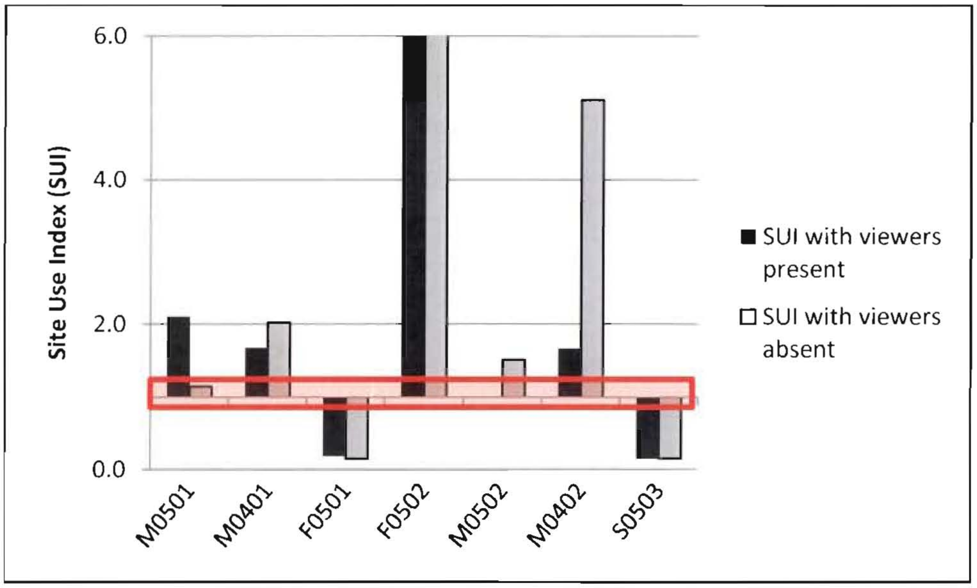

Figure 2-3. Site Use Index (SUI) for each grizzly bear with viewers present and absent to compare individual bear use around sites of higher and lower human use at the Fishing Branch River, Yukon, 2005. Site A data were from the entire season. SUI values greater than 1.2 indicate a fishing preference for Site A. SUI values less than 0.8 indicate a fishing preference for Site C. SUI values between 0.8 and 1.2 indicate no fishing site preference, which is shown by the red box. I truncated F0502's SUI to improve visibility of small SUIs; with viewers present her SUI was 34.751 and was 46.759 with viewers absent.

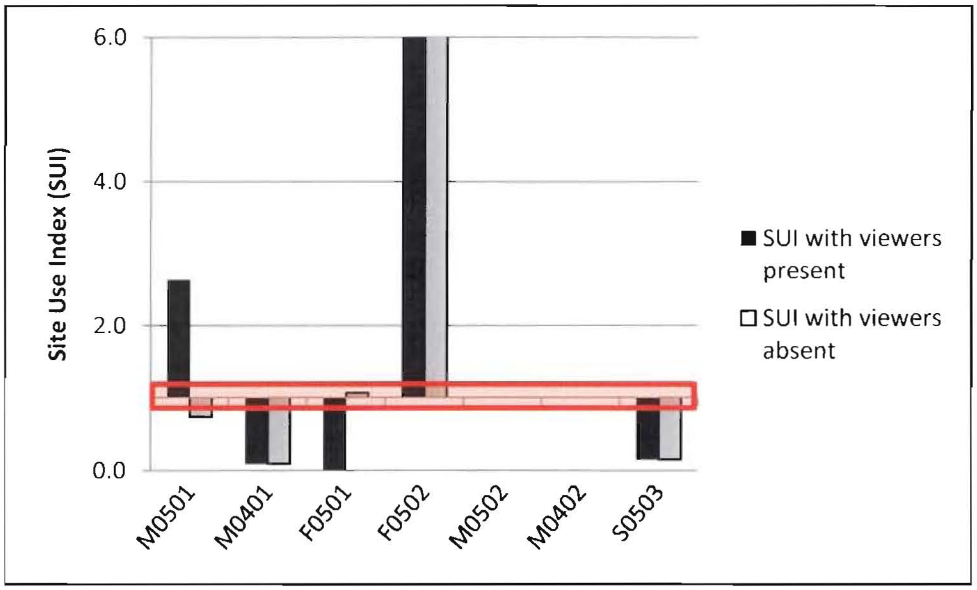

Figure 2-4. Site Use Index (SUI) for each grizzly bear with viewers present and absent to compare individual bear use around sites of higher and lower human use at the Fishing Branch River, Yukon, 2005. Data were from October 10 – 25, 2005, when the remote camera was operational. SUI values greater than 1.2 indicate a fishing preference for Site A. SUI values less than 0.8 indicate a fishing preference for Site C. SUI values between 0.8 and 1.2 indicate no fishing site preference, which is shown by the red box. I truncated F0502's SUI to improve visibility of small SUIs; with viewers present her SUI was 54.676 and was 16.687 with viewers absent.

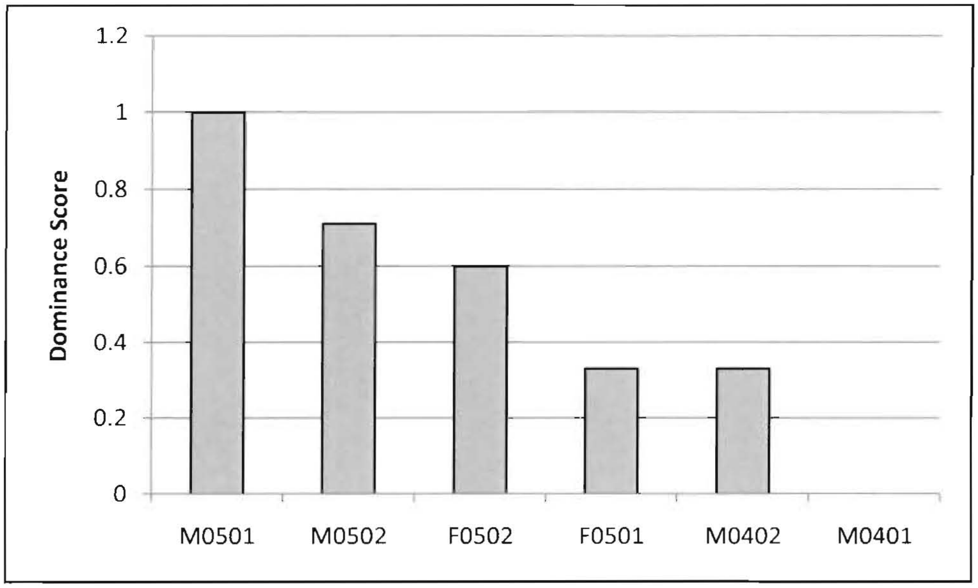

Figure 2-5. Dominance scores for grizzly bears along the Fishing Branch River, Yukon, 2005. Dominance scores range from zero to one, where one is the most dominant bear.

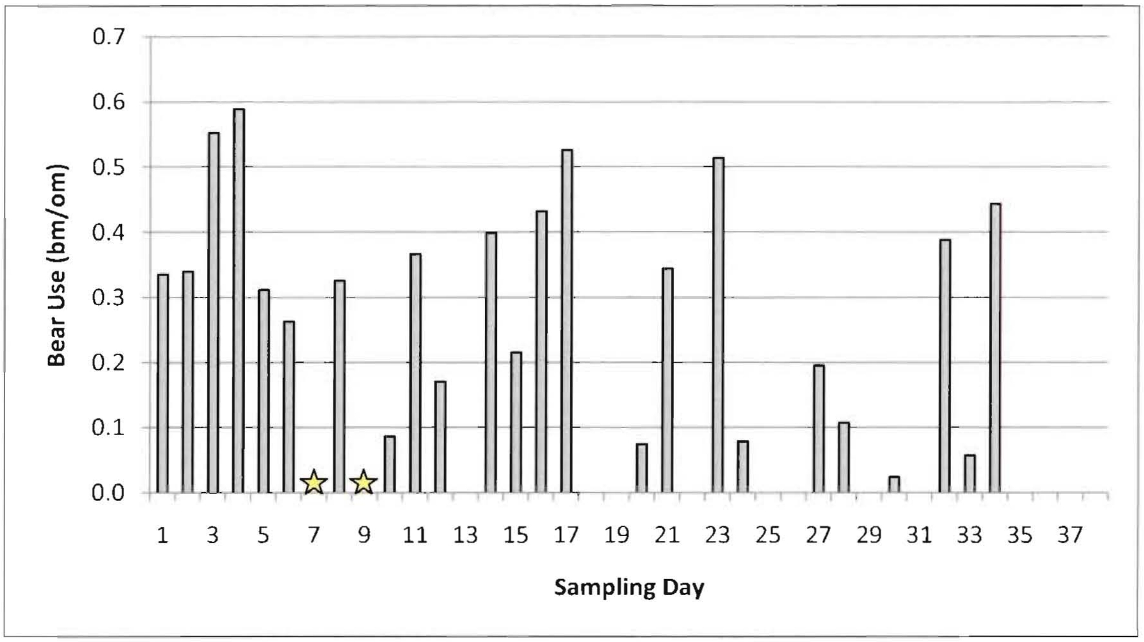

Figure 2-6. Bear use during daily sampling sessions, shown as a rate of bear minutes per observer minute (bm/om), along the Fishing Branch River, Yukon, 2005. Stars indicate unsampled days.

