

Sensory modes, foraging profitability, colour polymorphism and behavioural plasticity in  
coastal bear populations

by

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### Abstract

Mammalian carnivores can augment their temporal foraging niche by shifting to alternate sensory modes, and this can result in greater phenotypic and behavioural variability. Temporal shifts in activity patterns provide an opportunity to investigate changes in foraging strategies in species that exhibit such behavioural and phenotypic variability. To this end, I compared the diurnal and nocturnal foraging of two colour morphs of a polymorphic subspecies of black bear (*Ursus americanus kermodei*) on a salmon stream in British Columbia. I found that bears ( $N_{\text{White}}=4$ ,  $N_{\text{Black}}=37$ ) adjusted fishing behaviour according to light level and salmon abundance, and foraging efficiency varied between colour morphs and light level. Salmon were significantly more active but less timid during darkness, and were most timid towards the black morph during daylight which may have accounted for the significant differences in foraging efficiencies between morphs among light levels. Isotope analysis of hair segments obtained from a large scale sampling regime indicated dietary divergence between morphs among seasons and localities. White bears incorporated more marine derived nutrients into their diets than black morphs in many localities. Overall, both morphs were similar during non-foraging behaviours and social interactions among light levels. Bears spent 38% of observed time feeding which remained relatively consistent among light levels; however, scavenging was minimal during darkness. Of the 460 social interactions I observed, the majority (59%) were of low intensity and relatively few (15%) were of high intensity, and this was consistent among light levels. Among 45 high intensity encounters observed between black and white morphs, black was dominant to white more frequently than vice versa (58%), but this effect occurred only during darkness and twilight. This study indicates that bears are able to maximize foraging opportunities within multiple temporal regimes through shifts in sensory systems and by altering their behaviour according to light level.

**Keywords:** sensory modes; nocturnal behaviour; colour polymorphism; niche partitioning; foraging; black bear; *Ursus americanus*; Kermode bear; *Ursus arctos*; Salmon; *Oncorhynchus*; stable isotopes; activity patterns; social interactions; night vision; British Columbia

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## **1 General Introduction**

### **1.1 Sensory modes and body colour variability**

Many animals are active in a variety of environmental conditions that may vary in foraging profitabilities and/or predation risk, even though specialization and reliance on particular sensory modes tend to streamline activity to specific environmental conditions. One environmental condition that provides an opportunity to explore the degree of reliance on particular sensory modes is light level. Ambient light levels often strongly influence circadian rhythms, activity patterns, and foraging strategies as animals respond to changes in prey availability and vulnerability that are known to vary among light regimes. Theoretically, extending foraging behaviour into alternate temporal regimes will require different sensory modes, and produce different costs and benefits. For example, some of the benefits to nocturnal foraging are increased prey susceptibility and availability (McMahon and Evans 1992b, Thibault and McNeil 1995, Reimchen 1998b) and reduced predation risk and competition (Culp et al. 1991), while some of the costs of nocturnal foraging are associated with the compromise that comes with using primary sensory systems not ideally suited for depressed light regimes.

The primary sensory systems of an animal are shaped by the width and the time periods occupied by its preferred temporal niche and hunting modalities, and the behaviour of both its predators and prey. These factors may compromise an animal's ability to extend its activity into alternate light regimes. As a result, diurnally active predators tend to rely on visually based sensory systems while nocturnally active predators rely on tactile, chemical and auditory based sensory modes for prey detection

and pursuit (Montgomery and Milton 1993, Downes and Shine 1998). In contrast, animals occupying a wide temporal niche cope with non-specialized sensory systems by switching to alternate sensory modes during darkness (Beugnon and Fourcassie 1988, McMahon and Evans 1992a).

Sensory systems are also important during social interactions with conspecifics, notably in mammalian carnivores. For instance, it is known that agonistic signals in the form of visual cues are important in regulating social organization in large carnivores (Mech 1970, Stonorov and Stokes 1972, Egbert and Stokes 1976, Clutton-Brock et al. 1979, Latour 1981a, Latour 1981b, Reimchen 1998b). If visual cues are important in regulating social interactions then one might expect differences in the levels of agonistic interactions among light levels as it remains unclear how social dynamics are affected by the absence of visual cues.

For large mammals, the direct comparisons of behaviour among light levels have been historically limited due to logistical constraints with respect to night viewing equipment. With the development of light amplifying technologies, the importance of visual cues on numerous aspects of behaviour can be evaluated.

Flexibility in the use and utility of multiple sensory modes can result in greater phenotypic and behavioural variability, with some species exhibiting multiple trophic structures. Variability in trophic structure allows for the exploitation of different spatial conditions (multiple niches) and provides a mechanism for the establishment and persistence of variability within species. One striking example of variability within a species is colour polymorphism.

The highly variable colouration patterns and numerous colour polymorphisms observed in carnivores such as felids and canids (Mech 1970, Guggisberg 1975) and avian predators (Rohwer and Paulson 1987, Rohwer 1990, Galeotti et al. 2003) may be in part maintained by resource and niche partitioning (Recher and Recher 1972, Mock 1980, Rohwer 1990, Itoh 1991). Colour polymorphism may contribute to variable foraging success among morphs, as the visual and behavioural responses of prey may vary towards different coloured morphs. This effect could confer a temporary foraging advantage to the appropriate coloured morph (Murton 1971, Mock 1980). For instance, examples of multiple-niche partitioning are observed in the various colour morphs of wading shorebirds where different coloured morphs may vary in success in different habitats or in the same habitat under different light conditions (Galeotti et al. 2003). This is thought to be due to differences in foraging efficiency caused by variation in hunting camouflage (Cott 1940).

Although niche partitioning may involve a form of dietary divergence between morphs, direct measures of animal diets with conventional methods such as direct observation, scat or stomach analysis have been problematic for a variety of reasons. Unequal digestibility of food, inability to locate scat, elusive or wide ranging animals to ethical considerations and the practicalities of stomach analysis of rare or endangered species have all hampered our ability to investigate the diets of free ranging wildlife (Hilderbrand et al. 1996, Hobson et al. 2000, Darimont and Reimchen 2002). However, stable isotope analyses have recently been utilized to examine the trophic ecology of many animals, and its use has seen a dramatic increase and attention as it augments traditional dietary information (Kelly 2000).

Other forms of niche partitioning may involve aspects of behaviour unrelated to foraging. An example of this could be differences between morphs in social interactions (agonistic) possibly leading to spatial segregation among habitats. Another example might be attempts at avoiding predation through crypsis (Kettlewell 1955, Reimchen 1979, Palma and Steneck 2001).

Although the occurrence of polymorphic species is taxonomically widespread, the origin and the basic mechanisms maintaining most polymorphisms are not well understood (Jones et al. 1977, Losey et al. 1997), and there are no relevant data on most species to test competing hypotheses. One species that provides an excellent opportunity to explore the mechanisms maintaining colour polymorphism in a large mammalian carnivore is the Kermode bear (*Ursus americanus kermodei*) of British Columbia.

## 1.2 *Ursus americanus kermodei*

On the northwest coast of British Columbia (Fig. 1), a sub-species of black bear (*Ursus americanus kermodei*) has two distinct and heritable hair colour phenotypes (Fig. 2). The black-coloured form predominates over its range, but on some islands the white form or 'Spirit Bear' can occur in frequencies of 10%-20% (Ritland et al. 2001). Genetic models predict the loss of white morph due to allele fixation in small populations (Futuyma 1998). Gene flow from adjacent localities can mitigate effects of allele fixation, but data from Ritland et al. (2001) predict the loss of the white morph as gene flow from neighboring populations tends to increase the frequency of the dominant black allele while decreasing the frequency of the recessive white allele. A form of heterozygote advantage would increase the frequency of the white allele in the population; however,

current data indicate a deficit of heterozygotes on islands where the white morph is most common (Ritland et al. 2001, Marshall and Ritland 2002).

In light of these genetic data, it seems that some form of selection favoring the white morph is occurring. One form of niche partitioning that may be occurring is a form of dietary divergence between morphs, perhaps in their consumption of Pacific salmon. This seems like a reasonable hypothesis as coastal bears receive most (33-94%) of their yearly protein from salmon (Hilderbrand et al. 1996, Jacoby et al. 1999), making the spawning season a critical time period in which to gather sufficient food resources necessary for over wintering survival. Given this, natural selection should favour behavioural strategies which maximize foraging efficiency and consumption during the short period of prey availability, and colour morphs may differ in these foraging attributes.

Alternative explanations could be divergent spring, summer and fall diets or segregation of habitat use along spatial and temporal scales. Perhaps the white pelage of the Kermode bear could have thermoregulatory functions in reflecting heat energy (Marshall and Ritland 2002). However, thermoregulation seems unlikely to be important while foraging for salmon as bears of both colours are typically in water for long periods of time. However, thermoregulatory functions could have increased importance outside of spawning periods as black fur absorbs significant amounts of solar heat energy (Moen and Rogers 1985).

In addition to being a convenient system to evaluate foraging niche differentiation, the Kermode bears also enable an assessment of differential utilization of sensory systems among light regimes. Black bears have been classified as a diurnal

species throughout North America, but are known to expanding their activity patterns into darkness in areas where they compete for resources with brown bears (*U. arctos*) and where human activities occur during daylight (Lariviere et al. 1994a, Maehr 1997). While much research has been focused on their diurnal behaviour, the nocturnal foraging behaviour of bears has not been well documented. Also it was assumed that bears would be limited to scavenging on salmon since they lack visual cues during darkness necessary for visually-oriented predators. Thus nocturnal foraging by black bears was interpreted as an ecological exclusion from preferred foraging periods (Machutchon et al. 1997, Olson et al. 1998). This interpretation is not supported by Reimchen's (1998b), and Frame's (1974) observations of nocturnal foraging by black bears in salmon systems where both brown bears and human intrusion were absent. Some benefits to nocturnal foraging bears are decreased evasive responses of salmon, and fewer aggressive interactions with conspecifics.

In this thesis I will investigate how light levels are associated with sensory systems and examine evidence for multineche polymorphism between black and white bears that could be responsible for the maintenance of this colour polymorphism. In Chapter 3, I will examine feeding and locomotory behaviours between colour morphs among light levels. In Chapter 4, I will compare aspects of foraging behaviour (such as capture efficiencies) between colour morphs among light levels. In Chapter 5, I will examine evasive responses of salmon to a simulated polymorphic predator among light levels. In Chapter 6, I will evaluate niche partitioning between colour morphs through analysis of stable carbon and nitrogen isotope ratios of hair segments. In Chapter 7, I will investigate the dynamics of social interactions between morphs among light regimes in

order to evaluate the importance of visual cues in shaping the social interactions of this carnivore. In addition, I relate the social interactions to mechanisms maintaining the polymorphism in this bear population.

The simultaneous examination of multiple behavioural attributes of this polymorphic bear population provides an ideal setting to investigate ecological factors shaping the evolution of sensory systems, while at the same time allowing for the examination of the role of multineche differentiation in the maintenance of colour polymorphism.

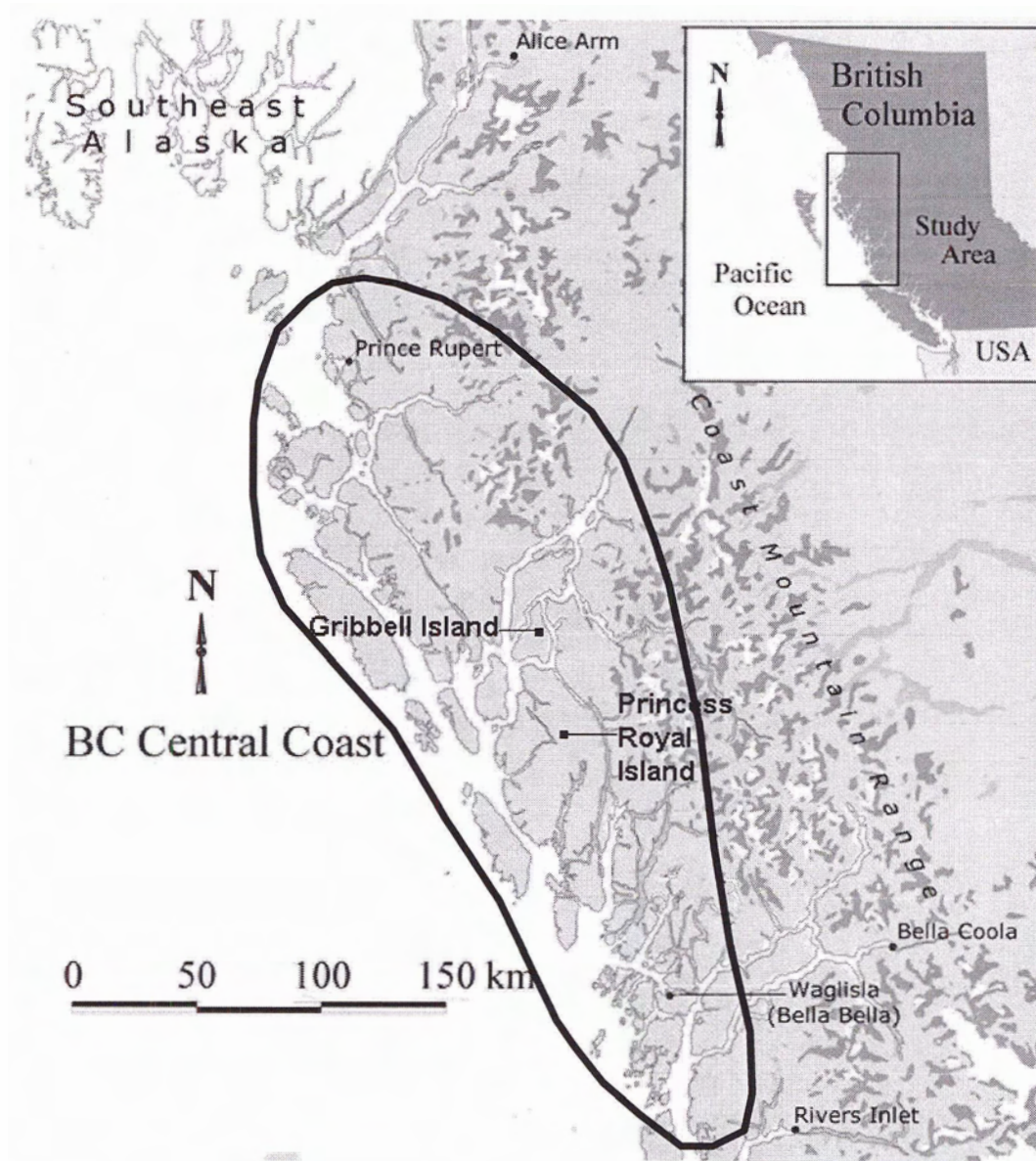


Figure 1. The northwest coast of British Columbia and the range of the Kermode bear (*Ursus americanus kermodei*).



Figure 2. Black and white colour morphs of the Kermode bear.

## 2 Site description and general methodology

### 2.1 Site description

From late August to early October, 2000-2002, I conducted detailed observations of bear fishing behaviour along Riordan Creek on Gribbell Island, on the northwest of BC (128°58'16'' W, 53°25'26'' N; Fig. 3.). Riordan Creek is situated in the very wet hyper-maritime (CWHvh2) sub zone of the Coastal Western Hemlock Biogeoclimatic Zone (Green and Klinka 1994). Climate is cool and wet with mean annual temperature of approximately 8C, and mean annual precipitation in excess of 4000 mm (Environment Canada 1991). Dominant tree species include Western Hemlock (*Tsuga heterophylla*), Sitka spruce (*Picea sitchensis*), Amabilis fir (*Abies amabilis*), Western redcedar (*Thuja plicata*), and Red alder (*Alnus rubra*). Common understory species include Alaskan blueberry (*Vaccinium alaskaense*), red huckleberry (*V. parvifolium*), false azalea (*Menziesia feruginea*), deer fern (*Blechnum spicant*), bunchberry (*Cornus canadensis*), lanky moss (*Rhytidiadelphus loreus*), step moss (*Hylocomium splendens*), and common green sphagnum (*Sphagnum girgensohnii*) on zonal sites, and salmonberry (*Rubus spectabilis*), red elderberry (*Sambucus racemosa*), stink current (*Ribes bracteosum*), and spiny-wood fern (*Dryopteris expansa*) on nutrient rich sites.

Riordan Creek is the outflow for a watershed shaped as a large bowl, and is surrounded by steep cliffs on both sides. During the late 1980's, this watershed was clear-cut up to the streamside in most locations except a portion near the mouth. As a consequence, Riordan Creek is subject to severe water fluctuations whereby heavy rains

cause severe flooding, while periods of dry weather cause the stream to drop substantially.

The Riordan Creek watershed supports a minor annual return of pink salmon (*Oncorhynchus gorbuscha*), along with some chum (*O. keta*) and coho salmon (*O. kisutch*). In the last ten years, pink, coho and chum salmon returns on Riordan Creek average 800, 100 and 20 individuals respectively (Department of Fisheries and Oceans Escapement data: 1990–2000). For all species, spawning begins in early September and is complete in early October.

Suitable spawning habitat extends for roughly 2.0 km from an upstream waterfall and lagoon. Although salmon can navigate past the waterfall, there are few suitable spawning areas upstream from the lagoon. Riordan Creek averages 12m in width and depths are typically less than 40cm. Fallen logs occasionally collect in certain areas along the spawning zone under which salmon will often pool during daylight hours.

Marten (*Martes americanus*), corvids and bald eagles (*Haliaeetus leucocephalus*) are active on the creek while salmon are spawning, but the dominant animal active during this time period are black bears (*Ursus americanus*). Bears capture large numbers of live salmon and consume them either on the bank or carry the carcass into the forest or heavy brush on the stream-bank. Bears and marten, along with birds and insects will typically scavenge the remnants of bear killed or naturally senescent salmon.



Figure 3. Satellite photo of the study area on Gribbell Island. Riordan Creek and IR10 creek are visible in NE and SW corners of the island. Neighbouring locality of Princess Royal Island is directly south. Photo available from <http://www.planlink.ca/>

## 2.2

### General Methodology

During the fall spawning runs in 2000-2002, I set up a research field camp near the mouth of the creek, which was approximately 1km from a favorable viewing site. Along with an assistant, we video-taped with a digital camcorder (SONY DCR-TRV720) and catalogued the bear-salmon interactions that form the majority of this thesis. Most observations of bears were from a fallen log spanning the river. The majority of observations were during daylight (average eight hours per day); however I staggered observation sessions to include times during twilight (average one hour per day) and three hours per day during darkness. However, no data were collected during Sept 4 to Sept 16, 2000, due to logistical constraints.

Human presence in the viewing area for the first two years of the study was restricted to myself and my assistant, however during the final year it consisted of various eco-tourism groups present for eight hour observation periods during daylight hours, three times per week.

Nocturnal observation sessions required light amplifying equipment and a voice recorder. All nocturnal observations were through a hand-held night vision monocular (ITT model CSC-N16140-DX, 50,000 X amplification, 0.95 cycles per milliradian resolution) aided with an infra-red emitter (880 nm) in extremely low light conditions. During darkness, I tape-recorded and later transcribed all my observations.

Over the duration of the study, I observed 37 individual black bears and four white bears. No brown bears were observed during the study. I used facial scaring

patterns to identify individual bears. I recorded fishing behaviour and interactions for all bears during the study period, including multiple observations per bear.

Bears were classified by colour morph (black or white), age-class (sub-adult, adult), and when possible, gender. Discrimination between adults and subadults was based on overall size of the bear, with larger bears (estimated mass >100 kg) classified as adults and smaller bears (estimated mass <100 kg) classified as sub-adults. Gender was determined by urinary posture and visual assessment of genitalia. No cubs were observed on the stream during the entire study.

## **Chapter 3: Behavioural activity patterns among light levels in a polymorphic bear population**

### **3.1 Introduction**

Animals show both seasonal and daily activity patterns that reflect behavioural adaptations in response to ecological factors such as fluctuating foraging profitabilities and competition. Animals seek to maximize foraging efficiency, resource availability and quality, and prey vulnerability (Lariviere and Messier 1997) while minimizing predation risk and competitive effects (herein defined as intraspecific competitive interference), thereby maximizing foraging profitability. Foraging profitabilities can be maximized with temporal shifts in diel foraging into more lucrative time periods and the investment of more time to feeding behaviours, while competitive interference can be reduced through temporal niche partitioning. In addition to the effects of minimizing competitive interference, niche partitioning is an especially useful mechanism contributing to our understanding of the maintenance of colour polymorphism in populations.

Color polymorphism occurs in many taxa (Rounds 1987, Colyn 1993, Franck et al. 2001, Johannesson and Ekendahl 2002, Galeotti et al. 2003) yet the origin and the basic mechanisms maintaining most polymorphisms are not well understood (Jones et al. 1977, Losey et al. 1997). Some hypotheses suggest that polymorphisms are functional traits maintained by multiple-niche partitioning (Smith 1990, Cook 1998). However, in most biological systems of interest, there are no relevant data on most species to test this hypothesis.

One form of niche partitioning is differential behaviour between colour morphs in areas relevant to foraging and locomotion. Varying the allocation of time to feeding on select food items that differ in nutritional content can significantly affect the total benefits (caloric intake) over time, especially during a period of abundant food availability (Krebs 1978). Similarly, maximum nutritional benefits are realized when allocating locomotory behaviours (standing, walking, and running) in such a manner as to minimize energy expenditure and maximize feeding opportunities. Optimum foraging and behavioural strategies may vary between colour morphs and across light levels, yet direct nocturnal observations of feeding and locomotory behaviour has been historically limited due to logistical constraints. The use of light-amplifying devices now enables such nocturnal-diurnal, and colour morph comparisons.

Black bears (*Ursus americanus*) are reported as being primarily diurnal throughout North America (Lariviere et al. 1994b, Machutcheon et al. 1997, Maehr 1997). However, with the aid of light-amplifying goggles, Reimchen (1994, 1998b) observed elevated nocturnal behaviour and stream visitation for black bears in British Columbia. In fact, bears in his study captured the majority of salmon during nocturnal foraging bouts, leading to the suggestion that night-time is preferred for foraging because of increased access to high quality feeding areas and reduced evasion by salmon, leading to high capture rates.

In addition to black bears, brown bears (*U. arctos*) also appear to exhibit extensive temporal variability in activity patterns. While they are well known to be diurnally active (Stonorov and Stokes 1972, Luque and Stokes 1976, Gilbert and Lanner 1995, Gende et al. 2001), crepuscular and nocturnal activity has also been reported (Gard

1971, Herrero 1985, Phillips 1987, Genov and Wanev 1992). Furthermore, Klinka and Reimchen (2002) recently reported substantial nocturnal foraging activity of a population of brown bears in coastal British Columbia.

In this paper I examine diurnal, crepuscular and nocturnal feeding and locomotory behaviours of a polymorphic subspecies of coastal black bear on a salmon stream in British Columbia. I predict that bears would exhibit behaviour comparable to that of other populations of black and brown bears on salmon streams, including foraging during the night. In addition, I predict that colour morphs would differ in measured feeding attributes in accordance with capture rates and efficiencies (see Chapter 4: Foraging).

### 3.1 **Methods and Materials**

#### 3.2.1 Temporal activity patterns: scan samples

I collected scan samples (Altmann 1974) by visually scanning the stream every 10 minutes during stream surveys within daylight, twilight and darkness. During scan samples, I recorded the total number of bears visible on the stream and segregated bears according to colour. I also assessed relative salmon abundance by counting the numbers of salmon in a delineated portion of the stream. With night vision goggles, my ability to detect bears on the stream was similar among light levels. To evaluate differences in diel patterns of stream visitation I used Kruskal-Wallis and Mann-Whitney U-tests. All time references are in 24 hour format.

#### 3.2.2 Individual time budgets

To evaluate overall time budgets of bears, I recorded the occurrence and duration of behaviours pertaining to their stream activities (Table 1), using focal animal sampling (Altmann 1974). Focal sampling of bears observed on the stream occurred during both 2001 and 2002 field seasons. I collected focal samples on adults that were readily recognizable by physical characteristics, namely scarring patterns, during daylight, twilight, and darkness. Only focal samples 5 minutes or longer in duration were included in subsequent analyses.

Behaviours recorded were similar between years but sampling methodologies differed slightly. During 2001, focal sampling occurred in the form of ‘focal interval

sampling', which is defined as recording a focal animal's behaviour at predetermined intervals. I recorded behaviour every 10 seconds for the duration of the observation session. Since during 'focal interval sampling' behaviours are not recorded continuously, there is a risk that rare behaviours of short duration will be omitted (Rose 2000). I identified two behaviours (attempts and successes) that were at risk to errors of omission and I attempted to compensate for this risk by recording them *ad libitum* independent of the focal sampling time interval. These *ad libitum* recordings were then incorporated into the overall focal animal sample. During 2002, focal animal sampling was recorded continuously.

The entire focal sample was manually entered into JWatcher (v 0.9), a behavioural analysis software package (Blumstein et al. 2000). I used this program to calculate the number of occurrences of behaviours, in addition to durations and the proportion of time occupied by individual behaviours. The data generated by JWatcher was then loaded into a database for statistical analysis using SPSS (v11.0).

I used both parametric and non-parametric statistics when comparing durations, and proportions of time among light levels and colour morphs. The proportion of time occupied by individual behaviours tended to be non-normal so I used non-parametric Kruskal-Wallis and Mann-Whitney U-tests to compare among light levels and bear colour. However, the actual mean durations of behaviours tended to be normally distributed after log transformation, and thus Student t-tests and ANOVA were used to compare among light levels and bear colour.

A total of 117 focal samples were included in the analysis ( $\bar{X}$  = 26.3 min  $\pm$  1.63 S.E.; range 5.7 min.-120.5 min.). These samples were distributed among light levels with

29 samples occurring during darkness ( $\bar{X}_{\text{Darkness}}=29.9 \text{ min} \pm 3.4 \text{ S.E.}$ ; range 6 min.-78 min.), 16 samples occurring during twilight ( $\bar{X}_{\text{Twilight}}=27.8 \text{ min} \pm 4.7 \text{ S.E.}$ ; range 11 min.-85 min.) and 72 samples occurring during daylight ( $\bar{X}_{\text{Daylight}}=24.5 \text{ min} \pm 2.0 \text{ S.E.}$ ; range 6 min.-120 min.). These samples included both black and white coloured bears ( $\bar{X}_{\text{Black}}=24.9 \text{ min} \pm 1.8 \text{ S.E.}$ ; range 6 min.-120 min.;  $\bar{X}_{\text{White}}=32.7 \text{ min} \pm 4.2 \text{ S.E.}$ ; range 10 min.-85 min.).

Table 1. Ethogram used for study of Gribbell Island bears in British Columbia during 2001-2002.

Behaviour	Description
Standing	Bear is stationary on stream but not feeding
Walking	Bear moves slowly along or within stream while fishing or accessing alternate fishing localities
Running	Bear moves quickly along or within stream typically while fishing
Scavenging	Bear feeds upon salmon carcass that it has not caught
Feeding fresh	Bear feeds upon salmon carcass that it has caught
Attempt	Bear attempts to capture salmon using a variety of techniques
Success	Bear successfully captures salmon

### 3.3

## RESULTS

#### 3.3.1 Temporal activity patterns: scan samples

##### 3.3.1.1 Overall

Overall, bears showed variation in diel stream visitation patterns while foraging ( $\chi^2=128.0$ ,  $df=11$ ,  $P<0.001$ , KW; Fig. 4). Bear activity was lowest during 10:00-16:00, and was highest during the remainder of the 24 hour period indicating a night-time foraging time preference. Stream visitation was similar during the night-time hours (20:00-08:00;  $\chi^2=4.17$ ,  $df=6$ ,  $P=0.65$ ; KW) and during the midday (10:00-16:00;  $\chi^2=1.42$ ,  $df=3$ ,  $P=0.70$ ; KW).

##### 3.3.1.2 Light level effects

Higher visitation counts during night-time and early morning are driven by the fact that bears foraged more actively in darkness than daylight ( $\chi^2=73.65$ ,  $df=2$ ,  $P<0.000$ , KW; Fig. 5). However, bears showed no detectable light level preference between darkness and twilight ( $Z=-1.05$ ,  $P=0.30$ ; MW).

##### 3.3.1.3 Colour morph effects

Black and white bears showed substantial variation in diel stream visitation patterns (Black:  $\chi^2=74.6$ ,  $df=11$ ,  $P<0.000$ , White:  $\chi^2=177.0$ ,  $df=11$ ,  $P<0.000$ , KW; Fig. 6). Peak stream visitation occurred during the night-time (20:00-8:00) relative to the midday (8:00-16:00) for both black and white bears (Black:  $Z=7.5$ ,  $P<0.001$ , White:  $Z=10.8$ ,  $P<0.001$ ; MW). Although black and white bears preferred foraging during the night (20:00-08:00), both colour morphs exhibited substantial variability in stream visitation during this time period (Black:  $\chi^2=14.4$ ,  $df=6$ ,  $P=0.025$ , White:  $\chi^2=49.2$ ,  $df=6$ ,  $P<0.001$ , KW).

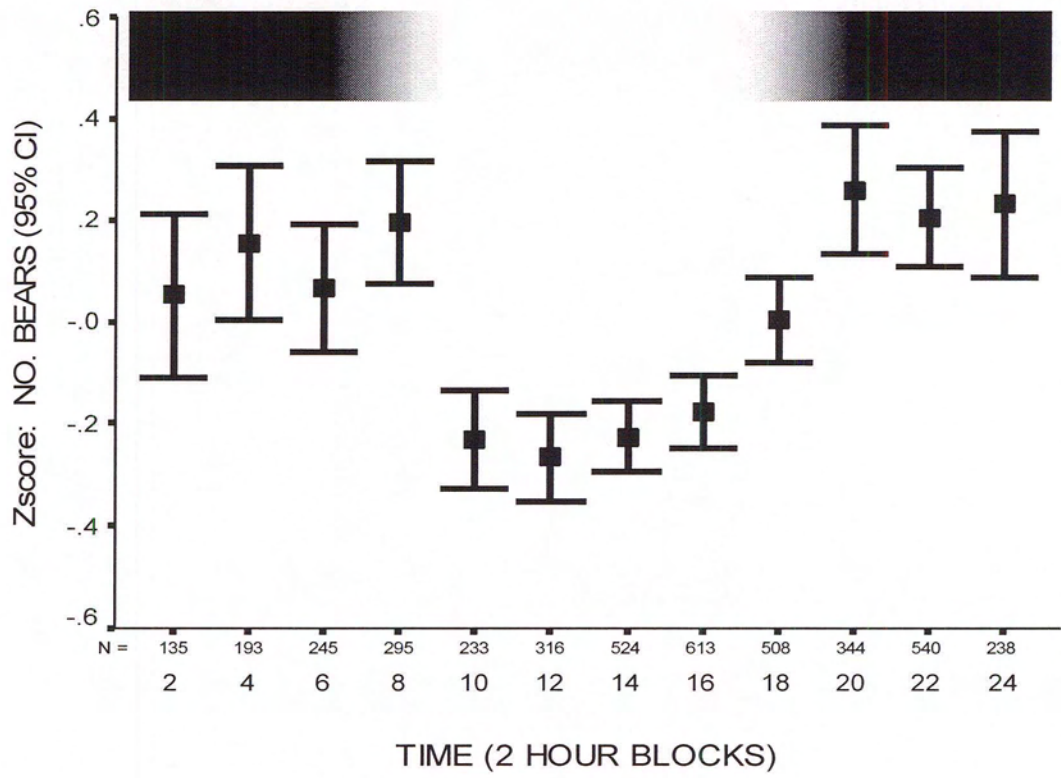


Figure 4. Stream visitation by bears within 2 hour time periods on Gribbell Island during the falls of 2000-2002. Light level is represented by horizontal bar where black is darkness and daylight is white. Error bars display 95% CI.

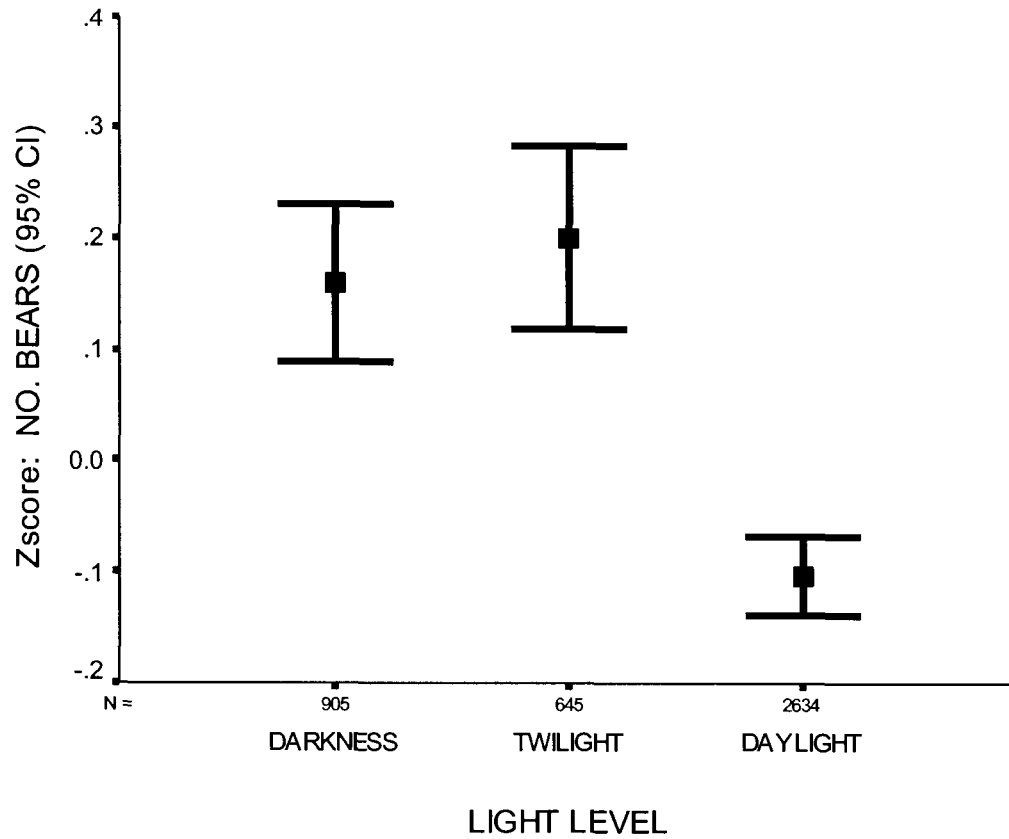


Figure 5. Stream visitation by bears within darkness, twilight and daylight on Gribbell Island during the falls of 2000-2002. Error bars display 95% CI.

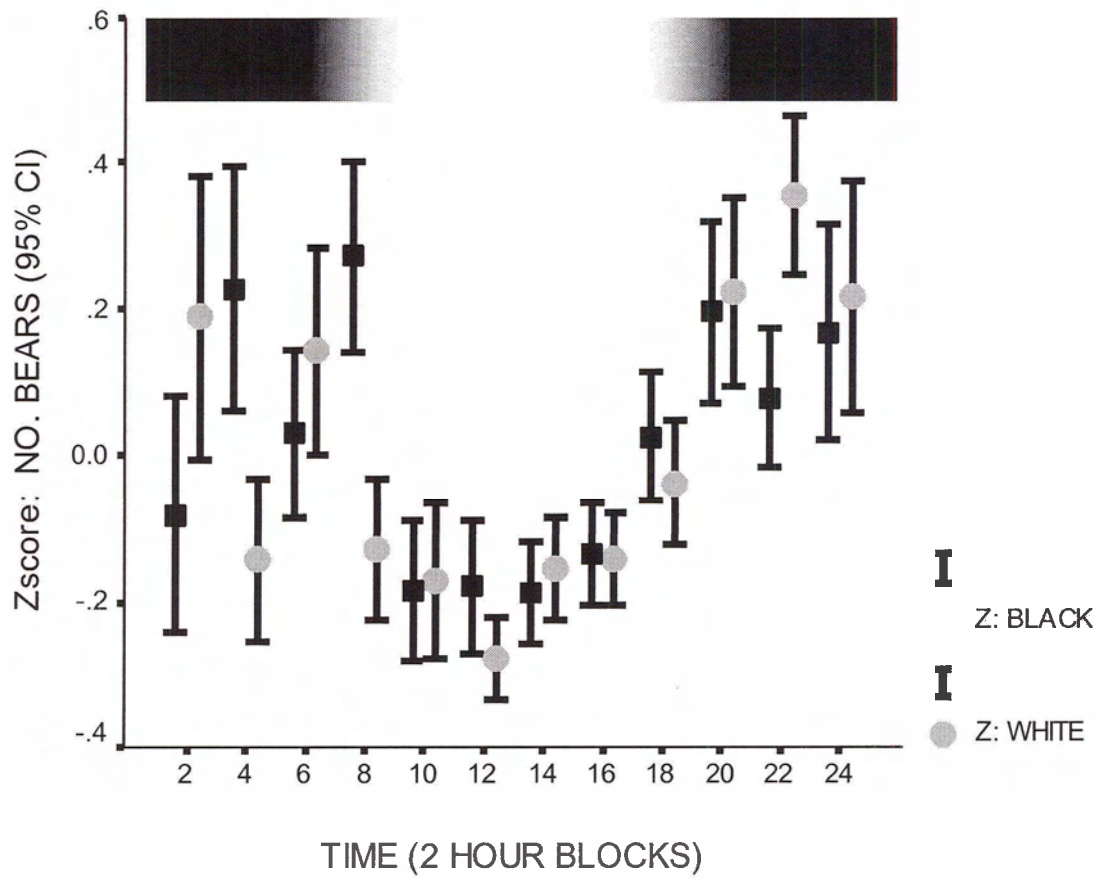


Figure 6. Standardized Z scores of stream visitation by black and white bears within 2 hour time periods on Gribbell Island during the falls of 2000-2002. Light level is represented by horizontal bar where black is darkness and daylight is white. Error bars display 95% CI.

#### 3.3.1.4 Colour and light level effects

The higher visitation counts during the night-time and early morning is again driven by black and white bears preferring to forage during darkness than during daylight (Black:  $Z=-3.79$ ,  $P<0.001$ ; White:  $Z=-6.65$ ,  $P<0.001$ ; Fig. 7). However, both colour morphs showed no detectable light level preference between darkness and twilight ( $Z=-0.90$ ,  $P=0.37$  and  $Z=-1.41$ ,  $P=0.16$ , respectively).

#### 3.3.1.5 Salmon density effects

Stream visitation by bears was heavily influenced by salmon spawning patterns. Salmon density increased during the spawning run from the end of August to mid-September, and then decreased towards the end of September and into October. Stream visitation by bears tended to increase with the density of salmon, and was infrequent during periods before and after the salmon run (Fig. 8).

Salmon density also influenced the diel activity patterns of bears. During the initial stages of the salmon run fish densities were still low and bears established an exclusively diurnal stream visitation pattern and did not visit the stream during darkness. However, as salmon densities increased, bears shifted towards a nocturnal pattern of stream visitation. Bears retained this nocturnal activity pattern until the salmon run had completed (typically near October 4), at which time they reverted back to their previous diurnal stream visitation pattern (Fig. 9).

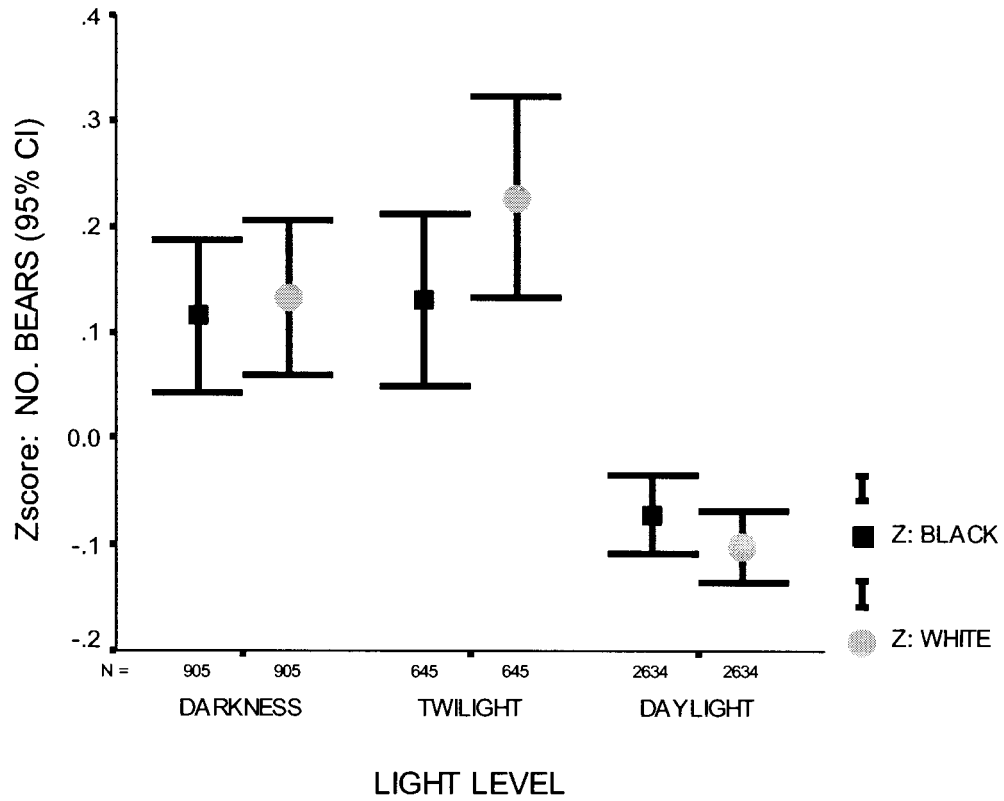


Figure 7. Standardized Z scores of stream visitation by black and white bears within darkness, twilight and daylight on Gribbell Island during the falls of 2000-2002. Error bars display 95% CI.

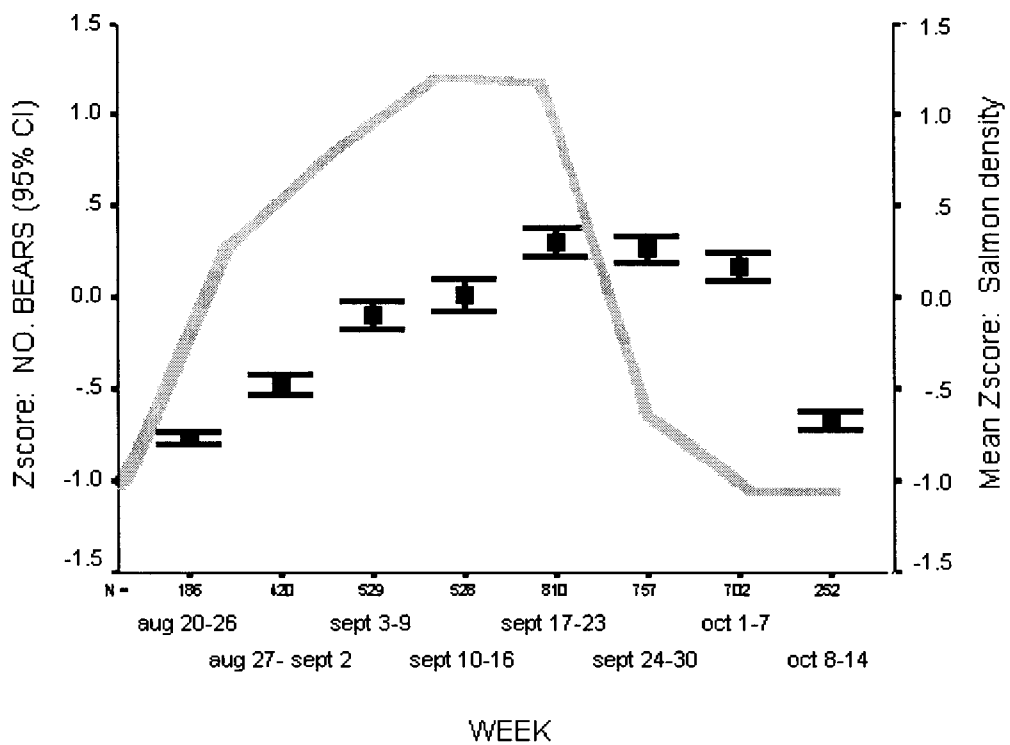


Figure 8. Stream visitation by bears and salmon abundance during the 8 weeks spanning the salmon run on Gribbell Island during the falls of 2000-2002. Error bars display 95% CI of Z scores of relative bear abundance; while mean Z score of relative salmon abundance is displayed by the grey line.