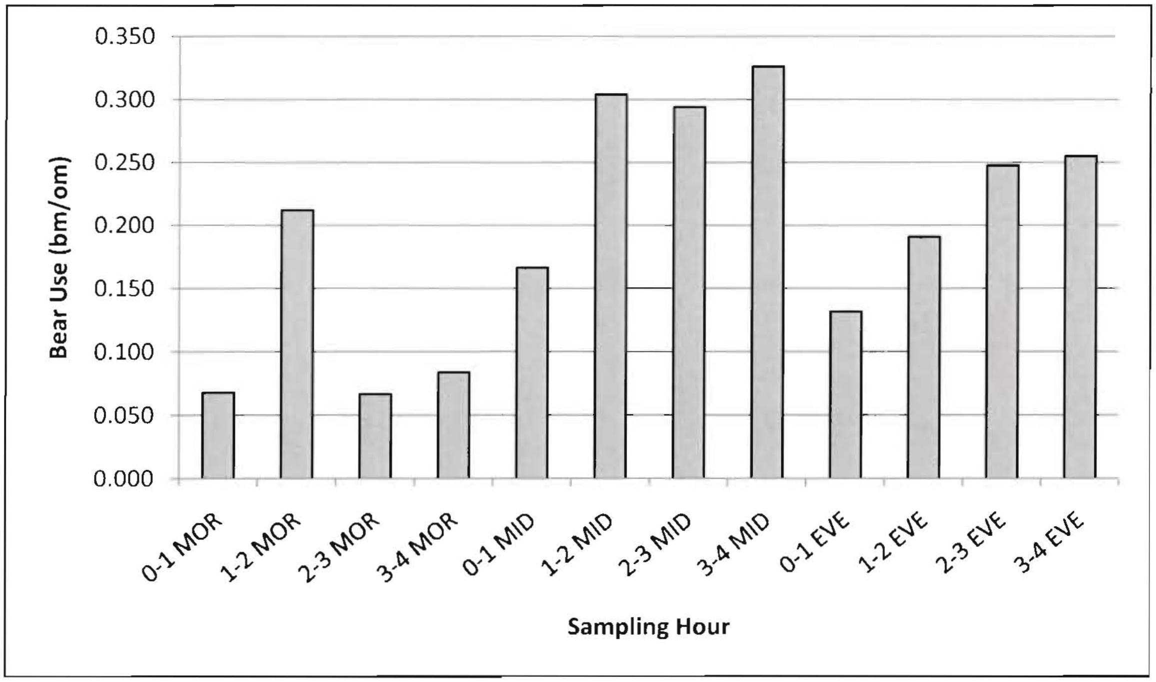

Figure 2-7. Bear use, shown as a rate of bear minutes per observer minute (bm/om), throughout the season categorized by hourly blocks within morning (MOR), midday (MID), and evening (EVE) sampling sessions along the Fishing Branch River, Yukon, 2005.

Chapter 3: Social interactions and their influence on feeding behaviour of grizzly bears along a salmon river in the northern Yukon

INTRODUCTION

For most of their lives, grizzly bears (*Ursus arctos*) are solitary creatures, with many population densities as low as 10 bears per 1000 km^2 (Poole et al. 2001). Grizzly bear forage is spatially and temporally distributed, usually in patchy clumps (Hamilton and Bunnell 1987, Barnes 1990). With patchy forage and few natural predators, bears gain no energetic benefit to foraging in groups (Herrero 1978). Usually grizzly bears congregate only for mating, feeding on concentrated resources (e.g., garbage dumps and salmon (*Oncorhychus* spp.)), and while females have dependent young (Herrero 1978, Chi 1999, Nevin and Gilbert 2005). As such, salmon spawning streams provide unique opportunities to study social dynamics of this normally solitary species.

Bears congregate along salmon-bearing streams to exploit a temporary increase in food availability, salmon, which is necessary for overwinter survival and reproduction (Hilderbrand et al. 1999, Gende and Quinn 2004). Dominant individuals gain access to prime feeding sites along salmon spawning streams by aggressively interacting with subordinate individuals or by pre-established dominance. Outcomes of prior social interactions form the basis for pre-established dominance. Pre-established dominance usually results in passive deferral interactions where the subordinate individual defers their position regardless of any overt reaction from the dominant individual (Chi 1999, Taillon and Cote 2006). Often, it is large male bears that dominate prime feeding sites (Egbert and Stokes 1976, Nevin and Gilbert 2005). Domination of feeding sites creates an agonistic situation that some subordinate bears perceive as too energetically costly; thus, subordinate individuals may feed at sub-optimal, but socially less risky fishing sites or abandon the fishing areas altogether (Egbert and Stokes 1976, Hilderbrand et al. 1996, Ben-David et al. 2004, Gende and Quinn 2004).

Social status affects individuals' resource access and feeding efficiency in many species. The result is increased energetic intake, potentially accompanied by increased fitness, for dominant individuals relative to subordinate individuals. Dominant Common Cranes (*Grus grus*) forced subordinate cranes from foraging sites with the highest food concentration, giving these dominant cranes higher consumption rates than subordinate cranes (Bautista et al. 1995). Dominant female chimpanzees (*Pan troglodytes*) in Gombe National Park, Tanzania, outcompeted lower ranking females for prime foraging sites, resulting in higher quality diets for these dominant females compared to lower ranking females (Murray et al. 2006). Similarly, some captive female gorillas (*Gorilla gorilla beringei*) dominated concentrations of high energy food sources, leaving subordinate females with the lower energy food available elsewhere in the enclosure (Scott and Lockard 2006). Foraging success of subordinate Ruddy Turnstones (*Arenaria interpres*) markedly declined with intraspecific competitors present (Vahl et al. 2005). In contrast, dominant Ruddy Turnstones maintained their level of foraging success with conspecifics present (Vahl et al. 2005). Dominant gobies (*Elacatinus prochilos*) in Barbados monopolized foraging areas with the highest food concentration; therefore, dominant gobies had higher foraging rates compared to subordinate gobies (Whiteman and Cote 2004). Many species exhibit dominance-dependent resource acquisition.

The interplay between social dominance in grizzly or black bears (*U. americanus*) and resource use has been examined at a few salmon streams to assess dominance-dependent resource acquisition and the compounding effects of human activity and dominance on resource acquisition. Dominant grizzly bears at McNeil River, Alaska, monopolized prime fishing locations forcing subordinate individuals into less efficient fishing positions (Egbert and Stokes 1976). At Anan Creek, Alaska, dominant black bears secured the best fishing locations and consumed fish at the capture location to reduce their energetic expenditures (Chi 1999). Subordinate bears used alternate foraging strategies to maintain fish consumption levels, such as occupying prime fishing sites after being vacated by dominant individuals or increasing their fishing time at lower quality areas where people were present (Chi 1999). Gende and Quinn (2004) found a positive relationship between grizzly bear dominance and fish consumption, whereas resource availability (salmon abundance) had little influence on bears' consumption at three streams in southeast Alaska. Grizzly and black bears display dominance-dependent resource access and consumption at some salmon spawning streams in Alaska.

I examined the social dynamics of grizzly bears congregating along the Fishing Branch River, Yukon, as part of my larger research project on the behavioural responses of grizzly bears to human activity at this site. Up to 20 grizzly bears congregate along the Fishing Branch River each fall because few other accessible salmon spawning grounds exist in the region. I investigated:

- whether a dominance hierarchy existed among grizzly bears along the Fishing Branch River,
- the nature of social interactions among these bears (i.e., aggressive or passive interactions, age/sex class involvement in interactions, and minimum distance maintained between individuals in passive interactions), and
- whether dominance status influenced bears' fishing behaviour, specifically their fishing bout lengths and fish consumption.

I hypothesized that a dominance hierarchy existed at the Fishing Branch River. I expected social interactions to be predominately aggressive in nature and initiated by dominant bears because of resource guarding (Milinski and Parker 1991). Pre-established dominance, tendency of the dominant individual to aggressively interact, and satiation of the subordinate individual should influence the minimum distance maintained between bears during passive interactions. I expected resource guarding to create a negative relationship between fishing bout length and dominance status. If dominant bears secured the most efficient fishing sites, they could consume more fish in less time compared to subordinate bears fishing in suboptimal sites. I hypothesized that a positive relationship would exist between fish consumption and dominance status because of the dominant-dependence of fishing location and fish acquisition found at other salmon spawning areas.

STUDY AREA

The study portion of the Fishing Branch River (N 66° 30' W 139° 20') was located within the Ni'iinlii Njik (Fishing Branch) protected area complex. This area protects the chum salmon (*O. keta*) run, grizzly bears that congregate here to consume the salmon, and their habitats (Yukon Government Department of Environment and Vuntut Gwitchin Government Department of Natural Resources 2000). The 7000 km^2 protected area was established in 1999 as part of the Vuntut Gwitchin First Nation Final Agreement and under the Yukon Protected Areas Strategy. Ni'iinlii Njik protected area complex protects a representative portion of the Northern Ogilvie Mountains Eco-region in the northern Yukon Territory. This protected area complex encompasses the Fishing Branch River watershed and parts of adjacent headwaters and is comprised of four components (Fig. 3-1): 5400 km^2 Wilderness Preserve, 1000 km^2 Habitat Protection Area, 165 km^2 Ecological Reserve, and 143 km^2 Vuntut Gwitchin Settlement Lands. My study site was at the newly established commercial bear viewing area in the Ecological Reserve and Settlement Lands immediately west of Bear Cave Mountain at the centre of the protected area (Fig. 3-1).

Unique characteristics of Ni'iinlii Njik protected area complex include limestone caves, year-round open water, and grizzly bear densities greater than any other place at this northern latitude (Yukon Government Department of Environment and Vuntut Gwitchin Government Department of Natural Resources 2000). Dissolving limestone creates nutrient-rich ecosystems, including calcium-enriched water from underwater limestone caverns. Thermal energy from summer waters is stored in underground reservoirs. This warm ground water resurfaces through upwellings, which creates permafrost-free areas around the river and maintains the river's non-frozen state during the severe northern winters. Permafrost-free conditions around the Fishing Branch River near Bear Cave Mountain create an opportunity for relatively dense white spruce (*Picea glauca*) forests to grow, with willow (*Salix* spp.) thickets that dominate riparian areas. Understory vegetation at the site contains many grizzly bear foods, including blueberry (*Vaccinium* spp.), soapberry (*Sheperdia canadensis*), bearberry (*Arctostaphylos rubra*), kinnickinnick (*A. uva-ursi*), rose (*Rosa* spp.), and highbush cranberry (*Viburnum edule*). The bear viewing area at the Fishing Branch River is located in an interior region, in contrast to the coastal habitats of most bear viewing sites.

The Ni'iinlii Njik protected area complex has limited human influence largely because of its isolation. Old Crow is the closest community to the study site at 120 km due north. Dawson City is the next closest community and is almost 280 km south. The study site and commercial bear viewing area were only accessible by helicopter, foot, or snowmobile. With the exception of commercial bear viewers, area visitors were largely limited to Yukon Government staff, Vuntut Gwitchin First Nation members, researchers, and Fisheries and Oceans Canada staff who maintain a live weir approximately 8 km downstream from the study site. Fisheries and Oceans Canada maintain the weir from mid-August to mid-October counting salmon daily. The chum run lasts from mid-August to early November, with escapement numbers as low as 5,000 (in 2000) and reaching highs of 301,000 (in 1975; Fisheries and Oceans Canada, unpublished data). Grizzly bears can be viewed at the study site from early September to early November.

My study site was the commercial viewing area along the Fishing Branch River, whose three bear viewing sites (A, B, C) provided approximately 500 m of continuous river viewing along chum salmon spawning grounds (Fig. 3-2). Site A was adjacent to the viewing camp and will be the primary viewing site. That is, Site A will have the most viewing hours by visitors. Sites B and C will be the secondary and tertiary sites for bear viewers, respectively. Bears displaced from the high human activity around camp and Site A may use the lower human activity area around Sites B and C as a refuge from human activity.

I based my research at the commercial bear viewing camp situated 20 m from the river in the forest adjacent to Site A. Camp infrastructure consisted of a main 5 m x 5 m cabin for cooking, two 3 m x 4 m sleeping cabins, a high cache, and outhouse. Bears were not deterred from camp unless they threatened property damage or physical harm. An electric fence protected the cabins during the non-viewing months. The commercial bear viewing program does not use viewing infrastructure (e.g., elevated platforms); rather, viewing occurs from natural river banks.

Habituation of bears is paramount to the success of commercial viewing operations because it creates safer and subsequently more optimal viewing opportunities (Aumiller and Matt 1994). Habituation efforts have been underway for over 10 years at the Fishing Branch River, with up to two months of active habituation annually (P. Timpany, personal communication). As a result, I characterize the social dynamic and behaviour of grizzly bears with previous exposure to human activity at the Fishing Branch River.

METHODS

Social Interactions

I identified individual bears by natural markings and morphological characteristics including coat colouration and scars. Individuals were photographed and distinctive characteristics sketched onto identification sheets. I updated the identification sheets as new defining characteristics became apparent (e.g., new scars, coat colouration changes, loss of young). I determined sex through direct observation of genitals, urination posture, or presence of cubs. Age class was assessed through prior knowledge of known bears, presence of cubs, and general body size.

I recorded all social interactions observed throughout the field season; not only those that occurred during sampling sessions. I defined a social interaction as any overt reaction to a conspecific, including passive deferrals and aggressive interactions (Chi 1999). Passive deferrals were when one bear, usually the subordinate, diverts around or away from the other bear to avoid an interaction. Aggressive interactions included physical contact, chases, bites, and jaw pops (Chi 1999, Gende and Quinn 2004). For all social interactions, I recorded individuals involved, interaction type (passive deferral, aggressive interaction, unknown), outcome (winner, loser, or tie), movements of each individual within subgrids, and minimum distance between individuals involved in passive deferrals (to the nearest 5 m). I classified interactions as 'unknown' when I did not observe the complete interaction. I divided the river and shore into six grid sections varying from 60 to 100 m in length to track bear movement during social interactions (Fig. 3-3). Grid sections were based on natural river features to eliminate the need to flag grid boundaries. I subdivided each grid section into five subsections to more accurately record bear position within each grid (Fig. 3-3). Table 3-1 describes the grid subsections.

Fishing Behaviour

I conducted 142.5 hours of grizzly bear observations from a stand erected 4 m up a tree at Site A between September 18 and October 25, 2005. During observations, I was approximately 20 m from the river's edge and 10 m from common travel paths of bears along the river shore. The tree stand masked my presence as much as possible creating a situation close to 'people absent' and elevated me above bears' travel paths giving them unimpeded movement through the observation area. I had an unobstructed view of 230 m downstream and a 50 % obstructed view of 160 m upstream from the tree stand; two spruce trees obstructed my upstream view. I selected the tree-stand location based on tree diameter, proximity to viewing Site A, level of safety while entering/exiting the stand, and view provided. Only the branches necessary to accommodate myself and the stand were removed from the tree. Branches were left to partially obscure bears' view of the tree stand.

I collected behaviour data for randomly chosen focal bears during one 4-hour sampling session per day (Altmann 1974). Throughout September and mid-October I used three 4-hour sampling sessions each day: morning, midday, and evening. I scheduled these daily sessions based on the length of sufficient daylight to identify individual bears. I used two sampling sessions per day starting in mid-October as available daylight declined. One 4-hour session was randomly chosen for sampling each day while ensuring equal coverage for all portions of the day throughout the bear viewing season. For each focal bear I recorded their:

1) identity,
2) age/sex class (adult (>5 years old), subadult (3-5 years old), 2-yr old, young-of-last-year, young-of-year),
3) fishing bout length (from arrival and departure times), and
4) length of each fish consumption activity within fishing bouts.

I collected behaviour information for independent bears only because behaviour of young is largely influenced by their mother's behaviour (Chi 1999).

I determined fishing bout lengths as the difference between each focal bear's fishing bout start and end time. I recorded fishing bout start times as the time each focal bear became visible unless it was on the river prior to commencing the sampling session. In this case, I recorded the sampling session start time as the focal bear's fishing bout start time because I had no knowledge of the bear's true fishing bout start time. I terminated focal observations if the focal bear became unobservable for more than 20 consecutive minutes but recorded the fishing bout end time as the time the focal bear left my field of view. This termination time was based on averaging the two longest fish consumption activities in 2004 (15 min) plus 33 % extra time (5 min) to account for any variation in fish consumption between years. I used a termination time to allow continuous fishing bouts for those bears that consumed a fish in vegetated cover and then resumed fishing. For bears still fishing on the river when a sampling session ended, I recorded the sampling session end time as their fishing bout end time because I did not know their actual fishing bout end time. Some fishing bout lengths were underestimated because of truncating fishing bouts that continued outside of sampling sessions. However, fishing bouts rarely began or continued beyond the sampling session. I measured the time (to the nearest second) the focal bear spent consuming each fish in a fishing bout, including biting, chewing, and manipulating fish position. These methods were based on research design from Chi (1999), Gende and Quinn (2004), and Nevin and Gilbert (2005).

I was accompanied by the commercial bear viewing guide during the sampling season for safety reasons. The guide remained out of view of the river during daily sampling sessions, usually staying in the main cabin. Two people affiliated with the commercial viewing operation were on-site from September 18 - 26, 2005. I excluded all data obtained while people were viewing bears to eliminate any direct human influence on bear behaviour. I was unable to exclude any effects my presence in the tree stand may have had on bear behaviour. Although general human activity at camp was minimized, the effect of the camp on bears could not be eliminated and thus, potentially influenced the social interactions and behaviour of the bears.

Analyses

Social Interactions

I created a dyadic interaction matrix using outcomes of social interactions between individual bears at the Fishing Branch River (Brown 1975, Martin and Bateson 1993, Lehner 1996). The dyadic interaction matrix shows the total wins, losses, and ties observed between all possible pairs of bears. I included interactions involving subadults in the matrix but excluded them from dominance analyses unless otherwise stated. I excluded subadult bears because I assumed they were always subordinate to adult bears (Chi 1999). With respect to social interactions, I defined a reversal as a win by individual

B when individual A won the majority of encounters between A and B (Brown 1975, Martin and Bateson 1993). Reversal situations were simply added into the dyadic interaction matrix as an additional win for the normally subordinate individual and as a loss for the normally dominant individual. I defined circularity as non-linear dominance where A dominates B, B dominates C, but C dominates A (Brown 1975, Martin and Bateson 1993). Potential circularities were determined through visual examination of a hierarchy diagram and included in the matrix as wins, losses, and ties for the respective individuals in a pair. I calculated the proportion of interactions that were reversals or circularities to obtain a rough estimate of linear dominance among these bears (Chi 1999). Linear dominance was where the top-ranking individual dominates all individuals, the second-ranking individual dominates all individuals except the top-ranking individual, and so on (Martin and Bateson 1993, Lehner 1996). I calculated Landau's index of linearity (h') for matrices containing unobserved dyad interactions, using Python 2.1, as more quantitative means to assess linear dominance (de Vries 1995, Python Software Foundation 2001; see Appendix 2 for Python code).

I assigned a rank order of dominance to the Fishing Branch River bears using two techniques: Dominance Rank and Dominance Score Rank. Each method varied in its treatment of the social interaction outcomes. As such, I compared results from both methods. I determined Dominance Rank (DR) by reordering the matrix to minimize the number of "wins" below the matrix diagonal (Martin and Bateson 1993). DR is an ordinal ranking system that assigns ranks according to the order of individual bears in the reordered matrix. I ranked the most dominant individual as one and assigned the most subordinate individual the highest number, equating to the number of independent bears in the matrix. To determine Dominance Score Ranks (DSR), I first calculated a Dominance Score (DS) for each bear as follows:

$$DS_y = \frac{W_y + 0.5 * T_y}{N_y}$$

where y = individual bear, W = number of interactions where the individual displaced another bear (wins), T = number of interactions where neither bear was supplanted by the other (ties), and N = total number of interactions involving the individual (Lehner 1996, Chi 1999, Koene et al. 2002). I ranked these DS giving DSR, where one is the most dominant individual corresponding to the highest DS.

Fishing Behaviour

I calculated fishing bout length and fish consumption for each bear during each sampling session in which they were a focal bear (i.e., one bout length and one consumption value per bear per day). Therefore, if an individual was a focal bear more than once during a sampling session, I averaged his fishing bout length and fish consumption from each focal observation in that sampling session. Creating one value for each fishing behaviour per bear per day reduced pseudoreplication in the data (Hurlbert 1984). Each fishing bout length and fish consumption was coded with the bear's dominance score. I excluded all fishing bouts with viewers present to minimize the direct influence of human activity on bears' fishing behaviour (see Chapter 2).