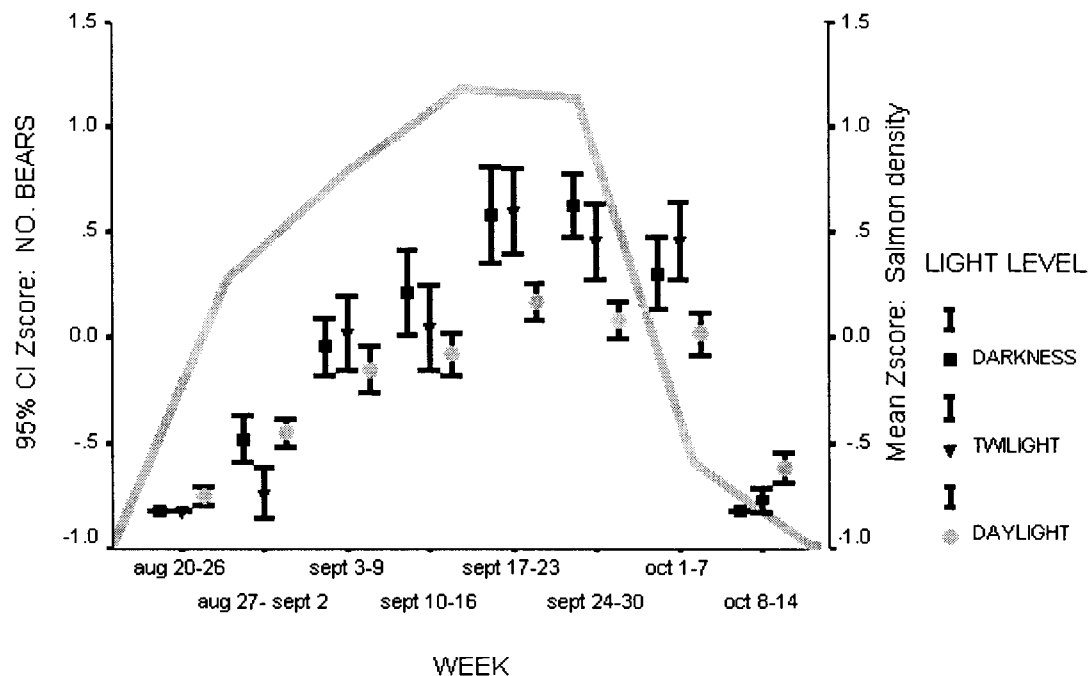


Figure 9. Stream visitation by bears within darkness, twilight and daylight and salmon abundance during the 8 weeks spanning the salmon run on Gribbell Island during the falls of 2000-2002. Error bars display 95% CI of Z scores of relative bear abundance, while mean Z score of relative salmon abundance is displayed by the grey line.

### 3.3.2 Individual time budgets

#### 3.3.2.1 Overall

While on salmon streams, the activities of coastal bears predominantly involve feeding and non-feeding behaviours (Fig. 10). Overall, bears spent 38% ( $\pm 0.02$  S.E.) of the time ingesting salmon and 58% ( $\pm 0.02$  S.E.) of the time moving about the stream or standing motionless in the water. Aspects of non-feeding behaviours are addressed in detail in subsequent sections of this chapter.

#### 3.3.2.2 Feeding time proportions

##### 3.3.2.2.1 Overall

Feeding by bears involved the handling and ingestion of both freshly caught salmon and scavenged carcasses. Bears spent more time feeding on freshly captured salmon than they spent feeding on scavenged carcasses, suggesting a preference for fresh salmon ( $\bar{X}_{\text{scavenge}}=16\%\pm 0.02$  S.E.;  $\bar{X}_{\text{fresh}}=22\%\pm 0.02$  S.E.;  $Z=-2.07$ ,  $P=0.038$ ; Fig. 11).

##### 3.3.2.2.2 Light level effects

Light levels were associated with the proportion of time spent scavenging ( $\chi^2 = 15.28$ ,  $df = 2$ ,  $P < 0.001$ ) but not the proportion of time spent consuming fresh salmon ( $\chi^2 = 5.03$ ,  $df = 2$ ,  $P = 0.08$ ; Fig. 12). Bears preferred to scavenge in twilight and daylight ( $21\% \pm 0.06$  S.E. and  $19\% \pm 0.03$  S.E., respectively) and avoided scavenging during darkness ( $3\% \pm 0.01$  S.E.). Although not statistically significant, bears spent more time consuming fresh salmon during darkness ( $29\% \pm 0.04$  S.E.), than during twilight ( $24\% \pm 0.06$  S.E.), and daylight ( $19\% \pm 0.02$  S.E.).

### 3.3.2.2.3 Colour morph effects

Black and white bears spent similar proportions of time scavenging and feeding on fresh salmon (Scavenging:  $Z=-1.32$ ,  $P=0.19$ ; Fresh:  $Z=-0.58$ ,  $P=0.56$ ; Fig. 13.). Black bears spent slightly less time scavenging relative to white bears ( $15\% \pm 0.02$  S.E. and  $19\% \pm 0.05$  S.E., respectively) but spent slightly more time feeding on fresh salmon ( $23\% \pm 0.02$  S.E. and  $18\% \pm 0.04$  S.E., respectively).

Black and white bears spent similar proportions of time scavenging and feeding on fresh salmon relative to one another among the three light regimes. Proportions of time spent scavenging were similar between black and white bears within darkness, twilight, and daylight (Table 2). Similarly, proportions of time spent feeding on fresh salmon were consistent between colour morphs among light levels.

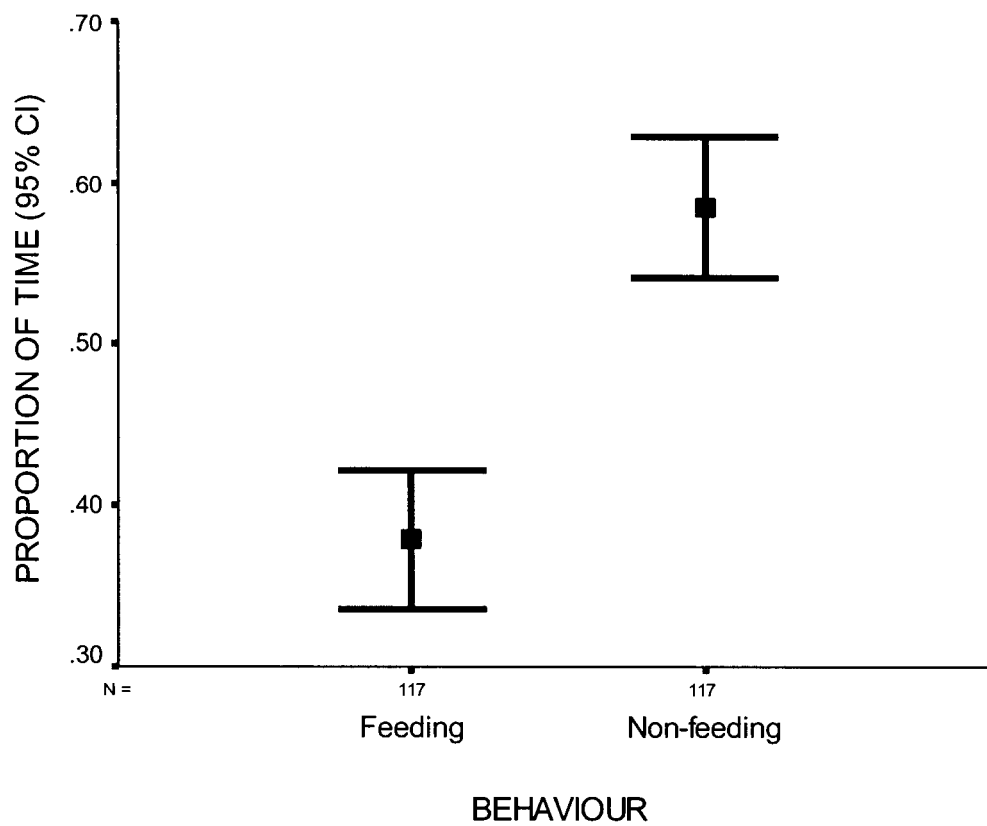


Figure 10. Overall proportions of time spent feeding and non-feeding by bears on Gribbell Island during the falls of 2000-2002. Error bars display 95% CI.

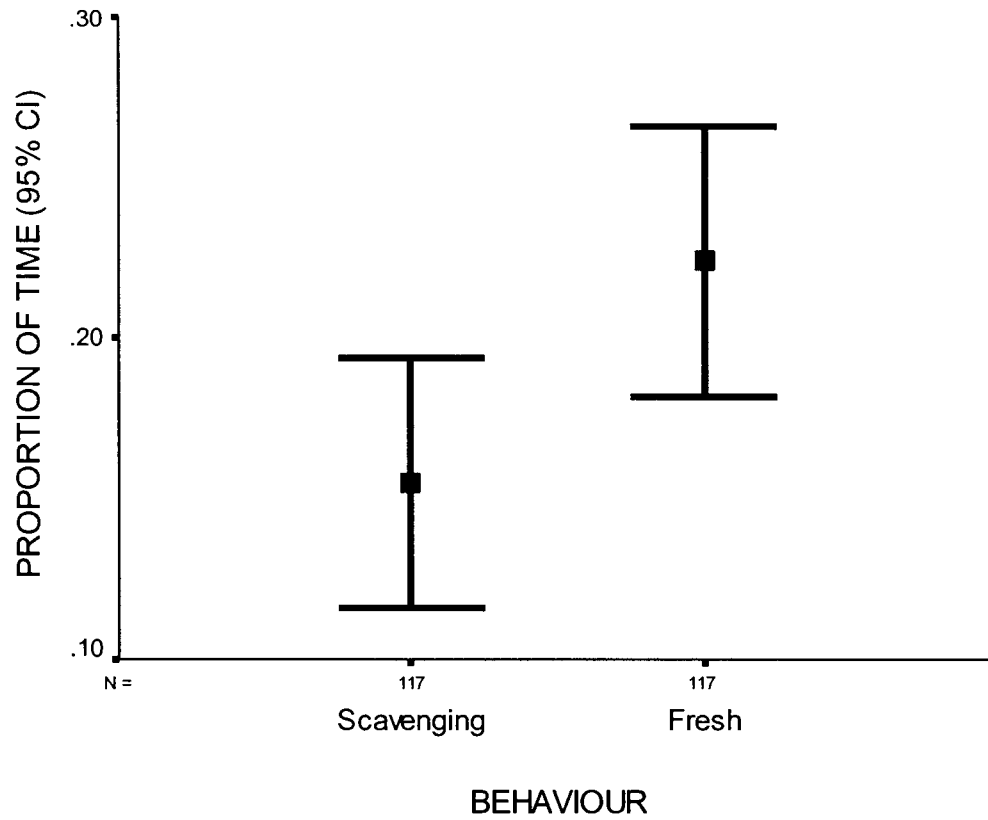


Figure 11. Overall proportions of time spent feeding on freshly caught and scavenged carcasses by bears on Gribbell Island during the falls of 2000-2002. Error bars display 95% CI.

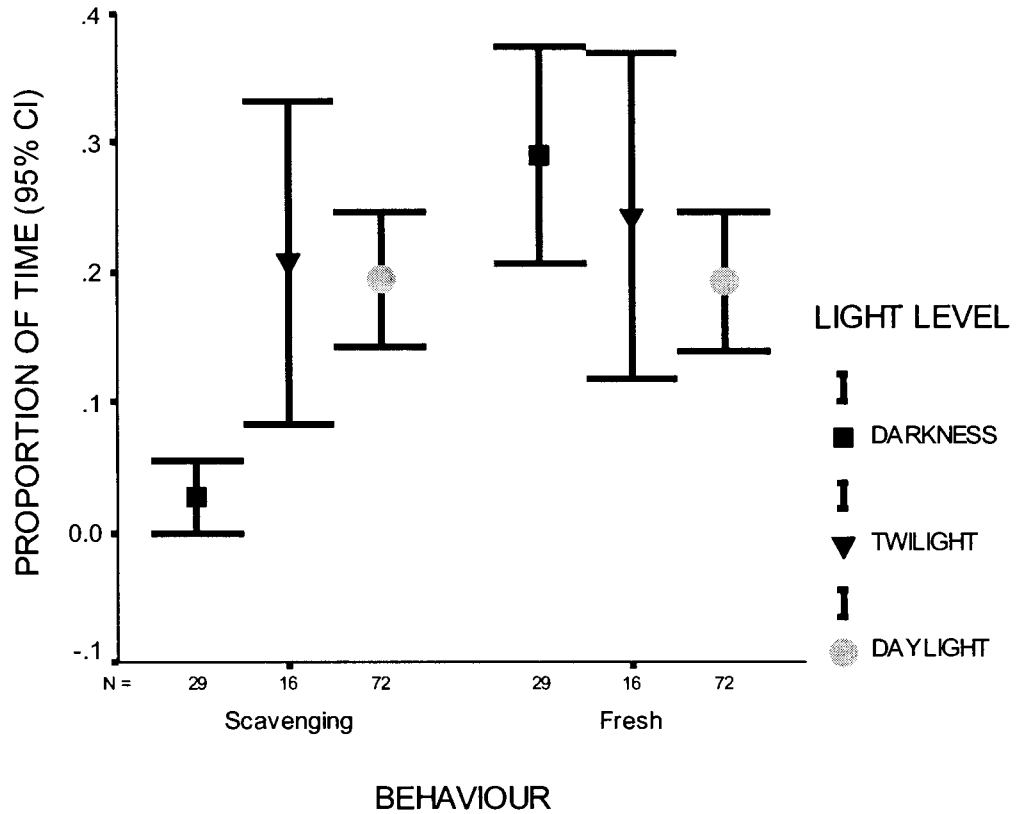


Figure 12. Overall proportions of time spent feeding on freshly caught and scavenged carcasses within darkness, twilight and daylight by bears on Gribbell Island during the falls of 2000-2002. Error bars display 95% CI.

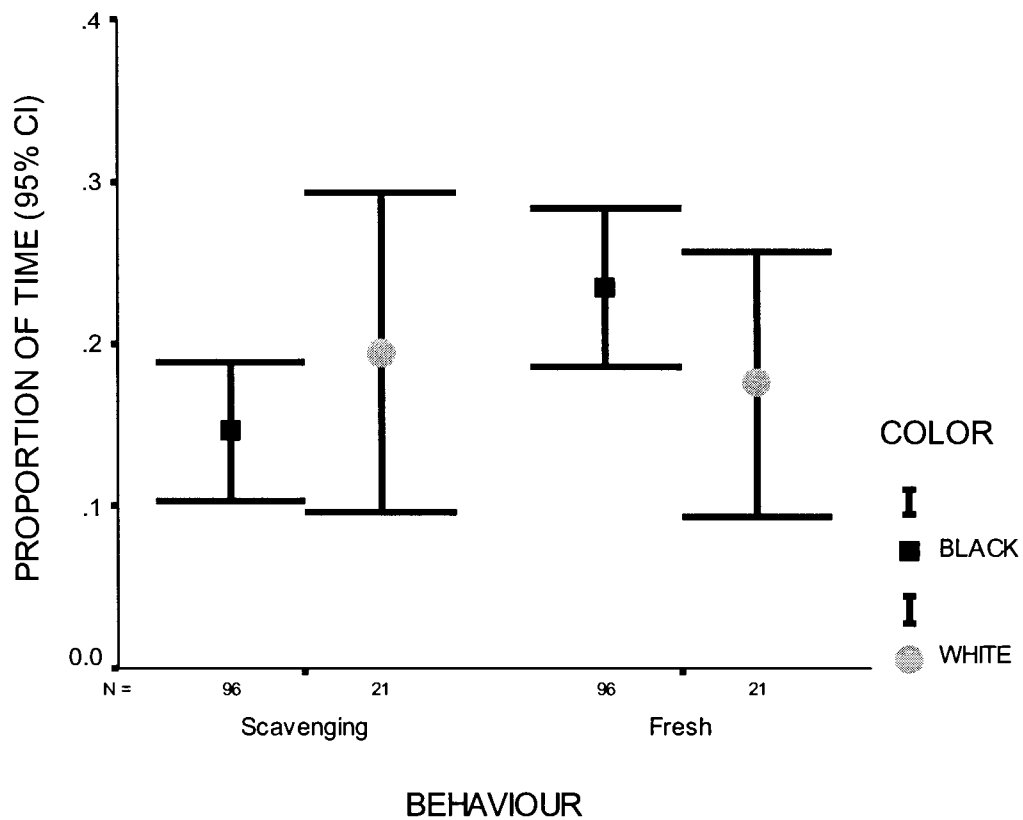


Figure 13. Overall proportions of time spent feeding on freshly caught and scavenged carcasses by black and white bears on Gribbell Island during the falls of 2000-2002. Error bars display 95% CI.

Table 2. Proportion of time spent scavenging and feeding on fresh salmon within darkness, twilight and daylight, and results of Kruskal Wallis ANOVA comparisons between colour morphs for bears on Gribbell Island during the falls of 2000-2002.

Behaviour	Light Level	Time (proportion $\pm$ S.E.)		Z	P
Scavenging		Black morph	White morph		
	Darkness	2.8 $\pm$ 1.6	2.1 $\pm$ 2.1	0.0	>0.99
	Twilight	25.1 $\pm$ 8.7	13.6 $\pm$ 5.6	-0.45	0.71
	Daylight	18.0 $\pm$ 2.8	26.7 $\pm$ 7.0	-1.31	0.19
Fresh	Darkness	28.6 $\pm$ 4.3	32.8 $\pm$ 16.5	-0.72	0.52
	Twilight	26.1 $\pm$ 9.0	21.5 $\pm$ 5.0	-0.28	0.78
	Daylight	20.7 $\pm$ 3.1	11.7 $\pm$ 4.6	-0.8	0.42

### 3.3.2.3 Feeding time durations

#### 3.3.2.3.1 Light level effects

Bears spent longer time periods consuming fresh salmon than scavenging carcasses ( $\bar{X}_{\text{scavenge}}=2.2 \text{ min} \pm 0.20 \text{ S.E.}$ ;  $\bar{X}_{\text{fresh}}=5.1 \text{ min} \pm 0.31 \text{ S.E.}$ ;  $t=-7.76$ ,  $df=137$ ,  $P<0.001$ ; Fig. 14) but these durations were not associated with light level (Scavenging:  $F_{2,65} = 1.16$ ,  $P = 0.32$ ; Fresh:  $F_{2,70} = 0.27$ ,  $P = 0.54$ ; ANOVA). Durations of scavenging bouts were shortest during darkness ( $\bar{X}=1.2 \text{ min} \pm 0.32 \text{ S.E.}$ ), and increased in twilight ( $\bar{X}=2.7 \text{ min} \pm 0.62 \text{ S.E.}$ ) and daylight ( $\bar{X}=2.3 \text{ min} \pm 0.23 \text{ S.E.}$ ). For bears feeding on fresh salmon, bout durations were similar within darkness ( $\bar{X}=4.7 \text{ min} \pm 0.39 \text{ S.E.}$ ), twilight ( $\bar{X}=4.6 \text{ min} \pm 0.42 \text{ S.E.}$ ), and daylight ( $\bar{X}=5.5 \text{ min} \pm 0.50 \text{ S.E.}$ ).

#### 3.3.2.3.2 Colour morph effects

Mean durations of scavenging, and fresh salmon feeding bouts were not associated with bear colour (Scavenging:  $F=0.04$ ,  $P=0.85$ ; Fresh:  $F=0.01$ ,  $P=0.94$ ; ANOVA; Fig. 15). Overall, scavenging bout durations for black bears were slightly shorter than that observed for white bears ( $\bar{X}_B=2.1 \text{ min} \pm 0.21 \text{ S.E.}$  and  $\bar{X}_w=2.6 \text{ min} \pm 0.53 \text{ S.E.}$ , respectively) while mean durations of fresh salmon feeding bouts for black bears were slightly longer than that observed for white bears ( $\bar{X}_B=5.2 \text{ min} \pm 0.36 \text{ S.E.}$  and  $\bar{X}_w=4.9 \text{ min} \pm 0.57 \text{ S.E.}$ , respectively).

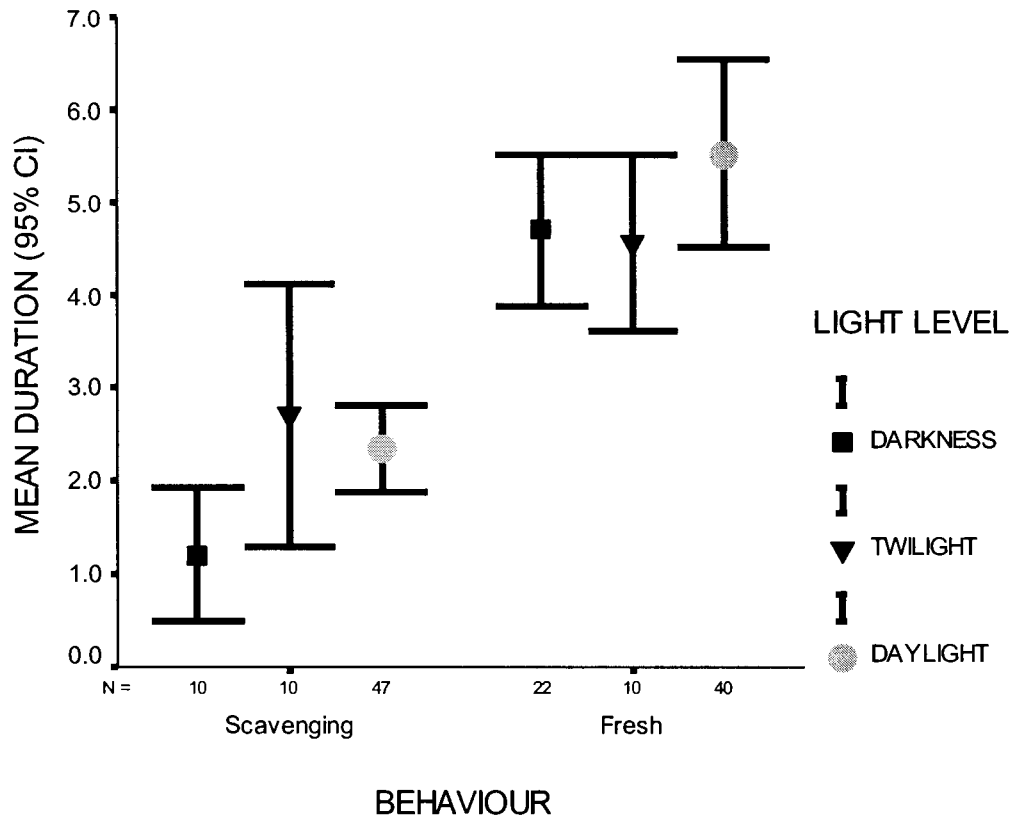


Figure 14. Mean feeding bout durations for freshly caught and scavenged carcasses by bears within darkness, twilight and daylight by bears on Gribbell Island during the falls of 2000-2002. Error bars display 95% CI.

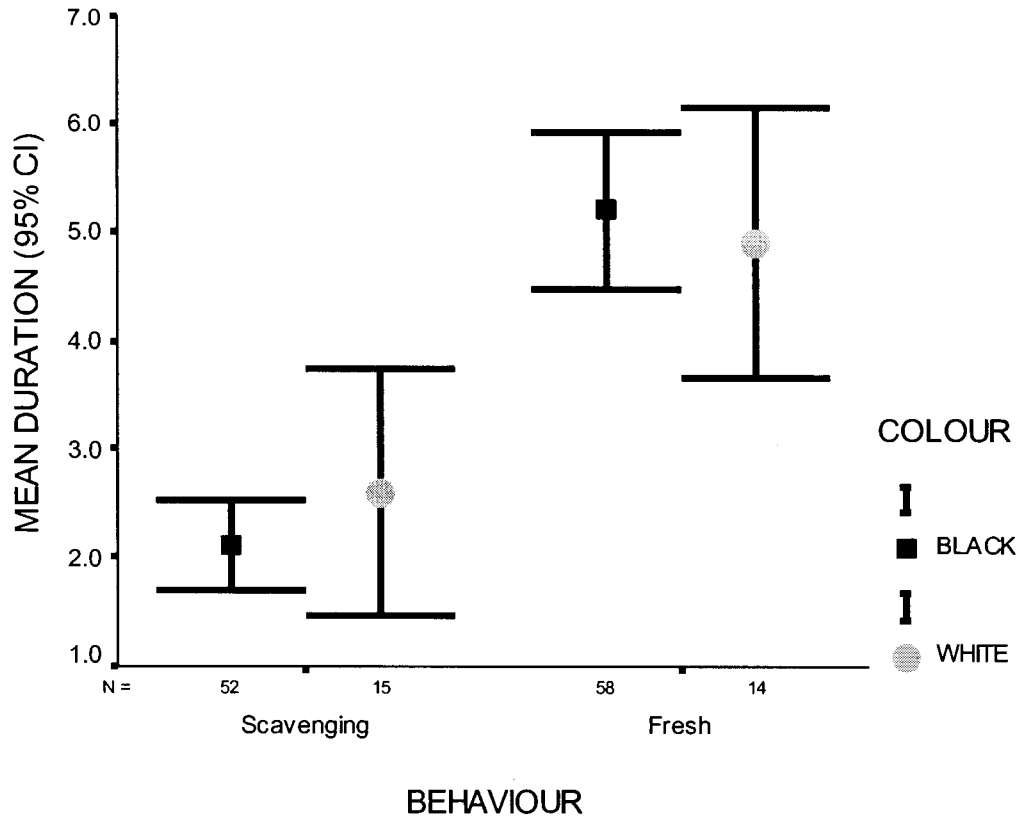


Figure 15. Mean feeding bout durations for freshly caught and scavenged carcasses by black and white bears on Gribbell Island during the falls of 2000-2002. Error bars display 95% CI.

### 3.3.2.4 Non-feeding time proportions

#### 3.3.2.4.1 Overall

When not feeding, bears spent much more of their time standing and walking than running ( $\chi^2 = 235.6$ ,  $df = 2$ ,  $P < 0.001$ ). Bears spent similar proportions of time standing and walking ( $29\% \pm 1.9$  S.E. and  $26\% \pm 1.4$  S.E., respectively) while running was rare ( $0.1\% \pm 0.03$  S.E.).

#### 3.3.2.4.2 Light level effects

Light levels were associated with the proportion of time bears spent standing ( $\chi^2 = 9.7$ ,  $df = 2$ ,  $P = 0.008$ ), but were not associated with the proportion of time spent walking ( $\chi^2 = 2.4$ ,  $df = 2$ ,  $P = 0.30$ ) or running ( $\chi^2 = 1.3$ ,  $df = 2$ ,  $P = 0.52$ ). The proportion of time spent standing was greatest during darkness and decreased into twilight and daylight ( $\bar{X}_{\text{darkness}}$ :  $38\% \pm 3.8$  S.E.;  $\bar{X}_{\text{twilight}}$ :  $25\% \pm 5.4$  S.E.;  $\bar{X}_{\text{daylight}}$ :  $26\% \pm 2.3$  S.E.; Fig. 16.), while the proportion of time spent walking was similar among light levels ( $\bar{X}_{\text{darkness}}$ :  $25\% \pm 2.8$  S.E.;  $\bar{X}_{\text{twilight}}$ :  $22\% \pm 3.2$  S.E.;  $\bar{X}_{\text{daylight}}$ :  $27\% \pm 1.8$  S.E.). Running was consistently rare among light levels ( $\bar{X}_{\text{darkness}}$ :  $0.05\% \pm 0.03$  S.E.;  $\bar{X}_{\text{twilight}}$ :  $0.1\% \pm 0.06$  S.E.;  $\bar{X}_{\text{daylight}}$ :  $0.1\% \pm 0.05$  S.E.).

#### 3.3.2.4.3 Colour morph effects

Overall, there were no detectable differences between black and white bears in the proportion of time spent standing ( $\bar{X}_{\text{B}}$ :  $28\% \pm 2.2$  S.E.;  $\bar{X}_{\text{W}}$ :  $29\% \pm 3.8$  S.E.;  $Z = -0.59$ ,  $P = 0.56$ ; MW) and walking ( $\bar{X}_{\text{B}}$ :  $26\% \pm 1.9$  S.E.;  $\bar{X}_{\text{W}}$ :  $26\% \pm 2.4$  S.E.;  $Z = -0.30$ ,  $P = 0.77$ ; MW). However, white bears spent a greater proportion of time running than did black

bears ( $\bar{X}_B$ : 0.10%  $\pm$  0.035 S.E.;  $\bar{X}_W$ : 0.14%  $\pm$  0.057 S.E.;  $Z=-2.3$ ,  $P=0.039$ ; MW; Fig. 17.).

The effects of light level on differences between black and white bears in the proportion of time spent performing non-feeding behaviours were variable. The proportion of time spent standing and walking did not differ between colour morphs among light levels, nor were there differences in the proportions of time spent running in twilight and daylight ( $P>0.05$  for all comparisons). However, black bears spent significantly less time running in darkness than did white bears ( $\bar{X}_B$ : 0.04%  $\pm$  0.03 S.E.;  $\bar{X}_W$ : 0.1%  $\pm$  0.05 S.E.;  $Z=-2.0$ ,  $P=0.04$ ).

### 3.3.2.5 Non-feeding time durations

#### 3.3.2.5.1 Light level effects

Light levels were associated with the durations of walking bouts, ( $F_{2,116} = 3.4$ ,  $P = 0.04$ ; Fig. 18), but were not associated with the durations of standing ( $F_{2,116} = 1.3$ ,  $P = 0.28$ ) or running bouts ( $F_{2,116} = 1.7$ ,  $P = 0.22$ ). The durations of standing bouts were greatest during darkness and decreased into twilight and daylight ( $\bar{X}_{\text{darkness}}$ : 1.18min.  $\pm$  0.14 S.E.;  $\bar{X}_{\text{twilight}}$ : 0.81min  $\pm$  0.35 S.E.;  $\bar{X}_{\text{daylight}}$ : 0.99min.  $\pm$  0.24 S.E.), while the durations of walking were greatest during daylight and decreased in twilight and darkness ( $\bar{X}_{\text{darkness}}$ : 0.59min.  $\pm$  0.7 S.E.;  $\bar{X}_{\text{twilight}}$ : 0.46min.  $\pm$  0.05 S.E.;  $\bar{X}_{\text{daylight}}$ : 0.68min.  $\pm$  0.6 S.E.). Running was consistently brief among light levels ( $\bar{X}_{\text{darkness}}$ : 0.07min.  $\pm$  0.01 S.E.;  $\bar{X}_{\text{twilight}}$ : 0.08min.  $\pm$  0.01 S.E.;  $\bar{X}_{\text{daylight}}$ : 0.07min.  $\pm$  0.01 S.E.).

### 3.3.2.5.2 Colour morph effects

Overall, there were no detectable differences between black and white bears in the duration of standing, walking, or running bouts (Standing:  $\bar{X}_B$ : 1.07min.  $\pm$  0.19 S.E.;  $\bar{X}_W$ : 0.77min.  $\pm$  0.11 S.E.;  $F_{1,116}=-0.41$ ,  $P=0.63$ ; Walking:  $\bar{X}_B$ : 0.63min.  $\pm$  0.5 S.E.;  $\bar{X}_W$ : 0.62min.  $\pm$  0.06 S.E.;  $F_{1,116}=-0.04$ ,  $P=0.85$ ; Running:  $\bar{X}_B$ : 0.08min.  $\pm$  0.01 S.E.;  $\bar{X}_W$ : 0.06min.  $\pm$  0.01 S.E.;  $F_{1,116}=-2.16$ ,  $P=0.17$ ; Fig. 19).

Light levels were not associated with differences between black and white bears in the duration of non-feeding behaviours. The durations of standing bouts for black and white bears were similar within darkness, twilight, and daylight (Table 3). Similarly, the durations of walking and running bouts for both colour morphs were similar among light levels.

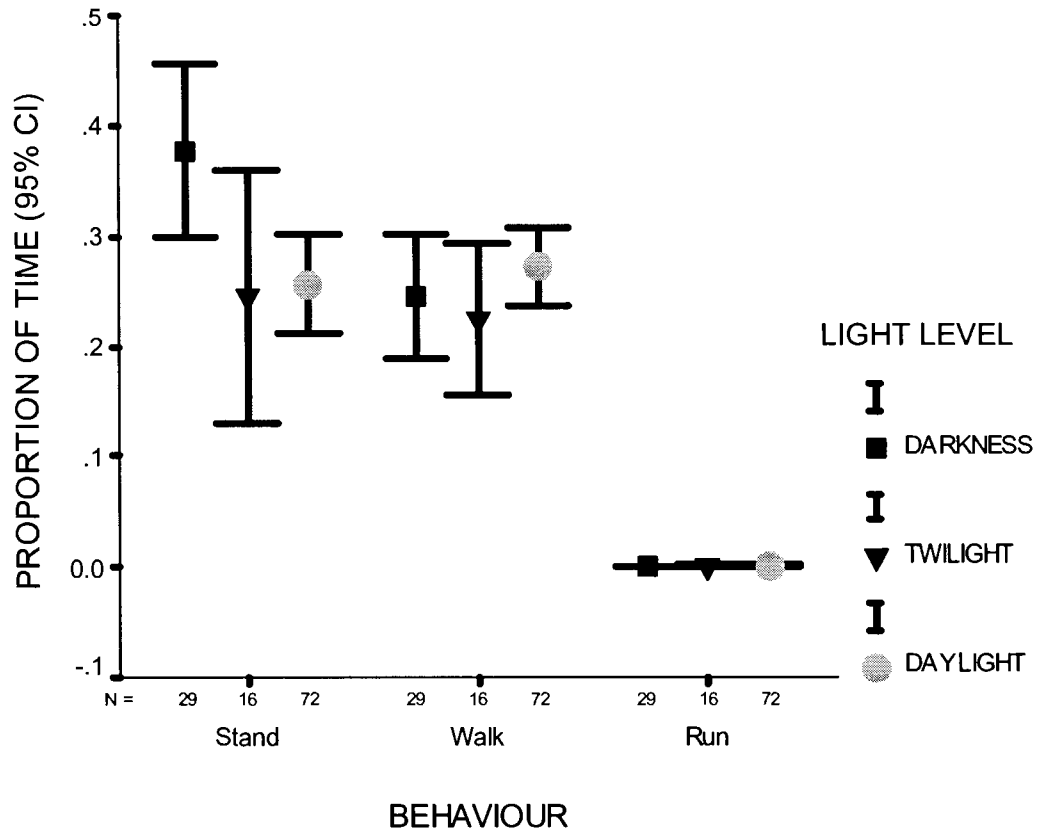


Figure 16 Proportion of time spent standing, walking and running within darkness, twilight and daylight by bears on Gribbell Island during the falls of 2000-2002. Error bars display 95% CI.

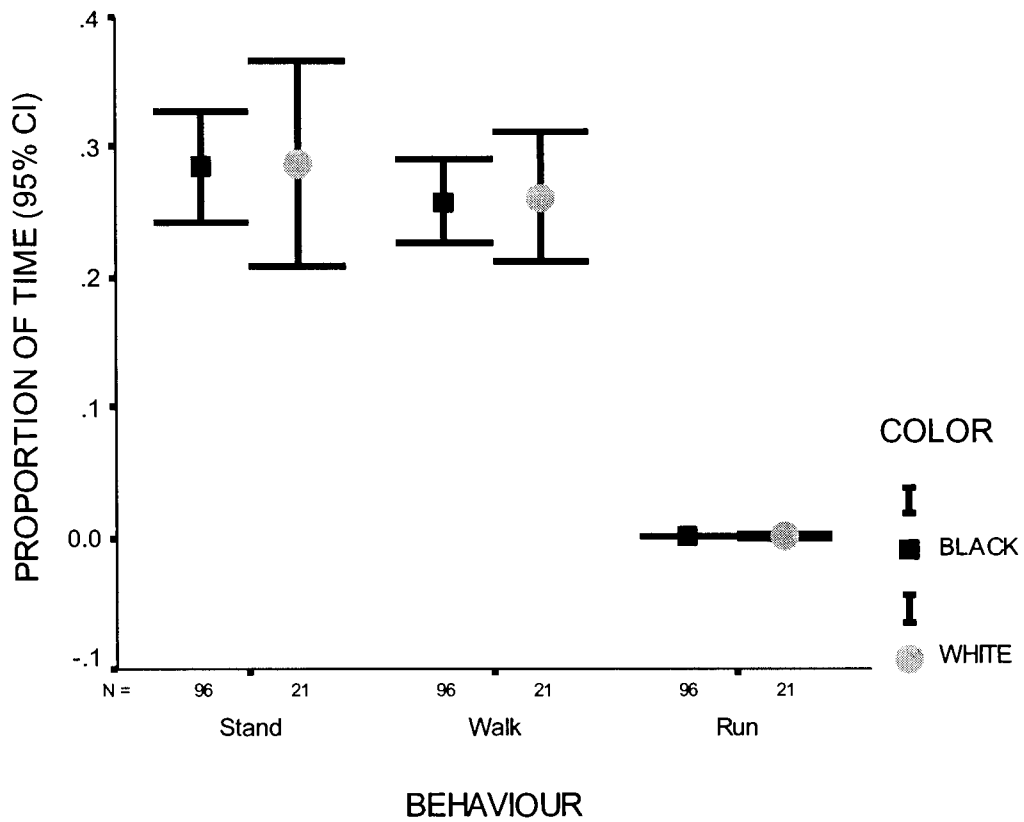


Figure 17. Proportions of time spent standing, walking and running by black and white bears on Gribbell Island during the falls of 2000-2002. Error bars display 95% CI.

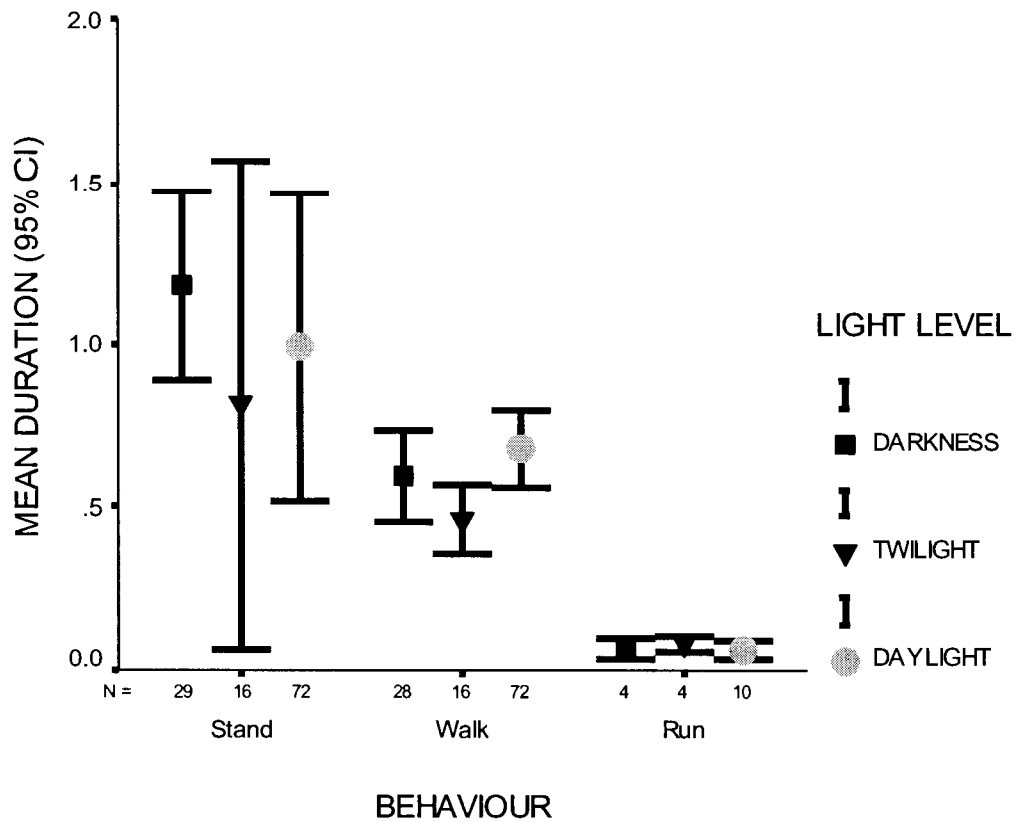


Figure 18. Durations of time spent standing, walking and running among light levels by bears on Gribbell Island during the falls of 2000-2002. Error bars display minutes and 95% CI.

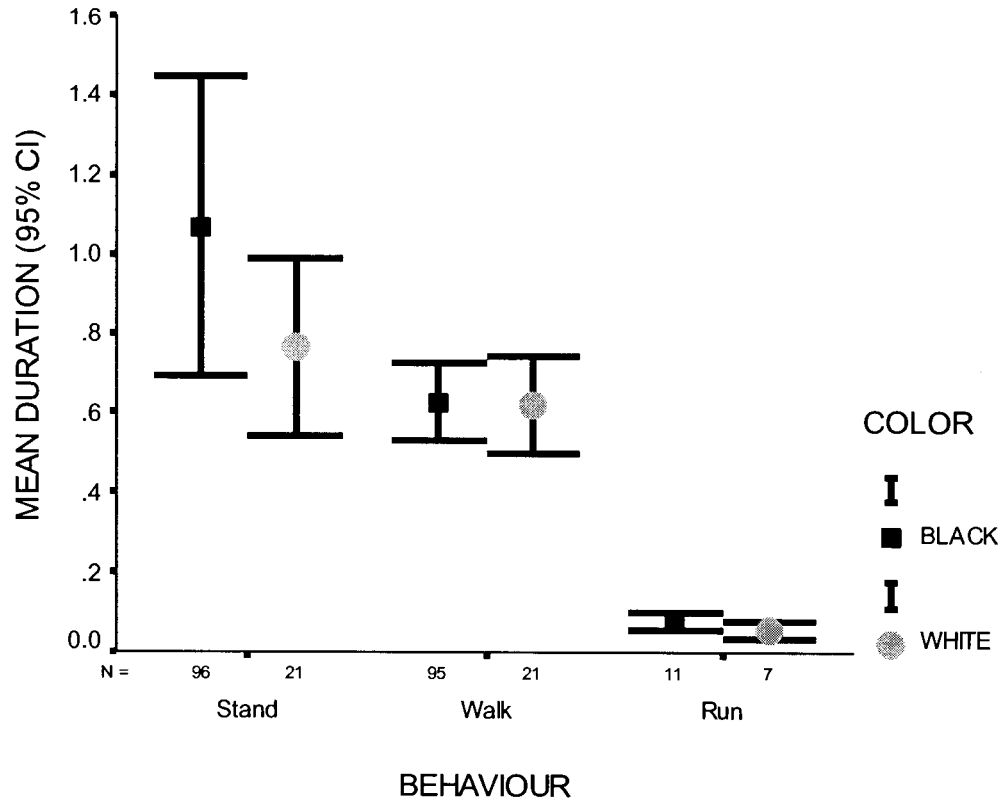


Figure 19. Durations of time spent standing, walking and running by black and white bears on Gribbell Island during the falls of 2000-2002. Error bars display minutes and 95% CI.