I calculated fishing bout length using the following formula:

$$L = T_d - T_a$$

where L = fishing bout length, T_d = departure time, and T_a = arrival time. I calculated fish consumption using the following formula:

$$F_x = \frac{C_x}{c}$$

where F = fish consumption, x = fishing bout, C = total length of consumption activities (min), and c = maximum overall consumption activity (min). With respect to calculating fish consumption, a consumption activity was a period of time within a fishing bout in which a bear continuously consumed fish. I defined maximum overall consumption activity (c) as the longest single consumption activity within all fishing bouts that was not 50 % greater than the next longest consumption activity. I used this 50 % rule to ensure that the maximum overall consumption activity was not uncharacteristically long as can occur when bears' focus deviates from consumption activities, such as concentrating on nearby conspecifics that slowed their chewing. I standardized consumption activities such that fish consumption per fishing bout (F_x) was a proportion of the maximum fish consumption activity. I did not create fish consumption values based on individual-specific maximum consumption activities, which would have accounted for any individual-specific variation in consumption rates. Use of individual-specific maximum consumption activities required the invalid assumption that each bear consumed approximately equal proportions of salmon in their maximum consumption activity.

Effects of Social Dominance on Fishing Behaviour

I examined whether fishing bout length and fish consumption differed by dominance score using an analysis of variance (ANOVA; Zar 1996). I used Pearson's correlation coefficient to examine the relationship between individual bear use throughout the field season (summed fishing bout lengths for each individual bear) and their number of social interactions to see whether interaction frequencies were related to the amount of time each bear spent on the river. I used JMP 6.0.0 for these analyses (SAS Institute 2005) and tested all dependent variable residuals for normality using the Shapiro-Wilk (W) goodness of fit test (Zar 1996). All points that were outliers from the fitted models were removed. I used a significance level of 0.05 for all analyses and reported 95 % confidence intervals.

RESULTS

Dominance Hierarchy

I observed 20 social interactions among the six adult and one subadult grizzly bears at the Fishing Branch River. The female subadult (S0503) deferred to the more dominant bear in her three interactions. Excluding the subadult from the interaction matrix, I observed 53 % of the possible dyad (pair) interactions, leaving 47 % unobserved (Table 3-2). I observed one reversal interaction (5.9 % of the total interactions) and no circularities or tied interactions. The dominance hierarchy of these grizzly bears appeared largely linear based on the lack of reversals, circularities, or ties. However, a visual assessment of the observed dominant-subordinate relationships shows a very non-linear hierarchy (Fig. 3-4). Quantitatively, I found that the linear hierarchy in the interaction matrix could have risen from chance alone (Landau's index of linearity: $P = 0.35$).

I observed up to four interactions for each pair of bears (Table 3-2). The number of wins and losses by each individual ranged from zero to nine (Table 3-2). Based on Dominance Rank, I found that M0501 was the most dominant individual (DR = 1) winning all his interactions. M0401 was the most subordinate individual (DR = 6) losing all his interactions (Table 3-2). Dominance Scores ranged from 0.00 to 1.00, meaning that one bear (M0501, DS = 1.00) dominated all their interactions and one bear (M0401, DS = 0.00) was subordinate in their interactions (Table 3-2). As a result, I ranked M0501 as most dominant (DSR = 1) and M0401 as most subordinate (DSR = 6; Table 3-2) for Dominance Score Ranks. DR and DSR differed in their ranking of intermediate bears despite producing identical most dominant and subordinate individuals. I broadly classified each bear as dominant (won nearly all or all of its interactions), intermediate (won and lost many interactions), or subordinate (lost nearly all or all of its interactions) to accommodate this ranking discrepancy (Table 3-2). I found no correlation between an individual bear's river use throughout the season and their number of social interactions ($r^2 = 0.296$, $P = 0.2066$, $n = 7$).

Nature of Social Interactions

Of the 20 social interactions I observed, 55 % were aggressive, 30 % were passive deferrals, and 15 % were unknown (Table 3-3). The dominant bear, M0501, won 73 % of aggressive interactions, all he was involved in. Play behaviour likely contributed to the aggressive interaction between M0502 and M0401, which was the only escalating to physical contact. I found that male bears were involved in 77 % of the 11 aggressive encounters (a male-male interaction counted as involvement of two males). Male bears won 82 % of aggressive encounters (Table 3-3). Females, females with young, and subadults were involved in the remaining 23 % of aggressive interactions and they won only 18 % of all aggressive interactions (Table 3-3).

I did not observe dominant individuals in any passive deferrals; all passive deferrals were between bears of intermediate or subordinate status. I observed substantial variation in the minimum distance between individuals in passive deferrals, even within interactions between the same individuals. I observed M0401 passively deferring to M0502 in three of their interactions with a minimum distance ranging from 20 to 80 m (Table 3-3).

Effects of Social Dominance on Fishing Behaviour

The maximum consumption activity I observed in 2005 was 17.0 min; however, this was >50 % longer than the next longest consumption activity (11.0 min). I excluded this absolute longest consumption activity and used 11.0 min as the maximum overall consumption activity for 2005. I found no significant difference in either fishing bout length or fish consumption between dominance scores (fishing bout length: $F_{4,19} = 1.732$, $P = 0.202$ and fish consumption: $F_{4,19} = 0.004$, $P = 0.954$; Figs. 3-5 and 3-6).

DISCUSSION

Dominance Hierarchy

I observed unequal interaction rates between grizzly bear pairs along the Fishing Branch River. I expected a positive relationship between river use by bears and their interaction rates because increased river time would translate into increased opportunities for social interactions. However, I found no evidence suggesting that river use affected interaction rates. Freeman et al. (1992) posed two explanations for a similar discrepancy in social interaction rates of male red deer (*Cervus elaphus*): 1) individuals vary in their tendency to participate in aggressive interactions and 2) a preferential pattern of social interactions exists where individuals may seek out one another at rates unequal to their encounter rates, supposedly a result of balancing potential risks and benefits of the interaction. Similarly, Moran (1982) found that 75 % of the social interactions among captive wolves (*Canis lupus*) were from four of the 28 possible wolf pairs. At the Fishing Branch River, two bear pairs accounted for 40 % of the observed interactions, with one individual occurring in both pairs. This large proportion of interactions by these three bears (two pairs) indicates that preferential interactions are likely occurring at the Fishing Branch River. I also attribute some of the variability in interaction rates to differences in the propensity of each bear to interact. F0502 was far more vigilant when fishing than any other bear, which may be indicative of her low tendency to interact. With frequent vigilance, F0502 could immediately react to any approaching conspecifics and move away before the social interaction (as I defined them) occurred. I found evidence that individual propensity to interact and preferential interactions may explain some variation in the social interaction rates of bears at the Fishing Branch River, rather than simply the amount of time on the river.

With nearly half of the possible pair interactions unobserved, I was unable to create a conclusive hierarchy of all dominant-subordinate relationships among grizzly bears using the Fishing Branch River. I may have missed pair interactions because they occurred beyond my observation area or during non-observation periods, particularly at night when researcher safety was a concern. Despite my incomplete observations, both dominance ranking methods were consistent with regard to the most dominant and subordinate bears but differed in their ranking of intermediate bears. Koene et al. (2002), when comparing methods, found similar ranking of individual grizzly bears on the hierarchy extremes but differences in ranking of intermediate individuals. I think the discrepancy in dominance ranking of Fishing Branch River bears occurred because I attempted to linearly rank individual bears when a linear hierarchy may not exist, especially among bears of intermediate dominance. Indistinct or fluctuating social structure is common among individuals of intermediate dominance (Chi 1999, Gende and Quinn 2004). Boyd and Silk (1983) suggest that individuals should not be ranked into a linear hierarchy if even one dominance relationship between two individuals remains unknown. I found support for a non-linear hierarchy at the Fishing Branch River with Landau's index of linearity, which found that the data provided insufficient evidence of a linear structure that could not have arisen by chance alone. Thus, my broad classification of bears into dominant, intermediate, and subordinate classes more accurately captured the dominance structure of bears at the Fishing Branch River.

More complex methods of assigning dominance rank exist that incorporate information lost in the assignment of the ordinal dominance scores I used here (Boyd and

Silk 1983). Cardinal dominance scores describe the amount of individual dominance on a continuous scale and can be statistically tested to assess whether individual scores significantly differ from one another (Boyd and Silk 1983). This testing would provide key insight into the social structure, or lack of, among the bears of intermediate dominance at the Fishing Branch River. Although cardinal dominance scores would provide more precise dominance information, I cannot meet two key assumptions of cardinal dominance: my sample size was too small and there were too few "wins" below the matrix diagonal (Boyd and Silk 1983). Thus, cardinal dominance scores were inappropriate for these data from the Fishing Branch River.

Independent of ranking scheme, I found an adult male, M0501, dominated the Fishing Branch River. The genders of dominant bears vary from stream to stream and may be explained by the abundance of spawning streams in bear home ranges. Larger home range size of male bears relative to females means that male bears presumably have more streams within their home range (Berns et al. 1980, Ballard et al. 1982, Barnes 1990). As such, male bears likely prefer fishing on larger streams where salmon are often more abundant (Gende and Quinn 2004) resulting in male bears being dominant at larger streams, such as Glendale River (Klinka and Reimchen 2002, Nevin and Gilbert 2005) and McNeil River (Egbert and Stokes 1976). Dominance by large females at two smaller spawning streams in Alaska (Himmel and Bear Creeks) may be an artifact of this varying abundance of salmon streams in home ranges (Gende and Quinn 2004). Large males were rarely observed at these smaller streams leading Gende and Quinn (2004) to suggest that male bears may be fishing at larger spawning streams where salmon were more abundant and accessible. Male bear dominance at the Fishing Branch River followed this pattern where male bears dominated this river because larger, more accessible salmon spawning streams do not exist within their home range.

Nature of Social Interactions

I observed largely aggressive social interactions along the Fishing Branch River, in contrast to the predominance of passive interactions at other salmon streams (e.g., Chi 1999). Almost all (73 %) of the Fishing Branch River aggressive interactions involved the most dominant individual, M0501. I do not think food resource guarding drove

M0501's high level of aggressive interactions because salmon were readily available. Resource guarding, leading to a despotic distribution, is usually only energetically beneficial when resources are scarce or clumped, such that the energetic gain achieved by excluding conspecifics from the resource outweighs the energetic cost of aggressive interactions to exclude conspecifics (Milinski and Parker 1991). A key assumption of despotic distribution is perfect knowledge of resource distribution (Milinski and Parker 1991). I think these bears were aware of the resource distribution within the 500 m river section around the viewing area as they often foraged this entire area at least once per day. As such, resource guarding could occur if it was energetically beneficial. M0501's high level of aggressive interactions in the presence of an abundant food resource suggests he was more aggressive relative to other bears along the Fishing Branch River. Perhaps M0501's absence on the river would create a substantially different social dynamic with minimal aggressive interactions because I observed no other bears with such prominent aggressive natures.

Optimality theory suggests that individuals should maximize their energetic gain to obtain the highest fitness levels possible (MacArthur and Pianka 1966). Bears can maximize caloric intake and/or minimize energetic loss to maximize their energetic gain. Thus, I expected Fishing Branch River grizzlies to consume the highest energetic portions of each salmon until limited by gut capacity and favour passive responses as opposed to aggressive ones whenever possible, due to the lower energetic cost of passive responses. Excluding M0501 because of his propensity to aggressively interact with conspecifics, grizzly bear social interactions were largely passive in nature. Although these passive tendencies lend support to Fishing Branch River bears abiding by the optimality theory, other factors likely contributed to the passive nature of these interactions. Pre-established dominance could result in largely passive responses because bears were aware of their hierarchical relation to other bears from the outcomes of previous interactions. In addition, I think the Fishing Branch River was below carrying capacity in 2005 with above-average salmon abundance and few bears relative to previous years. This situation precluded the need for aggressive interactions because the food resource was not limited.

Pre-established dominance, individual tendency to interact, and satiation all influenced the minimum distance maintained between two bears during passive social interactions. Presumably, bears that maintain large minimum distances during passive interactions perceive substantial "risk" from being in close proximity to the more dominant individual; thus, they defer their position from a greater distance. Subordinate individuals that permit dominant bears within a few meters before deferring their position may perceive lesser "risk" from the dominant individual. This "risk" perception can result from pre-established dominance and assessment of interaction tendencies. I observed a series of social interactions at the Fishing Branch River that follow these ideas of risk perception and assessment of interaction tendencies. I observed M0401 passively deferring to M0502 three times within 30 min. The initial deferral was at a minimum distance of 80 m, the second was 60 m, and the third was 20 m. M0401 permitted M0502 closer before deferring his position in each subsequent interaction, possibly because M0401 observed the lack of aggression in the preceding interactions and therefore M0502's low tendency to become aggressive. Unfortunately, this was the only pair of bears I observed passively interacting on multiple occasions, leaving me unable to assess how risk perception and assessment of interaction tendencies influenced the minimum distances between bears on a larger scale.

Satiation may have played a large role in determining the minimum distance maintained between bears in passive deferrals at the Fishing Branch River. When viewed in an energetic cost-benefit framework, cessation of feeding to passively defer to another individual translates into lost potential energetic intake, where the energy lost is proportional to the deferral distance. More satiated individuals would be at an energetic advantage to defer to the dominant individual at a greater distance because lost feeding opportunities were of lesser consequence given their satiation level. In contrast, less satiated individuals may allow the dominant individual much closer to maximize their foraging time. In this situation, dominant individuals would elicit a response parallel to predation risk in subordinate individuals. Milinski and Heller (1978) and Krebs and Kacelnik (1991) examined satiation effects on stickleback responses to predation risk. Hungry sticklebacks fed in areas with higher food concentrations, which also had a higher predation risk. In contrast, well-fed sticklebacks preferred areas with lower predation risk and less concentrated food. I think a similar satiation effect occurred with passive interactions at the Fishing Branch River. For example, a passive deferral occurred with 235 m between two bears. Perhaps M0401 deferred to F0501 at this great distance because he was relatively satiated having already fished 200 m of river. I was unable to gauge M0401's satiation prior to this deferral because the deferral occurred outside of a sampling session. As such, I had not collected fish consumption information. Small sample size precluded further investigation into the influence of satiation on passive deferral distances.

Effects of Social Dominance on Fishing Behaviour

Social status in many species influences individuals' access to resources and their feeding efficiency (Bautista et al. 1995, Whiteman and Cote 2004, Vahl et al. 2005, Murray et al. 2006, Scott and Lockard 2006). The result is increased energetic intake, potentially accompanied by increased fitness, for dominant individuals relative to subordinate individuals. Dominance status has influenced bears' fishing location choice, success rates, eating location (on river or in vegetative cover), and fishing bout length at various Alaskan salmon streams (Chi 1999, Gende and Quinn 2004). I hypothesized that dominant bears along the Fishing Branch River would have shorter fishing bouts and consume more fish relative to subordinate bears because dominant bears secure fishing sites with the highest feeding efficiency. However, I found no evidence that dominance status influenced fishing bout lengths or fish consumption of bears at the Fishing Branch River.

I think that bears' feeding behaviour was independent of their dominance status because there was little need for resource-driven intraspecific competition. Only eight bears used the Fishing Branch River during this season where salmon were five times more abundant than the 10-year average (Fisheries and Oceans Canada, unpublished data). Because resource competition drives the effects of dominance status on feeding behaviours (Hupp et al. 1996, Chi 1999, McCarthy et al. 1999, Gende and Quinn 2004), it follows that dominance would not influence feeding behaviours of these Fishing Branch River bears in years with abundant food. Fero et al. (2006) also found no relationship between dominance and feeding success of crayfish (*Orconectes rusticus*) when food was abundant. Perhaps years with low salmon abundance or accessibility (e.g., from high water) would create dominance-dependent effects on the feeding behaviour of these same bears at the Fishing Branch River. Egbert and Stokes (1976) found that reduced salmon abundance at McNeil River lead to increased intolerance among grizzly bears. This potential dominance-dependent fish consumption during years of low salmon abundance is particularly important in light of bears' reduced fish consumption when bear viewers were present (Chapter 2). I recommend monitoring feeding behaviour and dominance status of grizzly bears during a year with low salmon abundance at the Fishing Branch River to investigate the cumulative effects of bear viewers and limited forage on fish consumption by these bears.

CONCLUSION

Although a general dominance hierarchy was evident in the grizzly bears along the Fishing Branch River, dominance status had no measurable effect on the fishing behaviour of these bears. Above-average salmon abundance and few conspecifics using the river minimized competition driven by resource guarding. In turn, bears of all dominance status had temporally or spatially unimpeded access to salmon along the river. I expect dominance status to influence the feeding behaviour of these bears in years with less abundant salmon. As a result, I recommend monitoring dominance and feeding behaviour of bears along the Fishing Branch River during a year with low salmon abundance. Because these bears reduced their fish consumption with viewers present (Chapter 2), further reduction in consumption during low salmon years poses serious energetic consequences for less dominant bears. One main study limitation was my inability to exclude all effects of human presence on social interactions and behaviour of these bears. Although I excluded bear behaviour data collected with bear viewers present, I could not remove the general effect of human activity around camp or the camp infrastructure itself on these bears. As a result, my observations may overestimate the social interactions of habituated bears, that is, those bears opting to fish around human activity, and underestimate the interactions of bears wary of human activity.

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TABLES

Table 3-1. Physical description of subdivision (a-e) within movement grids for grizzly bear behaviour along the Fishing Branch River, Yukon, 2005.

Subsection	Description
A	Vegetated portion on the east side of each grid
B	Non-vegetated rocky shore east of the wetted portion of the riverbed
C	Wetted portion of the riverbed
D	Non-vegetated rocky shore west of the wetted portion of the riverbed
E	Vegetated portion on the west side of each grid

Table 3-2. Social interaction matrix for all grizzly bears along the Fishing Branch River, Yukon, 2005, where rows were the dominant individual in interactions with each column individual. The matrix shows the number of interactions between each dyad (pair) of individuals. Dashes (-) show unobserved interactions. I included dominance rank (DR), dominance score (DS), dominance score rank (DSR), and general dominance status for all individuals except the subadult.

Individual	M0501	M0502	M0402	F0502	F0501	M0401	S0503	Total # interactions	DR	DS	DSR	Dominance status
M0501		1	2	-	-	4	1	8	1	1.00	1	dominant
M0502	0		-	1	-	4	-	7	2	0.71	2	intermediate
M0402	0	-		1	-	-	-	3	3	0.33	5	intermediate
F0502	-	1	0		2	-	-	5	4	0.60	3	intermediate
F0501	-	-	-	0		1	2	5	5	0.33	5	intermediate
M0401	0	0	-	-	0		-	9	6	0.00	6	subordinate
S0503	0	-	-	-	0	-		3	n/a	n/a	n/a	n/a

Table 3-3. Social dominance interactions observed along the Fishing Branch River, Yukon, 2005, showing the interaction winner and loser, type, and description. Unknown interaction types were those where I did not observe the complete interaction.