Table 3. Duration of time spent standing, walking and running within darkness, twilight and daylight, and results of student's t-test comparisons between colour morphs for bears on Gribbell Island during the falls of 2000-2002.

Behaviour	Light Level	Time (minutes $\pm$ S.E.)		t	df	P
		Black morph	White morph			
<u>Standing</u>						
	Darkness	1.22 $\pm$ 0.16	0.87 $\pm$ 0.32	0.6	27	0.55
	Twilight	.97 $\pm$ .56	0.54 $\pm$ 0.08	-0.17	14	0.87
	Daylight	1.02 $\pm$ .28	0.85 $\pm$ 0.16	1.06	70	0.3
<u>Walking</u>						
	Darkness	0.61 $\pm$ 0.08	0.45 $\pm$ 0.02	0.57	26	0.57
	Twilight	0.44 $\pm$ .5	0.49 $\pm$ 0.1	-0.38	14	0.71
	Daylight	0.67 $\pm$ 0.07	0.73 $\pm$ 0.8	-1.13	70	0.26
<u>Running</u>						
	Darkness	0.07 $\pm$ 0.02	0.04 $\pm$ .02	0	2	>.99
	Twilight	0.1 $\pm$ .01	.07 $\pm$ 0.01	1.6	2	0.25
	Daylight	0.08 $\pm$ 0.02	0.04 $\pm$ 0.01	2.1	8	0.07

### 3.4

### Discussion

#### 3.4.1 Temporal activity patterns

Although brown and black bears are considered primarily diurnal throughout their range in North America, crepuscular and nocturnal activity is also observed (Gard 1971, Stonorov and Stokes 1972, Frame 1974, Egbert and Stokes 1976, Phillips 1987, Reimchen 1998b, Klinka and Reimchen 2002). Interference from other bears or disruptive human activity may displace bears to sub-optimal crepuscular or nocturnal foraging periods and limit individuals to scavenging (Machutchon et al. 1997, Olson et al. 1998). Our observation of preferential stream visitation by this population of black bears during darkness and twilight in the absence of brown bears and human activity imply that other factors are responsible in shaping the activity patterns of coastal bears.

One factor that may influence these data is the sampling methodology. The clear preference for low light levels exhibited by this population of bears may be an artefact of my sample design, as my observations were skewed towards daylight hours. However, it is highly unlikely that these distinct stream visitation patterns are an artefact of sampling protocol, as the scan sample sizes in the evening hours (20:00-22:00) are similar to those in the daytime (12:00-16:00) and the visitation pattern is dramatically different. Although stream visitation was more variable during the evening and early morning hours, visitation was consistently lower during daylight hours. Furthermore, the elevated nocturnal stream visitation observed during this study is consistent with other studies of bear behaviour on salmon streams (Frame 1974, Egbert and Stokes 1976, Reimchen 1998b, Klinka and Reimchen 2002).

A common thread linking the activity patterns of all coastal bear species to light levels is food availability; namely the seasonal availability of salmon (*Oncorhynchus spp.*). In the many documented cases of observed nocturnal behaviour in predominantly diurnal ursids, elevated foraging activity on salmon was a factor in the shift towards elevated activity during low light levels. In fact, Gard (1971) reported that brown bear predation on salmon is greatest at night while Egbert and Stokes (1976) reported substantial foraging activity by Alaskan brown bears late in the day and during early evening (1500-2200hr). Supporting these findings, brown bears have also been observed foraging on salmon throughout the day and night in British Columbia (Klinka and Reimchen 2002). Reimchen (1998a, 1998b) reported preferential nocturnal foraging by black bears owing mostly to decreased evasion by salmon and fewer aggressive interactions with conspecifics.

The pattern of elevated nocturnal stream visitation I observed is most likely driven by the increased susceptibility of salmon to bear predation during low light conditions, rather than a lower frequency of agonistic encounters with conspecifics, as the frequency of agonistic encounters actually increased during darkness (Chapter 7; Interactions). Salmon become more susceptible to predation as light levels drop due to their diminishing visual sensitivities and subsequent decreased evasive responses to proximal predators (see Chapter 5; Model Predator). This nocturnal “camouflage” increases bear foraging success during darkness (see Chapter 4; Foraging).

Stream visitation by bears was also heavily influenced by salmon spawning patterns, namely the timing of the salmon run. Although I was not able to record bear stream visitation patterns for extended periods before and after the salmon run, my data

suggest a diurnal activity pattern during periods devoid of salmon. Furthermore, stream visitation by bears increased dramatically when salmon began to enter the stream and it was only then that bears adopted their preference for low light levels. Further evidence that this preference also hinged upon salmon spawning patterns is the fact that bears abandoned their nocturnal preference and resumed their diurnal activity patterns and infrequent stream visits immediately following the completion of the salmon run. This diurnal activity pattern is consistent with black bear activity data from other coastal areas where brown bears are absent (Machutchon et al. 1997). However, the effects of salmon migration on black bear activity patterns were unclear in the study by Machutchon et al. (1997), as it was a locality primarily designed to focus on the effects of human use on black bear behaviour, and did not occur during the spawning run.

I observed both black and white bears foraging throughout the day and night and clearly demonstrated that both colour morphs prefer low light levels (darkness and twilight) over high light levels (daylight). However, it remains unclear why the white morphs preferred to forage during darkness when their apparent advantage occurred during daylight when salmon are less able to detect them (see Chapter 5; Model Predator). Although I may have predicted that white bears would prefer to forage during daylight over darkness due to their inherent advantage with visually sensitive salmon, I observed white bears preferentially foraging during darkness. White bears may prefer to forage during darkness when salmon were overall less responsive to bear movements, while during daylight white bears would need to remain still in order for their camouflage to be advantage.

### 3.4.2 Individual time budgets: Feeding

Not surprisingly, bears spent much of their time on the stream feeding on salmon. Since coastal bears receive 33-94% of their yearly protein from salmon (Hilderbrand et al. 1996, Jacoby et al. 1999), the spawning season is a critical time period to gather sufficient food resources necessary for over wintering.

Greater consumption of fresh salmon over scavenged carcasses suggests there are higher nutritional benefits to eating fresh fish, despite increased costs in foraging. Fresh salmon have been shown to contain more nutrition (Hendry and Berg 1999, Gende et al. 2001). As salmon senesce towards the end of their spawning cycle, somatic tissues contain less energy (Hendry and Berg 1999, Gende et al. 2001). This decrease is most apparent when comparing tissue energy content in senescent salmon to salmon that are still in ocean habitats prior to spawning. However, much of this energy is devoted to gonadal development and migrations to spawning grounds, and as such, once salmon arrive at potential spawning sites, the decrease in energy content of salmon tissue is less substantial. For instance, Hendry and Berg (1999) measured the energy content of somatic and gonadal tissues of sockeye salmon (*Oncorhynchus nerka*) in a chronological manner beginning in open ocean environments and ending at with senescent salmon. They report a substantial decline (62% for females and 57% for males) in somatic tissue energy content between these two periods. However, when one compares the tissue energy content between spawning and senescent time periods, the decrease in energy content is not as large (41% for females and 29% for males). These values are slightly greater than, but consistent with unpublished overall data from Hilderbrand et al. who documented a 23% drop in whole body tissue energy in female Pink salmon (*O.*

*gorbuscha*) and a 17% drop for males between salmon arriving in salmon spawning areas to spawned-out salmon.

This underlying energetics trade-off may prove useful in suggesting explanations as to why bears scavenged more during daylight than during darkness. Salmon are most susceptible to capture during darkness and as such, bears may increase their fishing efforts during this time period and abandon scavenging until daylight when capture may be more difficult. However, this is not supported by my foraging data where both capture efficiencies and capture rates were slightly lower during darkness relative to daylight and twilight (see Chapter 4; Foraging). The lower capture rates during darkness are undoubtedly linked to the prevailing fishing techniques during this time period where bears typically stood motionless in the stream waiting for salmon to swim within striking distance. Furthermore, the lack of scavenging during darkness is not likely to be linked to the absence of visual cues, as a bear's high olfactory fidelity would presumably be more than adequate to locate a decomposing salmon carcass on the stream bank. Unfortunately, bear colour does not provide additional insight into this dilemma as proportions of scavenging and feeding on fresh salmon were similar between black and white bears.

The durations of scavenging bouts were shorter than the durations observed for fresh salmon presumably due to the scavenged carcass being mostly consumed by other bears, and thus smaller in size. Typically, bears eat a portion of the fish, ingesting lipid rich zones such as the brain and eggs, if present (Reimchen 2000, Gende et al. 2001). The abandoned portions of fish are typically less nutritious parts of the fish such as viscera, gills, testes (if applicable) and some remnant musculature (Reimchen 2000).

Bears in this study spent 22% of the time feeding on fresh salmon, which is very similar to black bears in Alaska that fed on fresh salmon 20% of the time (Frame 1974). However, Frame (1974) reported that bears in his study spent 42% of the time scavenging salmon killed by other bears, and 7% eating salmon that had died of physiological breakdown. This leads to a total of 49% scavenging and when combined with the time spent feeding on fresh carcasses suggests that bears spent a total of 69% feeding. This is almost double the feeding estimate (38% for fresh and scavenging combined) in this study.

These discrepancies in feeding times between these two black bear populations can possibly be attributed to the large differences between the two study sites. Frame conducted his observations at Olsen Creek, Alaska, where the vast majority of spawning takes place within a relatively small tidal flat area (approximately 300m from mean high tide to stream forks; see Fig.1, Frame 1972), which would make for a relatively exposed fishing zone for bears. This combined with the much greater salmon run size (26,000 chum and 27,600 pink compared to 1500 pink in this study) would create a zone of extremely high salmon density where bears could come to the stream bank and immediately capture a salmon or begin scavenging a carcass. This seems supported by Frame's observations of bears only spending 9% of the time actively fishing, but 20% eating fresh salmon and 49% scavenging. Furthermore, the fact that he rarely observed bears on the tidal flat for more than 30 minutes at a time suggests that bears remained in the forest close to the tidal flat emerging primarily to feed and then returning to the forest. Bears in my study did not have the same amount of available salmon biomass

upon which to easily feed and consequently spent more time actively fishing and less time feeding.

### 3.4.3 Individual time budgets: Non-feeding behaviours

Light levels significantly influenced the proportion of time bears spent standing, but did not influence the proportion of time spent walking or running, suggesting that moving among different fishing localities is independent of light level. However, as standing is a precursor to an effective fishing technique, it also suggests that fishing strategies are directly influenced by light levels. This is consistent with my foraging data indicating the elevated use and high efficiency of standing techniques during darkness (see Chapter 4; Foraging).

Overall, bear colour morphs were similar in the proportion of time spent standing and walking. This suggests that aspects of behaviour independent of feeding activities were similar between black and white coloured bears. Differences detected in the proportion of time spent running between bear colour morphs is most likely an artefact of low sample size as this behaviour was relatively brief for both morphs and occurred only during running initiated fishing attempts.

In this study, bears spent almost twice the proportion of time walking as bears in Frame's (1974) study (29% compared to 17%). This again could also be attributed to the large differences between the two study sites. In Frame's study, bears could have remained outside of the tidal area until such time as they were sufficiently motivated to resume feeding. Due to the high density of salmon, bears could have either captured or scavenged carcasses without walking for long periods of time. This contrasts strongly

with my study as I observed bears only on a 90m stretch of stream, and salmon were distributed along it to a much greater extent than in Frame's study. Thus, bears in this study were motivated to move along the stream in order to encounter additional salmon. Consequently, bears would need to devote more time to walking and fishing and less time to feeding.

Although the mean durations of walking varied significantly among light levels, these differences were small and the ecological and behavioural significance of this result is unclear. Specifically, the most extreme duration time difference (between twilight and daylight) translated to only a 13 second difference between these two light levels. This makes it difficult to suggest reasonable advantages or disadvantages to bears among light levels for this behaviour, especially when black and white bears had nearly identical walking bout durations, suggesting that both colour morphs moved along the stream in a similar manner.

Taken together, these observations suggest that in terms of allocating time to feeding and locomotory activities, bear colour morphs are similar in most respects. Such behavioural similarities between bear colour morphs do not strongly support a form of behavioural niche partitioning.

## **Chapter 4: Foraging performance among different light environments of a polymorphic bear population.**

### **4.1 Introduction**

Foraging strategies are highly diverse, even within a species. In response to foraging demands, animals show behavioural adaptations to resource availability, quality and prey vulnerability (Lariviere and Messier 1997). In order to maximize foraging efficiency, individuals can alter both seasonal and daily activity patterns, including the expansion of foraging activities into darkness.

Many different taxa, including mammals (Wolfe and Summerlin 1989, Bowers 1990, Randall 1993), fish (Sjoberg 1989, Beers and Culp 1990, Metcalfe et al. 1997), birds (Robert et al. 1989) and insects (Bradley 1988, Beers and Culp 1990, Henschel 1994), specialize in strictly nocturnal foraging while many occasionally alternate between diurnal and nocturnal foraging (Robert et al. 1989, Sjoberg 1989, Jones et al. 1990, McMahon and Evans 1992b, Stander 1992, McNeil et al. 1993). The extent of nocturnal foraging can be classified as either supplementary, occurring only when an animal's food requirements are not met during the day, or preferential, occurring as a result of maximum profitability, and/or the safest foraging opportunities (Thibault and McNeil 1995).

The potential benefits of nocturnal foraging are many, with increased prey susceptibility (Sjoberg 1989, McMahon and Evans 1992b, Collins and Hinch 1993, McNeil et al. 1993, Thibault and McNeil 1995), availability (Robert et al. 1989, Warrant

et al. 1996, Lariviere and Messier 1997) and reduced risk of predation (Bradley 1988, Beers and Culp 1990, Jones et al. 1990, Culp et al. 1991, Thibault and McNeil 1995, Warrant et al. 1996) most frequently mentioned. Additional potential benefits of nocturnal foraging are increased prey abundance (Robert et al. 1989, Thibault and McNeil 1995), enhanced predatory efficiency (Sjoberg 1989, Reimchen 1998b, Klinka and Reimchen 2002), reduced competition (Warrant et al. 1996), and increased opportunities for targeting alternate prey species and size classes not available during strictly diurnal foraging periods (McMahon and Evans 1992b, Collins and Hinch 1993).

Many animals utilize one principal sensory system for all foraging behaviours. Most diurnally active animals use vision as a primary sensory mode while nocturnal animals tend to utilize non-visual sensory systems such as auditory, tactile, olfactory and echolocation systems (Griffin et al. 1965, Payne 1971, Beers and Culp 1990, Randall 1993, Henschel 1994). However, there are many examples of nocturnal foraging behaviours with primary sensory systems not ideally suited for depressed light regimes. Vision is the primary sensory mode during nocturnal foraging of numerous rodent species (Randall 1993), honeybees (Warrant et al. 1996), and numerous bird species (Robert et al. 1989, Jones et al. 1990, Brigham and Fenton 1991, Thibault and McNeil 1995). Alternately, auditory cues are used by many rodent species (Randall 1993) and owls (Payne 1971), while echolocation of sonar is utilized by bats (Griffin et al. 1965). Tactile-based sensory systems are primarily used by some spiders (Henschel 1994) and rodents during specific tasks during darkness such as dehusking seeds (Randall 1993). Olfactory and chemo-sensitive systems are the primary sensory modes for some rodents (Randall 1993), ants (Beugnon and Fourcassie 1988), geckos and snakes (Downes and

Shine 1998). Hydromechanical forces such as pressure waves are detected by the lateral lines and inner ears of fish (Beers and Culp 1990, Culp et al. 1991).

In contrast, many animals shift from a primary sensory mode utilized during daylight to alternate sensory modes during darkness. Many nocturnally-active animals, including birds (Robert et al. 1989, McMahon and Evans 1992b), fish (Collins and Hinch 1993) and ants (Beugnon and Fourcassie 1988), are capable of switching between diurnal sensory modes such as vision, to alternate modes such as tactile, auditory or chemo-sensory systems during darkness.

Ambient light levels vary during the night-time and can dramatically effect foraging efficiencies (Metcalf et al. 1997). As light levels increase during the night-time, several visually oriented species (Wolfe and Summerlin 1989, Beers and Culp 1990, Bowers 1990, Randall 1993, Metcalfe et al. 1997) are observed to have enhanced predatory efficiencies, while others show decreased predatory efficiencies (McMahon and Evans 1992b, Randall 1993). However, even non-visually-oriented species such as snakes can show enhanced predatory success during brighter nocturnal periods when changing light levels alter behaviour patterns of prey (Randall 1993).

Nocturnal predatory behaviour is driven by, and occurs in synchronization with the activities of prey (Culp et al. 1991, McMahon and Evans 1992b, Lariviere and Messier 1997). This can be demonstrated by seals pursuing nocturnally-active fish and cephalopods (Harcourt et al. 1995, Thomas and Thorne 2001), fish preying on nocturnally-active insects (Beers and Culp 1990), birds taking advantage of seasonally available nocturnal fishes (Sjoberg 1989), and ursids feeding on salmon during spawning

migrations (Stonorov and Stokes 1972, Frame 1974, Luque and Stokes 1976, Reimchen 1998b, Klinka and Reimchen 2002).

Predation occurs in three distinct phases: detection, pursuit, and subjugation (Vermeij 1982). Predator efficiencies can vary widely among these phases, among both temporal and spatial scales, and among taxa. Although some species achieve predation efficiencies near 100%, many species including some sea stars and spiders successfully capture less than 2% of targeted prey (Vermeij 1982). In fact, predatory failure is an inescapable aspect of predation, and is a necessary condition for the evolution of anti-predatory characteristics in prey (Vermeij 1982). Predation efficiencies for other large carnivores are usually less than 50% (Vermeij 1982), as shown by some African species such as lions (*Panthera leo*: 15%-39%), hyenas (*Crocuta crocuta*: 33%-44%) and jackals (*Canis aureus*: 33%) (Kruuk and Turner 1967, Schaller 1972, Stander 1992). Although these predators all show nocturnal activity peaks, their efficiency estimates were derived from diurnal observations due to visual limitations. Schaller (1972) restricted his nocturnal observations to bright, moonlit nights, during which times he reported lion efficiencies rising to 42%, from a diurnally-based estimate of 27%. Stander (1992) was the only author to use a light-amplifying device while observing lions and found lions restricted foraging activities to darkness and achieved an average 15% predation efficiency.

Black bears (*Ursus americanus*) are primarily diurnal throughout North America (Lariviere et al. 1994b, Machutchon et al. 1997, Maehr 1997), yet also expand their foraging activities into darkness while fishing for salmon (Reimchen 1994, Reimchen 1998b). However, it was presumed that nocturnal behaviour was due to disruptive human

activity or displacement by brown bears (Machutchon et al. 1997, Olson et al. 1998). Furthermore, it was speculated that bears would be limited to scavenging during darkness as they lack the visual capabilities necessary for the successful capture of salmon during these time periods (Machutchon et al. 1997, Olson et al. 1998). Yet, black bears on Haida Gwaii (formerly the Queen Charlotte Islands) captured the majority of salmon during nocturnal foraging bouts in the absence of brown bears and human disturbance (Reimchen 1998a, b), leading to the suggestion that night-time is preferred for foraging because of increased access to high quality feeding areas, reduced evasion by salmon, and high capture rates.

In addition to black bears, brown bears also appear to exhibit extensive temporal variability in activity patterns. While they are well known to be diurnally active (Stonorov and Stokes 1972, Luque and Stokes 1976, Gilbert and Lanner 1995, Gende et al. 2001), crepuscular and nocturnal activity has also been reported (Gard 1971, Herrero 1985, Phillips 1987, Genov and Wanev 1992). Furthermore, brown bears have been shown to utilize all light regimes while fishing for salmon and attain comparable foraging success among light levels (see Appendix 1).

If black bears prefer fishing during daylight, and are forced into foraging during darkness by the presence of brown bears or human disturbance (Machutchon et al. 1997, Olson et al. 1998), then nocturnal foraging by this bear population should be rare or absent. However, as this study site is devoid of brown bears and human disturbance, and coastal bears are successful fishers during darkness (Reimchen 1998b, Klinka and Reimchen 2002), this bear population should exhibit substantial nocturnal foraging behaviour with comparable capture efficiencies among light levels.

Coat colour polymorphism may contribute to variable foraging success between colour morphs. The visual and behavioural responses of prey (salmon) may differ between morphs. This effect could confer a temporary foraging advantage to the appropriate coloured morph (Murton 1971, Mock 1980). However, colour morph effects would presumably occur only during daylight and be absent during darkness.

Comparisons between colour morphs among light levels enable the examination of subtle aspects of foraging behaviour. Furthermore, differences in foraging attributes (such as capture efficiencies) between morphs may provide evidence for niche partitioning that could be responsible for the maintenance of this colour polymorphism.

## 4.2 **Methods and Materials**

I recorded fishing behaviour for all bears during the study period ( $N_{\text{White}}=4$ ,  $N_{\text{Black}}=37$ ), including multiple observations per bear. Only observations involving recognizable bears were included in subsequent analyses. I classified fishing techniques as three types; *Standing*, *Walking*, and *Running* (Luque and Stokes 1976, Klinka and Reimchen 2002).

I defined capture efficiency as the probability of a successful capture (number of successes /number of attempts) and fishing bout duration as the time (in minutes) an individual bear spent actively fishing on the stream within the observation area (100m of stream). Partial bouts consisted of observations where I did not observe either the initiation or termination of fishing, while transitory bouts were defined as bears fishing while constantly moving through the observation area and where fewer than three fishing

attempts were observed. Observations made within partial or transitory bouts not used in any subsequent analysis of foraging bout durations or capture rates. I defined capture rate as the number of fish captured per hour (number of successful captures/length of time foraging in hours).

I examined differences in foraging efficiencies among different bears in relation to fishing technique, light level and colour morph using non-parametric statistics. To test for interactions among Technique (*Standing, Walking, Running*), Light level (Darkness, Twilight, Daylight), Fishing Success (Fail, Success) and Colour (Black, White) I used log-linear models. I used Z values to assess the relative contributions of cells to the interaction and considered values  $> 1.96$  to be significant at a  $< 0.05$  (Norusis 1988). Distributions of data were tested for normality with the Kolmogorov–Smirnov test. As data tended to be non-normal, I used Kruskal–Wallis and Mann-Whitney U tests to analyze the relationships between foraging bout duration, number of salmon captured and salmon capture rates.

During spawning events and nest preparation, female salmon would make multiple splashes audible above background stream noise, and I assessed salmon activity patterns by counting these spawning events within multiple (N=60) 5 minute audio recordings extracted from a digital camcorder (SONY DCR-TRV720). One audio recording was made during each observation session.

To ensure that differences in salmon activity patterns that I recorded among light levels were not simply a consequence of differential sound transmission between contrasting air temperatures, I played pre-recorded splash sounds with a standard volume within peak daytime temperatures and nighttime low temperatures. I then calculated the

amplitude differences (difference in Decibels) of the splashes between the two temperatures (Day=22.4C, Night=8.2C). Mean decibels were greatest during daylight relative to darkness but these differences (less than 3%) were not statistically significant (Day:  $\bar{X}_{Db}=-17.7$ , S.D=0.57, N=2; Night:  $\bar{X}_{Db}=-18.1$ , S.D=0.15, N=2;  $t=1.4$ ,  $df=1$ ,  $P=0.40$ ; paired student's t-test). As the mean amplitude difference was not statistically different between the two temperatures, I feel that any effects of light level on salmon activity are not due to any temperature dependent sound propagation characteristics.

As bears seemed to respond to audible splash sounds made by salmon, I made attempts to lure bears towards me by mimicking these noises with a stick vibrating in the water. Although these early attempts were not properly quantified, bears moved towards the noises made by the vibrating stick and in subsequent years I attempted to isolate the sensory cues used by bears. To differentiate whether bears were using tactile or auditory cues during their search strategies I used a form of call playback where only auditory cues would be available to bears. I fabricated a waterproof speaker and small amplifier and played salmon spawning splashes while bears were within 40m. Playback experiments were conducted during all three light regimes and bear reaction was scored on a 5 point scale. A score of zero indicated that the bear ignored the call while positive integers indicated movement towards while negative integers indicated movement away from the speaker.

## 4.3

## Results

4.3.1 *Fishing technique*

Bears used different fishing techniques upon entering the stream. Of the 1769 attempts observed, the most common were *Standing* (47%), followed by *Running* (32%) then *Walking* (21%), and these were associated with light levels (Light\*Technique  $\chi^2 = 29.2$ ,  $df = 4$ ,  $P < 0.001$ ; Fig. 20). *Standing* was most common in darkness and least common during twilight while *Walking* was most common during twilight and least common during daylight. *Running* was least common during darkness and most common during daylight. Relatively high incidences of *Standing* during darkness ( $Z = 2.51$ ,  $P = 0.012$ ), contributed the greatest effect to the loglinear model. Although not reaching statistical significance, relatively high incidences of *Running* during daylight ( $Z = 1.89$ ,  $P = 0.058$ ), *Walking* during twilight ( $Z = 1.84$ ,  $P = 0.066$ ), and relatively low incidences of *Standing* during twilight ( $Z = -1.78$ ,  $P = 0.075$ ) all approached significance.

Fishing technique was also associated with bear colour (Technique\*Colour,  $\chi^2 = 8.48$ ,  $df = 2$ ,  $P = 0.014$ ; Fig. 21A). White bears had a greater preference for *Standing* (Black: 44.9%; White: 53.9%;  $Z = -2.01$ ,  $P = 0.044$ ), but there was no difference between the two morphs in the use of *Running* (Black: 33.2%; White: 29.3%;  $Z = 0.48$ ,  $P = 0.63$ ) or *Walking* (Black: 21.9%; White: 16.9%;  $Z = 1.07$ ,  $P = 0.28$ ). However, the strength of this relationship varied with light levels (Light\*Technique\*Colour,  $\chi^2 = 13.95$ ,  $df = 4$ ,  $P = 0.008$ ; Fig. 21B-D). White bears had lower frequencies of *Standing* during daylight but higher frequencies during twilight and darkness, (Daylight:  $Z = -3.42$ ,  $P < 0.001$ ;

Twilight:  $Z = 2.04$ ,  $P = 0.041$ ; Darkness:  $Z = 0.95$ ,  $P = 0.499$ ) and had higher frequencies of *Walking* during daylight ( $Z = 2.56$ ,  $P = 0.010$ ) but not darkness ( $Z = -2.00$ ,  $P = 0.045$ ).

#### 4.3.2 *Capture efficiency*

##### 4.3.2.1 *Light level effects*

Overall capture efficiency of salmon was 27.2% ( $N=1769$ ) but this varied among light levels (Light\*Success:  $\chi^2 = 11.67$ ,  $df = 2$ ,  $P = 0.003$ ; Fig. 22.). The highest efficiency occurred during twilight (33.6%), lower efficiencies occurred during daylight (26.5%) while the lowest efficiencies occurred during darkness (24.7%). Relatively high capture efficiency during twilight ( $Z = 2.51$ ,  $P = 0.012$ ) and relatively low capture efficiency during darkness ( $Z = -2.53$ ,  $P = 0.012$ ) contributed equally to the loglinear model.

##### 4.3.2.2 *Technique effects*

There were also interactions between capture efficiency and fishing technique (Technique\*Success  $\chi^2 = 72.26$ ,  $df = 2$ ,  $P < 0.001$ ). *Standing* was the most efficient technique (35.4%) while *Running* was less efficient (20.5%) and *Walking* was the least efficient (15.2%). *Standing* ( $Z = 7.01$ ,  $P < 0.001$ ) and *Walking* ( $Z = -4.50$ ,  $P < 0.001$ ) contributed most to the loglinear model because of their comparatively high and low capture efficiencies, respectively.

##### 4.3.2.3 *Light level and technique interactions*

These fishing techniques varied in their relative capture efficiencies among the three light levels (Fig. 23). The capture efficiency of *Standing* was lowest during

darkness (29.4%) climbing to its peak during twilight (44.2%) and declined during daylight (36.1%). *Walking* capture efficiency varied little among light levels and tended to decline from twilight (19.8%) to either darkness or daylight (14.0% and 13.8% respectively), while efficiencies of *Running* tended to decline from twilight (28.4%) to darkness (20.4%) or to daylight (18.4%). However the relationship between light level, technique use and capture efficiency was not statistically significant (Light\*Technique\*Success,  $\chi^2 = 1.55$ ,  $df = 4$ ,  $P = 0.82$ ).

#### 4.3.2.4 *Colour morph and interactions*

Overall capture efficiency was similar for both colour morphs (White: 30.0%; Black: 26.5%; Colour\*Success,  $\chi^2 = 0.55$ ,  $df = 1$ ,  $P = 0.46$ ), but differed among light regimes (Light Level\*Colour\*Success,  $\chi^2 = 6.63$ ,  $df = 2$ ,  $P = 0.036$ ; Fig. 24A.). White bears were less efficient than black bears during darkness (22.8% and 25.8% respectively;  $Z = -2.07$ ,  $P = 0.039$ ), but were more efficient than black bears during daylight and twilight, although this effect was only statistically significant in daylight. (Daylight: 34.1% and 25.3% respectively;  $Z = 2.33$ ,  $P = 0.020$ ; Twilight: 37.5% and 32.1% respectively;  $Z = 0.08$ ,  $P = 0.94$ ).

Although capture efficiencies were variable between colour morphs among fishing techniques and light levels, there was not an overall effect on efficiency when examining all variables simultaneously (Light Level\*Technique\*Colour\*Success,  $\chi^2 = 3.13$ ,  $df = 4$ ,  $P = 0.54$ ). During darkness, black bears tended to be more efficient than white bears while *Standing* (33.6% vs. 23.4% respectively;  $Z = 0.345$ ,  $P = 0.73$ ; Fig. 24B.) and *Walking* (15.3% vs. 9.5% respectively;  $Z = 1.43$ ,  $P = 0.15$ ) while both morphs had similar efficiencies in *Running* (20.0% vs. 21.1% respectively;  $Z = 1.44$ ,  $P = 0.15$ ).

However, during twilight, white bears were more efficient than black bears while *Walking* (33.3% vs. 16.7% respectively;  $Z = 0.53$ ,  $P = 0.59$ ; Fig. 24C), and there was little difference between the two morphs while *Standing* (20.0% vs. 21.1% respectively;  $Z = 0.028$ ,  $P = 0.97$ ) and *Running* (20.0% vs. 21.1% respectively;  $Z = 0.61$ ,  $P = 0.54$ ). Furthermore, white bears were more efficient than black bears among all three fishing techniques during daylight, although none of these differences reached statistical significance (*Standing*: 42.1% vs. 35.3% respectively;  $Z = 0.42$ ,  $P = 0.67$ ; *Walking*: 36.0% vs. 10.4% respectively;  $Z = 1.13$ ,  $P = 0.26$ ; *Running*: 22.4% vs. 17.7% respectively;  $Z = 0.94$ ,  $P = 0.35$ ; Fig. 24D).

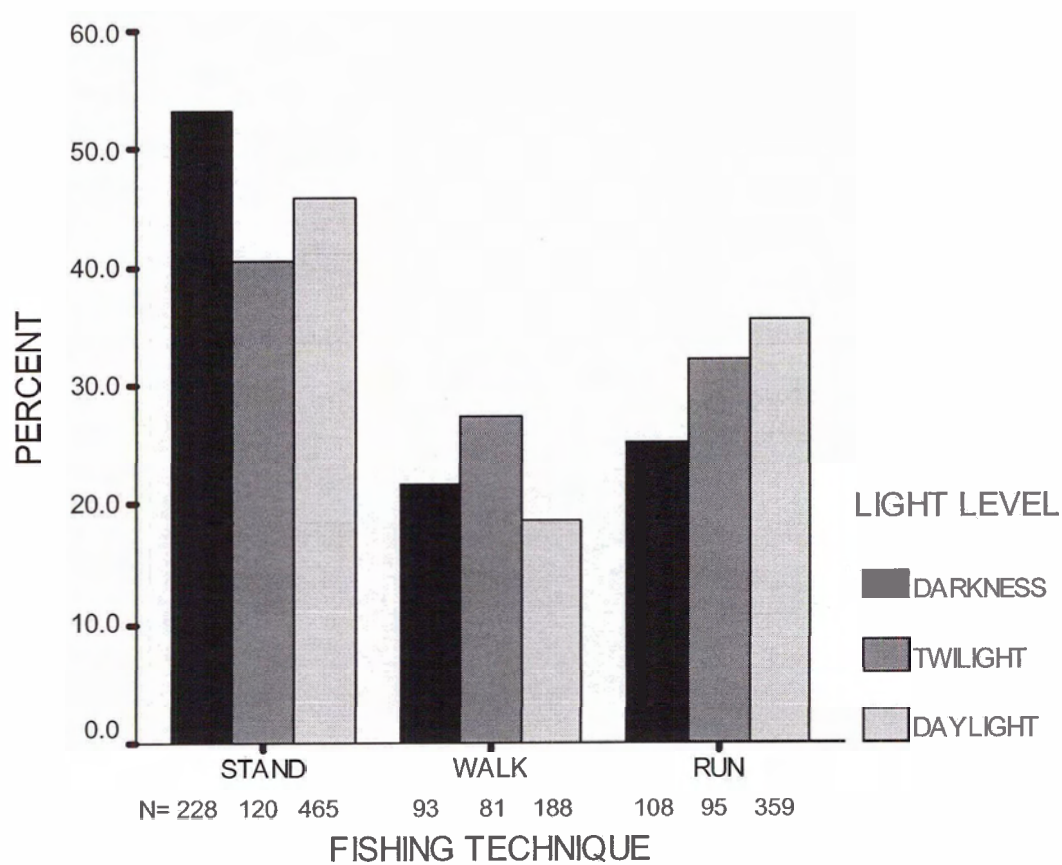


Figure 20. Observed proportions of the three fishing techniques used by all known bears within darkness, twilight and daylight ( $\chi^2 = 29.3$ ,  $df = 2$ ,  $P < 0.001$ ).

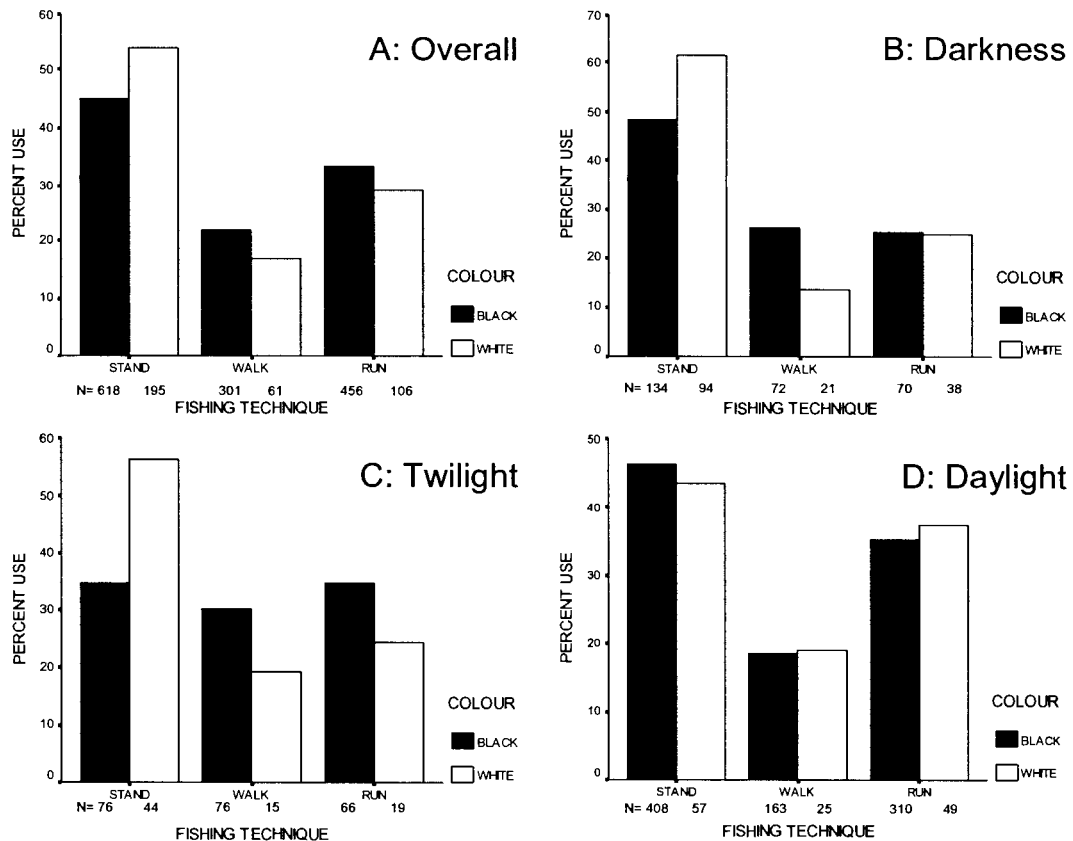


Figure 21A-D. Observed proportions of three fishing techniques used by black and white bears among three light regimes. **A.** Shows overall proportions for pooled light regimes ( $\chi^2 = 8.48$ ,  $df = 2$ ,  $P = 0.014$ ). **B.** Shows overall proportions during darkness. Colour morphs differed in *Standing* and *Walking* but not *Running*. **C.** Shows overall proportions during twilight. Colour morphs differed in *Standing* only. **D.** Shows overall proportions during daylight. Colour morphs differed in *Standing* and *Walking* but not *Running*.

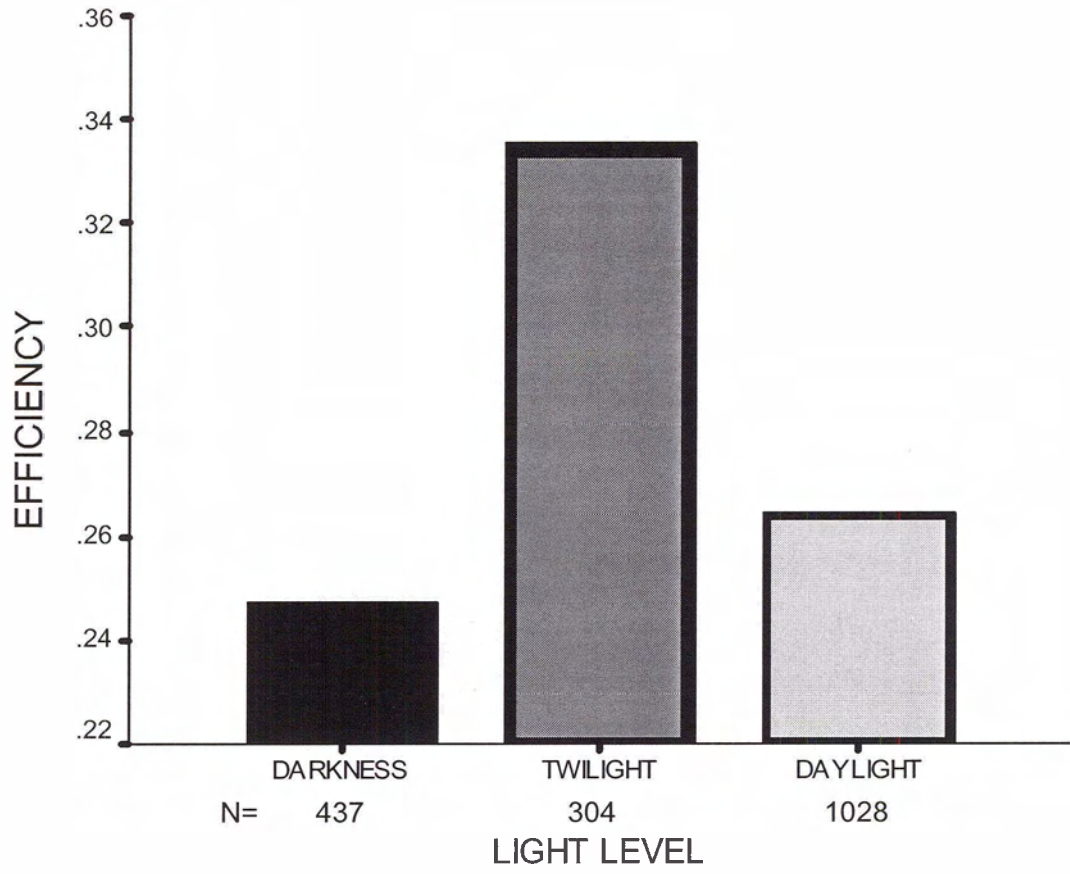


Figure 22. Overall capture efficiencies by all known bears within darkness, twilight and daylight ( $\chi^2 = 11.67$ ,  $df = 2$ ,  $P = 0.003$ ).

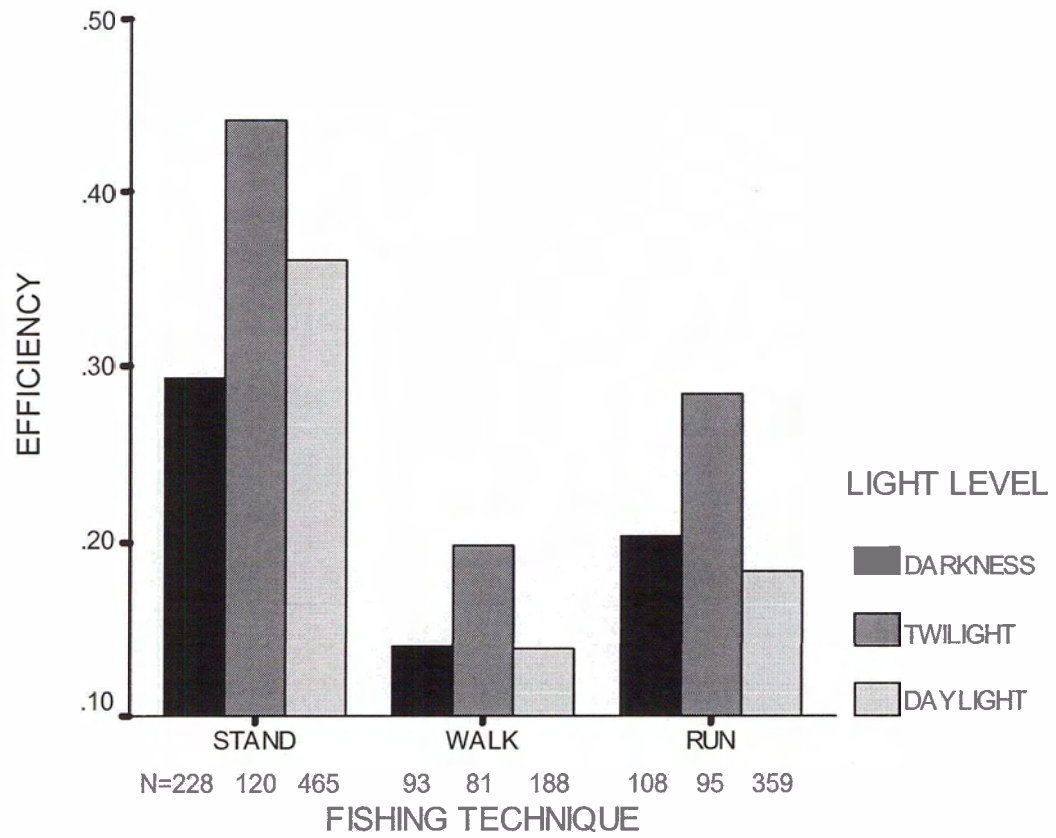


Figure 23. Capture efficiencies of the three fishing techniques by all known bears within darkness, twilight and darkness ( $\chi^2 = 1.55$ ,  $df = 4$ ,  $P = 0.82$ )

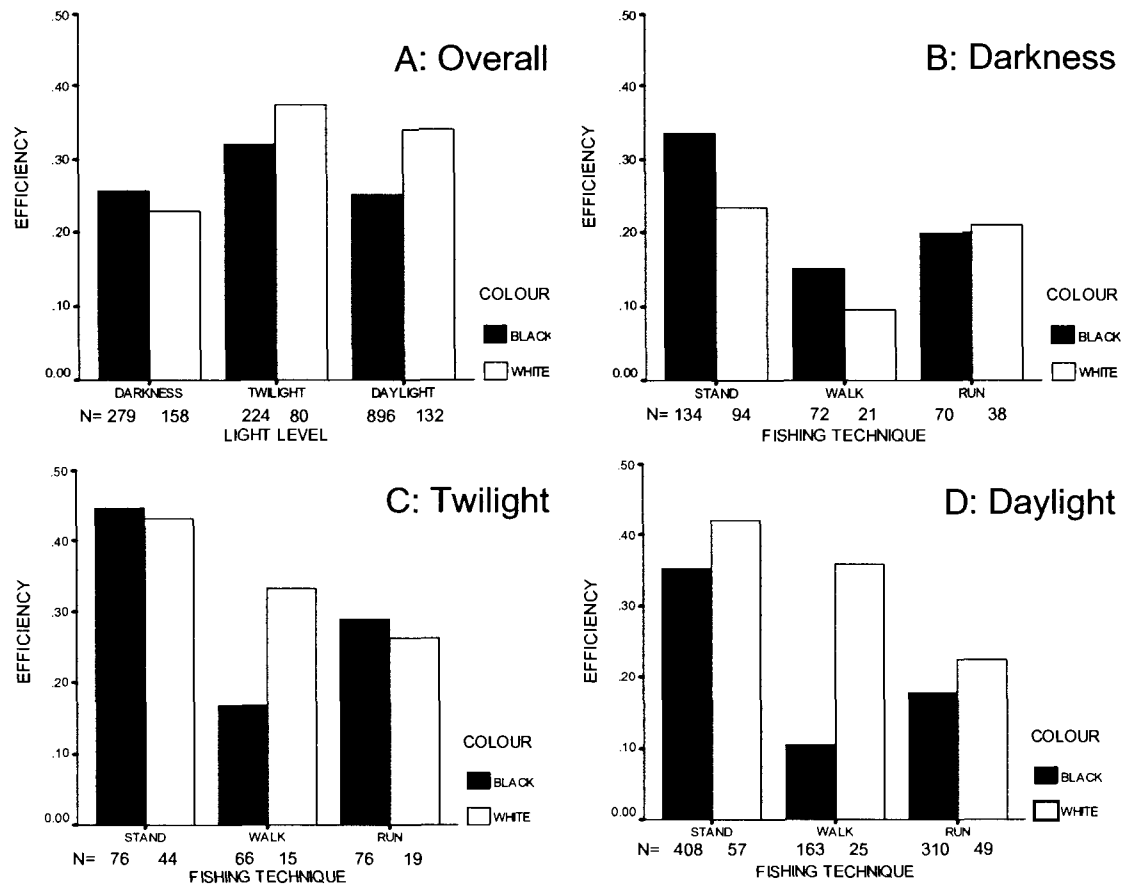


Figure 24A-D. Capture efficiencies of black and white bears among three light regimes. **A.** Shows overall efficiencies among light regimes. White bears were slightly more efficient twilight and daylight but not during darkness ( $\chi^2 = 6.63$ ,  $df = 2$ ,  $P = 0.036$ ). **B.** Shows overall efficiencies during darkness. Black bears were slightly more efficient while *Standing* and *Walking* but not *Running*. **C.** Shows overall efficiencies during twilight. White bears were slightly more efficient than black bears while *Walking*. **D.** Shows overall efficiencies during daylight. White bears were slightly more efficient than black bears for all techniques.

### 4.3.3 Capture rates

#### 4.3.3.1 Year effects

Overall capture rate was  $5.0 \pm 0.54$  SE fish/hour but this differed among years ( $\chi^2 = 7.39$ ,  $df = 2$ ,  $P = 0.025$ ; KW). Capture rates in 2000 ( $2.6 \pm 0.55$  SE fish/hour) were lower than rates observed during 2001 ( $6.0 \pm 0.77$  SE fish/hour) and 2002 ( $4.7 \pm 1.13$  SE fish/hour).

#### 4.3.3.2 Light level effects

Among years, capture rates were similar among light levels (Fig. 25). During 2000 capture rates were greatest during darkness (2000:  $\bar{X}_{\text{darkness}} = 2.9$  fish/hr  $\pm 1.3$  S.E.; twilight = 2.1 fish/hr;  $\bar{X}_{\text{daylight}} = 2.6$  fish/hr  $\pm 0.6$  S.E.;  $\chi^2 = 0.20$ ,  $df = 2$ ,  $P = 0.90$ ; KW) while during 2001, capture rates were greatest during daylight (2001:  $\bar{X}_{\text{darkness}} = 4.8$  fish/hr  $\pm 1.1$  S.E.;  $\bar{X}_{\text{twilight}} = 6.1$  fish/hr  $\pm 1.0$  S.E.;  $\bar{X}_{\text{daylight}} = 6.4$  fish/hr  $\pm 1.1$  S.E.;  $\chi^2 = 1.7$ ,  $df = 2$ ,  $P = 0.43$ ; KW). During 2002, capture rates during twilight were almost double the capture rates observed during daylight and darkness, and these differences approached statistical significance (2002:  $\bar{X}_{\text{darkness}} = 3.9$  fish/hr  $\pm 1.1$  S.E.;  $\bar{X}_{\text{twilight}} = 6.7$  fish/hr  $\pm 1.8$  S.E.;  $\bar{X}_{\text{daylight}} = 4.1$  fish/hr  $\pm 1.9$  S.E.;  $\chi^2 = 5.9$ ,  $df = 2$ ,  $P = 0.051$ ; KW).

#### 4.3.3.3 Colour morph and light level effects

Capture rates were similar between morphs among years (2000:  $\bar{X}_{\text{black}} = 2.7$  fish/hr  $\pm 0.6$  S.E.;  $\bar{X}_{\text{white}} = 2.5$  fish/hr  $\pm 1.4$  S.E.;  $Z = -0.19$ ,  $df = 2$ ,  $P = 0.85$ ; MW; 2001:  $\bar{X}_{\text{black}} = 6.1$  fish/hr  $\pm 0.9$  S.E.;  $\bar{X}_{\text{white}} = 5.6$  fish/hr  $\pm 1.1$  S.E.;  $Z = -0.19$ ,  $df = 2$ ,  $P = 0.85$ ; MW; 2002:  $\bar{X}_{\text{black}} = 4.8$  fish/hr  $\pm 1.5$  S.E.;  $\bar{X}_{\text{white}} = 4.2$  fish/hr  $\pm 1.1$  S.E.;  $Z = -0.19$ ,  $df = 2$ ,  $P =$

0.85; MW). Overall, black bears had slightly higher capture rates than white bears during all years, but none of these differences were statistically significant. Capture rates were also similar between morphs among light levels among years ( $P > 0.05$  for all comparisons)

#### 4.3.3.4 Foraging bout length effects

Fishing bout durations were highly variable (2000: 54.6 minutes  $\pm$  8.7 S.E., range=1-245; 2001: 38.1 minutes  $\pm$  3.2 S.E., range=1-155; 2002: 32.2 minutes  $\pm$  3.8 S.E., range=1-120) as bears would arrive on the stream, quickly capture a fish and then move out of sight, or remain visible on the stream for long periods of time and capture multiple fish. As a consequence, fishing bout durations had a strong effect on numbers of successful captures and capture rates. Numbers of successful captures were greater during long duration (>61 minutes) fishing bouts relative to short duration (<61 minutes) fishing bouts (2000:  $\bar{X}_{\text{short}} = 1.5 \pm 0.33$  S.E.,  $\bar{X}_{\text{long}} = 1.7 \pm 0.69$  S.E.;  $Z = -0.09$ ,  $P = 0.93$ ; 2001:  $\bar{X}_{\text{short}} = 1.8 \pm 0.16$  S.E.,  $\bar{X}_{\text{long}} = 4.9 \pm 0.66$  S.E.;  $Z = -4.5$ ,  $P < 0.001$ ; 2002:  $\bar{X}_{\text{short}} = 1.3 \pm 0.16$  S.E.,  $\bar{X}_{\text{long}} = 2.4 \pm 0.63$  S.E.;  $Z = -1.7$ ,  $P = 0.087$ ; Fig.26A-D), but capture rates were lower (2000:  $\bar{X}_{\text{short}} = 3.5 \pm 0.74$  S.E.,  $\bar{X}_{\text{long}} = 0.8 \pm 0.24$  S.E.;  $Z = -1.86$ ,  $P = 0.062$ ; 2001:  $\bar{X}_{\text{short}} = 6.8 \pm 0.97$  S.E.,  $\bar{X}_{\text{long}} = 3.5 \pm 0.53$  S.E.;  $Z = -1.90$ ,  $P = 0.057$ ; 2002:  $\bar{X}_{\text{short}} = 5.2 \pm 1.30$  S.E.,  $\bar{X}_{\text{long}} = 1.5 \pm 0.33$  S.E.;  $Z = -1.58$ ,  $P = 0.11$ ).

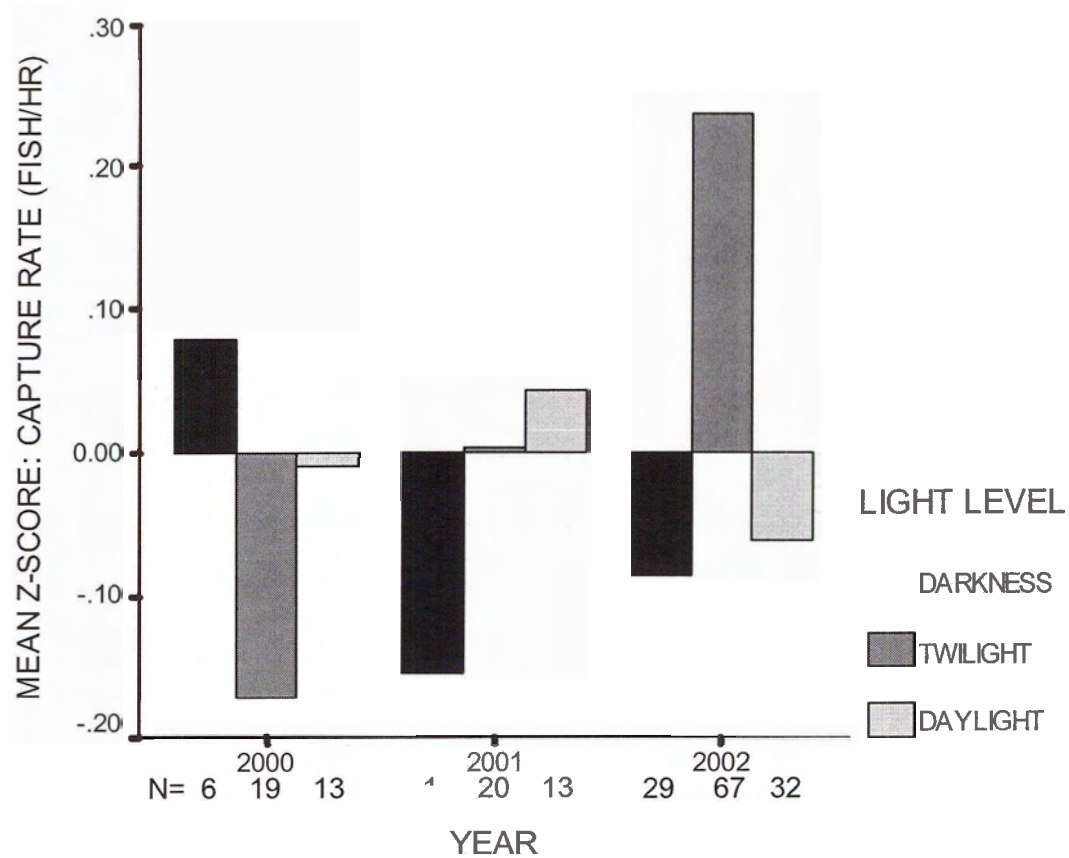


Figure 25. Capture rates (Z-scores standardized for year) were similar among light levels within years (2000:  $P = 0.90$ ; 2001:  $P = 0.43$ ), although the elevated rates in twilight approached statistical significance in 2002 ( $P = 0.051$ ).

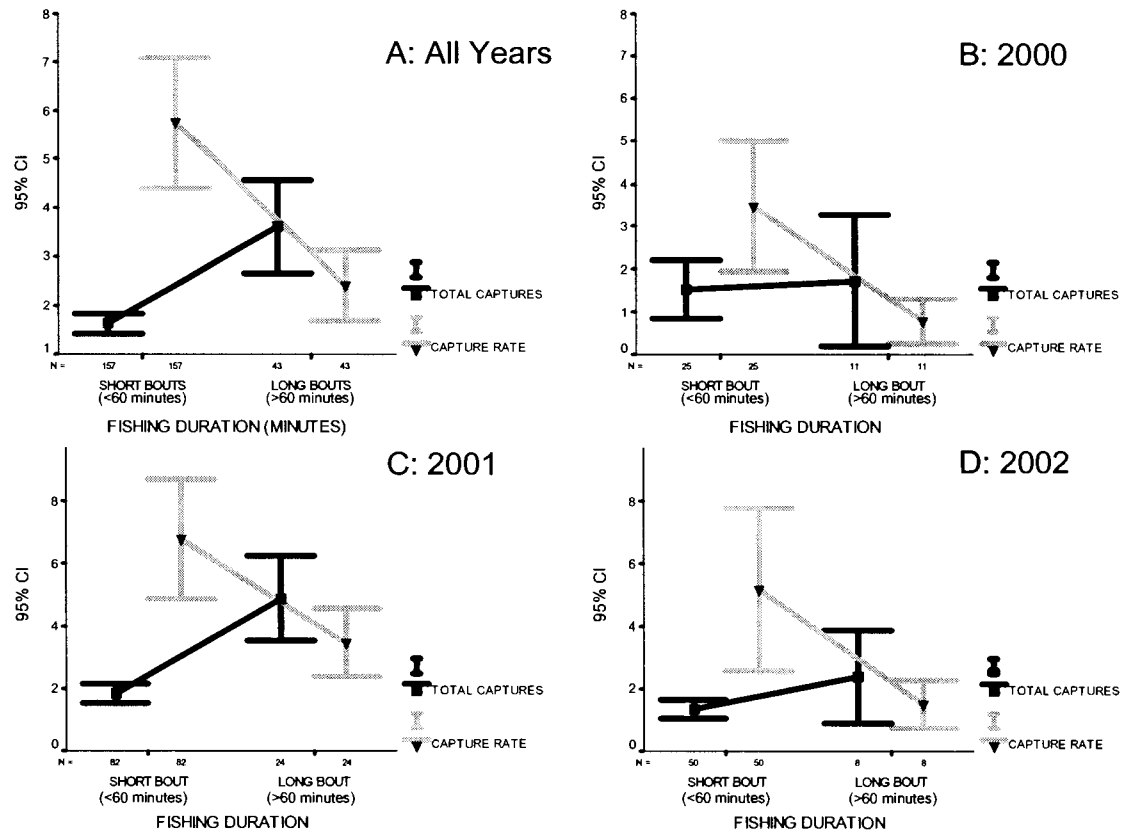


Figure 26A-D. The relationships between fishing bout duration for both bear morphs and number of fish captured, and the number of fish captured per hour among years. Within each year, total numbers of salmon captured tended to increase with bout length while capture rates tended to decrease. **A.** Shows the overall relationship between fishing bout duration and number of fish captured, and the number of fish captured per hour among all years. **B.** The relationship between fishing bout duration and number of fish captured, and the number of fish captured per hour during 2000. **C.** relationship between fishing bout duration and number of fish captured, and the number of fish captured per hour during 2001. **D.** relationship between fishing bout duration and number of fish captured, and the number of fish captured per hour during 2002.

#### 4.3.4 Salmon activity patterns

Overall salmon spawning activity rate differed among years ( $F_{1,60}=10.0$ ,  $P=0.003$ ) and light levels ( $F_{2,60}=23.6$ ,  $P<0.001$ ; Fig. 27). During 2001, overall salmon spawning activity rate was 5.0 spawn/min  $\pm$  4.0 S.E. and was greatest during darkness (9.8 spawn/min  $\pm$  1.6 S.E.), followed by twilight (4.9 spawn/min  $\pm$  0.6 S.E.) and was lowest during daylight (2.3 spawn/min  $\pm$  0.7 S.E.). Similarly, during 2002, overall salmon spawning activity rate was 3.3 spawn/min  $\pm$  2.4 S.E. and was also greatest during darkness (5.8 spawn/min  $\pm$  1.1 S.E.), followed by twilight (2.8 spawn/min  $\pm$  0.5 S.E.) and was lowest during daylight (2.3 spawn/min  $\pm$  0.5 S.E.).

#### 4.3.5 Acoustic cues: speaker

During call playback experiments, bears exhibited a range of responses to simulated salmon spawning noises and light levels had no detectable effect on bear response ( $\chi^2 = 3.51$ ,  $df = 2$ ,  $P=0.173$ ). Overall, bears tended to ignore or move away from the speaker in the playback trials. Of the 123 playback trials, there were 74 cases where bears ignored the speaker and 38 cases where bears moved slowly away from the speaker. In the other cases, bears either moved towards ( $N=2$ ) or ran away ( $N=9$ ) from the speaker. This suggests that bears did not use acoustic cues while fishing or the acoustic characteristics of the call playback were sufficiently different from the actual characteristics of salmon spawning and were ignored or avoided by bears.

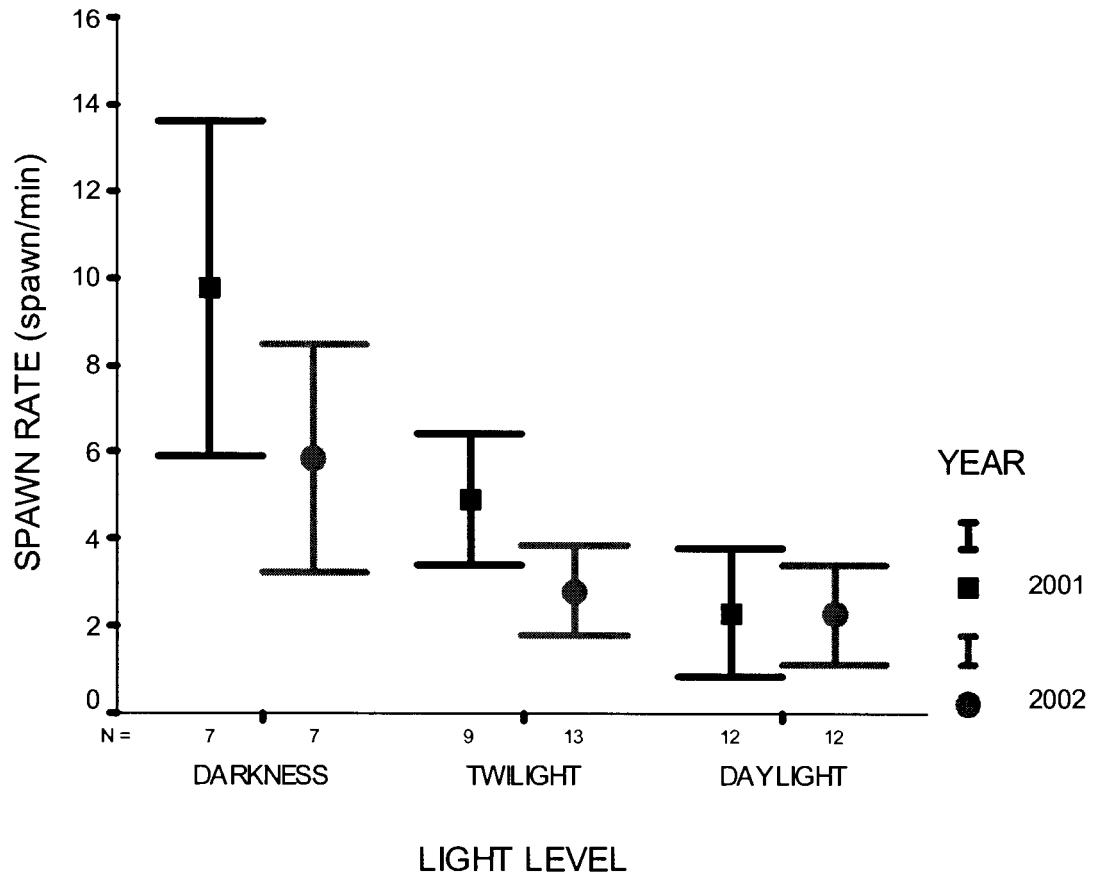


Figure 27. Salmon spawning rate (activity) observed within three light regimes.

Spawning activity was variable between years but consistently greatest during darkness and lowest during daylight ( $P < 0.001$ ; Tukey HSD post hoc test).

## 4.4

## Discussion

Consistent with previous studies, bears actively foraged for salmon during all light levels, including darkness (Frame 1974, Reimchen 1998b, Klinka and Reimchen 2002). Foraging during darkness occurred despite the absence of brown bears and human activity (for the first two years of the study) and can not be attributed to a restriction into sub-optimal foraging periods (Machutchon et al. 1997, Olson et al. 1998).

### 4.4.1 *Fishing technique*

Fishing techniques were variable among light levels. Bears in this study preferred *Standing* over *Running* and *Walking* among all three light regimes. This contrasts with observations of brown bears where *Standing* was preferred during darkness while *Standing* and *Running* were used with nearly equal frequency during daylight (Klinka and Reimchen 2002). However, *Running* was more common during high light levels in both studies. This is also most likely due to the reliance of visual systems for successful chase sequences as reported for brown bears. Although the frequency of *Running* was highest during daylight, it was during this time period that the efficiency of *Running* was lowest. This could be attributed to the increased evasive responsiveness of salmon during daylight (Chapter 5: Model Predator) or that fewer salmon are spawning in the stream shallows compared to darkness.

#### 4.4.2 *Efficiency*

During this study, overall capture efficiency averaged 27%, which is consistent with previously reported efficiencies for both black and brown bears. Observations of brown bears in Alaska and British Columbia have reported comparable capture efficiencies of 31% and 27% respectively (Luque and Stokes 1976, Klinka and Reimchen 2002), while studies of black bears from Alaska and British Columbia have reported daytime efficiencies of 26% and nocturnal efficiencies of 24% (Frame 1974, Reimchen 1998b). However, the black bears in this study had the greatest capture efficiencies during twilight (34%) and lowest efficiency during daylight (27%) and darkness (25%) whereas the brown bears reported in Klinka and Reimchen (2002) had the greatest capture efficiencies during darkness (36%) and lowest efficiency during daylight (20%).

Variability in reported efficiencies among studies could be related to the different stream characteristics and subsequent salmon behaviour among study sites (Luque and Stokes 1976). In Klinka and Reimchen (2002), salmon were limited to spawning in a stream section above and below a weir. This weir formed a partial barrier to upstream migration, resulting in large numbers of salmon to pool in the shallow waters directly beneath the weir. Consequently, bears concentrated their fishing efforts on these large aggregations of salmon beneath the weir, and not in the deeper water above it where the majority of spawning occurs. This dense aggregation of fish enabled bears to stand in the water and use primarily tactile cues to locate salmon during darkness. The availability of auditory cues to these brown bears could be limited by the fact that salmon did not concentrate their spawning efforts below the weir. Furthermore, elevated stream noise

caused by water moving down the weir could potentially limit the effectiveness of acoustic hunting strategies.

This contrasts with the stream characteristics in this study where salmon actively spawn along the length of the stream and are targeted by bears in multiple locations. Variable stream topography combined with the lack of a disruptive sound source (weir) enabled black bears to utilize multiple fishing techniques and sensory modes while foraging. This behavioural plasticity results in similar foraging efficiencies between daylight and darkness.

High capture efficiencies during low light levels could also be attributed to possible enhanced visual capabilities of bears relative to that of salmon during this time period (Reimchen 1998b, Klinka and Reimchen 2002). Enhanced visual acuity during low light levels has often been implicated as an important advantage that mammalian predators exploit, and probably accounts for their preference of crepuscular and nocturnal activity patterns. Bears possess a tapetum lucida that assists vision in low light situations by reflecting light back through the retina (Ronald and Lee 1981). Salmonids (*Oncorhynchus spp.*) lack a tapetum (Nicol et al. 1973) and as a consequence, may have difficulty, or be completely unable to visually detect the presence of an approaching bear during low light levels. However, salmon may shift reliance to lateral line sensory systems to detect proximal bears during darkness.

#### 4.4.3 *Fishing technique and efficiency*

Fishing techniques and efficiencies were variable among light levels. Among all three light levels, *Standing* was the most efficient of the three foraging techniques while

*Walking* was the least efficient. The low efficiencies of *Walking* could be attributed to the production of movement-induced pressure waves in the water which could alert salmon to the approach of a bear (Klinka and Reimchen 2002).

Consistent with optimal foraging theory and previously reported trends, bears used fishing techniques in accordance with their relative efficiencies among all light levels (Luque and Stokes 1976, Krebs 1978, Klinka and Reimchen 2002). *Standing* was most efficient in all light levels and was most freq used, while *Walking* was used least often and was the least efficient of all the techniques among all light regimes.

To my knowledge, this study is the first to document increased salmon spawning activity during darkness relative to daylight, and this shift in activity patterns has important consequences for the sensory systems and foraging ability of bears. It is possible that elevated nocturnal spawning activity allows bears to compensate for the reduced visibility during darkness and retain high capture efficiencies during this time period. Bears can exploit the acoustic and tactile cues given off by spawning salmon by shifting from visual pursuit strategies during daylight to alternate sensory modes during darkness (Reimchen 1998b, Klinka and Reimchen 2002).

It is not clear why salmon would display elevated nocturnal activity patterns, but possible scenarios could be decreased intraspecific competition between males over access to females, and between females over access to redds (McNeil 1967). Perhaps reductions in agonistic behaviour among salmon during darkness could be due to non-functioning visual systems. However, it is interesting to note that previous studies of the sensory mechanisms employed by salmon during spawning events indicate not only that visual systems are used alongside with tactile cues, but that both the visual and

vibrational cues are necessary for eliciting the male spawning behaviour (Satou et al. 1994b).

Bears seemed to respond to the audible splash sounds made by salmon. Early attempts to mimic salmon splashing noises with a vibrating stick were suggestive of acoustic or tactile based fishing as bears would look in the direction of the splash and often approach us to investigate the source more closely. Building upon these observations, I then attempted to isolate the sensory modes utilized by bears with a form of call playback where I played salmon splashes to bears. Since the speaker would not create the strong vibrations in the water as an actual salmon, this protocol made available only auditory cues to bears. It was hypothesized that bears would pay little attention to the splashes during daylight when visual systems were primarily utilized to capture prey, but would increase their attention given to the splashes during darkness where hearing and tactile sensory modalities were more active. However, my results from these experiments were inconclusive as it became evident that our recordings and subsequent playback of salmon splash noises were not of sufficient quality to accurately duplicate these sounds. As a consequence, bears tended to ignore the splashes within all three light regimes. Based upon these observations, I cannot completely discount the hypothesis of acoustic based foraging, but our experimental results neither support nor yield insight into the matter.

#### *4.4.4 Colour morph effects*

Owing to the increased visual responsiveness of salmon during daylight, bear colour effects on technique use and efficiency should occur during daylight and twilight,

but not during darkness. Consistent with this theory, I detected significant differences in the use of *Standing* and *Walking* during daylight and twilight but not during darkness. *Standing* was preferred by white bears in twilight while black bears preferred *Standing* during daylight. However, this is contrary to what I would have predicted given that salmon are less timid towards white bears than towards black bears (See Chapter 5: Model Predator). I expected white bears to stand more during the day relative to black bears to exploit this behaviour observed in salmon.

It is difficult to identify factors contributing to why *Standing* and *Walking* are favoured between the two morphs among the different light regimes as both techniques have their respective advantages and disadvantages, and the two morphs alternate their technique preference between daylight and twilight. Bears favouring *Standing* employ 'sit and wait' ambush strategies and may be seeking to minimize movements that provide salmon with visual and tactile cues to their location. Conversely, bears that prefer *Walking* may seek to intentionally disturb the water, thereby alarming salmon that attempt escape by rapidly swimming away. This may seem counterproductive, but spawning fish are typically in shallow water and their escape attempts often send them into shallower water or up onto the shore itself where capture becomes less difficult. It is also possible that bears walk in the water to elicit movements from salmon, which would facilitate detection against a uniform background. However, bears may be walking in the water simply to move to alternate fishing localities, and in doing so opportunistically attempt to capture salmon.

Bear colour and light levels were associated with capture efficiency. Overall capture efficiencies were similar between colour morphs, yet efficiency differences were

detected among the three light regimes with white bears being more efficient than black bears during daylight, contrasting with the elevated capture efficiency of black bears during darkness. A possible mechanism for why colour morphs differ in foraging efficiencies among light levels could be related to the visual and behavioural responses of salmon to an approaching bear. There is evidence for reduced evasive response by salmon to white bears and this effect is strongest during daylight and absent during darkness (see Chapter 5: Model Predator). From the salmon's visual perspective, a white bear would contrast less against a bright sky background than a black bear. This would make the white morph effectively more camouflaged than the black bear, and confer a foraging advantage in a similar manner to the white underparts of seabirds facilitating foraging because of their inconspicuousness to aquatic prey against the bright sky (Gotmark et al. 1986, Gotmark 1987). Presumably, such an advantage would be strongest in daylight, weaker during twilight and absent during darkness. This may explain why black bears prefer *Standing* during daylight, but does not explain why they do not prefer *Standing* during twilight.

Capture efficiencies for both morphs also varied with fishing technique among light regimes. While *Walking* during daylight, black bears had capture efficiencies of only 10%, yet while *Standing* their efficiency rose to 35%. Conversely, white bears had capture efficiencies of 36% while *Walking*, and a comparable 42% efficiency while *Standing*. Perhaps this is a form of niche partitioning in differential fishing technique as seen in other taxa where foraging niches differ among morphs (Adams and Huntingford 2002, Guiguer et al. 2002, Andersson 2003).

#### 4.4.5 *Capture rates*

Capture rates were influenced by the duration of foraging bouts but not by light levels or colour morph. Capture rates were approximately three times higher during short duration compared to long duration fishing bouts. Short duration fishing bouts were often characterized by bears arriving on the stream and quickly capturing a fish and then moving out of sight, whereas during longer foraging bouts, individuals remained visible on the stream for long periods of time and captured multiple fish. As a consequence, short duration bouts tend to overestimate capture rates while long duration fishing bouts probably reflect a more realistic estimate of capture rate over time. This effect may be a result of reduced fishing effort as bears become increasingly satiated during longer foraging bouts (Klinka and Reimchen 2002).

Capture rates of salmon by both brown and black bears appear to be similar in most coastal areas. Bears in this study area had overall capture rates (for bouts in excess of 60 minutes) ranging from 0.6 - 3.5 fish/hour from 2000-2002. These rates are comparable to 2.1 fish/hour reported for black bears in Alaska (Frame 1974), and 13 fish/day (roughly 0.5 fish/hour) for black bears on the Queen Charlotte Islands (Reimchen 2000). Furthermore, the capture rates in this study are also comparable to those reported for British Columbian brown bears which caught an average of 4.2 fish/hour for bouts in excess of 60 minutes (Klinka and Reimchen 2002), and to dominant Alaskan brown bears which caught an average of 1.0 to 3.4 fish per hour (Egbert and Stokes 1976, Luque and Stokes 1976).

This study illustrates the behavioural plasticity inherent to coastal bears in their ability to exploit and successfully forage in multiple temporal regimes. By tailoring

appropriate fishing techniques among light levels, bears are able to capitalize on changes in salmon vulnerability and maintain high capture rates in a variety of lighting environments. Furthermore, bears may shift to alternate sensory systems depending upon lighting environments and the behaviour of prey, as elevated nocturnal spawning behaviour of salmon may increase their susceptibility to predation by creating acoustic cues.

This type of pelage polymorphism appears to be a functional adaptation to foraging strategies. The variability in coat colours may enable bears to successfully forage in different lighting environments, as white bears appear to have higher foraging success during daylight while black bears appear to have higher foraging success during darkness. If it is true that colour morphs differ in capture efficiencies among light levels, then this has implications for their ability to utilize salmon resources, and suggests a niche polymorphism. Increased utilization of salmon resources confers fitness benefits to coastal bear populations (Hilderbrand et al. 1999a, Hilderbrand et al. 1999b), thus increased utilization of salmon by a particular colour morph could confer a selective advantage to that morph and promote the long term maintenance of the polymorphism. As Kermode bears have few natural predators, the maintenance of the polymorphism is not likely due to frequency dependent effect due to the actions of selective predation or apostatic selection, rather it is likely the result of niche partitioning between morphs.

## **Chapter 5: Behavioural responses of salmon to a model predator among variable light regimes**

### **5.1 Introduction**

Predation occurs in three distinct phases: detection, pursuit, and subjugation, with each phase being a necessary component of a successful capture (Vermeij 1982).

Predators attempting to capture highly maneuverable prey may seek to minimize detection to allow closer proximity thereby facilitating successful capture, and prey may seek to minimize detection to avoid the subsequent phases of predation. One method of minimizing detection is to camouflage your form into that of the background and examples of crypsis have long fascinated evolutionary biologists (Cott 1940, Endler 1978).

Color polymorphism occurs in many taxa (Rounds 1987, Colyn 1993, Franck et al. 2001, Johannesson and Eken Dahl 2002, Galeotti et al. 2003) yet the origin and the basic mechanisms maintaining most polymorphisms are not well understood (Jones et al. 1977, Losey et al. 1997). Some hypotheses suggest that polymorphisms are functional traits maintained by frequency dependent selection (such as apostatic selection) or multiple-niche partitioning (Paulson 1973, Smith 1990, Cook 1998).

In apostatic selection, a given phenotype is favoured in direct proportion to its rarity through frequency-dependent predator pressure. Prey encounter a common predator morph with sufficient frequency to form a search image of the predator thereby increasing their ability to detect it. There may be a threshold of abundance before a

search image is formed, thus rarer morphs would be favoured if they were not present in numbers sufficient to permit the formation of the search image. Thus a rare predator has an opportunity to exploit naïve prey and have a greater chance for successful capture of that individual. This slight advantage of the rarer morph could lead to balanced polymorphism in the population (Paulson 1973). However, apostatic selection has been difficult to demonstrate in nature (Preston 1980).

Examples of multiple-niche partitioning are observed in the various morphs of wading shorebirds. Different morphs may vary in success in different habitats or in the same habitat under different light conditions (Galeotti et al. 2003). This is thought to be due to differences in foraging efficiency caused by variation in hunting camouflage. It is speculated that white morphs may be more cryptic when viewed against bright sky during daylight, whereas dark morphs may be more cryptic when viewed against a dark background. Based on experimental data on herons, Mock (1980) suggested that white morphs predominate in clear shallow waters on sunny days and open habitats as found along sea coasts and coral reefs, whereas dark morphs could predominate in cloudy water in closed habitat as found along inland waterways. In addition, the white underparts of seabirds have been shown to facilitate foraging because of their inconspicuousness to aquatic prey against the bright sky (Gotmark et al. 1986, Gotmark 1987)

Murton (1971) suggested that white and dark morphs in herons are maintained because the white forms are less visible to prey and have an advantage in situations demanding stealth or surprise while the dark morphs have an advantage in scaring or flushing prey out of hiding or into movement. However, this hypothesis was not supported by direct observations of Eastern Reef Herons or in Polynesian Egrets where

foraging patterns were similar between the two morphs (Recher and Recher 1972, Holyoak 1973).

In this paper I examine evasive responses of salmon to a simulated polymorphic predator during diurnal, crepuscular and nocturnal periods. I predict that salmon would exhibit increased evasive swimming behaviour towards black colours compared to white colours in daylight and twilight but not during darkness. Such differences in potential prey susceptibility between colour morphs confer a foraging advantage to one morph over the other, and may provide a portion of a mechanism maintaining this polymorphism.

## **5.2 Methods and Materials**

### *5.2.1 Experimental Pool*

In a suitable area of the stream where salmon were either actively spawning or holding, I setup an observational pool (hereafter called the arena) consisting of two circular rings delineated by white painted rocks that were clearly visible from above the stream surface. One ring had a 2m radius from the origin (centre), and the other had a radius of 4m. The stream substrate and depth (approximately 50cm) were consistent within the entire observational area (Fig. 28A).

### *5.2.2 Simulating colour morph effects*

To simulate an individual black or white morph bear standing in the water I draped myself in either black or white linen (Fig. 28B). The fabric costume covered my

entire body except for small eye openings. The fabric did not break the surface of the water, typically stopping a few centimetres above the water surface. As this study was concerned with salmon response to above water visual stimuli, green coloured rubber boots were worn during all trials thus standardizing below water visual stimuli.

### *5.2.3 Simulating colour morph effects for two individuals*

I was also interested in whether salmon reacted differently to two bears in close proximity. If salmon were more timid around multiple bears than towards individual bears, then there could be motivation to competitively exclude proximal conspecifics. To investigate potential competitive interference effects between bears, my field assistant also wore a costume during appropriate trials.

### *5.2.4 Experimental protocol*

I conducted 38 trial sets over a four week period in Sept 2002 during the salmon migration within three light regimes; complete darkness, twilight, and daylight. Nocturnal trials were made possible with night vision equipment (ITT model CSC-N16140-DX, 50,000x amplification, 0.95 cycles per milliradian resolution) and infrared light emitters. In total there were 5 different treatments; individual black (B), individual white (W), two black (BB), two white (WW), and one mixed treatment consisting of one white one black costume (BW). I alternated trial order for each set. Occasionally, bears would approach to within 5m of me and my assistant as we stood in the arena, at which point we terminated the trial and waited for the bear to vacate the area before resuming. However, interrupted trials during twilight were typically abandoned as light levels did

not remain constant for the time periods necessary to repeat the trial. Interrupted trials were not used in subsequent analysis.

For trials simulating individual bears the experimental protocol was identical for each treatment. While wearing the costume, I entered the water from the shore and walked directly to the centre of the arena. I would stay at this central position for the duration of each trial. The disturbance of entering the stream caused the salmon to scatter, but they typically returned within a few minutes. Once every minute I rotated 360 degrees about the origin and counted the number of visible salmon. I simultaneously recorded salmon numbers within the 2m ring (0-2m) and the zone outside the 2 m but within the 4 m ring (2-4m). I was the only individual performing salmon counts for the entire study. After initial trials, I determined that the majority of salmon had returned to the arena after 5 minutes. I therefore set the trial duration at a conservative 7 minutes for each treatment giving a total of 7 counts. After the seventh count I exited the arena and walked onto the shore which was out of sight of the salmon in the arena. I also determined that when I was not the arena, a three-minute latency period between trials was sufficient for the salmon to return to the trial pool. During this latency period, I would change into the appropriate costume for the next treatment. This enabled comparisons within all light levels possible as twilight typically lasts for 50 minutes, the time required to conduct all treatments.

Trials involving multiple costumes were identical to those involving individual costumes in all respects except my assistant stood at a set location at the edge of the 4m ring delineating the arena boundary. My assistant also wore an appropriate coloured costume, and assumed their set location in synchrony as I assumed my count location. At

no time were visible spectrum flashlights used while in the arena, but my assistant did occasionally scan areas outside the arena for approaching bears during nocturnal trials with a small flashlight.

#### *5.2.5 Count verification*

I assessed observer bias and measurement error with video analysis. I compared salmon counts which were scored on the ground (in the field), to counts made by student volunteers from video filmed simultaneously from a tree above the arena (Fig. 29). Both the volunteers and I were blind as to the treatment being scored. There was a 13.7% measurement error rate in salmon counts made in the pool over the study duration with no bias with respect to colour morph or direction. This implies that my counts were relatively consistent and repeatable.

#### *5.2.6 Statistical procedures*

To test for differences in salmon timidity among light levels and between colour morphs I used a combination of parametric and non-parametric statistics. I tested data distributions for normality with the Kolmogorov–Smirnov test. As data tended to be normal for counts within the 2-4m zone and within the 4m arena I used T-Tests and ANOVA to test for differences in salmon response between colour (black, white), competition (individual, multiple) and among light level (darkness, twilight, daylight). As data tended to be non-normal for counts within 0-2m zone, I used Kruskal–Wallis and Mann-Whitney U tests to test the same criteria. I used Wilcoxon signed rank tests to compare salmon counts within 0-2m zone to counts within 2-4m zone. However, each

trial consists of multiple counts taken within a 7 minute time period in which salmon may enter and leave the arena, possibly violating the assumption of identical individuals inherent to paired tests. I feel that the use of a paired test is justified in this case as the trial data are means of the multiple counts taken simultaneously within 0-2m and 2-4m zones over the 7 minutes, and thus are not independent.