Date	Winner	Loser	Interaction Type	Interaction Description
Sep 19	M0502	M0401	passive deferral	displaced off river
Sep 19	M0502	M0401	passive deferral	displaced off river
Sep 19	M0502	M0401	passive deferral	displaced up river but not off river
Sep 19	M0502	F0502	unknown	displaced off river
Sep 20	F0502	M0502	unknown	unknown
Sep 21	M0501	M0402	aggressive	chase, vocalizations
Sep 22	M0501	M0402	aggressive	chase, vocalizations
Sep 22	M0502	M0401	aggressive	chase, biting, vocalizations
Sep 22	M0501	M0401	aggressive	chase
Oct 01	M0501	M0502	aggressive	chase
Oct 01	M0501	M0401	aggressive	chase
Oct 02	M0501	M0401	aggressive	chase
Oct 03	M0501	M0401	aggressive	chase
Oct 06	F0501	S0503	aggressive	chase
Oct 08	F0502	F0501	passive deferral	displaced off river
Oct 08	M0402	F0502	passive deferral	displaced up river but not off river
Oct 11	F0502	F0501	unknown	displaced off river
Oct 13	F0501	M0401	passive deferral	displaced off river
Oct 14	F0501	S0503	aggressive	chase
Oct 17	M0501	S0503	aggressive	chase

FIGURES

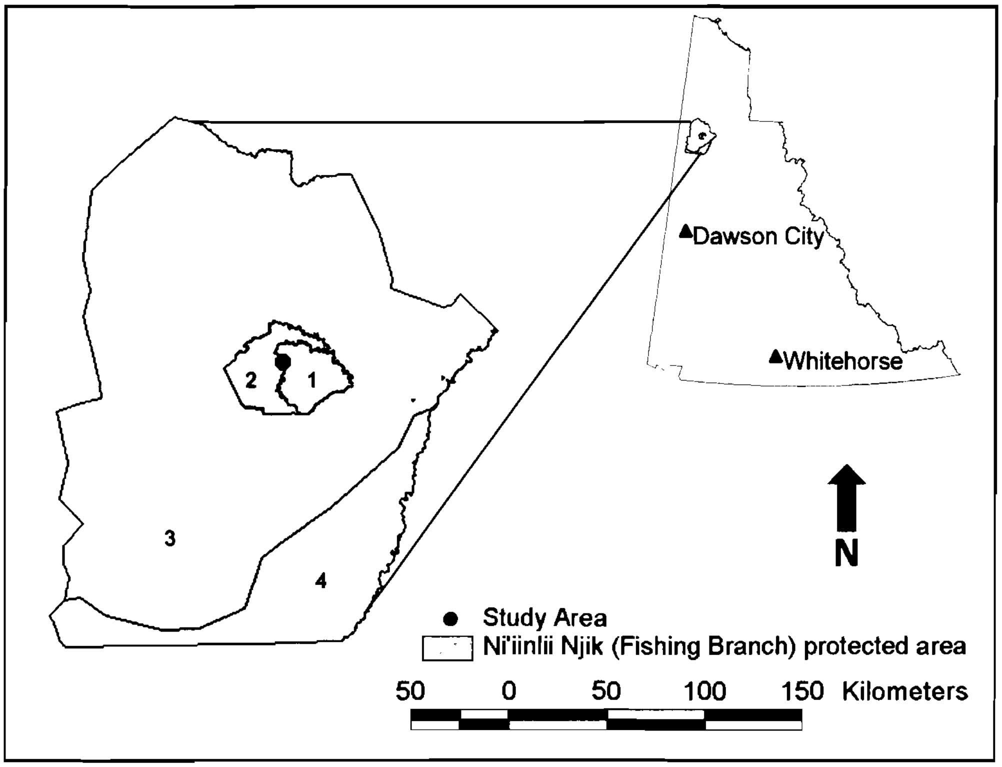

Figure 3-1. Study area in the Ni'iinlii Njik (Fishing Branch) protected area complex, Yukon. Divisions within the protected area represent the Vuntut Gwitchin Settlement Lands (1), Ecological Reserve (2), Wilderness Preserve (3), and Habitat Protection Area (4).

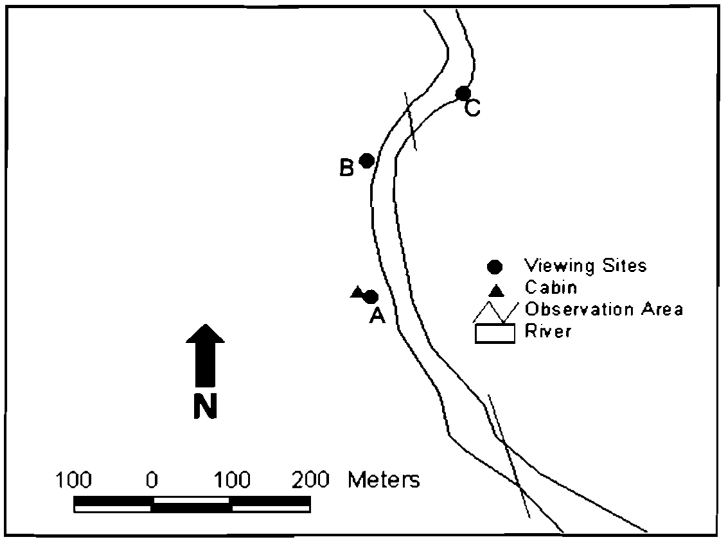

Figure 3-2. Commercial bear viewing area and research site along the Fishing Branch River, Yukon, 2005.

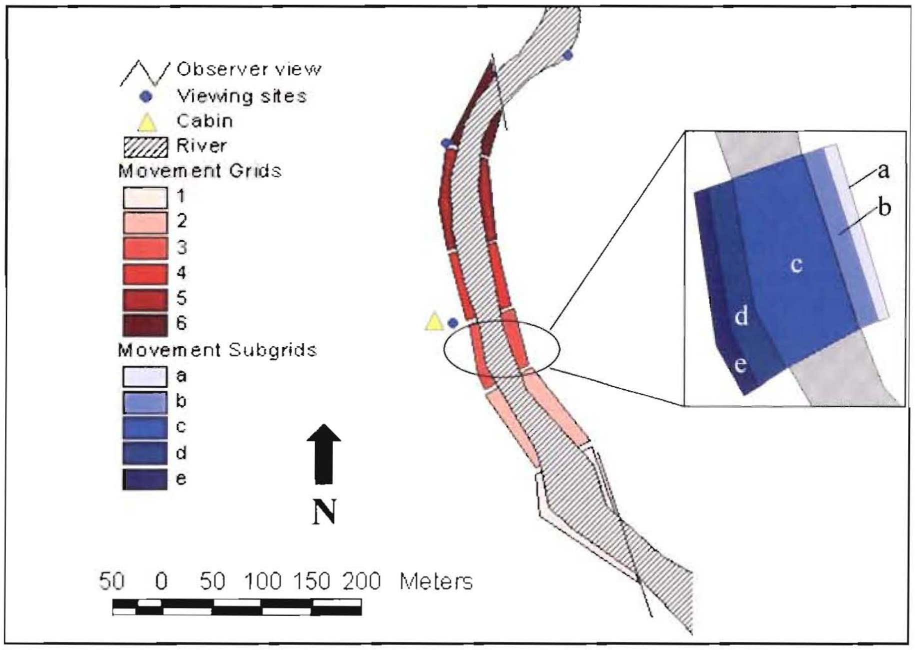

Figure 3-3. Grids (1-6) and an example of subdivision within each grid (a-e) used to monitor grizzly bear movement along the Fishing Branch River, Yukon, 2005.

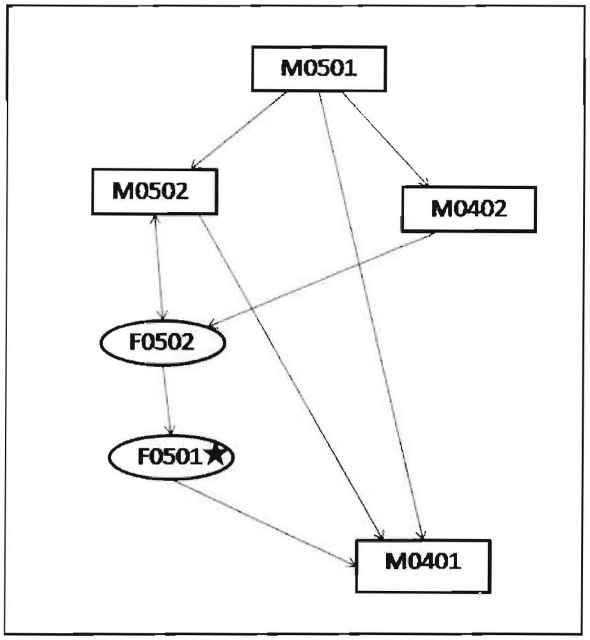

Figure 3-4. Dominant-subordinate relationships observed between the six adult grizzly bears along the Fishing Branch River, Yukon, 2005. I did not observe interactions between all possible pairs of bears, which was reflected in the loose organization of this hierarchy diagram. Square outlines indicate male bears, circle outlines indicate female bears, and stars indicate females with young. Single direction arrows point at the subordinate individual in the connected pair. Two-way arrows indicate reversal interactions where both individuals in the pair dominated at least one interaction.

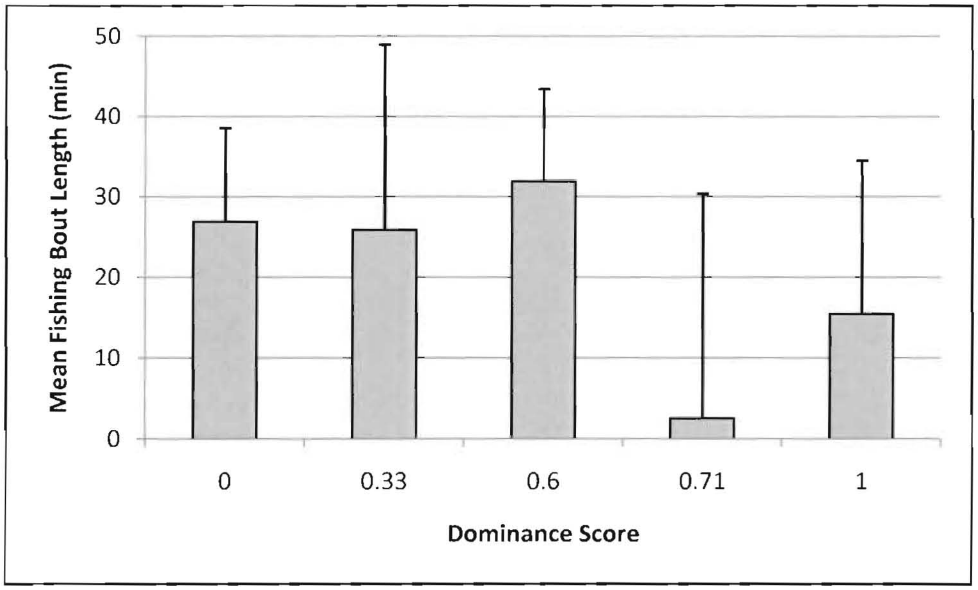

Figure 3-5. Mean fishing bout length by dominance score of grizzly bears along the Fishing Branch River, Yukon, 2005. Dominance scores ranged from zero to one where zero was the most subordinate individual and one was the most dominant individual. Error bars indicate 95 % confidence intervals.