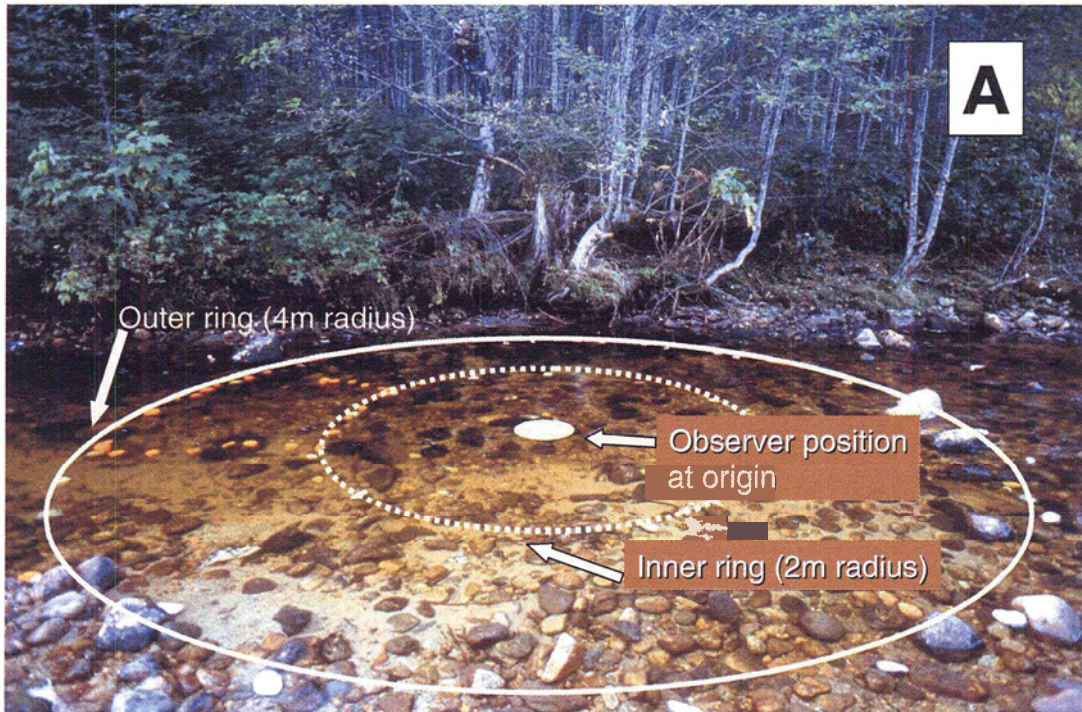


Figure 28A-B. Observational pool (arena) consisting of two circular rings delineated by white painted rocks that were clearly visible from above the stream surface. **A:** Displays inner (2m radius) and outer (4m radius) ring of arena. **B:** Displays white costume treatment with observer at origin (centre).

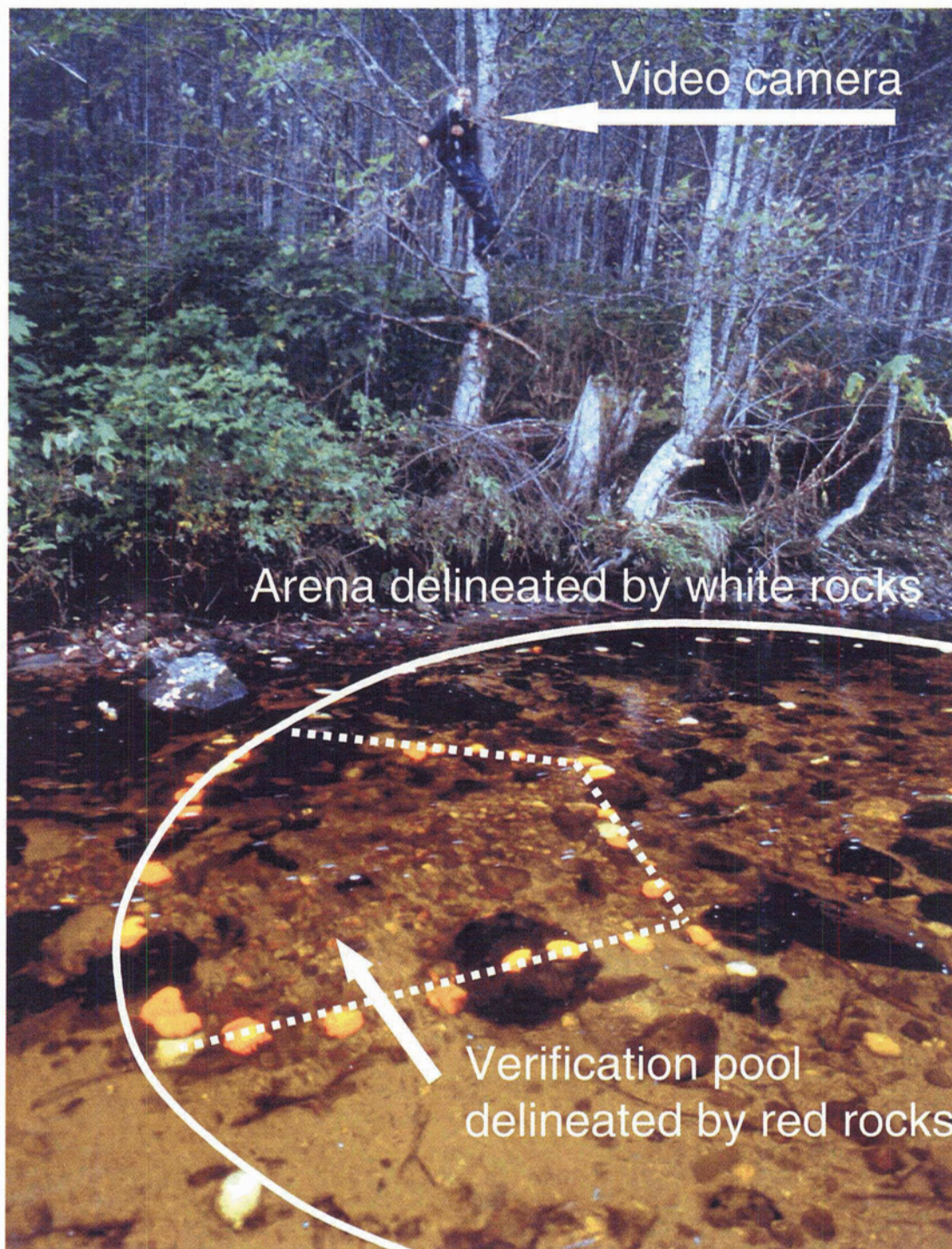


Figure 29. Verification portion of arena is delineated by red painted rocks. Assistant video-tapes salmon activity from tree as observed counts from origin (not visible). Measurement error in counts was a 13.7% with no bias with respect to colour morph.

### 5.3

## Results

#### 5.3.1 *Distance effects*

Overall, fewer salmon were observed within the 0-2m zone ( $\bar{X}=1.05 \pm 0.10$  S.E.) than within the 2-4m zone ( $\bar{X}=11.94 \pm 0.46$  S.E.) among all trials ( $Z=-11.89$ ,  $P<0.001$ ; Wilcoxon; Fig. 30). This effect was strong even after compensating for area differences between the two zones ( $Z=-11.72$ ,  $P<0.001$ ; Wilcoxon) and among light levels (Darkness:  $Z=-6.15$ ,  $P<0.001$ ; Twilight:  $Z=-7.22$ ,  $P<0.001$ ; Daylight:  $Z=-7.22$ ,  $P<0.001$ ; Wilcoxon).

#### 5.3.2 *Colour morph effects for individuals*

##### 5.3.2.1 *Colour morph effects for individuals: Overall*

Overall, salmon response was highly dependent upon costume colour. Within the 4m arena, salmon counts were highest during white costume treatments (W:  $\bar{X}=15.50 \pm 1.07$  S.E.) compared to black costume treatments (B:  $\bar{X}=11.56 \pm .97$  S.E.;  $t=-2.73$ ,  $df=74$ ,  $P=0.008$ ; Fig. 31A.).

##### 5.3.2.2 *Colour morph effects for individuals: Distance effects*

Within the 0-2m zone, salmon counts were significantly higher for the white treatment (W:  $\bar{X}=1.31 \pm 0.22$  S.E.) than for the black treatment (B:  $\bar{X}=0.82 \pm 0.17$  S.E.;  $Z=-1.96$ ,  $P=0.050$ ; MW; Fig. 31B). Similarly, within the 2-4m zone, salmon were significantly more numerous in the white treatments (W:  $\bar{X}=14.19 \pm 0.99$  S.E.) than in the black treatments (B:  $\bar{X}=10.74 \pm 0.87$  S.E.;  $Z=-2.54$ ,  $P=0.011$ ; MW; Fig. 31C.).

### 5.3.3 *Colour morph effects for two individuals*

#### 5.3.3.1 *Colour morph effects for two individuals: Overall*

Overall, there was little difference in counts between trials involving individual and multiple costumes (Fig. 32A.). Salmon counts for individual black treatments (B) were slightly higher than for multiple black treatments (BB), but were slightly lower than the mixed treatment (BW), however, these differences did not reach statistical significance ( $F=2.01$ ,  $df=2$ ,  $P=0.139$ ). Similarly, there was little difference in salmon counts among trials of single white (W), multiple white (WW) and mixed trials (BW). Salmon counts for individual white treatments were highest compared to the multiple white treatment and the mixed colour treatment, but these differences were not statistically significant ( $F=1.41$ ,  $df=2$ ,  $P=0.248$ ).

#### 5.3.3.2 *Colour morph effects for two individuals: Distance effects*

There was little difference in counts between trials involving individual and multiple costumes within the 0-2m zone. Similar to the overall effects, salmon counts for individual black treatments (B) were slightly higher than for multiple black treatments (BB), but were slightly lower than the mixed treatment (BW), however, these differences did not reach statistical significance ( $\chi^2=3.90$ ,  $df=2$ ,  $P=0.142$ ; KW; Fig. 32B). There was also no difference in salmon counts among trials of single white (W), multiple white (WW) and mixed trials (BW). Salmon counts for individual white treatments (W) were almost identical to the multiple white treatments (WW) while the mixed colour treatments (BW) had lower salmon counts, but these differences were not statistically significant ( $\chi^2=0.59$ ,  $df=2$ ,  $P=0.744$ ; KW).

Within the 2-4m zone, the trends were identical to those observed in the 0-2m

zone, namely counts for individual black treatments (B) were slightly higher than for multiple black treatments (BB), but were slightly lower than the mixed treatment (BW), but these differences were not significantly different ( $F=1.61$ ,  $df=2$ ,  $P=0.20$ ; Fig. 32C.). Furthermore, I again detected little difference in salmon counts among trials of single white (W), multiple white (WW) and mixed trials (BW). Salmon counts for individual white treatments (W) were highest compared to the multiple white treatments (WW) and the mixed colour treatments (BW), but these differences were not statistically significant ( $F=1.51$ ,  $df=2$ ,  $P=0.23$ ).

#### 5.3.4 Light level effects

##### 5.3.4.1 Light level effects: Overall

Salmon counts were highly dependent upon light levels ( $F=35.48$ ,  $df=2$ ,  $P<0.001$ ; Fig. 33A-C.). Counts within the 4m arena were highest during darkness ( $\bar{X}=18.63 \pm 0.80$  S.E.; Fig. 33A), less during twilight ( $\bar{X}=11.92 \pm 0.68$  S.E.) and lowest during daylight ( $\bar{X}=10.03 \pm 0.68$  S.E.). Salmon counts were significantly higher during darkness compared to both daylight and twilight ( $P<0.001$ ; Tukey HSD), however, there was no difference in counts between daylight and twilight ( $P=0.16$ ; Tukey HSD).

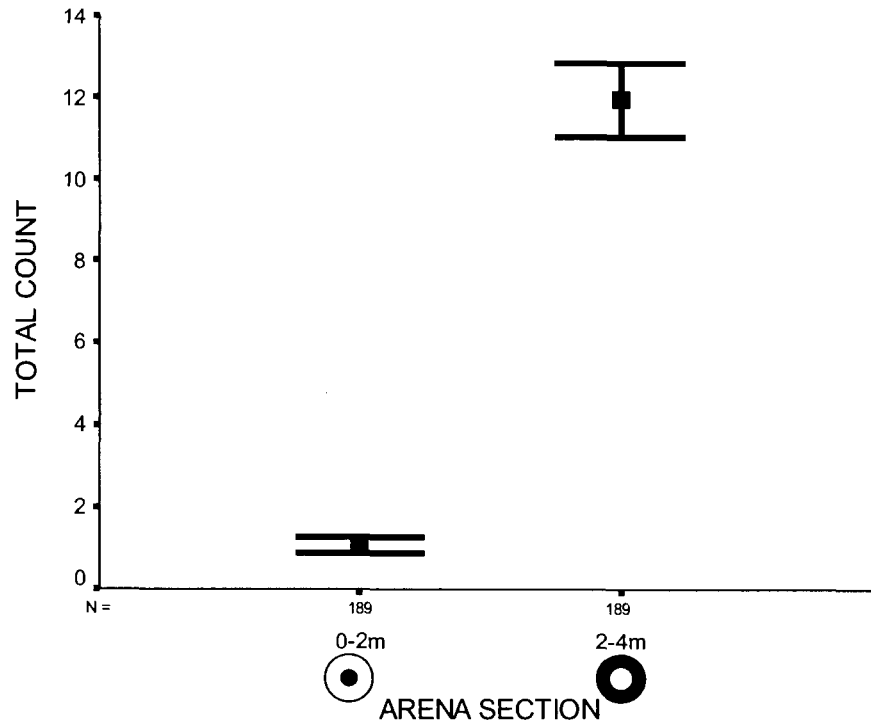


Figure 30. Number of salmon returning to the arena after disturbance. Salmon counts differed between near (0-2m) and distant (2-4m) zones ( $Z=-11.89$ ,  $P<0.001$ ). Displayed are 95 % confidence intervals.

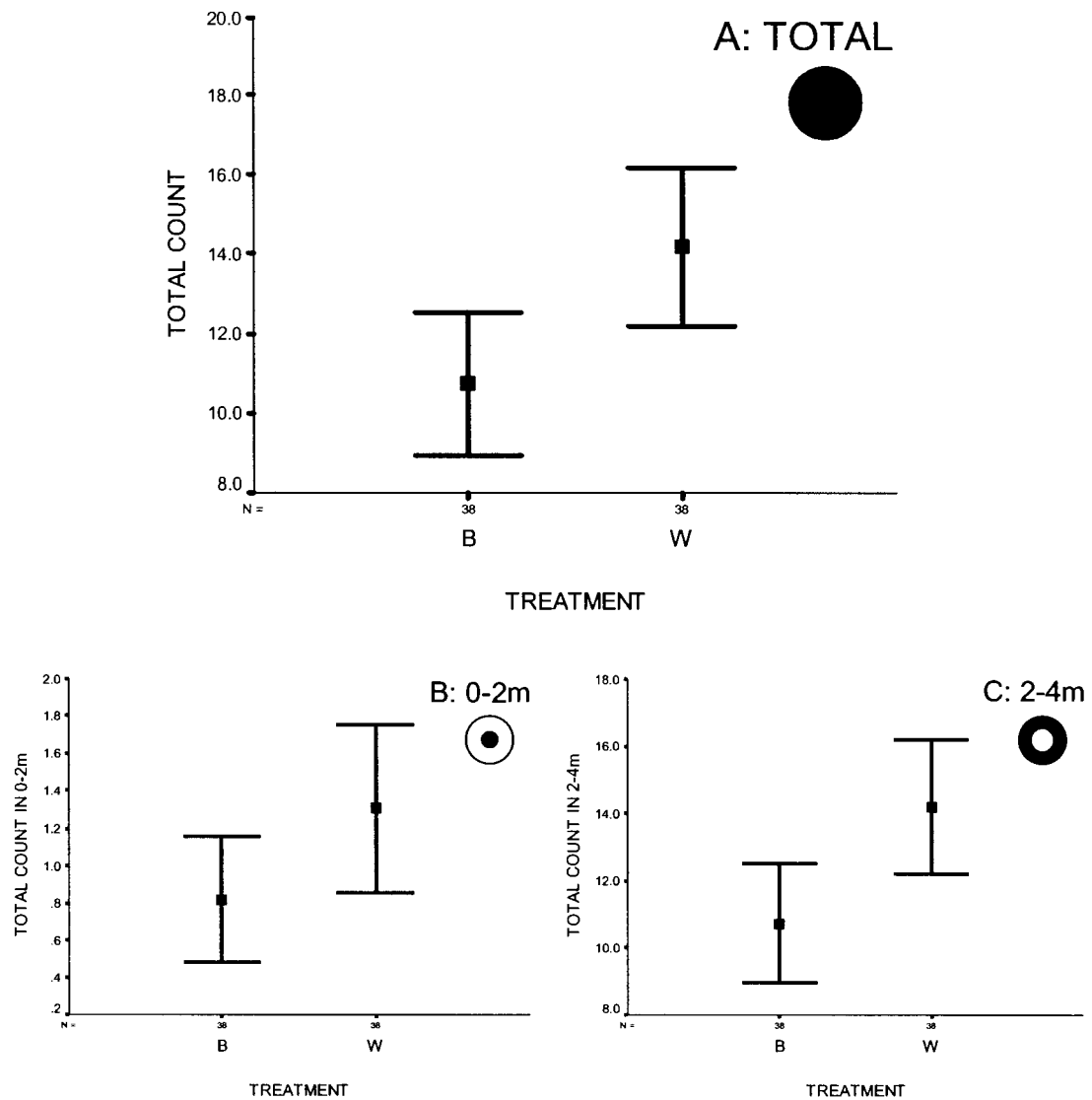


Figure 31A-C. Number of salmon returning to the arena after disturbance towards black and white colours. Salmon counts differed between Black (B) and White (W) treatments **A:** Displays Number of salmon returning to 4m arena. ( $t=-2.73$ ,  $P=0.008$ ). **B:** Displays Number of salmon returning to the 0-2m zone ( $Z=-1.96$ ,  $P=0.050$ ). **C:** Displays Number of salmon returning to the 2-4m zone ( $Z=-2.54$ ,  $P=0.011$ ). Displayed are 95 % confidence intervals.

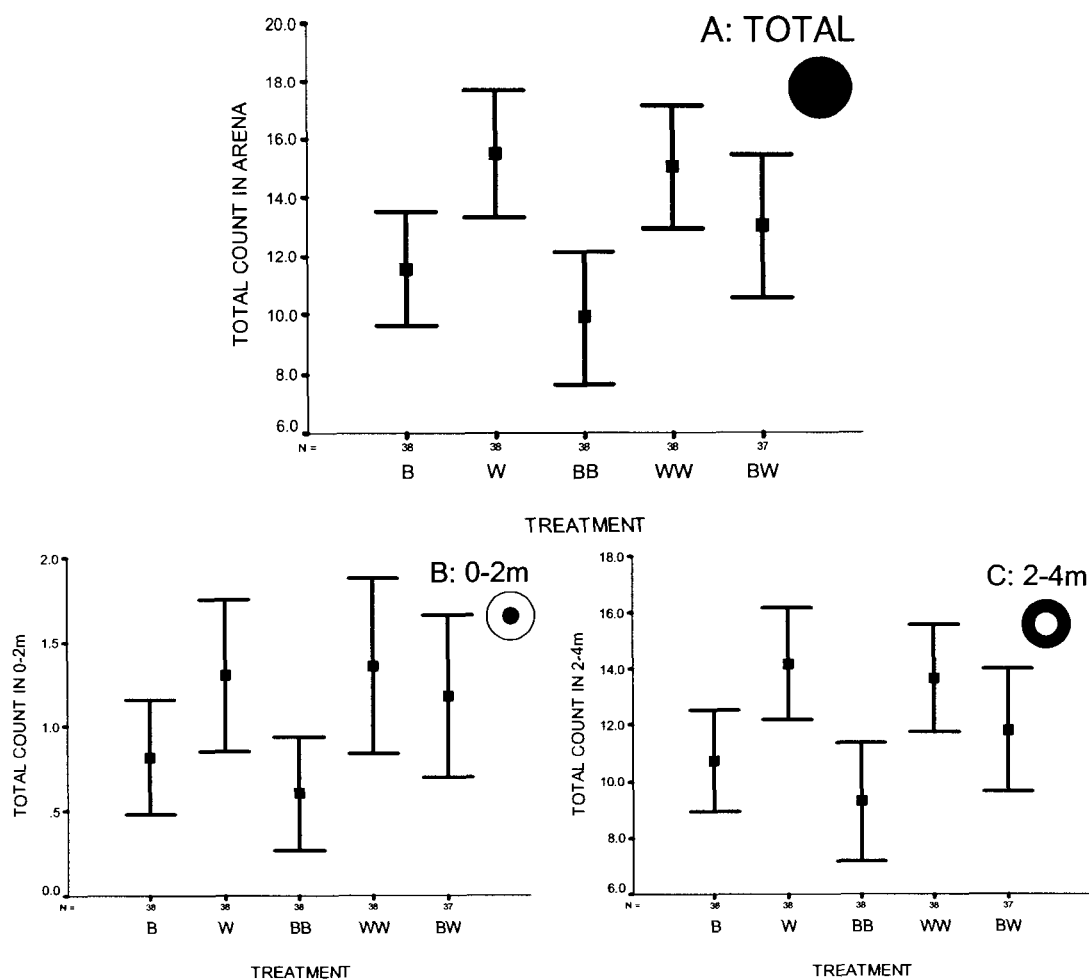


Figure 32A-C. Number of salmon returning to the arena after disturbance from two individuals. Salmon counts were similar between treatments of individual and two individuals. **A:** Displays number of salmon returning to 4m arena for all treatments; B, BB, BW were statistically similar ( $F=2.01$ ,  $P=0.139$ ) as were white treatments W, WW, BW ( $F=1.41$ ,  $P=0.248$ ). **B:** Displays number of salmon returning to the 0-2m zone for all treatments; B, BB, BW were statistically similar ( $F=2.01$ ,  $P=0.139$ ) as were white treatments W, WW, BW ( $F=1.41$ ,  $P=0.248$ ). **C:** Displays number of salmon returning to 2-4m zone for all treatments; B, BB, BW were statistically similar ( $F=2.01$ ,  $P=0.139$ ) as were white treatments W, WW, BW ( $F=1.41$ ,  $P=0.248$ ). Displayed are 95 % confidence intervals.

### 5.3.4.2 *Light level effects: Distance effects*

Within the 0-2m zone, salmon counts were substantially lower than for the 4m arena, but were also highly dependent upon light levels ( $\chi^2=56.06$ ,  $df=2$ ,  $P<0.001$ ; Fig. 33B). Counts were highest during darkness ( $\bar{X}=1.80 \pm 0.22$  S.E.), less during twilight ( $\bar{X}=1.35 \pm 0.16$  S.E.) and lowest during daylight ( $\bar{X}=0.23 \pm 0.04$  S.E.). Salmon counts during daylight were significantly lower than both darkness and twilight ( $P<0.001$ ), however, there was no difference in counts between darkness and twilight ( $Z=-1.66$ ,  $P=0.097$ ).

Similar to counts within the 4m arena, salmon counts within the 2-4m zone were highly dependent upon light levels ( $F=26.41$ ,  $df=2$ ,  $P<0.001$ ; Fig. 33C). Counts for the 4m arena were highest during darkness ( $\bar{X}=16.83 \pm 0.86$  S.E.), less during twilight ( $10.57 \pm 0.61$  S.E.) and lowest during daylight ( $\bar{X}=9.80 \pm 0.68$  S.E.). Salmon counts were significantly higher during darkness compared to both daylight and twilight ( $P<0.001$ ; Tukey HSD), however, there was no difference in counts between daylight and twilight ( $P=0.70$ ; Tukey HSD).

### 5.3.5 *Colour morph effects for individuals among light regimes*

#### 5.3.5.1 *Colour morph effects for individuals among light regimes: Overall*

Salmon counts were also highly dependent upon treatment among light levels ( $F=8.42$ ,  $df=2$ ,  $P=0.005$ ; Fig. 34A-C.). During daylight, salmon counts for the 4m arena were significantly higher for the W treatment (W:  $\bar{X}=15.05 \pm 1.00$  S.E.) than for the B treatment (B:  $\bar{X}=8.13 \pm 1.00$  S.E.;  $F=23.75$ ,  $df=1$ ,  $P<0.001$ ; Fig.34A.), however, I did not detect differences between colours during darkness (B:  $\bar{X}=16.88 \pm 2.20$  S.E.; W:

$\bar{X}=19.49 \pm 2.20$  S.E.;  $F=0.70$ ,  $df=1$ ,  $P=0.41$ ) or twilight (B:  $\bar{X}=11.18 \pm 1.67$  S.E.; W:  $\bar{X}=13.10 \pm 1.67$  S.E.;  $F=0.67$ ,  $df=1$ ,  $P=0.42$ ).

#### 5.3.5.2 *Colour morph effects for individuals among light regimes: Distance effects*

Within the 0-2m zone, salmon counts were also dependent upon treatment colour among light levels (Fig. 34B). During daylight, salmon counts for the 0-2m zone were significantly higher for the single White treatment (W:  $\bar{X}=0.47 \pm 0.13$  S.E.) than for the single Black treatment (B:  $\bar{X}=0.07 \pm 0.04$  S.E.;  $\chi^2=5.43$ ,  $df=1$ ,  $P=0.020$ ), however, I did not detect differences between colours during darkness (B:  $\bar{X}=1.17 \pm 0.34$  S.E.; W:  $\bar{X}=1.91 \pm 0.46$  S.E.;  $\chi^2=2.53$ ,  $df=1$ ,  $P=0.111$ ) or twilight (B:  $\bar{X}=1.32 \pm 0.30$  S.E.; W:  $\bar{X}=1.71 \pm 0.41$  S.E.;  $\chi^2=0.51$ ,  $df=1$ ,  $P=0.47$ ).

Within the 2-4m zone, salmon counts were also dependent upon treatment colour among light levels ( $F=7.48$ ,  $df=1$ ,  $P=0.008$ ; Fig. 34C). During daylight, salmon counts for the 2-4m zone were significantly higher for the W treatment (W:  $\bar{X}=14.58 \pm 1.08$  S.E.) than for the B treatment (B:  $\bar{X}=8.06 \pm 0.85$  S.E.;  $F=22.51$ ,  $df=1$ ,  $P<0.001$ ), however, I did not detect differences between colours during darkness (B:  $\bar{X}=15.70 \pm 1.69$  S.E.; W:  $\bar{X}=17.57 \pm 2.27$  S.E.;  $F=1.64$ ,  $df=1$ ,  $P=0.22$ ) or twilight (B:  $\bar{X}=9.86 \pm 1.41$  S.E.; W:  $\bar{X}=11.39 \pm 1.60$  S.E.;  $F=0.44$ ,  $df=1$ ,  $P=0.52$ ).

#### 5.3.6 *Colour morph effects for two individuals among light regimes*

##### 5.3.6.1 *Colour morph effects for two individuals among light regimes: Overall*

Within the 4m arena, salmon counts among black (B), multiple black (BB), and mixed treatments (BW), were highly influenced by ambient light levels ( $F=33.28$ ,  $df=2$ ,

$P < 0.001$ ; Fig. 35A) but not by treatment ( $F = 2.73$ ,  $df = 2$ ,  $P = 0.070$ ). Similarly, counts among white (W), multiple white (WW), and mixed treatments (BW) within the 4m arena were highly influenced by ambient light levels ( $F = 13.68$ ,  $df = 2$ ,  $P < 0.001$ ) but not by treatment ( $F = 1.47$ ,  $df = 2$ ,  $P = 0.234$ ; Fig. 35B).

#### *5.3.6.2 Colour morph effects for two individuals among light regimes: Distance effects.*

Within the 0-2m zone, salmon counts among black (B), multiple black (BB), and mixed treatments (BW), were influenced by both ambient light levels ( $F = 20.89$ ,  $df = 2$ ,  $P < 0.001$ ; Fig. 35C) and by treatment ( $F = 3.44$ ,  $df = 2$ ,  $P = 0.039$ ). However, when isolating each light regime, counts did not differ among treatments (darkness:  $F = 1.07$ ,  $df = 2$ ,  $P = 0.356$ ; twilight:  $F = 2.42$ ,  $df = 2$ ,  $P = 0.102$ ; daylight:  $F = 2.26$ ,  $df = 2$ ,  $P = 0.118$ ). Counts among white (W), multiple white (WW), and mixed treatments (BW), were only influenced by light level (Light Level:  $F = 19.38$ ,  $df = 2$ ,  $P < 0.001$ ; Treatment:  $F = 0.201$ ,  $df = 2$ ,  $P = 0.818$ ; Fig. 35D).

Within the 2-4m zone, salmon counts among black (B), multiple black (BB), and mixed treatments (BW), were influenced by ambient light levels ( $F = 28.86$ ,  $df = 2$ ,  $P < 0.001$ ; Fig. 35E) but not by treatment ( $F = 1.98$ ,  $df = 2$ ,  $P = 0.143$ ). Similarly, counts among white (W), multiple white (WW), and mixed treatments (BW), were only influenced by light level (Light Level:  $F = 10.86$ ,  $df = 2$ ,  $P < 0.001$ ; Treatment:  $F = 1.52$ ,  $df = 2$ ,  $P = 0.223$ ; Fig. 35F).

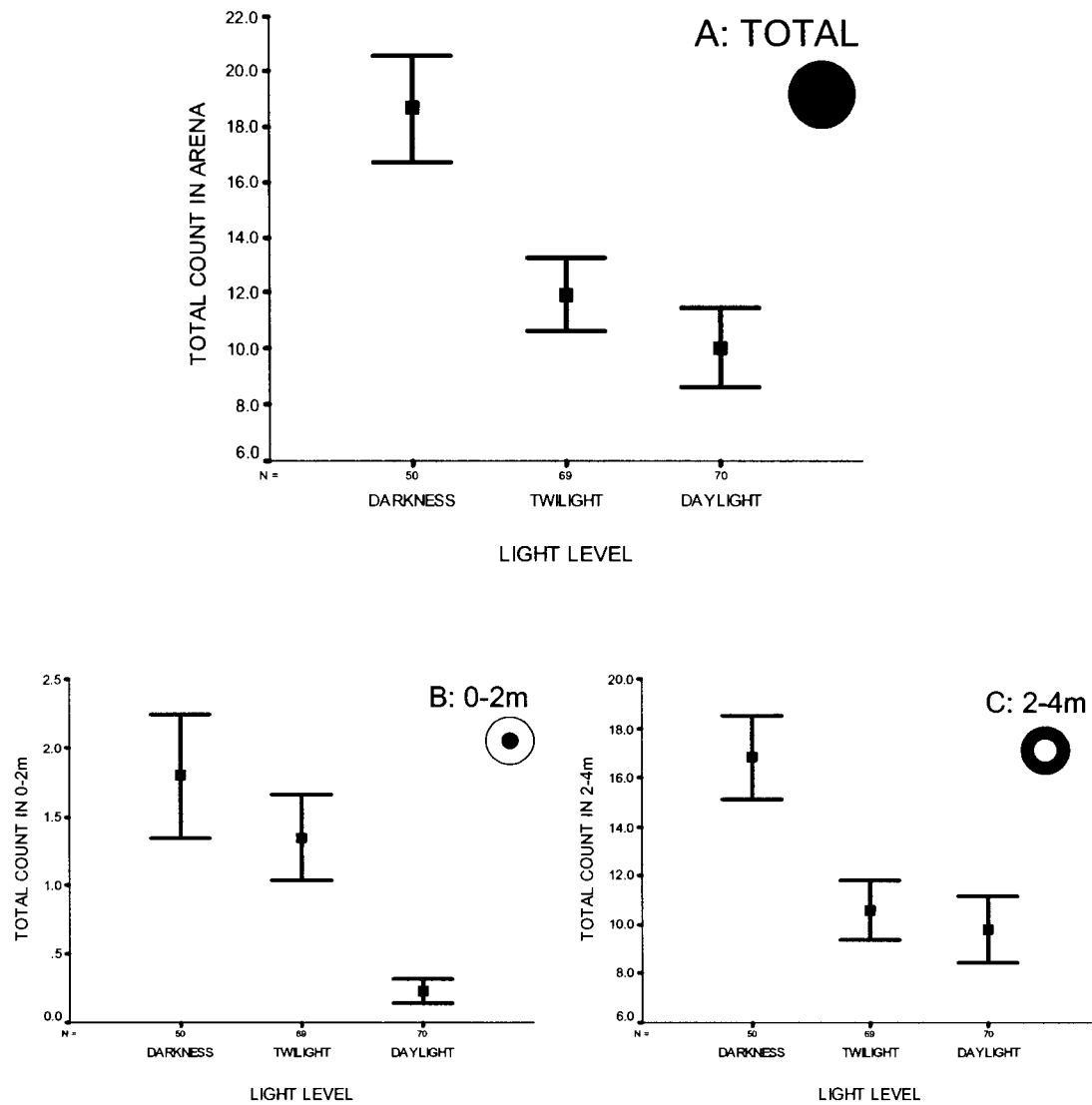


Figure 33A-C. Number of salmon returning to the arena after disturbance within darkness, twilight and daylight. **A:** Displays number of salmon returning to 4m arena ( $F=35.48$ ,  $P<0.001$ ). **B:** Displays number of salmon returning to the 0-2m zone ( $\chi^2=56.06$ ,  $df=2$ ,  $P<0.001$ ). **C:** Displays number of salmon returning to the 2-4m zone ( $F=26.41$ ,  $P<0.001$ ). Displayed are 95 % confidence intervals.

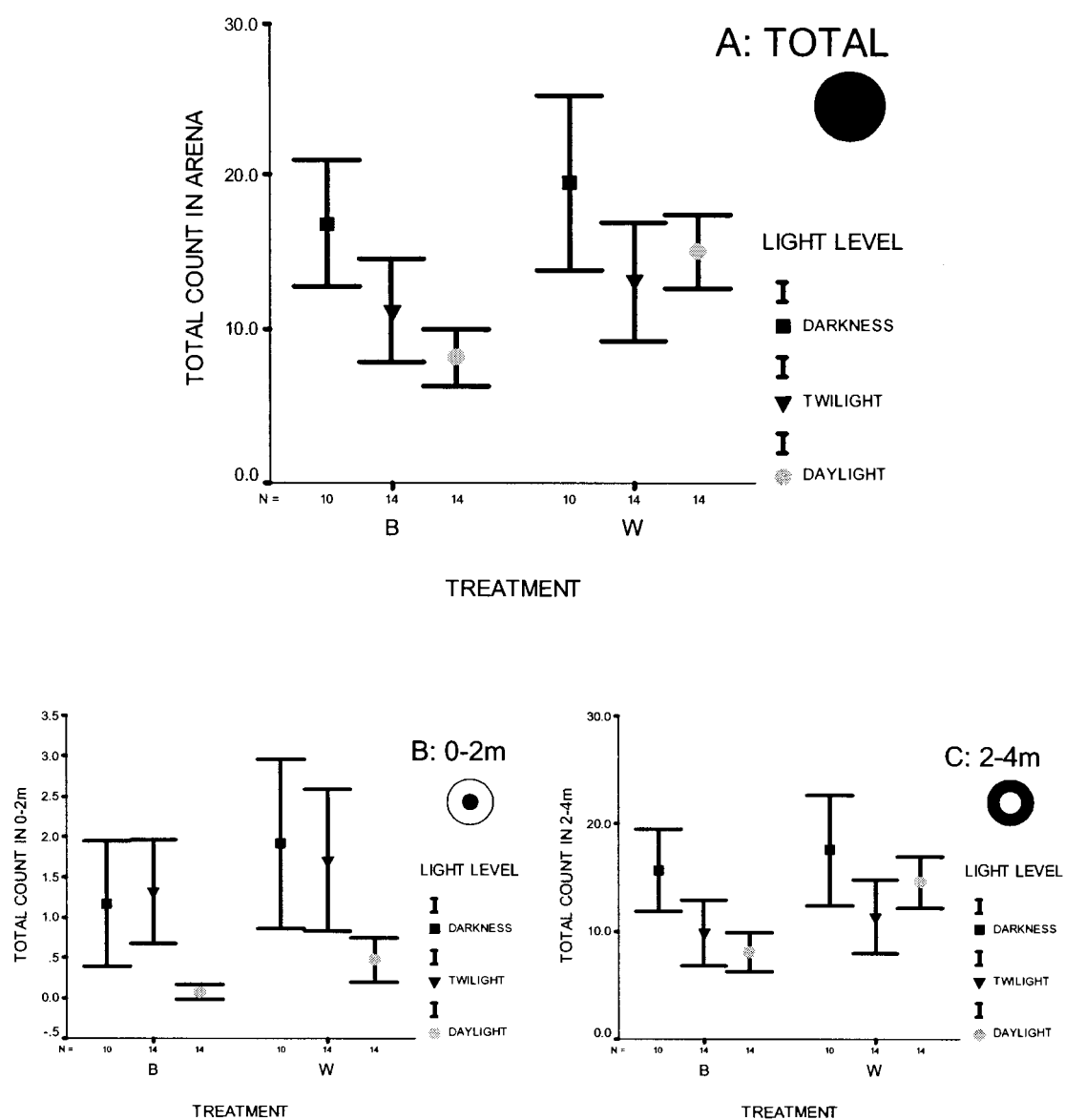


Figure 34A-C. Number of salmon returning to arena after disturbance towards black and white colours within darkness, twilight and daylight. Salmon counts differed between colours only during daylight. **A:** Displays number of salmon returning to the 4m arena ( $F=8.42$ ,  $P=0.005$ ). **B:** Displays number of salmon returning to the 0-2m zone ( $\chi^2=5.43$ ,  $P=0.020$ ; daylight). **C:** Displays number of salmon returning to the 2-4m zone ( $F=7.48$ ,  $P=0.008$ ). Displayed are 95 % confidence intervals.

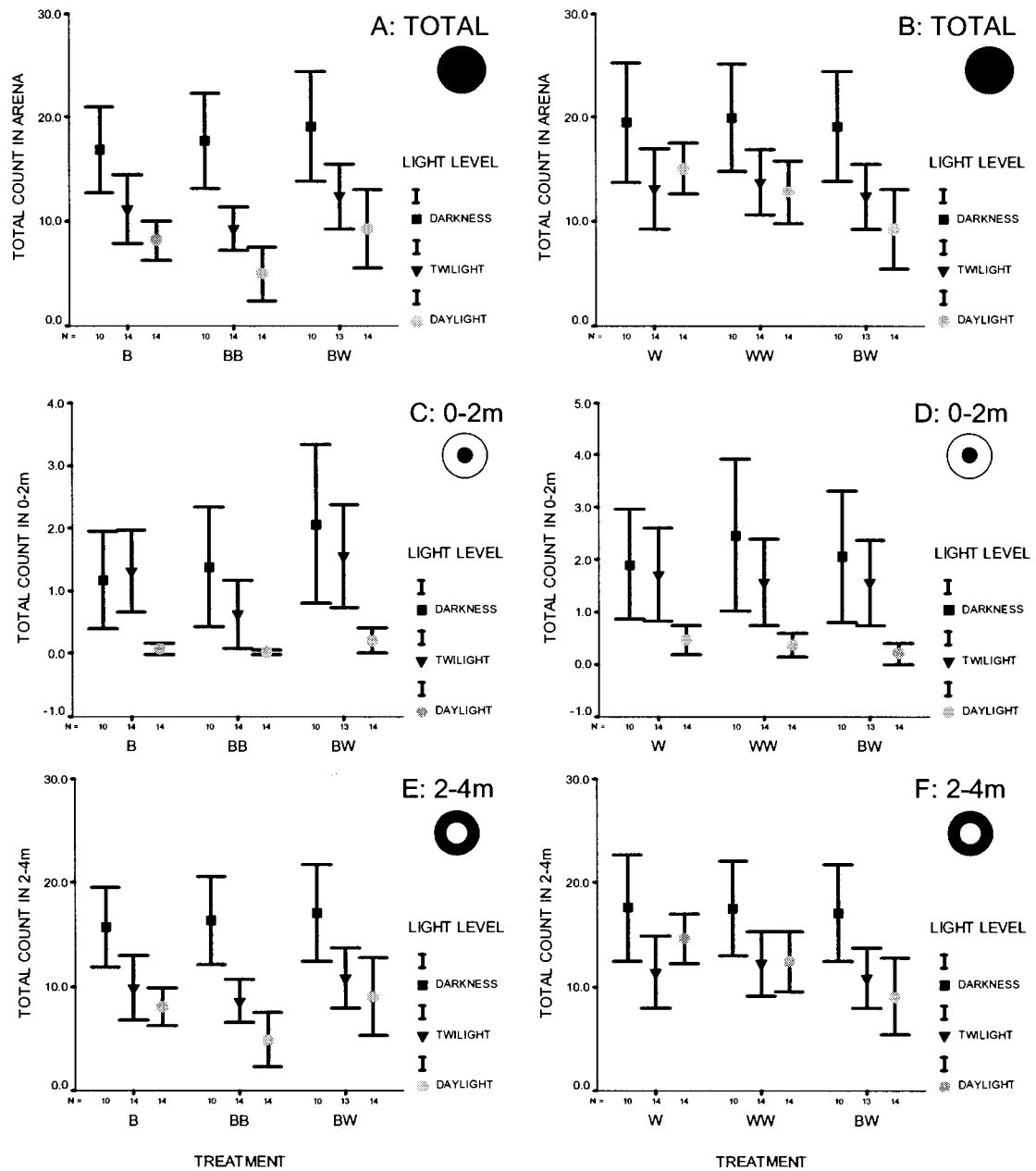


Figure 35A-F. Number of salmon returning to arena after disturbance from two individuals within darkness, twilight and daylight. **A-B**: Displays number of salmon returning to the 4m arena ( $F=2.73$ ,  $P=0.070$ ). **C-D**: Displays number of salmon returning to the 0-2m zone ( $F=3.44$ ,  $df=2$ ,  $P=0.039$ ). **E-F**: Displays number of salmon returning to the 2-4m zone ( $F=1.98$ ,  $df=2$ ,  $P=0.143$ ). Displayed are 95 % confidence intervals.

## 5.4

## Discussion

### 5.4.1 *Distance effects*

Salmon counts were lowest for all treatments within 0-2m compared to the 2-4m zone, indicating high timidity towards proximate sources of disturbance. This effect was strong even after size corrections were made to compensate for the differences in area between the two zones. Disturbances were not limited to those of a visual nature, as this effect was also present during darkness. However, counts within the 0-2m zone were higher during darkness, suggesting that the capacity to visually detect potential predators had a strong effect on salmon timidity. Proximate vibrational disturbances most probably detected by the lateral line sensory system of salmon (Satou et al. 1991, Montgomery and Milton 1993, Satou et al. 1994a), could also affect timidity and may account for the lower counts in the 0-2m zone. While standing in the arena, I was undoubtedly the source of these vibrational disturbances. Although I did not change my location within the centre of the arena, I was altering my orientation 360 degrees every minute during my counts. In doing so I would have created slight vibrations on the stream substrate with my feet which may have alerted salmon to a possible risk especially during darkness. Although this may be the case, there were numerous instances during trials in darkness where salmon would inadvertently bump into my leg and not swim quickly away, but rather remained in the area. It is possible that in these instances the salmon mistook my leg for a piece of woody debris in the stream, but these fish typically did not move while I was rotating during my counts.

Within the 2-4m zone, counts were much higher suggesting that salmon preferred to remain at a further distance away rather than directly beside the observer. This preference by salmon would have consequences for the fishing techniques used by bears. In instances when fish are at a distance, bears would be forced to either chase, or plunge after fish rather than simply grasping at nearby fish with its paws. However, the opposite would be true during darkness, where fish tend to be more numerous and in closer proximity, in which case bears would presumably be able to pounce on nearby fish. Foraging data of bears from this locality suggests that bears stand most often during darkness, perhaps to exploit the decreased timidity of salmon during this time period. In fact, on many occasions I have seen salmon that were completely unaware of a standing bear, and bump into the bear's leg while it was either moving or actively spawning. Since the visual sensory system of bears is not as useful during darkness as compared to during daylight, such tactile cues by naive salmon may assist in bear foraging during darkness.