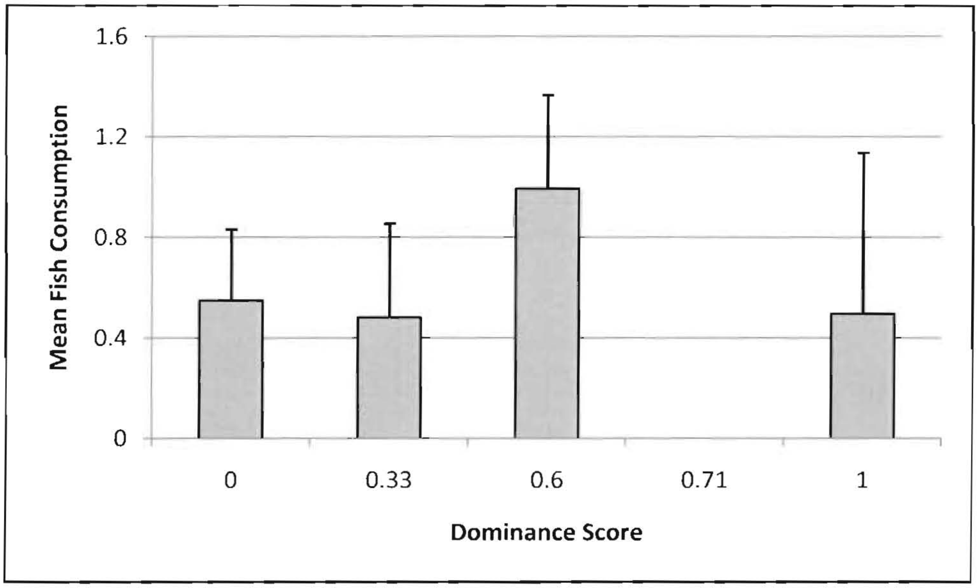

Figure 3-6. Mean fish consumption per fishing bout by dominance score of grizzly bears along the Fishing Branch River, Yukon, 2005. Dominance scores ranged from zero to one where zero was the most subordinate individual and one was the most dominant individual. Error bars indicate 95 % confidence intervals.

Chapter 4: General discussion

SUMMARY

Tourism is the largest industry in the global economy, employing an estimated 200 million people and creating approximately $3.5 trillion in economic activity (The International Ecotourism Society 2005). In the Yukon, tourism is the largest private employer with approximately 80 % of all employed Yukon residents working for businesses that reported some amount of tourism revenue (Yukon Government Department of Tourism and Culture 2007). Wildlife-based ecotourism featuring large mammals in their natural environment has rapidly grown in popularity. In particular, bear viewing is overwhelmingly popular, prompting managers to limit viewer numbers at many sites to minimize human impacts on bears and their habitat (U.S. Forest Service 1989, Aumiller and Matt 1994). Bear viewing has shifted bears' behaviour and activity patterns spatially and/or temporally, in some cases reducing their energetic intake (Olson and Gilbert 1994, Chi and Gilbert 1999, Crupi 2003).

Given the popularity of bear viewing and negative viewer effects at other bear viewing sites, the managing agencies for the Yukon's Ni'iinlii Njik (Fishing Branch) protected area complex required an investigation into the potential effects of a bear viewing program on grizzly bears (*Ursus arctos*) at the Fishing Branch River prior to the onset of commercial viewing. Bear viewing at the Fishing Branch River occurs during the fall chum salmon (*Oncorhynchus keta*) run because bears congregate along the river to exploit this high energy resource. My research goals were to investigate the potential effects of bear viewing on these grizzly bears at the Fishing Branch River and provide area managers with recommendations for further research, management of the viewing program, and measures to mitigate negative viewer effects on bears. I also assessed whether a dominance hierarchy existed among these bears at the Fishing Branch River, the nature of their intraspecific social interactions, and the influence of social dominance on fishing behaviour. My primary interest with social dominance was to characterize any dominance effect on fish consumption by grizzly bears because these dominance-dependent effects could compound any viewer-induced changes to fish consumption.

Habituated bears characteristically show little response to human presence and are commonly observed fishing near human activity when it coincides with high salmon availability or minimal conspecific competition (Olson and Gilbert 1994, Chi and Gilbert 1999, Nevin and Gilbert 2005, Tollefson et al. 2005). Olson and Gilbert (1994) found grizzly bears wary of human activity fed in suboptimal fishing areas of Brooks River where human activity was lowest. In contrast, habituated bears exploited highly efficient fishing sites regardless of their proximity to human activity (Olson and Gilbert 1994). At Anan Creek, almost half of the black bears (*U. americanus*) were spatially displaced by bear viewers and moved to viewer prohibited areas where they could fish undisturbed (Chi and Gilbert 1999). The habituation status of bears at the Fishing Branch River largely explained their fishing site preferences. Viewer presence and the indirect effects of camp (e.g., infrastructure and human odors) influenced bears' spatial use of the Fishing Branch River. Bears wary of human activity were negatively influenced by viewers or camp preferring to fish away from human activity or in viewer absence.

Bears reduced their fish consumption by 24 % when viewers were present, which likely resulted from their 17 % less time spent fishing with viewers present. Viewer presence was the second-most important variable for predicting fish consumption, second only to fishing bout length. Conspecific activity, resource availability, and dominance status had little influence on fish consumption. Although the 24 % reduction in fish consumption can have drastic effects on bears' health, I was unable to evaluate any potential spatio-temporal compensation for viewer presence. Bear behaviour is very adaptable giving them the ability to compensate for factors that alter their natural behaviour, such as the presence of bear viewers (Gilbert 1989). Spatio-temporal compensation for human activity at bear viewing areas has been documented on numerous occasions (e.g., Klinka and Reimchen 2002, Smith 2002, Crupi 2003, Rode et al. 2006). Bears along the Fishing Branch River may have taken similar compensatory approaches by increasing their nocturnal foraging or maximizing their foraging in areas with lower human activity. However, spatio-temporal compensatory feeding can only occur if sufficient feeding opportunities exist. Other bears may fully occupy these potential compensatory times and locations leaving limited opportunity for bears displaced by viewer activity. I found little evidence that uncontrollable, between-year environmental factors (e.g., salmon abundance or summer forage quality) influenced fish consumption by these bears. I think that the negligible influence of uncontrollable year factors means that the viewer effects I found on fish consumption were not an artifact of the state of these uncontrollable year effects that particular year, 2005.

Bear use of the Fishing Branch River varied greatly throughout the season, ranging from 0 – 60 % during sampling sessions. Low bear numbers, high salmon abundance, and increased number of fishing locations due to abnormally low water levels all contributed to this variability in bear use. As the season progressed, the prevalence of sampling sessions without bear use increased drastically. This pattern could result from a natural decline in consumption (Crupi 2003) or reduced fishing effort required to reach satiation because of increased availability of live salmon and carcasses towards the season's end. Hourly bear use was lowest in the first hour of sampling sessions and lowest during morning sampling sessions. I think low bear use during morning sampling sessions was an artifact of preferential fishing during the twilight hours prior to the morning sampling session. I was unable to sample these twilight periods because of insufficient light conditions. High bear use at this time is common at other fishing sites (Warner 1987, Olson et al. 1998, Smith 2002, Crupi 2003, Nevin and Gilbert 2005). Thus, many bears probably reached satiation prior to my morning sampling sessions and consequently were off the river, likely resting, for part of the morning sessions. Reduced bear use in the first hour of sampling sessions has been attributed to the movement of viewer groups to viewing sites (Rode et al. 2006). Viewer movement was an unlikely cause of this observed pattern because viewer activity was minimal at the Fishing Branch River. Although I travelled to the tree-stand for each sampling session, the travel distance was less than 15 m and largely concealed from fishing bears by vegetation. With human activity as an unlikely cause of the seasonal and daily use patterns of these bears, I anticipate these patterns largely reflect the natural use patterns of these bears along the Fishing Branch River.

Variability in bears' tendency to interact and propensity to interact with particular individuals better explained their unequal interaction rates than the amount of time they spent on the river. I detected a loose dominance hierarchy among these bears, with inconclusive structure among individuals of intermediate dominance. I found the majority of social interactions along the Fishing Branch River were aggressive in nature, mostly involving the dominant individual. Resource guarding was an unlikely explanation for the aggressive nature of these interactions because this behaviour is only energetically favourable when resources are limited. I think the predominance of aggressive interactions resulted from the propensity of the dominant individual to aggressively interact independent of resource availability. Pre-established dominance, individual tendency to interact, and satiation all contributed to the minimum distance maintained between bears during passive interactions. Although a general dominance hierarchy was evident in the grizzly bears along the Fishing Branch River, I found that dominance status had no measurable effect on bears' fishing bout length or fish consumption. Above-average salmon abundance and few conspecifics using the river minimized competition driven by resource guarding. Hence, bears of all dominance status had temporally or spatially unimpeded access to salmon along the river.

FURTHER RESEARCH

I strongly recommend further investigation into potential spatio-temporal compensation for the viewer-induced reduction of fish consumption by bears around high human activity. Research must include a well designed sampling regime that includes the presence/absence of viewers and samples fish consumption in areas of higher and lower human activity within a single viewing season. I recommend incorporating three additional variables into the analysis of viewer effects on bears' fish consumption: index of body condition upon arrival at river, time spent in vigilant activities, and an index of bear use by bears more dominant than the focal bear in the 24 hours preceding the focal bear's fishing bout. My study design and sample size did not permit inclusion of these variables despite their potential to alter the importance and magnitude of viewer effects on fish consumption by bears.

I was unable to incorporate the year variable into the analysis of viewer effects on fish consumption because of inconsistent data collection techniques between 2004 and 2005. Any future research should be designed with consistent between-year sampling to accommodate all variables in one analysis. Small sample size may have influenced my assessment of behavioural changes by bears in response to viewer presence. I recommend further investigation into the behavioural adaptability of these Fishing Branch River bears in response to viewer activity with emphasis on increased sample sizes to help reduce variation in individual behaviours. With human activity an unlikely cause of the seasonal and daily patterns of bear use, I anticipate these patterns largely reflect the natural use patterns of bears at the Fishing Branch River. I recommend assessing seasonal and daily use patterns of these bears during a commercial viewing season to evaluate whether consistent viewer activity alters their pre-viewing patterns of use.