Reaction to predation risk could also depend upon the reproductive state of the salmon. Female Pink salmon typically have a spawning cycle of 2-3 days but can remain alive for 10-14 days, while males have a cycle lasting up 14 days before they die (Chebanov 1980). This short time span available for spawning could make females more risk prone, as reaction to each stream disturbance would reduce time devoted to spawning, digging and defending redds. As the physical condition of salmon deteriorates during their spawning cycle, their sensitivity or escape threshold may be raised to ensure maximal spawning opportunities, at the expense of higher predation risk. It is likely that differences in the reproductive state of individual fish would be accounted for as this study consisted of multiple trials over 4 weeks. These results are based on a mean count

calculated from 7 sub-counts involving many fish. I measured the average response from many salmon at the same time (scan sampling) as opposed to measuring the response of individual fish (focal animal sampling) which may have been more prone to reproductive condition effects among salmon.

During this study, I observed elevated nocturnal spawning behaviour by salmon (See Chapter 4: Foraging). It is not clear why salmon would display elevated nocturnal activity patterns, but possible scenarios could be decreased intraspecific competition between males over access to females, and between females over access to redds (McNeil 1967). It is possible that reductions in agonistic behaviour among salmon during darkness could be due to non-functioning visual systems. The decreased utility of visual systems in salmon during darkness may provide the elevated motivation to spawn as a predator out of sight is a predator out of mind. A strong motivation to spawn may account for the higher counts in the arena during darkness. However, it is interesting to note that previous studies of the sensory mechanisms employed by salmon during spawning events indicate not only that visual systems are used alongside with tactile cues, but that both the visual and vibrational cues are necessary for eliciting the male spawning behaviour (Satou et al. 1994b).

#### *5.4.2 Colour morph effects for individuals*

These results strongly illustrate that salmon were more timid towards the black coloured treatments than towards the white treatments. This effect occurred within the 0-2m and the 2-4m zones. High measurement error could have reduced the association between colour and timidity, but my results had relatively low error (13%) indicating my

salmon counts were relatively consistent. Further, the effect size of this experiment exceeded 50% difference between colour morphs, which greatly exceeds the 13% measurement error. These factors strongly suggest that predation risk perceived by salmon differs between bear colour morphs. This pattern of differential response may depend on differential crypsis of the two morphs in different light conditions (Gotmark 1987). White morphs may be more cryptic when viewed against bright sky during daylight, whereas dark morphs may be more cryptic when viewed against a dark background as occurs in a forest or at night. This seems a reasonable hypothesis in light of previous investigations examining foraging differences between colour morphs of piscivorous wading birds and seabirds (Murton 1971, Mock 1980, Gotmark et al. 1986, Gotmark 1987).

However, timidity of salmon towards the black morph could be also due to lower perception of risk from a rare predator morph as in apostatic selection. Salmon could be less likely to recognize a rare colour morph, and less likely to react adversely to it, which would be to the rare morphs advantage. This slight advantage of the rare morph could lead to balanced polymorphism in the population. Apostatic selection would be facilitated by the rapid turn-over of prey population, in which there are many young and naïve individuals among the prey each year (Paulson 1973). This is indeed the case in the predator-prey relationship between bears and salmon, where spawning occurs only once in their lifetime, and adults do not pass learned experiences onto young before they die.

Although the response of salmon was clear, it remains difficult to isolate which mechanism is responsible for the observed timidity of salmon towards the black morph. Aspects of bear fishing behaviour tend to support the camouflage hypothesis. I

sometimes observed black bears standing very still directly under an overhanging log, presumably to match its own silhouette with the black silhouette cast by the log. I called this technique ‘Shadow fishing’, and interestingly, I never observed the white morph fishing in this manner. While ‘Shadow fishing’, black bears would stand very still and wait for salmon to come within approximately 2m before plunging forward in an attempt to capture the fish.

Salmon response was highly influenced by the ambient light level, with high numbers of salmon counted among all treatments during darkness. In fact, counts for the black treatments made during darkness were almost double the counts made during daylight; while for white treatments, there was not a large change in counts between daylight and darkness. This suggests that salmon may primarily rely on visual-based sensory systems to assess predation risk, and when relied upon, these visual systems can discriminate between colour morphs, favouring white morphs over blacks.

Daily activity patterns of different morphs may be an important factor in explaining the maintenance of colour polymorphism in birds (Galeotti et al. 2003), and presumably could be an important factor in explaining the polymorphism expressed in this bear population. It is interesting that polymorphic Eastern reef herons (*Egretta sacra*) are active at night as well as in the daytime (Itoh 1991), considering that nocturnal species in *Ardeidae* all have dark plumage. Perhaps foraging differences exist between heron colour morphs during nocturnal foraging bouts and these studies predated the availability of night vision equipment which would enable such diurnal nocturnal comparisons.

In this study, both colour morphs fished during darkness more often than during daylight (See Chapter 4: Foraging). This is counter to prediction based on Heron colouration with respect to diel activity patterns where black morphs are considered nocturnal. However, colour morphs differed in fishing technique use and foraging success among light levels (See Chapter 4: Foraging).

#### *5.4.3 Colour morph effects for two individuals*

My data suggest that there were few differences in salmon timidity between individual and multiple bears. Although counts for multiple black treatments were lower than for individual black treatments, this difference was not statistically significant, leaving ambient light levels as the most important predictor of salmon timidity.

This was somewhat unexpected as competitive interference between conspecifics typically results in decreased foraging opportunities for each individual (Van Der Meer 1997). However, Gotmark et al. (1986) found that individuals obtained more food while foraging as members of a group than foraging as individuals. He argued that schooling fish were more likely to break from the school when attacked by multiple predators. This argument is not directly comparable to salmon because they act as individuals in freshwater lakes and rivers while trying to maximize spawning opportunities, even though they school in marine environments.

Differences in salmon proximity towards single or multiple bears could motivate bears to either co-operatively forage, or to competitively exclude proximal conspecifics. As these data do not support the prerequisites for competitive interference, the motivation to aggressively defend a fishing area would be low. I would not predict co-operative foraging behaviour in this population. Bears are typically solitary and I have not seen co-

operative fishing behaviour at any time during the course of this study. Predictions of intraspecific tolerance among this bear population based upon salmon response would be of weak intolerance, as tolerance thresholds would vary among individuals. This is indeed the case, as most interactions of bears tend to be of low intensity, with one bear walking away to alternate fishing areas, or ignoring each other completely sometimes within close proximity (See Chapter 7: Interactions).

Differential evasive responses by salmon towards colour morphs may have implications for the potential availability and susceptibility of salmon resources. An increased utilization of salmon confers fitness benefits to coastal bear populations (Hilderbrand et al. 1999a, Hilderbrand et al. 1999b), thus increased utilization of salmon by a particular colour morph could confer a selective advantage to that morph possibly promoting the long term maintenance of the polymorphism.

This study illustrates the behavioural plasticity of salmon in their response to colour morphs among light levels and highlights their reliance on visual cues to assess predation risk. It provides an important piece to the ecological and behavioural puzzle clouding the possible mechanisms of the maintenance of this colour polymorphism. Furthermore, it predicts that interactions between bears would be predominantly of low intensity.

## **Chapter 6: Stable isotope analysis suggest possible niche partitioning of a polymorphic bear population**

### **6.1 Introduction**

Color polymorphism occurs in many taxa (Cain and Sheppard 1950, Ford 1964, Reimchen 1979, Rounds 1987, Colyn 1993, Franck et al. 2001, Johannesson and Ekendahl 2002, Galeotti et al. 2003) yet the origin and the basic mechanisms maintaining most polymorphisms are not well understood (Jones et al. 1977, Losey et al. 1997). Some hypotheses suggest that colour variations are selectively neutral traits with frequencies dependent on founder effects and random genetic drift (Futuyma 1998). Alternately, colour polymorphisms are maintained by a form of heterozygote advantage (Futuyma 1998) or are functional traits maintained by frequency dependent selection (such as apostatic selection) or multiple-niche partitioning (Levene 1953, Levins and MacArthur 1966, Maynard Smith 1970, Paulson 1973, Smith 1990, Cook 1998).

The highly variable colouration patterns and numerous colour polymorphisms observed in carnivores such as felids and canids (Mech 1970, Guggisberg 1975), and avian predators (Rohwer and Paulson 1987, Rohwer 1990, Galeotti et al. 2003) may be in part maintained by resource and niche partitioning (Recher and Recher 1972, Mock 1980, Rohwer 1990, Itoh 1991). Colour polymorphism may contribute to variable foraging success among morphs, as the visual and behavioural responses of prey may vary towards different coloured morphs. This effect could confer a temporary foraging advantage to the appropriate coloured morph (Murton 1971, Mock 1980). For instance, examples of

multiple-niche partitioning are observed in the various colour morphs of wading shorebirds where different coloured morphs may vary in success in different habitats or in the same habitat under different light conditions (Galeotti et al. 2003). This is thought to be due to differences in foraging efficiency caused by variation in hunting camouflage (Cott 1940).

Knowledge of dietary differences between sympatric colour morphs could yield important insights into the role of niche partitioning in the maintenance of colour polymorphism; however, direct measures of animal diets with conventional methods such as direct observation, scat or stomach analysis have been problematic for a variety of reasons. Unequal digestibility of food, inability to locate scat, elusive or wide ranging animals to ethical considerations and the practicalities of stomach analysis of rare or endangered species have all hampered our ability to investigate the diets of free-ranging wildlife (Hilderbrand et al. 1996, Hobson et al. 2000, Darimont and Reimchen 2002).

Stable isotope analyses have recently been utilized to examine the trophic ecology of many birds and mammals, and its use has seen a dramatic increase and attention as it augments traditional dietary information (Kelly 2000). Isotopic information is incorporated into tissue and tends to reflect the diets of consumers (DeNiro and Epstein 1978, 1981). Stable isotopes of nitrogen ( $N^{15}$ ) are enriched by approximately 3 ‰ between trophic levels, thus revealing information on trophic association (Peterson and Fry 1987), while stable isotopes of carbon ( $C^{13}$ ) reveal information on the source of carbon, enabling assessments of the use of plants, terrestrial meat and salmon in diets. Depleted  $C^{13}$  signatures tend to indicate terrestrial sources of carbon while enriched  $C^{13}$  signatures indicate marine inputs. With a dual isotope approach, analysis of animal tissue

can be a valuable tool in elucidating subtle dietary differences between colour morphs of a species, and can provide evidence for niche partitioning which can be difficult to otherwise measure. However, stable isotope analysis does not directly assess the level of biomass consumed but rather what foods are assimilated, and this is influenced by digestibility and metabolizability, which differ among food items (Pritchard and Robbins 1990, Hilderbrand et al. 1996, Jacoby et al. 1999).

Isotopic information is incorporated into metabolically-active tissues during the period of tissue growth and can reflect diets over periods as short as days (blood), months (nail and hair) to years (bone). In ursids, hair growth begins in early May following a spring molt, and continues until hibernation (Robbins et al. 2002). Assuming hair growth rates are constant throughout the duration of growth, specific hair sections reflect dietary information during the period of hair growth; namely proximal (base) sections represent most recent (fall) diets, while medial sections represent summer diets and distal (tip) sections represent spring diets.

In this chapter I evaluate niche partitioning between colour morphs through analysis of stable carbon and nitrogen isotope ratios of hair segments in a polymorphic black bear (*U. a. kermodei*). I utilize a regional perspective encompassing the entire known range of this subspecies over a three-year sampling regime, in combination with a local perspective where I sampled bears during my behavioural investigations of bears on Riordan Creek, Gribbell Island. I examine intra-hair values of stable carbon and nitrogen isotopes to elucidate dietary overlap between colour morphs of bears during the spring, summer and fall seasons.

To investigate potential historical insight into bear diets, I also examined pelts from bears killed at the turn of the century. I examine intra-hair values of stable carbon and nitrogen isotopes to investigate potential dietary change over the spring, summer and fall seasons.

Proximal (base) sections of hair are predicted to be elevated in both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values relative to medial and distal (tip) sections due to the incorporation of marine derived nutrients (assumed to be mainly salmon) into the fall diet. Distal (tip) and medial (mid) sections should be similar and indicate a plant-based diet. Differences in the degree of incorporation of salmon into the diet, or more subtle differences in niche space between colour morphs can confer an advantage to one morph over the other, and may provide a portion of a mechanism maintaining this polymorphism.

## **6.2 Methods and Materials**

### *6.2.1 Coastal and local assessment*

Kermit Ritland at the University of British Columbia provided bear hair samples comprising of 197 individuals that were collected during September and October, 1997-1999, over the known range of the Kermode bear on the coast of British Columbia (Ritland et al. 2001).

Of the 197 genotyped bear samples, 176 were black morphs while 18 were white. Of these I sampled 35 bears of which 17 were black, and 18 were white. I paired black and white samples from the same locality, and when paired samples from the same locality were not available, I paired samples from nearby (< 10 km) localities.

During 2001, I collected bear hair by placing hair snares at select locations along bear travel routes on the stream (Riordan Creek). In addition, I collected hair directly

from bears as they passed underneath me from a log which spanned the stream. In order to do this safely, I made a “bear comb” consisting of 2 strips of carpet edging (with nails dulled) nailed along a long branch. One end of the comb was anchored into the stream bank and I attached a rope to the other end. This allowed me to raise and lower the comb while sitting on the mid-point or the other end of the observation log. As bears moved underneath the comb, I gently lowered it onto their backs and then raised it again after they had passed (Fig. 36). This allowed me to identify the bear and ensure that the sample was not contaminated by hairs from other bears. The inability to verify whether samples were of individuals or of multiple bears was the main criterion forcing me to eventually abandon the use of multiple hair snares around the study site. As I was not genotyping individuals (as per Ritland et al.), and the inability to discriminate hairs between individual bears taken from snares, I used only hair samples taken from the comb in 2002.

### *6.2.2 Historical assessment*

Pelts of two adult and one sub-adult white morph Kermode bears that were killed at the turn of the century were made available by the B.C. Royal Museum. Although the exact dates are somewhat ambiguous, these bears were killed on Princess Royal Island (May 22, 1910) and Gribbell Island (May 22, 1906) according to museum records.



Figure 36. The “bear comb” allowed me collect hair from individual bears without fear of contamination by other bears. I could lower the comb onto the bears back and then raise it after they had passed.

### 6.2.3 Hair sample protocol

I washed guard hairs with a 2:1 mixture of chloroform and ethanol to remove surface debris and oils (Hilderbrand et al. 1996, Hobson et al. 2000). After drying at 60°C for at least 48 h, I cut the hairs into 3 equal sections comprising of the base (most proximal), mid-section (medial), tip (distal). These sections were then cut into small pieces (<1mm) and approximately 1 mg dry weight was loaded into tin cups. Mass spectrometry analysis of carbon and nitrogen isotopes was conducted at the stable isotope facility, University of Saskatchewan, Saskatoon, Canada using a Europa Scientific ANCA NT gas/solid/liquid preparation module coupled to a Europa Scientific Tracer/ 20 mass spectrometer.

### 6.2.4 Calculations and statistical analysis

Isotopic contents are expressed in  $\delta$  (delta) notation representing the difference between the isotopic content of the sample and known isotopic standards (atmospheric N<sub>2</sub> for nitrogen and PeeDee Belemnite (PDB) limestone for carbon). This is expressed in parts per thousand (‰) according to the formula (1):

$$1) \delta^{15}\text{N} \text{ or } \delta^{13}\text{C} (\text{‰}) = (R_{\text{sample}} / R_{\text{standard}} - 1) * 1000, \text{ where } R \text{ is the ratio of the heavy isotope } (^{15}\text{N} \text{ or } ^{13}\text{C}) / \text{light isotope } (^{14}\text{N} \text{ or } ^{12}\text{C}).$$

In order to compare the isotopic signatures in hair sections to the whole hair isotope values reported in the literature, I present average  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values

((proximal+medial+distal)/3) as whole hair values, in addition to  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values from proximal, medial and distal hair sections.

I calculated standardized residual Z scores of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  using SPSS (v.10) to remove the effects of locality and season. I then calculated Euclidean distances of standardized residual Z scores of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  to examine how far individual bears deviated from the central tendency of the entire sampled bear population according the formula (2).

2) Euclidean distance=  $c^2 = a^2 + b^2$  where  $a^2 = \delta^{15}\text{N}$  and  $b^2 = \delta^{13}\text{C}$

$$c = \sqrt{a^2 + b^2}$$

$$= \sqrt{(\delta\text{N15} - \text{Median } \delta\text{N15})^2 - (\delta\text{C13} - \text{Median } \delta\text{C13})^2}$$

I converted  $d^{15}\text{N}$  values to percentage of marine-derived nitrogen (MDN) using the equation (Helfield and Naiman 2001, Mathewson et al. 2003).

$$3) \% \text{MDN} = [(\text{Obs} - \text{TEM}) / (\text{MEM} - \text{TEM})] \times 100$$

Where Obs is the  $d^{15}\text{N}$  value of the proximal hair sample, TEM is the  $d^{15}\text{N}$  value of the terrestrial end member (spring value of hair for all bears in sample), and MEM is the  $d^{15}\text{N}$  value of the marine end member (salmon tissue corrected for trophic fractionation of 3.5‰). I used 13.01‰ for MEM (Ben-David et al. 1998, Mathewson et al. 2003). I assumed that salmon were not available to bears during the spring and thus spring diets are based on vegetation. Rather than using published isotope values for the many food

items of bears, this method of using the spring levels as the TEM allows bears to do the plant sampling.

To explore the level of dietary segregation between colour morphs in relation to the frequency of the allele responsible for the white morph. I calculated the magnitude of separation between the 2 colour morphs by subtracting the isotopic values of the blacks from the isotopic values of the whites according to the formulae (4), (5):

$$4) \delta^{13}\text{C} (\text{white morph}) - \delta^{13}\text{C} (\text{black morph})$$

$$5) \delta^{15}\text{N} (\text{white morph}) - \delta^{15}\text{N} (\text{black morph})$$

Thus positive values of (4) and (5) reflect increased enrichment of the white morph relative to black morph, while negative values reflect increased enrichment of the black morph relative to the white morph. The frequency of the white coat allele (G) was taken from Ritland et al. (2001).

We used ANOVA with Tukey's post hoc tests, T-Tests, and Wilcoxon Signed Rank Tests to examine differences in isotopic values among bears, localities and hair sections using SPSS (v.10).

## 6.3

## Results

## 6.3.1 Coastal assessment

## 6.3.1.1 Isotope values for whole hair samples

Overall isotope values for whole hair samples (N=35) varied widely among individuals among all localities (Fig. 37). Mean  $\delta^{13}\text{C}$  was  $-22.8\text{‰} \pm 1.1$  SD and ranged from  $-25.0$  to  $-20.8\text{‰}$  (N=41), while mean  $\delta^{15}\text{N}$  was  $4.3\text{‰} \pm 1.86$  SD and ranged from  $0.8$  to  $7.9\text{‰}$ . Low values of both isotopes (typically  $-26$  to  $-22\text{‰}$  for  $\delta^{13}\text{C}$  and  $0$ - $5\text{‰}$   $\delta^{15}\text{N}$ ) indicate a diet based predominantly on terrestrial plants, while high values of both isotopes (typically  $-17$  to  $-20\text{‰}$  for  $\delta^{13}\text{C}$  and  $8$ - $15\text{‰}$   $\delta^{15}\text{N}$ ) indicate increased incorporation of marine resources, predominantly salmon, into diet. Localities differed in both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ( $\delta^{13}\text{C}$ :  $F_{10,40}=4.54$ ,  $P=0.001$ ;  $\delta^{15}\text{N}$ :  $F_{10,40}=4.35$ ,  $P=0.001$ ), and I detected no differences between black and white morphs for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  within localities ( $\delta^{13}\text{C}$ :  $Z= -0.314$ ,  $P=0.754$ ;  $\delta^{15}\text{N}$ :  $Z=-1.18$ ,  $P=0.24$ ; Wilcoxon Signed Rank Test).

When removing locality effects using Z scores there were no differences in isotopic signatures between colour morphs ( $\delta^{13}\text{C}$ :  $t= -0.43$ ,  $df=38$ ,  $P=0.67$ ;  $\delta^{15}\text{N}$ :  $t=-0.83$ ,  $P=0.41$ ; Fig. 38). However, Euclidean distances (deviations from central tendency) were statistically different between colour morphs with black morphs having higher Euclidean distances than white bears ( $\bar{X}_B$ :  $1.30 \pm 0.52$  SD,  $N=22$ ;  $\bar{X}_W$ :  $0.98 \pm 0.38$  SD,  $N=18$ ;  $t= -2.18$ ,  $df=38$ ,  $P=0.035$ ). To test whether these effects were similar among localities, I more closely examined Gribbell and Princess Royal Islands.

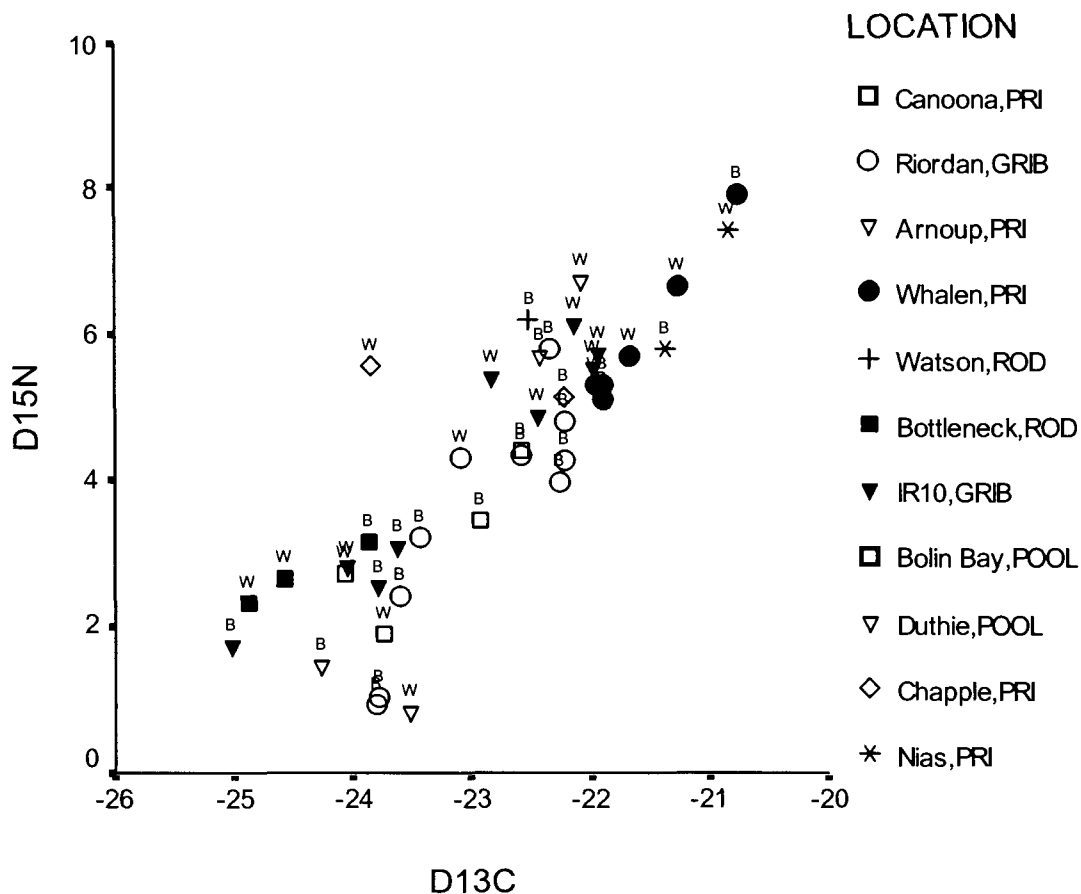


Figure 37. Whole hair  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for all bears among all localities sampled in 1997-2001. Colour morphs are indicated as B (black) and W (white). Localities are indicated as Creek name, and island or mainland name. PRI=Princess Royal Island; ROD= Roderick Island; GRIB= Gribbell Island; POOL= Pooley Island. Bolin Bay is the only mainland locality and is immediately north of Pooley Island.

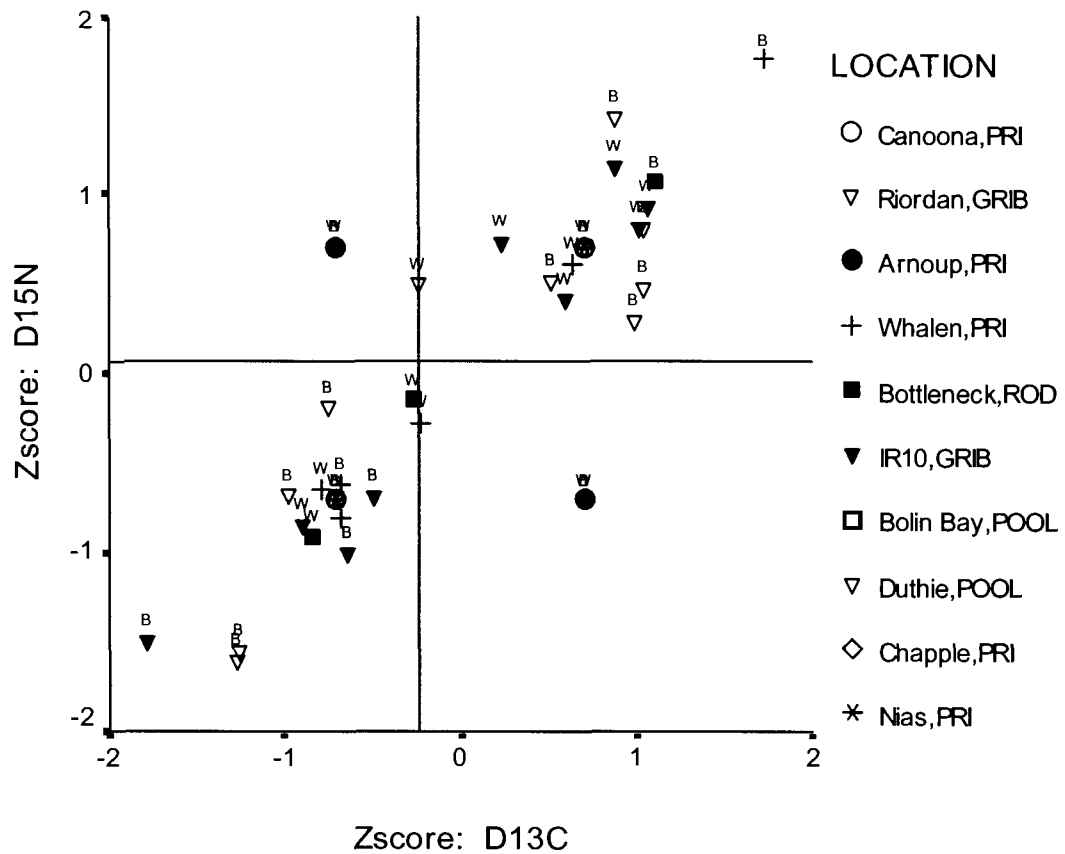


Fig. 38. Z scores of whole hair  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for all bears among all localities sampled in 1997-2001. Colour morphs are indicated as B (black) and W (white). Z scores are displayed as Standard Deviations. Reference lines indicate median  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  Z score values. Localities are indicated as Creek name, and island or mainland name. PRI=Princess Royal Island; ROD= Roderick Island; GRIB= Gribbell Island; POOL= Pooley Island. Bolin Bay is the only mainland locality and is immediately north of Pooley Island.

### 6.3.1.1.1 *Whole hair isotope values from Gribbell Island*

There is a separation of isotopic signatures between the 2 colour morphs on Gribbell Island (N=19; Fig. 39). White morphs were significantly more enriched in  $\delta^{15}\text{N}$  (white:  $5.0\text{‰} \pm 1.12\text{SD}$ ; black:  $3.2\text{‰} \pm 1.52\text{SD}$ ;  $t = -2.71$ ,  $df=17$ ,  $P=0.015$ ) but not in  $\delta^{13}\text{C}$  ( $\bar{X}_w$ :  $-22.6\text{‰} \pm 0.76\text{SD}$ ;  $\bar{X}_B$ :  $-23.2\text{‰} \pm 0.89\text{SD}$ ;  $t = -1.45$ ,  $df=17$ ,  $P=0.17$ ).

When removing site effects on Gribbell island white bears appeared to have elevated signatures in both isotopes relative to black bears, but these differences were not statistically significant ( $\delta^{13}\text{C}$ :  $t = -1.34$ ,  $df=17$ ,  $P=0.20$ ;  $\delta^{15}\text{N}$ :  $t = -1.94$ ,  $df=17$ ,  $P=0.07$ ; Fig. 40). Although Euclidean distances were not statistically different between morphs, black morphs had greater Euclidean distances than the white morphs, consistent in the direction and magnitude of the differences between morphs among all localities. ( $\bar{X}_B$ :  $1.36 \pm 0.51\text{SD}$ ,  $N=12$ ;  $\bar{X}_w$ :  $1.11 \pm 0.43\text{SD}$ ,  $N=7$ ;  $t = 1.06$ ,  $df=17$ ,  $P=0.30$ ). On Riordan Creek, there were no differences between black and white morphs for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ( $\delta^{13}\text{C}$ :  $t = -0.24$ ,  $df=8$ ,  $P=0.82$ ;  $\delta^{15}\text{N}$ :  $Z = -0.50$ ,  $df=8$ ,  $P=0.63$ ). However, on the neighbouring IR10 creek, there were significant differences between black and white morphs for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ( $\delta^{13}\text{C}$ :  $t = -2.82$ ,  $df=9$ ,  $P=0.020$ ;  $\delta^{15}\text{N}$ :  $t = -3.74$ ,  $df=9$ ,  $P=0.005$ ) as white morphs were enriched in both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  relative to black morphs. White morphs were enriched in both isotopes relative to black morphs on IR10 during each of the three years sampled (1997-1999), and during one year on Riordan Creek in 1998.

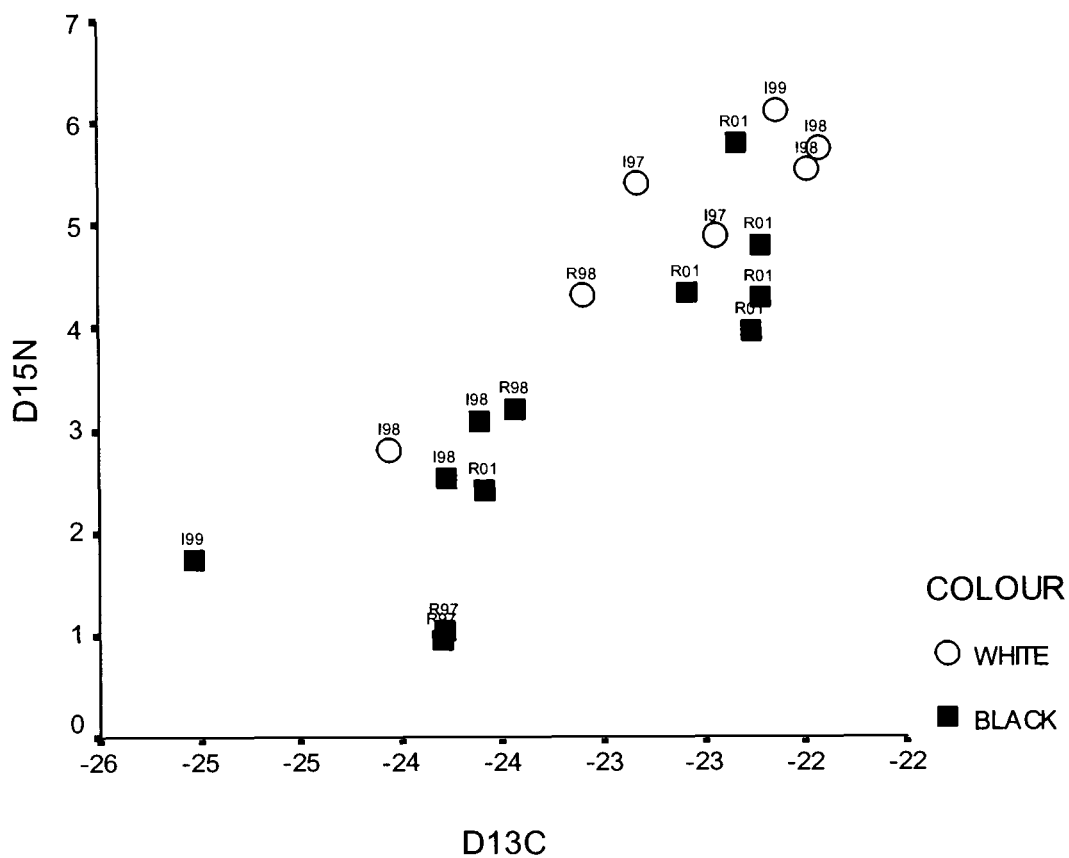


Figure 39. Whole hair  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for black and white morphs sampled in 1997-2001 on Gribbell Island, British Columbia. Site locations are indicated as creek, and year sampled. I97=IR10, 1997; I98=IR10, 1998; I99=IR10, 1999; R97=Riordan Creek, 1997; R98=Riordan Creek, 1998; R99=Riordan Creek, 1999; R01=Riordan Creek, 2001.

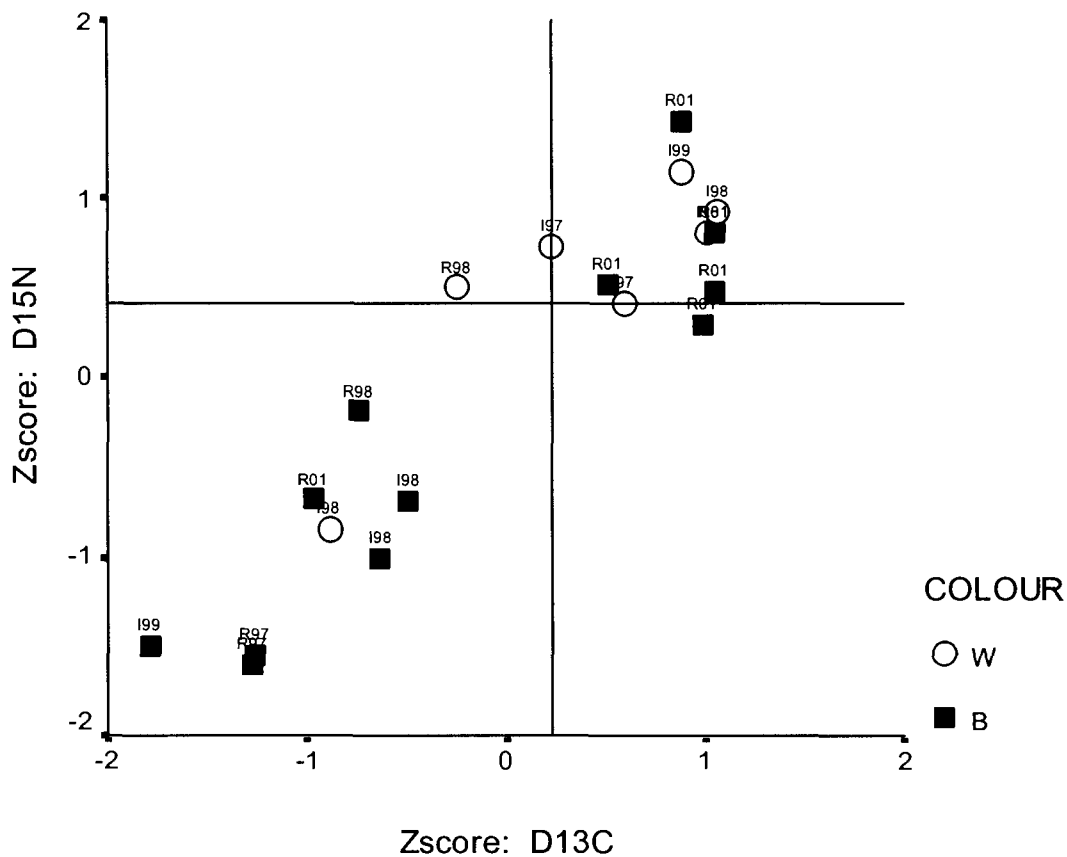


Figure 40. Z scores of whole hair  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for black and white morphs sampled in 1997-2001 on Gribbell Island, British Columbia. Z scores are displayed as Standard Deviations. Reference lines indicate median  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  Z score values. Site locations are indicated as creek, and year sampled. I97=IR10, 1997; I98=IR10, 1998; I99=IR10, 1999; R97=Riordan, 1997; R98=Riordan, 1998; R99=Riordan, 1999; R01=Riordan, 2001.

### 6.3.1.1.2 *Whole hair isotope values from Princess Royal Island*

On a neighbouring island (Princess Royal Island), there is high variability of isotope signatures with no clear relationship between colour morph (N=14; Fig. 41). White morph bears were isotopically indistinguishable from black morph bears in both  $\delta^{13}\text{C}$  (white:  $-22.4\text{‰} \pm 1.26\text{SD}$ ; black:  $-22.2\text{‰} \pm 1.14\text{SD}$ ;  $t=0.335$ ,  $df=12$ ,  $P=0.743$ ) and  $\delta^{15}\text{N}$  (white:  $4.8\text{‰} \pm 2.45\text{SD}$ ; black:  $4.9\text{‰} \pm 2.00\text{SD}$ ;  $t=0.097$ ,  $df=12$ ,  $P=0.925$ ). Among the five localities on Princess Royal Island, there was no detectable relationship in either  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  between black and white morphs ( $\delta^{13}\text{C}$ :  $Z=-0.674$ ,  $P=0.50$ ;  $\delta^{15}\text{N}$ :  $Z=-0.135$ ,  $P=0.89$ ; Wilcoxon Signed Rank Test).

When removing site effects on Princess Royal Island there were no differences in isotopic signatures between colour morphs ( $\delta^{13}\text{C}$ :  $t= -0.23$ ,  $df=12$ ,  $P=0.82$ ;  $\delta^{15}\text{N}$ :  $t=-0.20$ ,  $df=12$ ,  $P=0.85$ ; Fig. 42). Similar to Gribbell Island, Euclidean distances were not statistically different between morphs, yet black morphs had greater Euclidean distances than the white morphs, consistent in the direction and magnitude of the differences between morphs among all localities. ( $\bar{X}_B$ :  $1.21 \pm 0.63\text{SD}$ ,  $N=7$ ;  $\bar{X}_W$ :  $0.90 \pm 0.28\text{SD}$ ,  $N=7$ ;  $t= 1.17$ ,  $df=12$ ,  $P=0.27$ ).

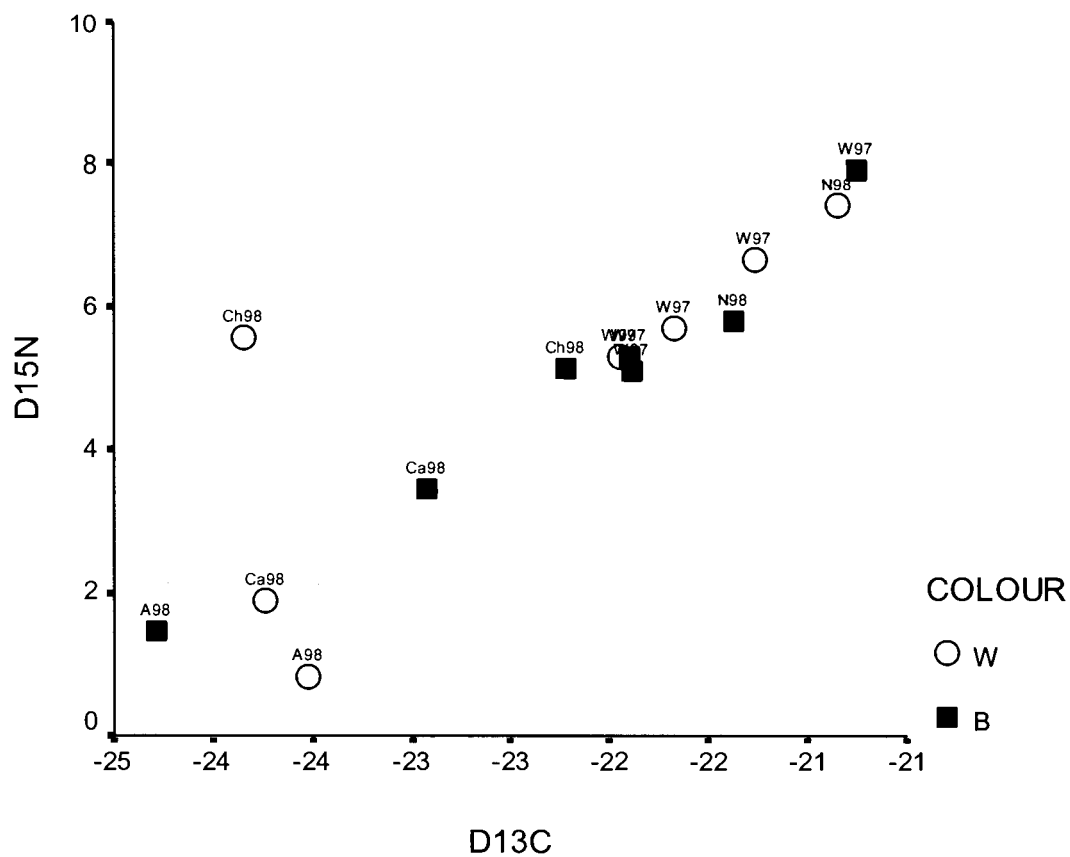


Figure 41. Whole hair  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for black and white morphs sampled in 1997-1999 on Princess Royal Island, British Columbia. Site locations are indicated as creek, and year sampled. A98=Arnoup, 1998; Ca98=Canoona, 1998; Ch98=Chapple, 1998; N98=Nias, 1998; W97=Whalen, 1997.