I expect dominance status to influence fishing behaviour of bears in years with less abundant salmon. As a result, I recommend monitoring dominance and fish consumption of bears along the Fishing Branch River during a year with low salmon abundance. Because these bears reduced their fish consumption with viewers present, further reduction in consumption during low salmon years poses serious energetic consequences for less dominant bears. If this compounding reduction in fish consumption occurs, managers should alter the viewing program to create human-free fishing times for bears to compensate for their reduced fish consumption when viewers are present.

Similar to research at other bear viewing sites, I found that habituation reduces the negative effects of viewers on bears. Managing for habituation of bears along the Fishing Branch River may be an effective means to minimize viewer impacts on these bears. The negative effects of viewers could be temporary and become minimal as bears increasingly habituate to bear viewers. A literature review of habituation by grizzly bears should be conducted with particular notice of the length of time it takes for bears to become habituated in relation to the amount and nature of human contact.

RECOMMENDATIONS FOR BEAR VIEWING

I provide the following recommendations for bear viewing based on my research.

- Outline viewer prohibited areas on a map to clarify human-free zones. Include with the map, an explanation about the effects of viewing on energy intake (Tables 2-5 and 2-6), spatial river use of these bears (Figs. 2-3 and 2-4), and why human-free zones are needed to ensure bears can feed unimpeded.

- Develop indices of habituation into the monitoring program. Only the spatial river use of wary bears was negatively influenced by human activity (Figs. 2-3 and 2-4). If bears become habituated over time to commercial viewing activities, perhaps additional viewing opportunities could be permitted.
- Develop special viewing protocols in years with low salmon availability to minimize effects of viewers on bears if dominance status appears to influence fish consumption by these bears (e.g., create consistent human-free daylight periods giving bears unimpeded access to the river).
- Maintain the current limit of five people using the viewing area to minimize impacts on the bears at least until it can be shown that bears compensate for the negative effects of viewers on their fish consumption.

I have other recommendations that would minimize effects on bears during the viewing season based on my experiences at the commercial bear viewing site.

- Continue using the three identified viewing sites. These sites are well placed with respect to visibility for high quality viewing and safety and they create a human-free zone immediately downstream of the viewing area in a heavily spawned area where compensatory feeding by bears can potentially occur.
- Do not stop and view bears on the trails between viewing sites. Viewing bears from trails turns a briefly-used travel corridor for viewers into an additional viewing area. Viewers should only stop on trails for safety reasons such as encountering a bear along the trail.
- Prohibit bear viewing during darkness because safety is highly compromised from the difficulty in detecting bears.
- Continue monitoring viewer effects on bears with the annual monitoring program, ideally with a managing agency staff member collecting data rather than the guide to maximize data quality.
- Continue to collect bear hair samples annually to confirm presence of individual bears and to track annual changes in diet as found through isotope analysis.

RECOMMENDATIONS TO MITIGATE EFFECTS ON BEARS

I recommend several measures to mitigate viewer effects on grizzly bears of the Fishing Branch River, particularly if minimal spatio-temporal compensatory behaviours are found. Daily viewing hours should be restricted. Many other bear viewing sites (e.g., Pack Creek, Brooks River, Glendale Cove, and Khutzeymateen Sanctuary) limit daily viewing hours to permit bears daylight fishing hours free of human activity (U.S. Forest Service 1988, National Park Service 2001, Pitts 2001, McGrady 2003). Consistently maintaining these viewing hour restrictions creates predictable viewing patterns where bears learn which hours are free of human activity and thus, fish accordingly. Based on the patterns of bear use at the Fishing Branch River, designating non-viewing days in the first half of the viewing season and/or either midday or evening human-free times would be effective measures to mitigate any negative viewer effects on bears because they coincide with the highest bear use periods.

Secondly, I recommend developing a consistent viewing schedule for each of the three viewing sites but staggered among sites. Movement of viewer groups to and from viewing sites has reduced bear activity (Rode et al. 2006). Scheduling consistent viewing times at specific viewing sites allows bears to learn these patterns of viewer movement and respond accordingly, either by avoiding or becoming accustomed to this predictable viewer movement.

Lastly, I recommend further restricting the movement of bear viewers around the viewing area. I acknowledge current restrictions on viewer movement; however, crossing the Fishing Branch River to reach a denning cave or to summit Bear Cave Mountain is potentially quite disruptive because it requires viewer presence in a highly used bear resting area and travel corridor. These hikes should be reduced or stopped because they enlarge the footprint of human activity. Many other bear viewing sites greatly restrict viewer movement, such that viewers are only permitted at the viewing sites or on the trails between viewing sites and hikes equivalent to those at the Fishing Branch River are prohibited (U.S. Forest Service 1988, Aumiller and Matt 1994, McGrady 2003).

I recommend employing these mitigating measures one per season if insufficient spatio-temporal compensatory feeding behaviours are found. By implementing one measure per season, the effectiveness of each measure can be assessed individually rather than the mixed effect of all mitigating measures. In addition, implementing only the necessary mitigation measures will minimize restrictions on the viewing program.

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APPENDICES

APPENDIX 1. REMOTE VIDEO CAMERA

The remote camera system was comprised of three subsystems: video camera, energy system, and base station. This system was designed to operate for four hours in temperatures as low as –15°C. The laptop, video recorder, and video link must be operated at temperatures above 0°C and were thus stored in the cabin. Batteries were charged at room temperature. Below are the technical specifications for the components of each subsystem.

Subsystem	Component	Model Number
Camera	Video Camera	Panasonic® WV-CP484 1/3" Colour Video Camera
	Weather-Proof Enclosure	Pelco® EH5723
	Lens	Tamron 1/3" 20-100mm A/I SQ 13VG20100
	Video Link	Analog video transmitter 2.4GHz, 3W, 8 channels
	Heater	12W foil heating element
	Datalink	MaxStream™ Serial Datalink 19.2 kbaud, 900 MHz
	Controller	Homemade microcontroller board (based on a Atmega8), features: - temperature monitoring and regulation - battery over-discharge protection - camera on/off remote control - low temperature protection for batteries - conformally coded
	External Connectors and Cables	Waterproof, armoured
Energy System	Rechargeable Battery	Panasonic® lead acid 12V, 33Ah
	Enclosure	NATO ammunition box
	Charger	Lead acid battery charger, 12V 10A
Base Station	Commercial Laptop	Dell™ Inspiron 6000 with Microsoft XP®
	Control Software	Homemade, features: - based on QT4.0 platform independent (UNIX and Microsoft) - on/off camera control - monitor camera temperature and battery voltage - data logging
	Video Receiver	Analog video receiver 2.4GHz, 3W, 8 channels
	External Antenna	
	Video Encoder	WinTV PVR2® Personal Video Recorder, USB
	Data Storage	External USB Harddrives (2 @ 230GB each)
	Datalink	MaxStream™ Serial Datalink 19.2 kbaud, 900 MHz

APPENDIX 2. PYTHON 2.1 CODE TO CALCULATE LANDAU'S INDEX OF LINEARITY (H') FOR SOCIAL DOMINANCE MATRICES CONTAINING UNOBSERVED DYAD INTERACTIONS

```
# import one of the numeric array modules
#
from numarray import *
from random import *

rows =
((5,1,1,0,0,1,1),(0,5,0,0.5,0,1,0),(0,0,5,1,0,0,0),(0,0.5,0,5,1,0,0),(0,0,0,0,5,1,1),(0,0,0,0,0,5
,0),(0,0,0,0,0,0,5))

numbears = 7
repetitions = 10000

# fill dominance matrix

dommat = zeros((numbears+1,numbears+1), Float)
tempmat = zeros((numbears+1,numbears+1), Float)
randmat = zeros((numbears+1,numbears+1), Float)

for i in range (0,numbears):
    for j in range (0,numbears):
        dommat[i+1,j+1] = rows[i][j]

# set counters

counter = 0.0
hrGTEh0 = 0.0
hrLTEh0 = 0.0

for k in range (1,repetitions+1):

# make temporary matrix

    for i in range (1,numbears):
        for j in range (i+1,numbears+1):
            if dommat[i,j] == 0 and dommat[j,i] == 0:
 #                print i,",",j," is an unknown pair"
                y = random()
 #                print "random = ",y
                if y <= 0.5:
                    tempmat[i,j] = 1
                    tempmat[j,i] = 0
```

```
          else:
             tempmat[i,j] = 0
             tempmat[j,i] = 1
       else:
          tempmat[i,j] = dommat[i,j]
          tempmat[j,i] = dommat[j,i]

# calculate h0

   totsum=0
   for i in range (1,numbears+1):
      rowsum = 0.0
      sumsign = 0.0
      for j in range(1,numbears+1):
         rowsum = rowsum + tempmat[i,j]
#        print "rowsum = ", rowsum
      sumsign = power((rowsum-(numbears-1)/2),2)
      totsum = totsum + sumsign

   h0 = 12*totsum/(numbears*numbears*numbears-numbears)


# make random matrix

   for i in range (1,numbears):
      for j in range (i+1,numbears+1):
         y = random()
         if y <= 0.5:
            randmat[i,j] = 1
            randmat[j,i] = 0
         else:
            randmat[i,j] = 0
            randmat[j,i] = 1

#   print " "
# calculate hr
   totsum=0
   for i in range (1,numbears+1):
      rowsum = 0.0
      sumsign = 0.0
      for j in range(1,numbears+1):
         rowsum = rowsum + randmat[i,j]
#        print "rowsum = ",rowsum
      sumsign = power((rowsum-(numbears-1)/2),2)
      totsum = totsum + sumsign
```

```
    hr = 12*totsum/(numbears*numbears*numbears-numbears)

# update counters
    counter = counter + 1
    if hr >= h0:
        hrGTEh0 = hrGTEh0 + 1
#           print "hr >= h0", hrGTEh0
    elif hr <= h0:
        hrLTEh0 = hrLTEh0 + 1
#           print "hr <= h0"
#       print "hr = ",hr," h0 = ",h0

# calculate probabilities
Pr = hrGTEh0/counter
Pl = hrLTEh0/counter

print "total repetitions: ",counter
print "Pr = ",Pr
print "Pl = ",Pl
```