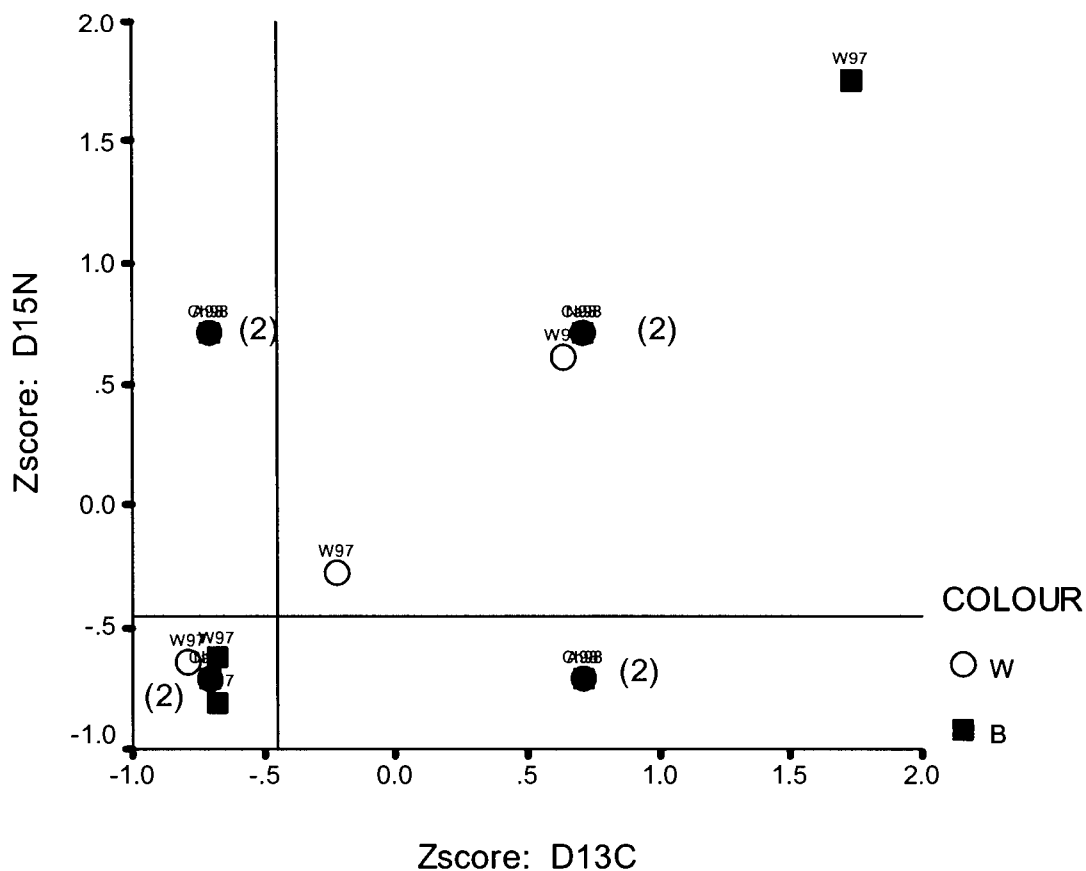


Figure 42. Z scores of whole hair  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for black and white morphs sampled in 1997-1999 on Princess Royal Island, British Columbia. Z scores are displayed as Standard Deviations. Reference lines indicate median  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  Z score values. Numbers in brackets beside points indicate the number of individuals with identical isotopic signatures. Site locations are indicated as creek, and year sampled. A98=Arnoup, 1998; Ca98=Canoona, 1998; Ch98=Chapple, 1998; N98=Nias, 1998; W97=Whalen, 1997.

### 6.3.1.2 *Isotope values for hair segments*

Distal, medial and proximal hair segments differed in isotopic signatures of both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  indicating detectable seasonal shifts in the diets of bears ( $\delta^{15}\text{N}$ :  $F_{2,121}=52.94$ ,  $P<0.001$ ;  $\delta^{13}\text{C}$ :  $F_{2,121}=42.91$ ,  $P<0.001$ ; Fig. 43A). For distal hair segments, mean  $\delta^{13}\text{C}$  was  $-23.9\text{‰} \pm 0.79\text{ SD}$  (range= $-25.5\text{‰}$  to  $-22.4\text{‰}$ ), while mean  $\delta^{15}\text{N}$  was  $2.3\text{‰} \pm 1.3\text{ SD}$  (range  $0.3\text{‰}$  to  $5.6\text{‰}$ ) indicating a spring diet based on vegetation (Fig. 43B). Medial hair segments also had relatively low isotope signatures with mean  $\delta^{13}\text{C}$  values of  $-23.3\text{‰} \pm 0.80\text{ SD}$  and (range  $-25.2\text{‰}$  to  $-21.50\text{‰}$ ), while mean  $\delta^{15}\text{N}$  was  $3.1\text{‰} \pm 1.3\text{ SD}$  (range  $1.2\text{‰}$  to  $6.7\text{‰}$ ) indicating that summer diets were also based on vegetation (Fig. 43C). However, there is a clear separation of isotopic values between spring and fall ( $P<0.001$  Tukey HSD), and between summer and fall ( $P<0.001$  Tukey HSD), as proximal hair sections had elevated isotope values compared to distal and medial hair sections (Fig. 43D). Proximal hair segments had mean  $\delta^{13}\text{C}$  values of  $-21.3\text{‰} \pm 2.0\text{ SD}$  and (range  $-24.6\text{‰}$  to  $-17.4\text{‰}$ ), while mean  $\delta^{15}\text{N}$  was  $7.5\text{‰} \pm 3.3\text{ SD}$  (range  $1.3\text{‰}$  to  $13.6\text{‰}$ ). The enriched isotopic values of the proximal hair sections indicate that the majority of bears switch to increased salmon consumption during the fall.

Although distal hair sections did not differ from medial sections for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  among bears ( $P=0.12$  and  $P=0.29$  respectively; Tukey HSD), there was a significant shift in both isotopes within individual bears between these two hair segments, ( $\delta^{13}\text{C}$ :  $t=6.6$ ,  $df=40$ ,  $P<0.001$ ;  $\delta^{15}\text{N}$ :  $t=5.6$ ,  $df=40$ ,  $P<0.001$ ; paired t-tests) indicating dietary shifts from the spring to summer.

When using a generic sign test, there was a significant difference in  $\delta^{15}\text{N}$  for distal hair segments indicating divergent spring diets between colour morphs ( $Z=-2.43$ ,  $P=0.15$ ; Wilcoxon Signed Rank Test). However, no differences were detected in  $\delta^{15}\text{N}$  between the colour morphs for mid or proximal hair sections within each locality (mid:  $Z=-1.18$ ,  $P=0.24$ ; base:  $Z=-0.62$ ,  $P=0.53$ ; Wilcoxon Signed Rank Test). Furthermore, I did not detect differences in  $\delta^{13}\text{C}$  among hair segments between black and white morphs (tip:  $Z=-1.098$ ,  $P=0.272$ , mid:  $Z=-0.314$ ,  $P=0.754$ , base:  $Z=-0.00$ ,  $P=1.00$ ).

A finer scale analysis of the dietary differences between colour morphs is possible through the use of standardized Z scores. After removing locality and seasonal effects using Z scores there were differences in isotopic signatures in  $\delta^{15}\text{N}$  but not in  $\delta^{13}\text{C}$  between colour morphs ( $\delta^{13}\text{C}$ :  $t=-1.14$ ,  $df=116$ ,  $P=0.26$ ;  $\delta^{15}\text{N}$ :  $t=-2.34$ ,  $P=0.021$ ; Fig. 44A-D). However, Euclidean distances were not statistically different between colour morphs indicating that morphs were similar in their deviations from central tendency in diet among localities and seasons ( $\bar{X}_B$ :  $1.21 \pm 0.65$  SD,  $N=69$ ;  $\bar{X}_W$ :  $1.29 \pm 0.65$  SD,  $N=53$ ;  $t=-0.66$ ,  $df=120$ ,  $P=0.51$ ).

Using spring diets as a control (presuming salmon is not available to bears during the spring), the calculated percent of marine derived nitrogen in the fall diets of bears was  $\bar{X}=34.8\% \pm 28\%$  with a maximum value recorded as 80%. It is interesting to note that there is a subset of bears which do not appear to utilize salmon during the fall.

To test whether these effects were similar among localities, I more closely examined the most complete data sets of Gribbell and Princess Royal Islands.

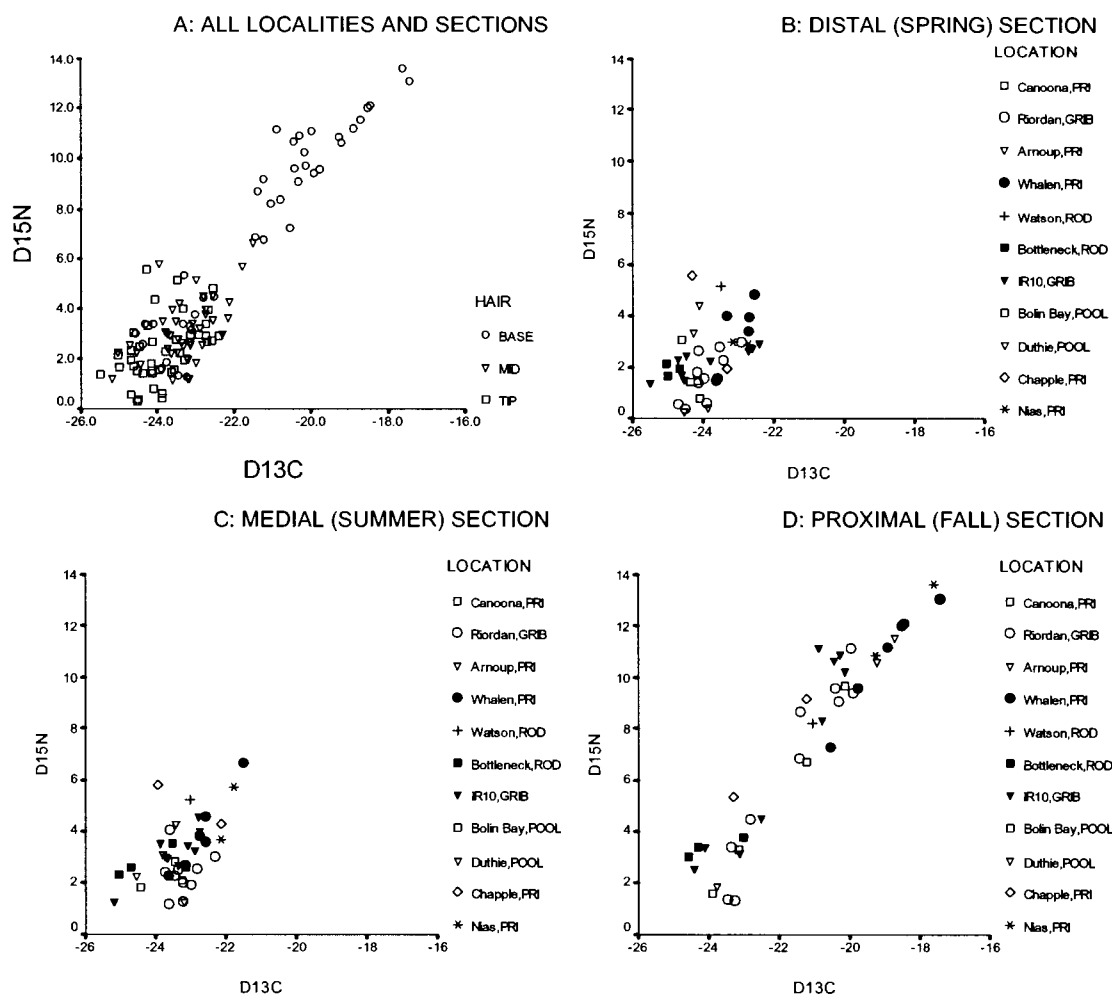


Figure 43A-D.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for hair segments of bears sampled during a broad geographic survey in 1997-1999. **A:**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for proximal, medial and distal hair sections among all localities. **B:**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for distal hair sections representing spring diets among all localities. **C:**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for medial hair sections representing summer diets among all localities. **D:**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for proximal hair sections representing fall diets among all localities.

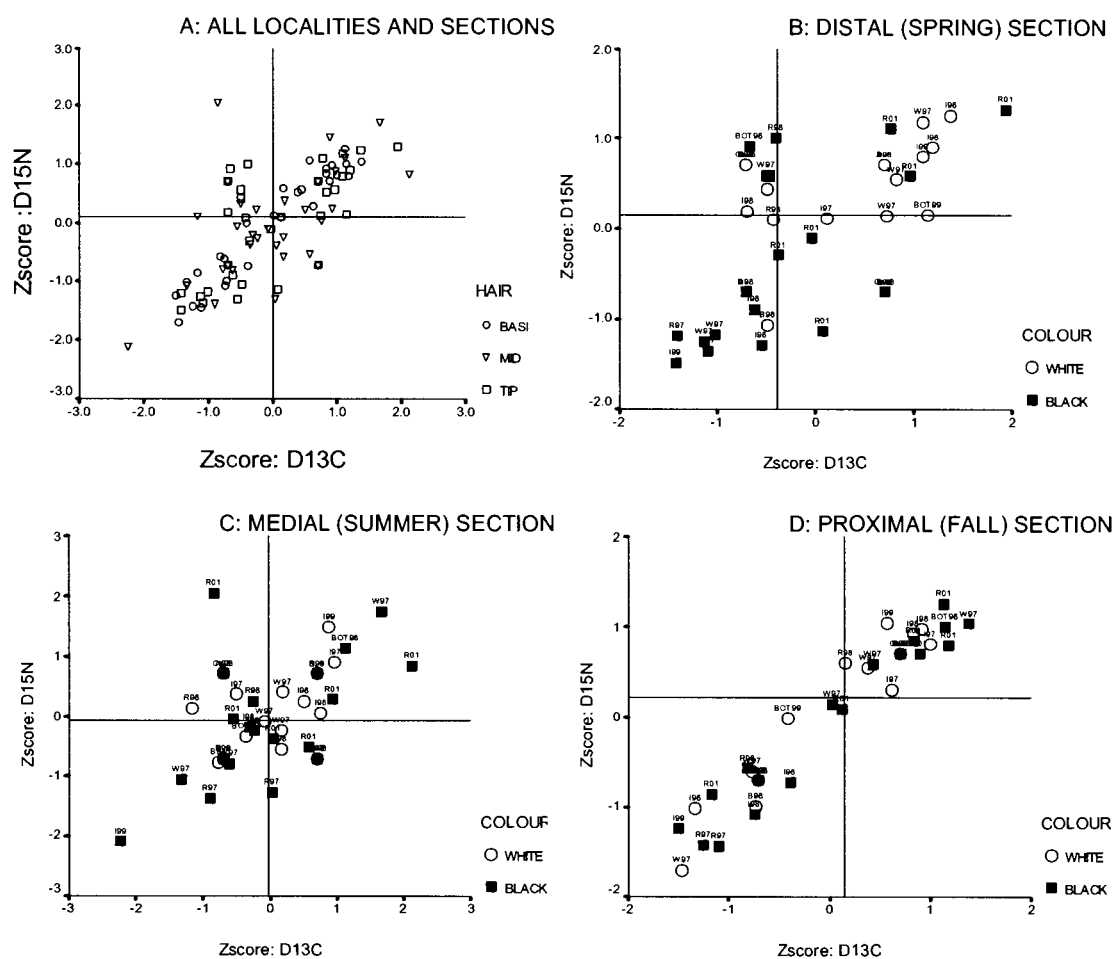


Figure 44A-D. Z scores (standardized for location and season) of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for hair segments of bears sampled during a broad geographic survey in 1997-1999. Z scores are displayed as Standard Deviations. Reference lines indicate median  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  Z score values. **A:** Z scores for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for proximal, medial and distal hair sections among all localities. **B:** Z scores for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for distal hair sections representing spring diets for black and white morphs among all localities. **C:** Z scores for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for medial hair sections representing summer diets for black and white morphs among all localities. **D:** Z scores for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for proximal hair sections representing fall diets for black and white morphs among all localities.

### 6.3.1.2.1 *Isotope values for hair segments for Gribbell Island*

#### **Spring**

Distal hair segments for both colour morphs had low isotope signatures for both  $\delta^{13}\text{C}$  (white:  $-23.55 \text{‰} \pm 0.96\text{SD}$ ; black:  $-24.16 \text{‰} \pm 0.69 \text{SD}$ ) and  $\delta^{15}\text{N}$  (white:  $2.45 \text{‰} \pm 0.36 \text{SD}$ ; black:  $1.65 \text{‰} \pm 0.87 \text{SD}$ ) indicating a vegetarian diet for both colour morphs (Fig. 45A). However, although the effect is slight, there is a significant separation between the two colour morphs in  $\delta^{15}\text{N}$  but not in  $\delta^{13}\text{C}$  where white bears were slightly more enriched than black bears ( $\delta^{13}\text{C}$ :  $t=-1.61$ ,  $df=17$ ,  $P=0.13$ ;  $\delta^{15}\text{N}$ :  $t=-2.29$ ,  $df=17$ ,  $P=0.035$ ).

Euclidean distances were not statistically different between morphs, yet black morphs had greater Euclidean distances than the white morphs, ( $\bar{X}_B$ :  $1.17 \pm 0.59 \text{SD}$ ,  $N=12$ ;  $\bar{X}_W$ :  $1.10 \pm 0.61 \text{SD}$ ,  $N=7$ ;  $t=0.24$ ,  $df=17$ ,  $P=0.82$ ; Fig. 45B).

#### **Summer**

A similar trend is seen in the medial hair segments with low  $\delta^{13}\text{C}$  (white:  $-23.21 \text{‰} \pm 0.45 \text{SD}$ ; black:  $-23.43 \text{‰} \pm 0.69 \text{SD}$ ) and  $\delta^{15}\text{N}$  (white:  $3.40 \text{‰} \pm 0.73 \text{SD}$ ; black:  $2.32 \text{‰} \pm 0.86 \text{SD}$ ) values which characterise a summer diet based on vegetation (Fig. 45C). Again, although the effect is slight, there is a significant enrichment of  $\delta^{15}\text{N}$  in white bears relative to black bears ( $t=-2.77$ ,  $df=17$ ,  $P=0.013$ ), however the level of enrichment of  $\delta^{13}\text{C}$  does not reach statistical significance ( $t=-0.75$ ,  $df=17$ ,  $P=0.46$ ).

Euclidean distances were not statistically different between morphs, yet black morphs had greater Euclidean distances than the white morphs, ( $\bar{X}_B$ :  $1.14 \pm 0.67 \text{SD}$ ,  $N=12$ ;  $\bar{X}_W$ :  $0.71 \pm 0.30 \text{SD}$ ,  $N=7$ ;  $t=1.61$ ,  $df=17$ ,  $P=0.13$ ; Fig. 45D).

***Fall***

Within the proximal hair segments, white bears are enriched in  $\delta^{15}\text{N}$  but not in  $\delta^{13}\text{C}$  relative to the black bears ( $\delta^{13}\text{C}$ :  $t = -1.29, df = 17, P = 0.22$ ;  $\delta^{15}\text{N}$ :  $t = -2.27, df = 17, P = 0.037$ ; Fig. 45E). Proximal hair segments for the white colour morph had high isotope signatures for both  $\delta^{13}\text{C}$  ( $-21.15 \text{‰} \pm 1.37 \text{ SD}$ ) and  $\delta^{15}\text{N}$  ( $9.06 \text{‰} \pm 2.72 \text{ SD}$ ) indicating a diet high in the direct consumption of salmon. White bears assimilated  $47\% \pm 19\%$  of dietary N from salmon. Proximal hair segments for the black colour morph had lower isotope signatures and higher standard deviations for both  $\delta^{13}\text{C}$  ( $-22.07 \text{‰} \pm 1.58 \text{ SD}$ ) and  $\delta^{15}\text{N}$  ( $5.56 \text{‰} \pm 3.49 \text{ SD}$ ) relative to the white morph. Black bears assimilated  $22.4\% \pm 24\%$  of dietary N from salmon.

Euclidean distances were not statistically different between morphs, yet black morphs had greater Euclidean distances than the white morphs ( $\bar{X}_B$ :  $1.24 \pm 0.62 \text{ SD}$ ,  $N = 12$ ;  $\bar{X}_W$ :  $0.83 \pm 0.54 \text{ SD}$ ,  $N = 7$ ;  $t = 1.49, df = 17, P = 0.16$ ; Fig. 45F).

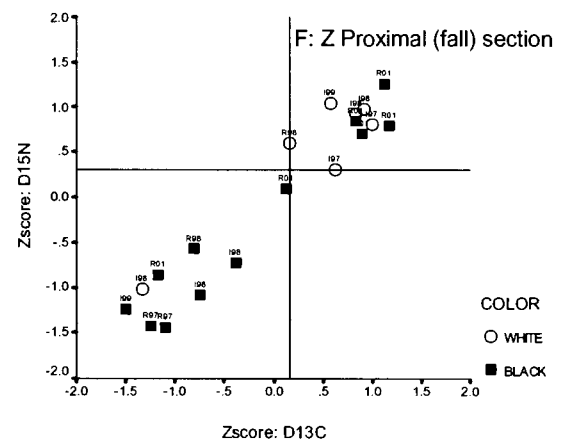
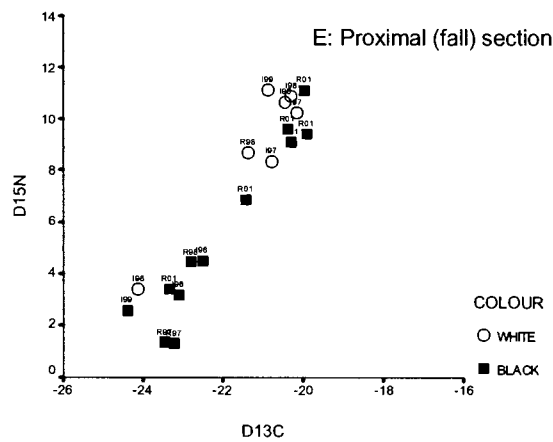
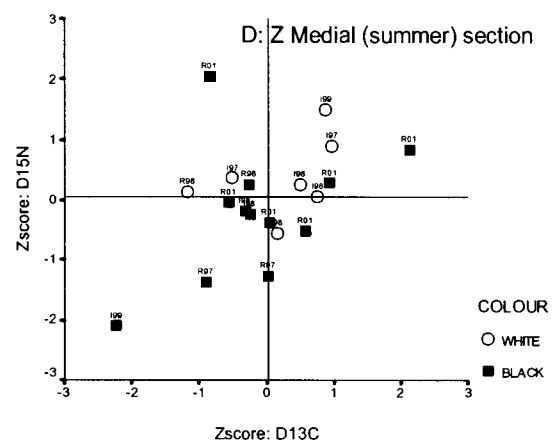
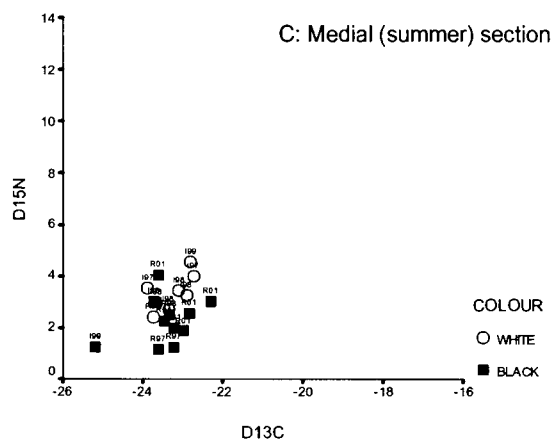
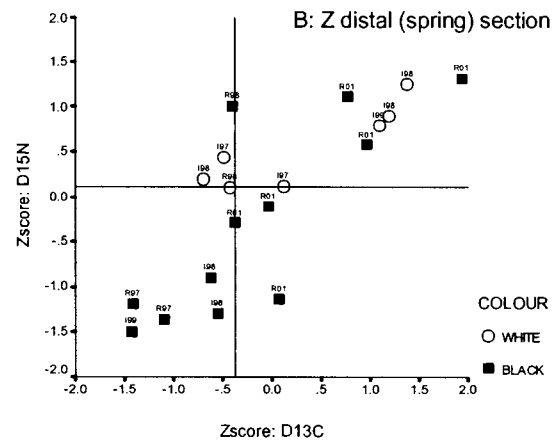
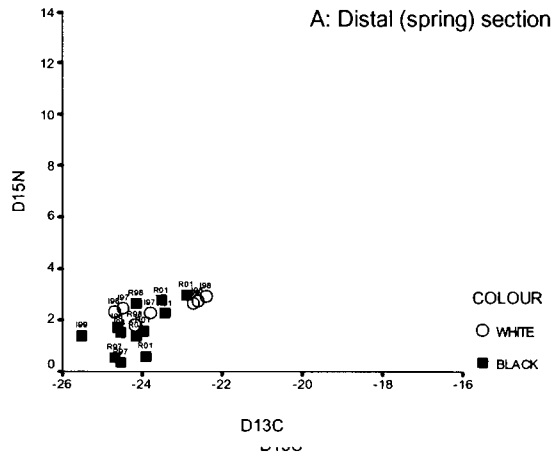


Figure 45A-F.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values and Z scores (standardized for location and season) and for hair segments of black and white bears sampled on Gribbell island 1997-2001. Z scores are displayed as Standard Deviations. Reference lines indicate median  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  Z score values. **A:**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for distal hair sections representing spring diets. **B:** Z scores for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for distal hair sections representing spring diets **C:**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for medial hair sections representing summer diets. **D:** Z scores for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for medial hair sections representing summer diets **E:**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for proximal hair sections representing fall diets among all localities. **F:** Z scores for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for proximal hair sections representing fall diets.

### 6.3.1.2.2 *Isotope values for hair segments for Princess Royal Island*

#### ***Spring***

Distal hair segments for both colour morphs had low isotope signatures for both  $\delta^{13}\text{C}$  (white:  $-23.35\text{‰} \pm 0.75\text{SD}$ ; black:  $-23.60\text{‰} \pm 0.58\text{SD}$ ) and  $\delta^{15}\text{N}$  (white:  $3.24\text{‰} \pm 1.80\text{SD}$ ; black:  $1.85\text{‰} \pm 1.80\text{SD}$ ) indicating a vegetarian diet for both colour morphs. There appeared to be isotopic separation between the two colour morphs; however, this did not reach statistical significance ( $\delta^{13}\text{C}$ :  $t=-0.71$ ,  $df=12$ ,  $p=0.494$ ;  $\delta^{15}\text{N}$ :  $t=-1.67$ ,  $df=12$ ,  $P=0.121$ ; Fig. 46A). Euclidean distances were not statistically different between morphs ( $\bar{X}_B$ :  $1.23 \pm 0.42$  SD,  $N=7$ ;  $\bar{X}_W$ :  $1.70 \pm 0.63$  SD,  $N=7$ ;  $t= 1.61$ ,  $df=12$ ,  $P=0.13$ ; Fig. 46B).

#### ***Summer***

A similar trend is seen in the medial hair segments with low  $\delta^{13}\text{C}$  (white:  $-22.84\text{‰} \pm 0.67\text{SD}$ ; black:  $-22.94\text{‰} \pm 1.06\text{SD}$ ) and  $\delta^{15}\text{N}$  (white:  $3.89\text{‰} \pm 1.64\text{SD}$ ; black:  $3.52\text{‰} \pm 1.57\text{SD}$ ) values for both colour morphs, characterizing a summer diet based predominantly on vegetation. Isotopic signatures did not differ between the two colour morphs ( $\delta^{13}\text{C}$ :  $t=-0.19$ ,  $df=12$ ,  $p=0.851$ ;  $\delta^{15}\text{N}$ :  $t=-0.43$ ,  $df=12$ ,  $P=0.673$ ; Fig. 46C).

Euclidean distances were not statistically different between morphs ( $\bar{X}_B$ :  $1.46 \pm 1.03$  SD,  $N=12$ ;  $\bar{X}_W$ :  $1.44 \pm 0.75$  SD,  $N=7$ ;  $t= 0.41$ ,  $df=12$ ,  $P=0.97$ ; Fig. 46D).

#### ***Fall***

Proximal hair segments for both colour morphs had high isotope signatures for both  $\delta^{13}\text{C}$  (white:  $-20.60\text{‰} \pm 2.54\text{SD}$ ; black:  $-20.03\text{‰} \pm 2.16\text{SD}$ ) and  $\delta^{15}\text{N}$  (white:  $8.23\text{‰} \pm 4.44\text{SD}$ ; black:  $9.28\text{‰} \pm 3.88\text{SD}$ ) indicating fall diets high in the direct consumption of salmon (Fig. 46E). White bears assimilated  $41\% \pm 31\%$  of dietary N

from salmon, while black bears assimilated  $49\% \pm 28\%$  of dietary N from salmon. However, there is no evident trend of ecological separation as isotopic signatures did not differ between the two colour morphs ( $\delta^{13}\text{C}$ :  $t=-0.19$ ,  $df=12$ ,  $p=0.851$ ;  $\delta^{15}\text{N}$ :  $t=-0.43$ ,  $df=12$ ,  $P=0.673$ ).

Euclidean distances were not statistically different between morphs ( $\bar{X}_B$ :  $1.36 \pm 0.79$  SD,  $N=7$ ;  $\bar{X}_W$ :  $1.45 \pm 0.76$  SD,  $N=6$ ;  $t=0.21$ ,  $df=11$ ,  $P=0.84$ ; Fig. 46F).

### 6.3.1.3 *Magnitude of dietary separation relative to gene frequency*

There is a positive relationship between the magnitude of isotopic differentiation between black and white morphs and the frequency of the white coat allele (Fig. 47A-B). The magnitude of separation between the 2 colour morphs is displayed on the X axis. As the frequency of the white coat allele increases in the population, the degree of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  enrichment in white bears relative to black bears becomes more pronounced ( $\delta^{13}\text{C}$ : Pearson Correlation = 0.577,  $P=0.049$ ;  $\delta^{15}\text{N}$ : Pearson Correlation = 0.666,  $P=0.018$ ).

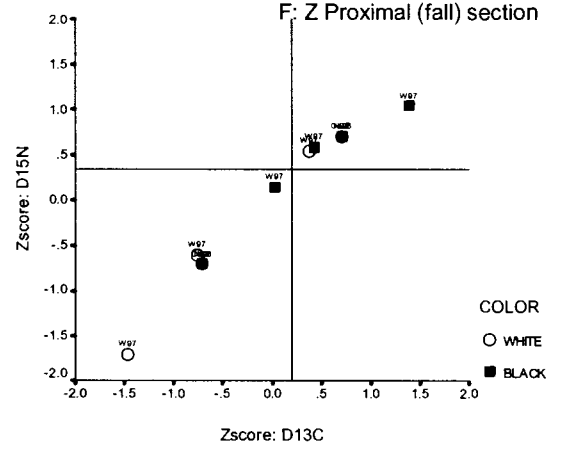
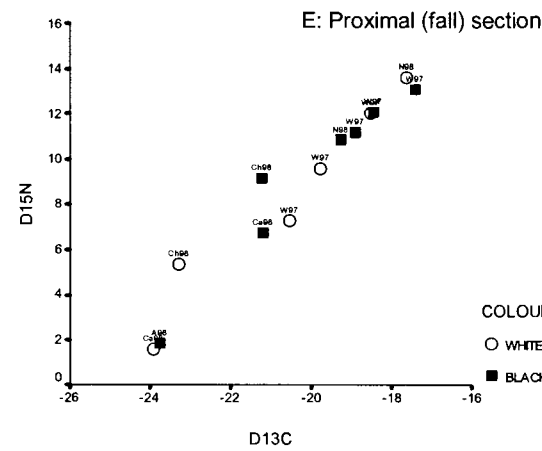
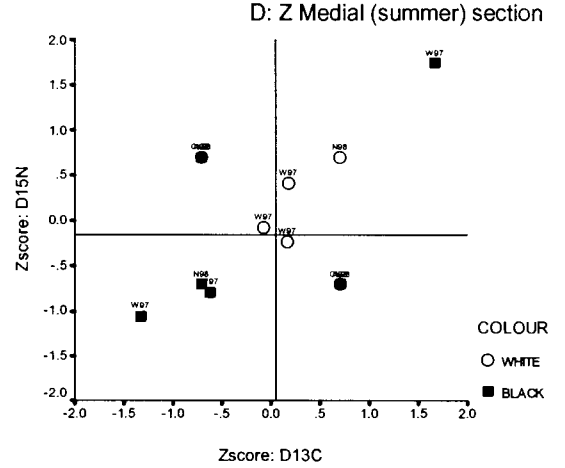
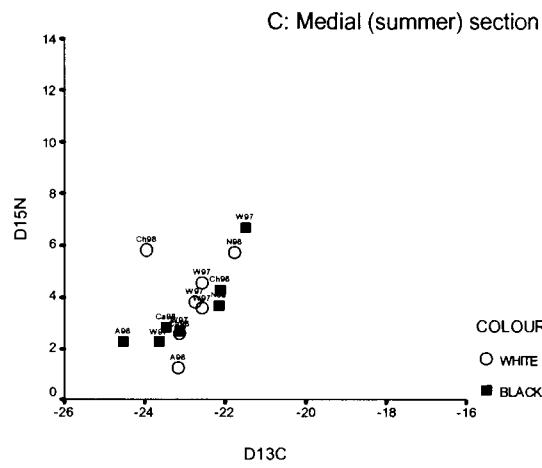
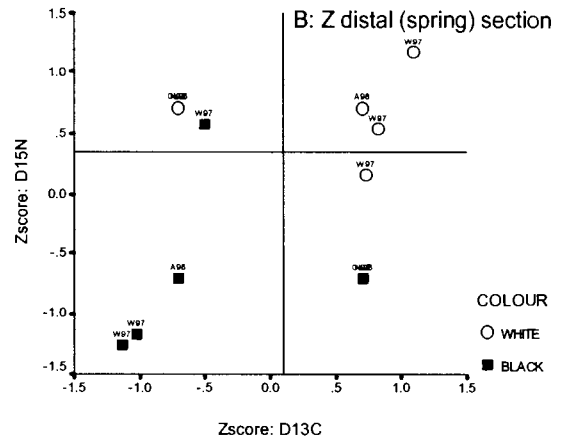
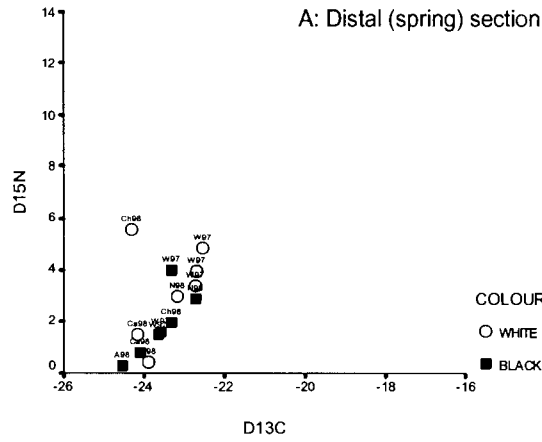


Figure 46A-F.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values and Z scores (standardized for location and season) and for hair segments of black and white bears sampled on Princess Royal Island 1997-1999. Z scores are displayed as Standard Deviations. Reference lines indicate median  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  Z score values. **A:**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for distal hair sections representing spring diets. **B:** Z scores for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for distal hair sections representing spring diets **C:**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for medial hair sections representing summer diets. **D:** Z scores for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for medial hair sections representing summer diets **E:**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for proximal hair sections representing fall diets among all localities. **F:** Z scores for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for proximal hair sections representing fall diets.

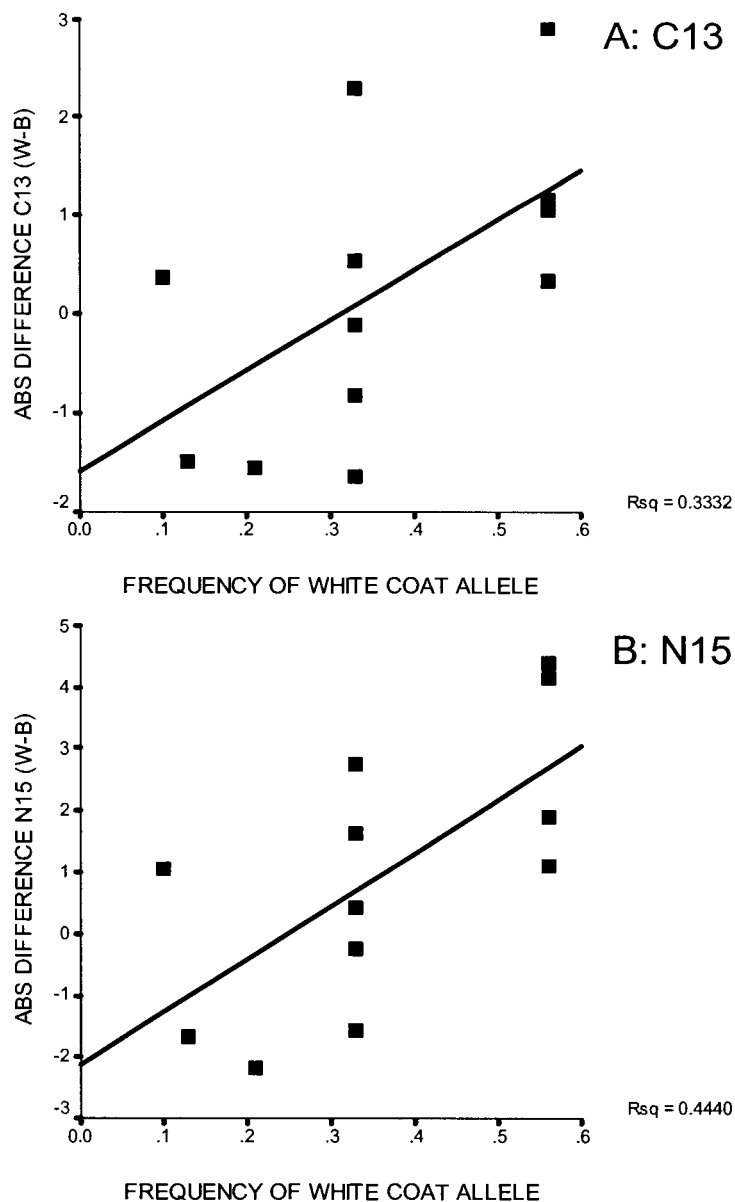


Figure 47A-B. The relationship between magnitude of isotopic differentiation and the white coat allele frequency between colour morphs of Kermode bears in British Columbia. **A:** The relationship in  $\delta^{13}\text{C}$  (raw values) separation between black and white morphs and the frequency of G ( $P=0.049$ ). **B:** The relationship in  $\delta^{15}\text{N}$  (raw values) separation between black and white morphs and the frequency of G ( $P=0.018$ ).

### 6.3.2 *Historical assessment*

#### 6.3.2.1 *Isotope values for whole hair samples*

Overall isotope values for whole hair samples of four white bears from Gribbell and Princess Royal Island varied little among individuals (Fig. 48). Mean  $\delta^{13}\text{C}$  was  $-22.5\text{‰} \pm 0.58$  SD and ranged from  $(-23.2$  to  $-21.8\text{‰})$ , while mean  $\delta^{15}\text{N}$  was  $2.25\text{‰} \pm 2.15$  SD and ranged from  $(0.56$  to  $4.4\text{‰})$ .

#### 6.3.2.2 *Isotope values for hair segments*

Distal, medial and proximal hair segments were similar in isotopic signatures of both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  indicating similar seasonal diets of bears ( $\delta^{13}\text{C}$ :  $F=0.40$ ,  $df=2$ ,  $P=0.685$ ;  $\delta^{15}\text{N}$ :  $F=0.247$ ,  $df=2$ ,  $P=0.789$ ; Fig. 49). For distal hair segments, mean  $\delta^{13}\text{C}$  was  $-22.43\text{‰} \pm 0.53$  SD and (range  $-22.74\text{‰}$  to  $-21.81\text{‰}$ ), while mean  $\delta^{15}\text{N}$  was  $1.17\text{‰} \pm 2.09$  SD (range  $-1.18$  to  $2.83\text{‰}$ ) indicating a spring diet based on vegetation. Medial hair segments also had relatively low isotope signatures with mean  $\delta^{13}\text{C}$  values of  $-22.43\text{‰} \pm 0.57$  SD and (range  $-22.94\text{‰}$  to  $-21.82\text{‰}$ ), while mean  $\delta^{15}\text{N}$  was  $1.24\text{‰} \pm 3.87$  SD (range  $-0.95\text{‰}$  to  $2.85\text{‰}$ ) indicating that summer diets were also based on vegetation. However, unlike in the broad geographic survey and in the local assessment, there was not a clear separation of isotopic values among hair segments ( $\delta^{13}\text{C}$ :  $F=0.40$ ,  $df=2$ ,  $P=0.685$ ;  $\delta^{15}\text{N}$ :  $F=0.25$ ,  $df=2$ ,  $P=0.789$ ). Proximal hair segments had mean  $\delta^{13}\text{C}$  values of  $-22.11\text{‰} \pm 0.36$  SD and (range  $-22.50$  to  $-21.80\text{‰}$ ), while mean  $\delta^{15}\text{N}$  was  $2.21\text{‰} \pm 2.01$  SD (range  $0.44$  to  $4.40\text{‰}$ ). The similarity of isotopic values among hair sections indicate that the majority of bears had a diet based on plant matter up to when they were shot.

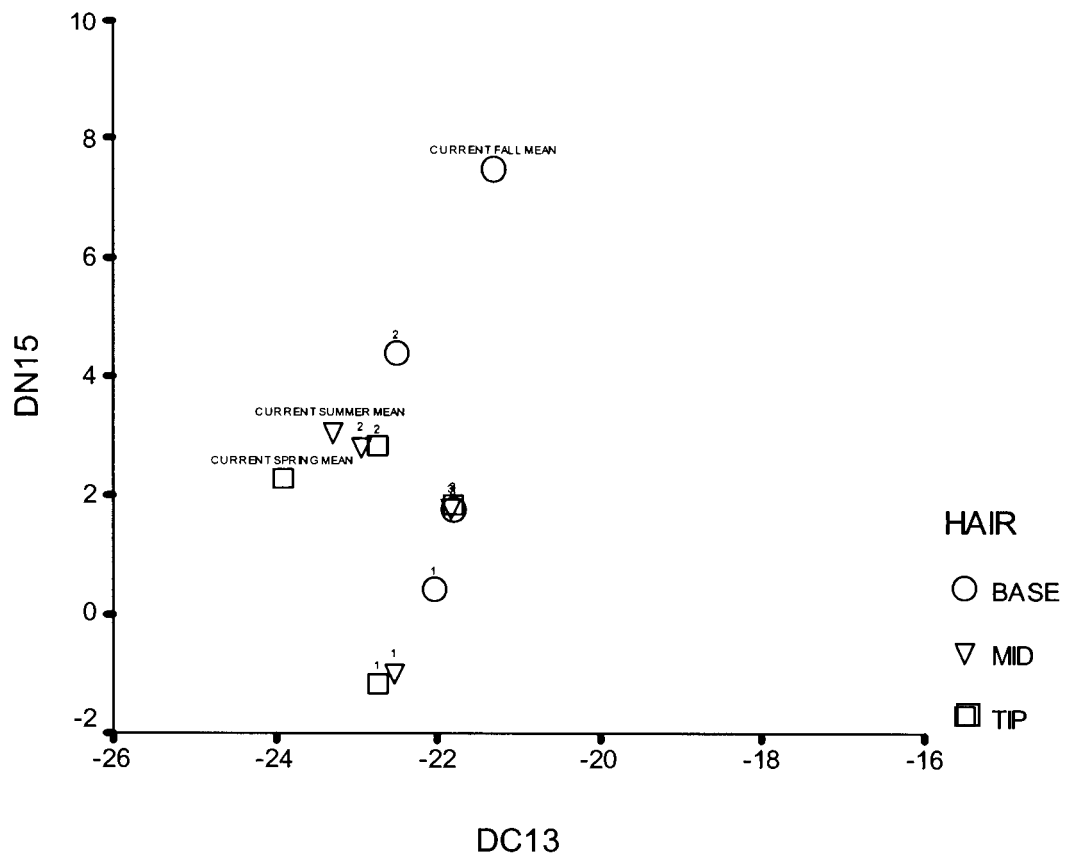


Figure 49.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for hair segments of four white bears shot at the turn of the century on Gribbell Island and Princess Royal Island.

## 6.4

## Discussion

### 6.4.1 Coastal assessment

Overall isotope values for whole hair samples varied widely among individuals indicating a broad potential niche breadth. This is not surprising, as brown and black bears (*U. arctos* and *U. americanus*) are well known to be omnivorous, consuming a variety of plants and animals (Mattson et al. 1991).

Jacoby et al. (1999) reported mean  $\delta^{13}\text{C}$  of -22.5 ‰ and  $\delta^{15}\text{N}$  of 4.9 ‰ in black bears sympatric with brown bears but observed an enrichment (increase) to -20.1 ‰ for  $\delta^{13}\text{C}$  and to 7.6 ‰ for  $\delta^{15}\text{N}$  in black bears allopatric with brown bears on the Kenai Peninsula, Alaska. Our results for whole hair samples when solely looking at isotope values are most consistent with black bears sympatric with brown bears, which incorporated little salmon into the diet, even though bears in our study are typically allopatric with brown bears except on Princess Royal island and on the mainland. This is true prior to salmon spawning migrations when bears consume mainly vegetation as their primary food source. However, bears living in coastal areas have easy access to inter-tidal zones, and can supplement their diets with alternative protein sources such as crabs, barnacles and bivalves. Yet, once salmon become plentiful during the fall, bears typically switch to this food source. It is possible that our overall isotope values were low relative to the Kenai black bears allopatric with brown bears because salmon typically run for the majority of the summer months in Alaska, making this resource available for an increased proportion of time relative to time spent hibernating during the winter months. This is most evident in brown bears where  $\delta^{13}\text{C}$  values typically range from -20 ‰ to -18 ‰ and

$\delta^{15}\text{N}$  values typically range between 9 ‰-11.5 ‰ indicating substantial incorporation of salmon into annual diets (Hilderbrand et al. 1996, Jacoby et al. 1999). However, when looking at calculated % MDN in diets, our bears are most similar to Kenai black bears allopatric with brown bears, with approximately 53% MDN in the diet comparable to bears in this study which incorporate slightly less MDN into their diets (38%).

It is interesting that the variability in isotope values for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were much higher in our study than for the Kenai black bears (Jacoby et al. 1999), even with similar sample sizes (35 vs. 37, respectively). This could be due to increased diversity of habitats spanning the many islands in the large sampling area in our study, while the Kenai Peninsula may not be as large or diverse in habitat attributes.

Stable isotope ratios derived from segments of hair tissue allows for an examination of a dietary window spanning the period of hair growth which, in ursids, approximates spring to fall. Isotope values among hair segments differed between spring and fall and between the summer and fall indicating that seasonal dietary shifts can be detected through analysis of hair segments. This clearly demonstrates that examination of multiple sections of hair along the hair shaft can provide finer scale analysis of diets over seasons than through analysis of whole hair samples. This technique is an expansion of the previous work by Darimont and Reimchen (2002) where the importance of salmon in the diets of wolves was assessed by measuring isotopes in two hair segments (base and tip). Other authors have used segments of alternate tissues to reconstruct diets over finer time scales than is possible by whole tissue analysis. Some examples include the use of tooth annuli to reconstruct the diets of pinnipeds and bovids (Hobson and Sease 1998, Wiedemann et al. 1999), while feather segments were used to in diet reconstructions of

fulmars (Thompson and Furness 1995). Segments of baleen have even been used to elucidate seasonal shifts in the location of feeding grounds of Bowhead whales (Schell et al. 1989). This theory has also been applied to the reconstruction of historic salmon abundance, and assessment of nutrient cycling in the Pacific Northwest through analysis of tree cores from ancient stream-side residents (Reimchen et al. 2002).

Seasonal variation in diet is difficult to detect when using whole hair samples. Dietary reconstruction involving isotopic results derived solely from whole hair samples may be misleading as seasonal changes are lost. This study is the first to examine temporal variability in black bear diet using segments of hair and produced insights into niche space that would not have been possible with whole hair analysis.

Isotope values in distal and medial hair segments indicate a predominantly vegetative diet during the spring and summer seasons. This was expected as salmon have not yet begun to spawn during these time periods. Comparisons between distal and medial hair segments within individual bears revealed dietary shifts between spring and summer; however, this effect was not detected in analyses among all bears. This was also expected as bears shift to alternate plants as sources become depleted and alternate species become available or more nutritious. This process can vary with many environmental factors including topography, elevation, temperature, precipitation patterns to name a few. Thus individual shifts in dietary preferences will vary with the diversity of the landscape and as this study encompasses a vast area and many different bears, these subtle shifts are likely to be difficult to detect unless analysed in a paired fashion.

Isotope values in proximal hair segments indicate a substantial shift towards increased incorporation of salmon in the fall diets of bears on the west coast of British

Columbia. This was expected as salmon are an accessible and critically important nutritional resource for bear populations which have access to coastal streams and rivers. The high nutritive value of salmon combined with its high digestibility, has been shown to influence bear size, population density, fecundity, and overwintering survival by allowing the development of large fat reserves required during hibernation (Hilderbrand et al. 1999b, Gende et al. 2001).

However, there were many bears which did not have enriched isotope signatures in proximal hair segments suggesting that they did not utilize salmon resources during the fall. This is surprising given the availability of such an important resource. Furthermore, salmon naturally die after spawning or are partially consumed and abandoned, typically resulting in carcasses littering the stream banks and riparian zone. Even for bears unable to successfully capture live salmon (which are more nutritious than senescent salmon), the availability of carcasses presents opportunities for scavenging unparalleled during other times of the year. Although isotopic analysis can not currently differentiate between actively predated or scavenged dietary sources (Jacoby et al. 1999), the assimilation of salmon in the diet by any means would be detected. In addition, all hair samples were collected on bear trails along salmon streams during the fall, thus proximity to salmon sources may not sufficiently account for the lack of salmon in diets. One possible explanation for the lack of enrichment in some proximal hair segments could be the timing of bears returning to the salmon stream. If a bear was delayed in arriving at the salmon stream, the isotopic signal may not have had sufficient time to incorporate into the hair shaft. However, I examined all hair collection dates and there appeared to be sufficient time to allow for isotopic signals to incorporate into the hair shaft, and many

samples with enriched isotopic signatures were collected early in the fall which should have limited the extent of enrichment if it is subject to incorporation time effects. The avoidance of salmon streams has been shown for some bear populations (Hilderbrand et al. 1996) and for mothers and cubs during darkness (Klinka and Reimchen 2002) possibly to prevent potentially costly agonistic interactions among bears which tend to congregate at such feeding sites.

One interesting question that remains difficult to address is how numerous adult bears can survive on Gribbell Island which has so few salmon. Reimchen (2002) observed 8 bears feeding on approximately 13 chum salmon per day over the duration of the salmon run (5000 salmon/run) on the Haida Gwaii (Queen Charlotte Islands), while the salmon run on Gribbell Island (Riordan Creek) averages only 950 salmon. Throughout the study, I observed 41 individual bears feeding on Riordan Creek. Although 41 bears are not simultaneously active on the stream, it seems improbable that the relatively small numbers of salmon observed in Riordan Creek could support a large population of bears. One possible explanation could be that bears supplement their diets with vegetation. This is supported by anecdotal evidence whereby I frequently encountered bear scat along the stream and in wooded areas, and within each scat I found abundant evidence of terrestrial forage including undigested berries, leaves and other vegetation. Another possible explanation could be increased and/or continued reliance on intertidal foraging. Furthermore, it is entirely possible that bears from Gribbell Island swim to neighbouring localities to access alternate salmon runs or other sources of nutrition.

Our analysis of stable isotope signatures in the hair of Kermode bear yielded interesting insights into the role of ecological segregation between colour morphs. Localities varied widely in both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  but it was possible to detect some trends of ecological segregation between the two colour morphs. Yet, using whole hair samples that derive a mean isotopic signature from a large (6 month) dietary window, I did not detect differences in the isotope signatures between colour morphs. However, Euclidean distances tended to be larger for black bears rather than white bears indicating that black morphs tended to have more variable overall diets than white morphs. Although diet variability was not found to be statistically different between colour morphs across all localities, the directions and magnitudes of the differences were consistent among the two largest sample sites; Gribbell Island and Princess Royal Island. This suggests that similar ecological processes occur within these localities, and are shaping the niche space of this bear population in a similar manner.

Strong evidence for ecological segregation between colour morphs exists in some localities, namely those on Gribbell Island, while on a neighbouring island (Princess Royal Island), this relationship is not as consistent. On Gribbell Island, both whole hair samples and all three hair segments indicated that white bears were significantly elevated in  $\delta^{15}\text{N}$  relative to black bears. Although the evidence for niche segregation between morphs is strongest in some localities, it is not isolated to those localities *per se*, as the strongest evidence for segregation comes from the analysis of standardized Z scores which compares isotopic signatures between morphs after removing the effects of locality and season.

When analysing standardized Z scores,  $d^{15}\text{N}$  values were significantly elevated in white morphs relative to black morphs among all localities and seasons. Since the analysis of Z scores removes the effects of locality and season, this is the strongest evidence for ecological segregation between colour morphs. However, it remains somewhat problematic to isolate exactly what differences in diet are reflected in the elevated signatures of  $d^{15}\text{N}$ , but consistent values of  $d^{13}\text{C}$ . Elevated signatures of  $d^{15}\text{N}$  with consistent values of  $d^{13}\text{C}$  typically indicate indirect assimilation of marine-derived nutrients rather than direct consumption of salmon tissue which is indicated by elevated signatures for both isotopes.

It is possible that this isotopic separation between colour morphs reflects differential foraging on certain plants or in segregated habitat use, such as differential use of riparian or intertidal habitats. Plant species can differ in  $d^{15}\text{N}$  signatures due to a variety of factors namely mycorrhizal associations, soil differences, rooting depth and site productivity (Nadelhoffer and Fry 1994, Schulze et al. 1994, Reimchen et al. 2002, Mathewson et al. 2003). Thus plants found in the riparian zone may differ isotopically from plants found elsewhere in the forest and these site differences may be reflected in the isotope values in hair if colour morphs partition habitat use along spatial scales within the forest environment. Thus habitat partitioning on spatial scales can influence a bear's exposure to specific plants and animals which may differ in isotopic values and are reflected in hair throughout the seasons.

Another possible source of enrichment may be due to feeding on inter-tidal organisms and estuarine grasses. Grasses tend to be slightly enriched in  $d^{13}\text{C}$  due to carbon fixation via a C4 pathway rather than a C3 pathway, and inter-tidal organisms are

enriched in  $d^{13}C$  due to marine influences, while the  $d^{15}N$  signatures of inter-tidal organisms and grasses would be relatively low reflecting their trophic position. Thus a spring and summer diet based predominantly on grasses and inter-tidal organisms would have relatively low  $d^{15}N$  but high  $d^{13}C$ . During the fall when bears shift their diets to incorporate salmon, the result is a large increase in  $d^{15}N$  but a relatively small increase in  $d^{13}C$  relative to  $d^{15}N$ . This creates a large  $d^{15}N$  flux from spring/summer to fall diets that will be easier to detect statistically than the smaller flux in  $d^{13}C$  from spring/summer to fall diets. Perhaps the statistically significant difference between colour morphs in  $d^{15}N$  but not  $d^{13}C$  is due to the different sized isotopic fluxes set in motion by inter-tidal feeding.

If it is true that white bears spend more time feeding on inter-tidal organisms in the spring and fall relative to black bears, then their white pelage may assist them in overcoming heat stress. Although it may seem unlikely that bears in the temperate regions of the Pacific North West suffer from heat stress, black pelage has been shown to absorb up to 90 percent of available solar radiation (Kelley et al. 1954). In fact when black bears are exposed to sunlight, radiant temperatures rapidly increase. For instance, radiant temperature readings of  $34^{\circ}C$  were recorded off the back of a black bear even though ambient temperature readings were only  $2^{\circ}C$ , and additional readings indicated a  $25^{\circ}C$  increase in radiant temperature relative to ambient temperatures when exposed to direct sunlight (Moen and Rogers 1985). These temperature effects do not seem trivial and the white morph would seem to have a thermoregulatory advantage and perhaps are better able to tolerate feeding in exposed areas such as inter-tidal estuaries and shorelines for extended periods of time.

There was a significant relationship between the magnitude of isotopic differentiation between black and white morphs and the frequency of the white coat allele. This is interesting as it indicates that white bears incorporate more MDN into their diets in areas with high frequencies of the allele giving rise to white coat colour.

This data set provides evidence for the possible existence of niche segregation between colour morphs suggesting a balanced polymorphism. Niche segregation may allow the frequency of white alleles to increase, and eventually flow to neighbouring localities. In fact, gene flow from Gribbell island to Princess Royal is speculated as the colonizing agent when the white mutation occurred (Ritland et al. 2001, Marshall and Ritland 2002).

#### *6.4.2 Historical assessment*

Isotope values from the white bears shot at the turn of the century provide potential insight into historical diets, and these values were surprising in that they indicated a predominantly vegetative diet. It is possible that these bears were shot in the spring or summer prior to the arrival of salmon in the streams. However, if the bears were shot prior to the commencement of moulting (moult begins in May) then hairs would reflect the previous year's diet, but if shot in the middle of the summer when moulting is well underway, hairs could reflect previous years diets and the spring and summer diets.

Diets of these historically sampled bears appear to be similar to the spring and summer diets of contemporary bears. It is possible that the preservation process and storage methods of these hides may have influenced the isotopic signature, but this is doubtful as authors have successfully used pelts in isotopic investigations of mammals killed decades ago (Hilderbrand et al. 1996, Jacoby et al. 1999)

This study illustrates the variable nature of bear diets over temporal and spatial scales. The importance of salmon is showcased in that the majority of coastal bears sampled consume appreciable quantities of this critical resource. This research also demonstrates the usefulness of stable isotope analysis as a tool in elucidating subtle niche partitioning between species or between colour morphs, which can be difficult to measure in strictly observational studies.

## **Chapter 7: Conspecific behavioural interactions among light levels in a polymorphic bear population**

### **7.1 Introduction**

Carnivores exist on a continuum of social systems ranging from gregarious species such as the African wild dog (*Lycaon pictus*), and the African lion (*Panthera leo*), to the solitary leopard (*Panthera pardus*) and wolverine (*Gulo gulo*). Investigations into the behavioural ecology of the most solitary species have been difficult, and excluding observations of captive animals, there are relatively few studies in the literature. However, individuals of solitary species are occasionally forced in communal coexistence, forming temporary aggregations during breeding periods and at kill sites or other localized food resources (Schaller 1967, Latour 1981a). These aggregations represent opportunities to study some of the social behaviour and interactions of otherwise solitary carnivores.

Bears are typically solitary but will form aggregations around food resources such as carrion and salmon streams and ecologically less interesting sites such as garbage dumps. There are also aggregations resulting from kinship and brief male-female associations that occur during the breeding season (Stonorov and Stokes 1972, Egbert and Stokes 1976).

Previous investigations of brown bear interactions on salmon streams have indicated that a dominance hierarchy is established and maintained by aggressive

interactions among individuals (Stonorov and Stokes 1972). However, black bears tended to either avoid visual contact with one another (Reimchen 1998b) or interact without direct physical contact (Frame 1974).

Ursids evolved from a canid lineage during the upper Pliocene (Herrero 1972), yet the social displays of these two groups have retained many common characteristics despite the numerous morphological, ecological and physiological differences between ursids and canids (Henry and Herrero 1974). For instance, it is known that agonistic signals in the form of visual cues are important in regulating social organization in both bears and wolves (Mech 1970, Stonorov and Stokes 1972, Egbert and Stokes 1976, Latour 1981a, Latour 1981b, Reimchen 1998b).

If visual cues are important in regulating social interactions then one might expect differences in the levels of agonistic interactions among light levels as it remains unclear how the social dynamics of bear aggregations are affected by the absence of visual cues (Reimchen 1998b). Direct comparisons of behaviour among light levels have been historically limited due to logistical constraints. With the development of light amplifying technologies, the importance of visual cues on the agonistic interactions among bears can be evaluated.

Color polymorphism occurs in many taxa (Rounds 1987, Colyn 1993, Franck et al. 2001, Johannesson and Ekendahl 2002, Galeotti et al. 2003) yet the origin and the basic mechanisms maintaining most polymorphisms are not well understood (Jones et al. 1977, Losey et al. 1997). Some hypotheses suggest that colour variations are selectively neutral traits with frequencies dependent on founder effects and random genetic drift (Futuyma 1998). Alternately, colour polymorphisms are maintained by a form of

heterozygote advantage (Futuyma 1998) or are functional traits maintained by frequency dependent selection (such as apostatic selection) or multiple-niche partitioning (Levene 1953, Levins and MacArthur 1966, Maynard Smith 1970, Paulson 1973, Smith 1990, Cook 1998). However, there is no relevant data on most species to test these competing hypotheses. Niche partitioning might be facilitated by agonistic interactions between colour morphs which may lead to differential access to food resources.

In this chapter I examine the dynamics of interactions in a polymorphic bear population within different light regimes in order to evaluate the importance of visual cues in shaping the social interactions of this carnivore. In addition, I relate the social interactions of this bear population to mechanisms maintaining the polymorphism in this bear population.

## 7.2

### **Methods and Materials**

During my observations of bear fishing behaviour, I observed (N=460) interactions during darkness, twilight and daylight. These interactions were recorded and quantified by myself but most (58%) were also video-taped. All interactions were coded as black-black (B-B), black-white (B-W) and white-white (W-W).

I classified interactions with respect to the nearest inter-bear distance. For non video-taped interactions, I estimated inter-bear distance using measured streamside landmarks. These measured streamside landmarks were also used for video-taped interactions and further accuracy was attained by measuring bear lengths on a viewing monitor.

I also classified interactions with respect to intensity. Low intensity interactions appear as though the bears ignored one another while medium and high intensity interactions are characterized by outcomes where dominance and subordination are established by one bear moving away from the other (Table 1.). I was also interested in the possible effects of coat colour on dominance. During medium and high intensity interactions of B-W dyads, I recorded which bear was dominant (did not move away).

I examined the effects of light levels, inter-bear distance and dyad colour composition on interaction intensity using Loglinear models. I used Z values to assess the relative contributions of cells to the interaction and considered values  $> 1.96$  to be significant at a  $< 0.05$  (Norusis 1988, Klinka and Reimchen 2002).

Table 4. Definitions of interaction intensities between bears on Gribbell Island during the falls of 2000-2002.

Interaction intensity	Description
Low	No visible reaction to presence or actions of a conspecifics
Medium	One or both bears walk away from the stream area due to the approach or presence of a conspecific
High	One bear either runs away (escape) or runs towards (charge) a conspecific

## 7.3

## Results

### 7.3.1 Interaction intensity

Overall, of the 460 interactions I observed, the majority tended to be of low intensity (58.5%), followed by medium intensity interactions (26.7%), while high intensity interactions were least common (14.8%; par  $\chi^2 = 142.0$ ,  $df=2$ ,  $P < 0.001$ ; Fig. 50). Direct contact and fighting was extremely rare, and only observed twice during the 3 field seasons.

### 7.3.2 Light level effects on interaction intensity

Among each of the light levels, low intensity interactions were most common, medium intensity interactions were less common, while high intensity interactions were least common (Light\*Intensity:  $\chi^2 = 1.6$ ,  $df = 4$ ,  $P = 0.81$ ; Fig. 51).

#### 7.3.2.1 Proximity effects on interaction intensity

Interaction intensities were also associated with proximity (Intensity \*Distance  $\chi^2 = 35.2$ ,  $df = 4$ ,  $P = 0.016$ ; Fig. 52.). As proximity increased to within 5m the frequency of high interaction intensities increased six fold, while the frequency of low intensity interactions was roughly halved (0-5m: 43.1%; 6-10m: 56.6%; 11-15m: 75.0%; 16m+: 76.0%). Relatively high incidences of low intensity interactions ( $Z = 1.96$ ,  $P = 0.05$ ) and rare incidences of high intensity interactions ( $Z = 2.56$ ,  $P = 0.010$ ) contributed to the loglinear model.

Distance effects on interaction intensities were relatively consistent among light levels (Light level\*Intensity \*Distance  $\chi^2 = 15.8$ ,  $df = 12$ ,  $P = 0.20$ ; Fig. 53.). As proximity increased, the frequencies of high intensity interactions approximately doubled, while the frequencies of low intensity interactions were roughly halved, and this occurred within all light levels.

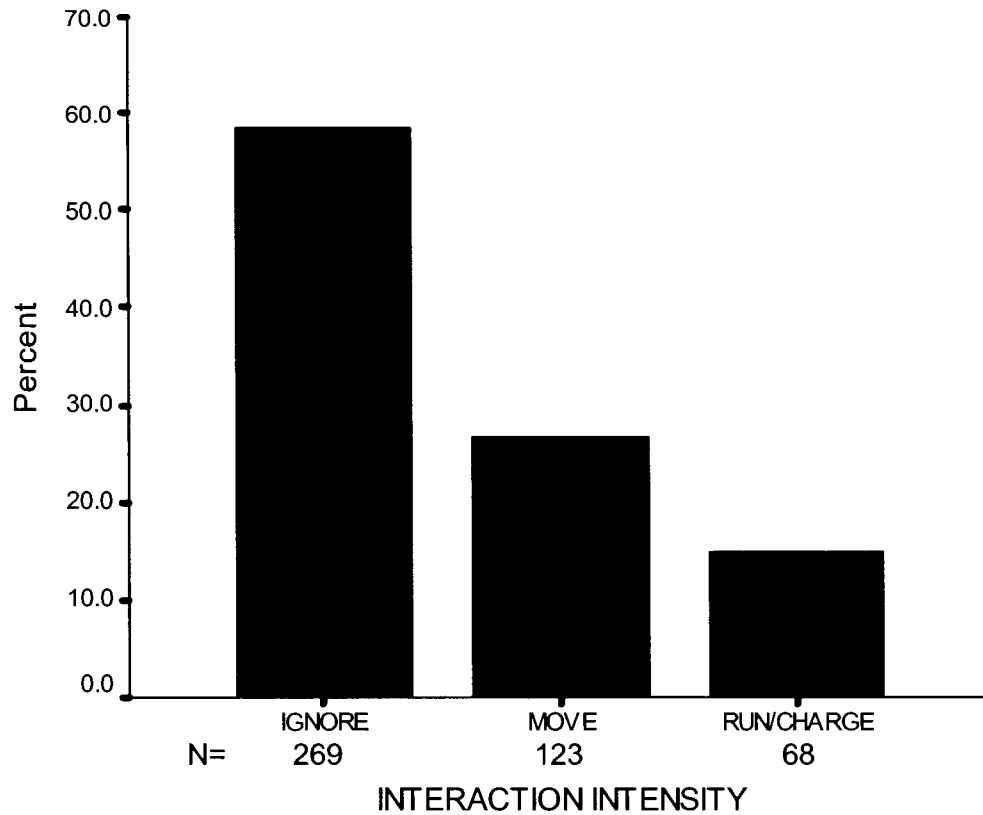


Figure 50. Overall proportions of interaction intensities between bears on Gribbell Island during the falls of 2000-2002.

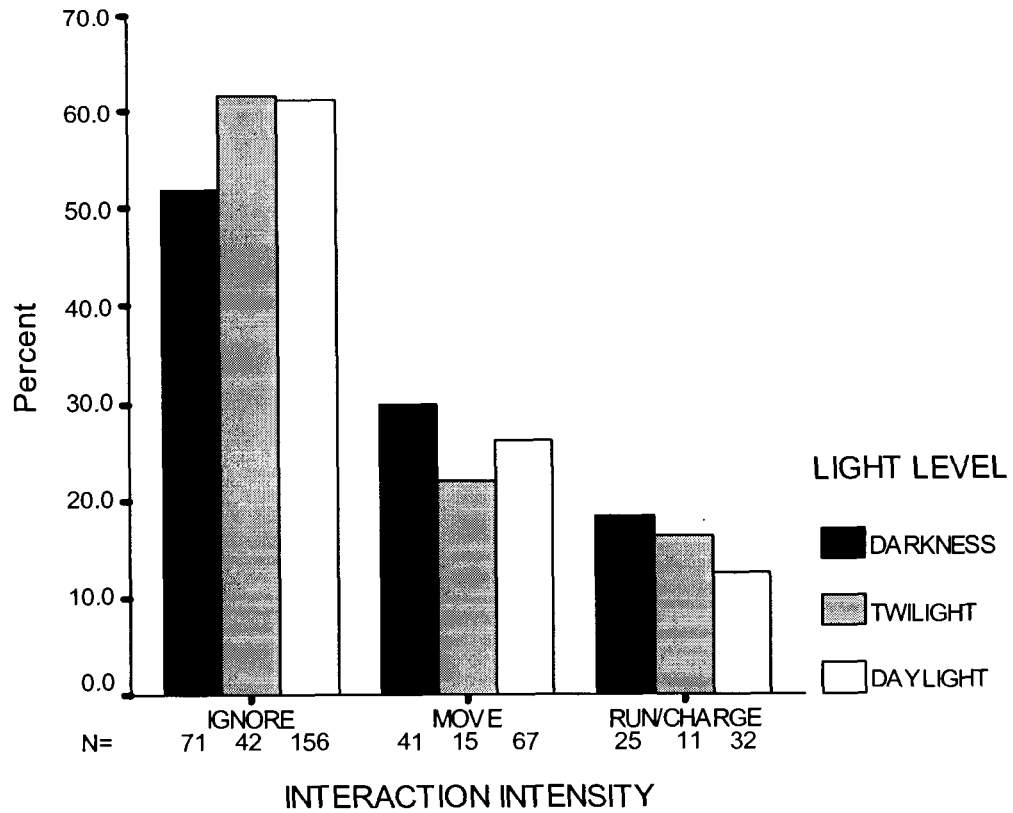


Figure 51. Overall proportions of interaction intensities between bears within darkness, twilight and daylight on Gribbell Island during the falls of 2000-2002.

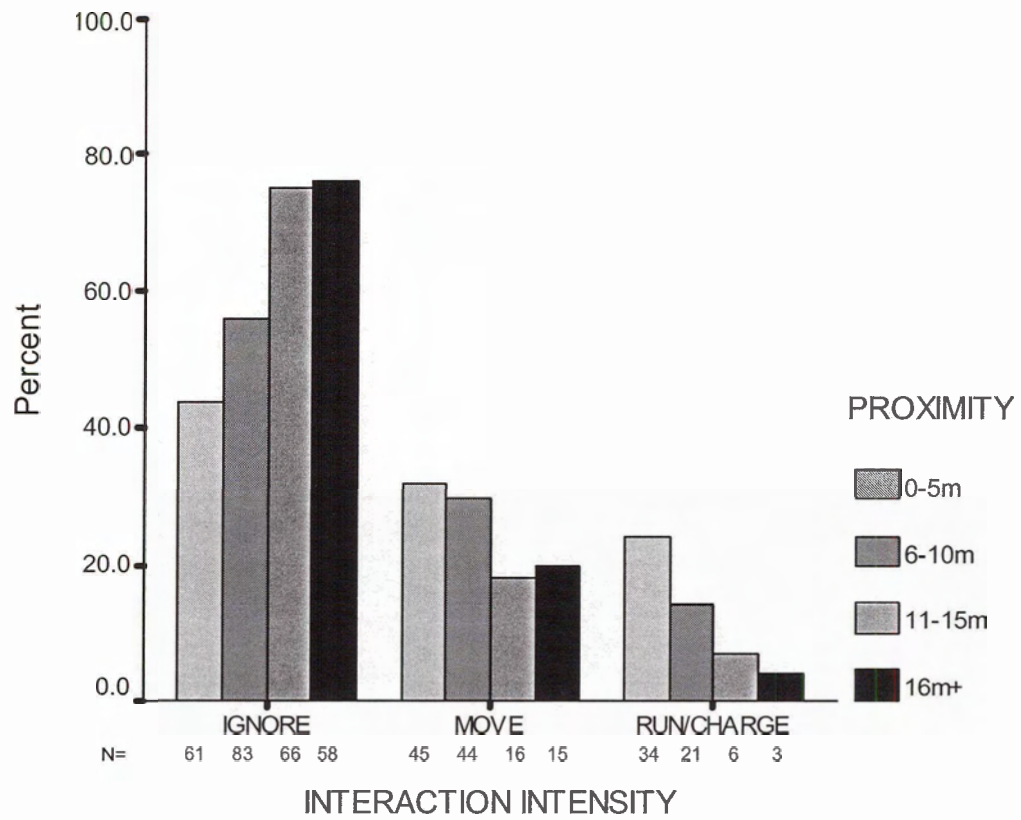


Figure 52. Overall proportions of interaction intensities between bears within 0-5m, 6-10m, 11-15m, 16m+ on Gribbell Island during the falls of 2000-2002.

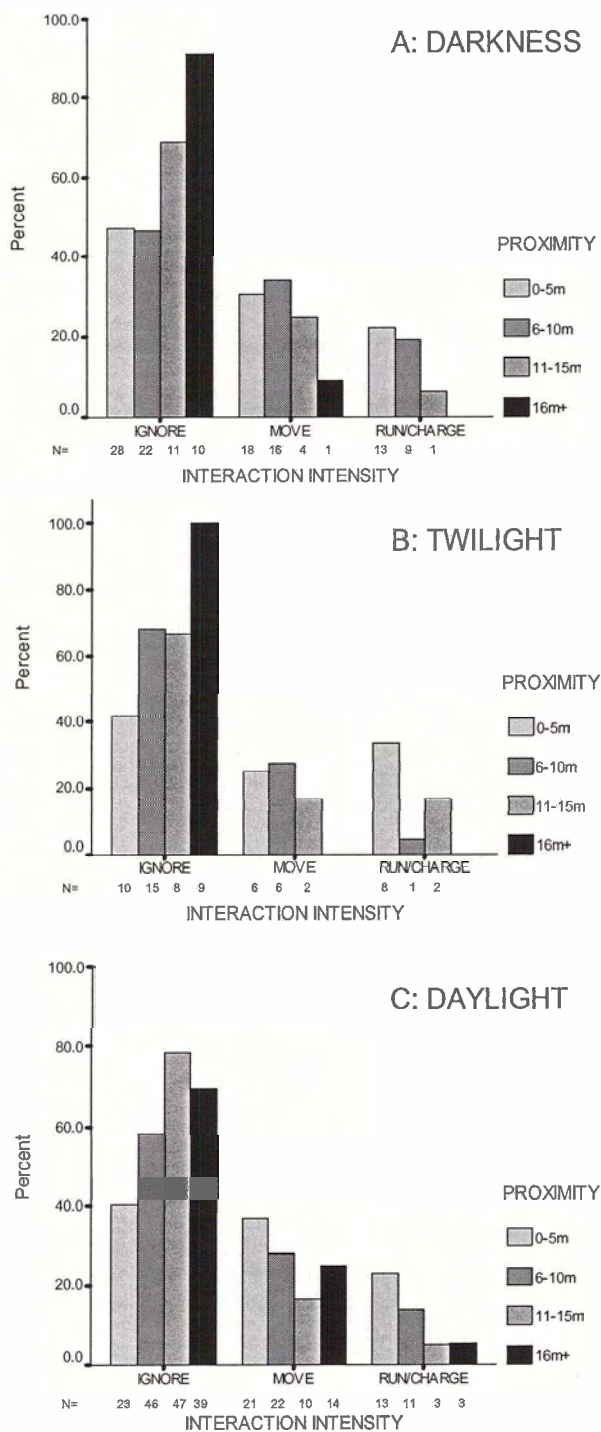


Figure 53. Proportions of interaction intensities between bears within 0-5m, 6-10m, 11-15m, 16m+ within A) Darkness, B) Twilight and C) Daylight on Gribbell Island during the falls of 2000-2002.

#### 7.3.4 Colour morph effects

Overall, the majority of interactions consisted of black-black dyads (B-B: 71.3%), followed by black-white dyads (B-W: 27.4%), and white-white dyads were rare (W-W: 1.3%), and this was associated with light level (Light level \*Dyad:  $\chi^2 = 8.3$ ,  $df=2$ ,  $P=0.016$ ; Fig. 54). Within all light levels, B-B dyads remained most common, followed by B-W and W-W dyads. Frequencies of B-B dyads decreased from darkness into daylight, while the frequency of B-W dyads increased during the same time periods. Although rare in all light levels, the frequency of W-W dyads also decreased from darkness into daylight.

Interactions within B-B and B-W dyads were of similar intensities (Intensity \*Dyad  $\chi^2 = 3.8$ ,  $df = 2$ ,  $P = 0.15$ ; Fig. 55). Low intensity interactions were most common for both B-B and B-W dyads, followed by medium intensities and high intensity interactions, and this was consistent among light levels (Light level\*Intensity \*Dyad  $\chi^2 = 6.4$ ,  $df = 4$ ,  $P = 0.17$ )

#### 7.3.5 Colour morph and dominance

Overall, within B-W dyads, black bears were more frequently observed to be dominant (other bear moved out of area) than white bears by winning 26/45 interactions, however this effect was not statistically significant (Colour  $\chi^2 = 0.82$ ,  $df = 1$ ,  $P = 0.37$ ).

Frequencies of dominance for black and white bears within B-W dyads were consistent among light levels (Light level\*Colour:  $\chi^2 = 4.08$ ,  $df = 2$ ,  $P = 0.13$ ; Fig. 56). However, black bears were frequently more dominant during darkness and twilight, but both morphs had identical frequencies of dominance during daylight.

Frequencies of dominance for black and white bears within B-W dyads were also similar between interaction intensities (Intensity\*Colour:  $\chi^2 = 1.37$ ,  $df = 2$ ,  $P = 0.50$ ; Fig. 57). However, black bears were more dominant in medium intensity interactions yet both morphs had identical frequencies of dominance during high intensity interactions.

Frequencies of dominance for black and white bears within B-W dyads were also similar between interaction intensities among light levels (Light level\*Intensity\*Colour:  $\chi^2 = 0.77$ ,  $df = 4$ ,  $P = 0.94$ ; Fig. 58). Although not statistically significant, black bears were more dominant in medium intensity interactions, and in all high intensity interactions during darkness, while during twilight they were more dominant in high intensity interactions and in all medium intensity interactions. However, during daylight, white bears tended to be dominant in high intensity interactions but not in medium intensity interactions.

Frequencies of dominance for black and white bears within B-W dyads were also associated with inter-bear distance (Distance\*Colour:  $\chi^2 = 7.98$ ,  $df = 2$ ,  $P = 0.047$ ; Fig. 59). White bears tended to be more dominant in close proximity (0-5m:  $Z=-0.73$ ,  $P=0.46$ ), while black bears tended to be more dominant at farther distances (6-10m:  $Z=-0.72$ ,  $P=0.47$ ; 11-15m:  $Z=-0.14$ ,  $P=0.89$ ; 16m+:  $Z=-0.16$ ,  $P=0.87$ ).

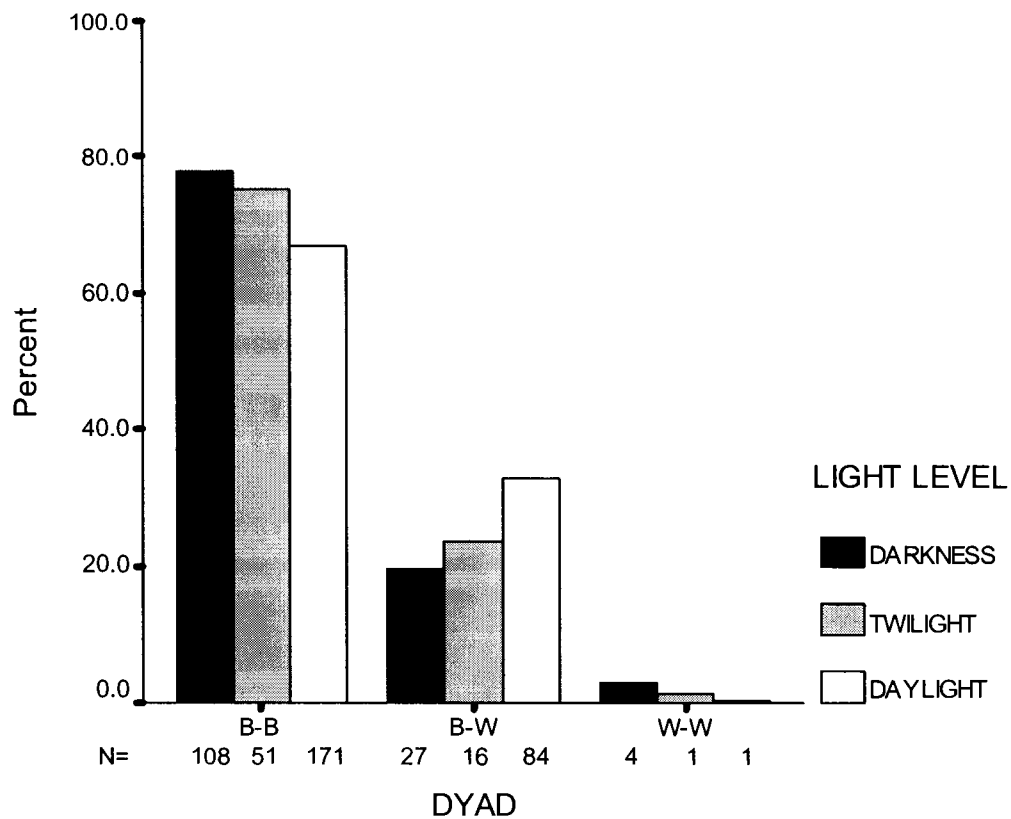


Figure 54. Proportions of interactions between black-black (B-B), black-white (B-W) and white-white (W-W) dyads within darkness, twilight and daylight on Gribbell Island during the falls of 2000-2002.

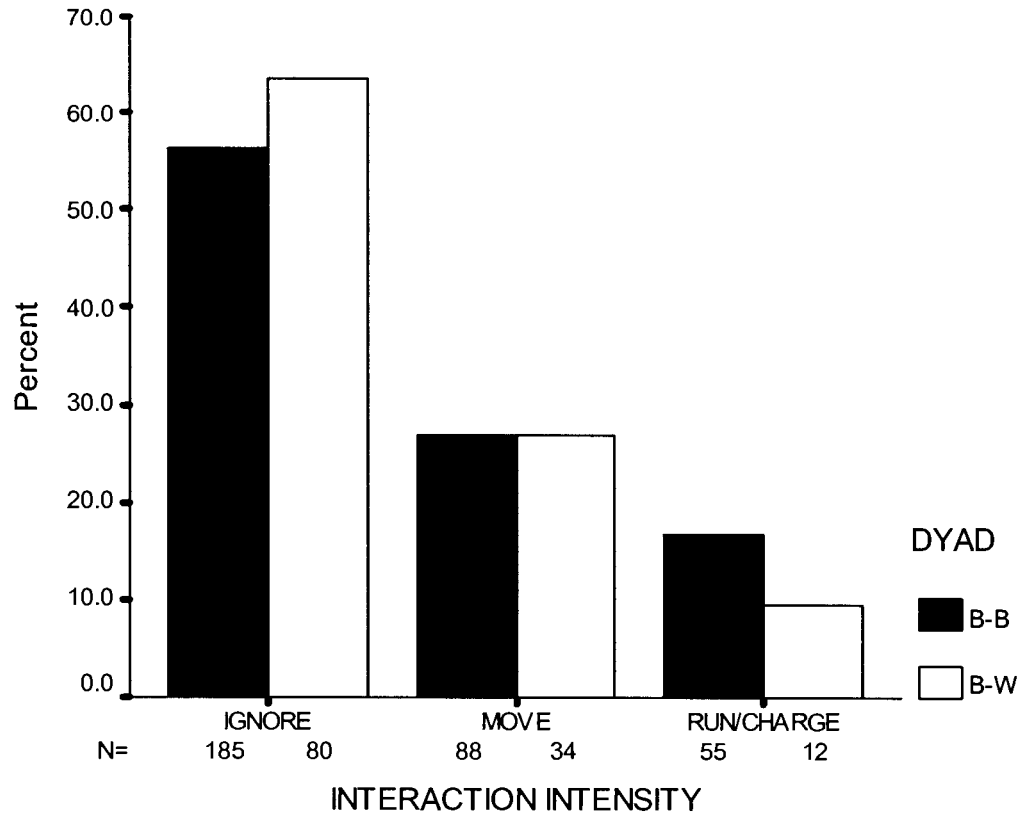


Figure 55. Proportions of interaction intensities between black-black (B-B) and black-white (B-W) dyads on Gribbell Island during the falls of 2000-2002.

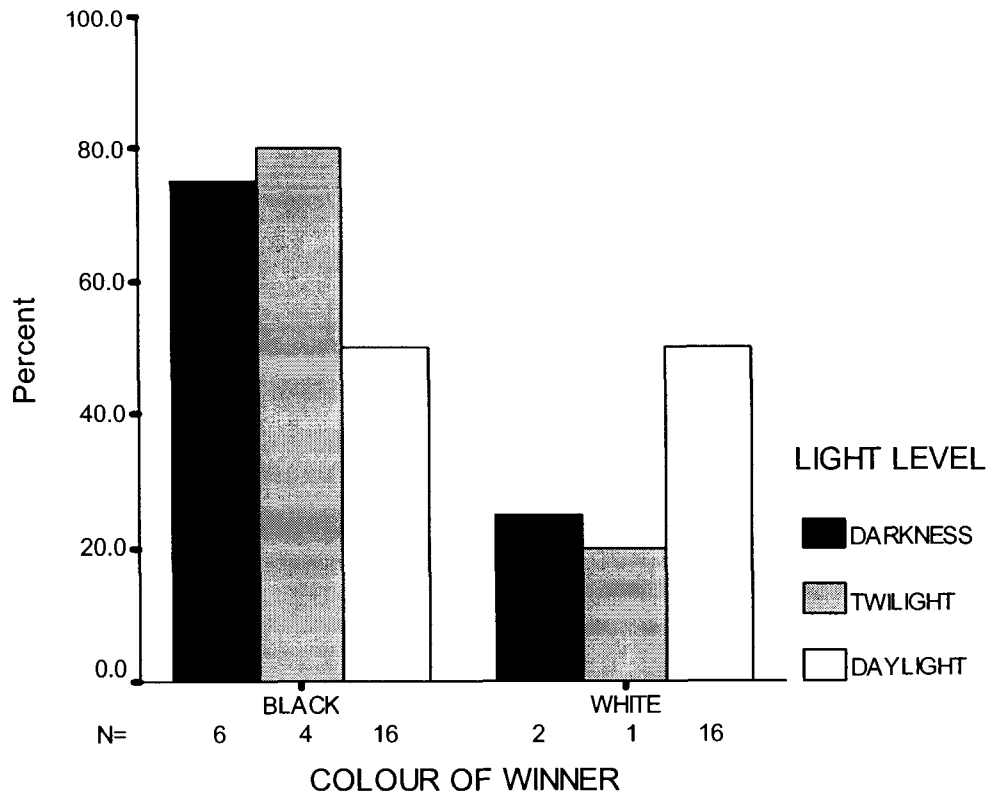


Figure 56. Light level effects on frequencies of dominance for black (B) and white (W) bears within black-white (B-W) dyads during darkness, twilight and daylight on Gribbell Island during the falls of 2000-2002. Displayed are medium and high level interaction intensities.

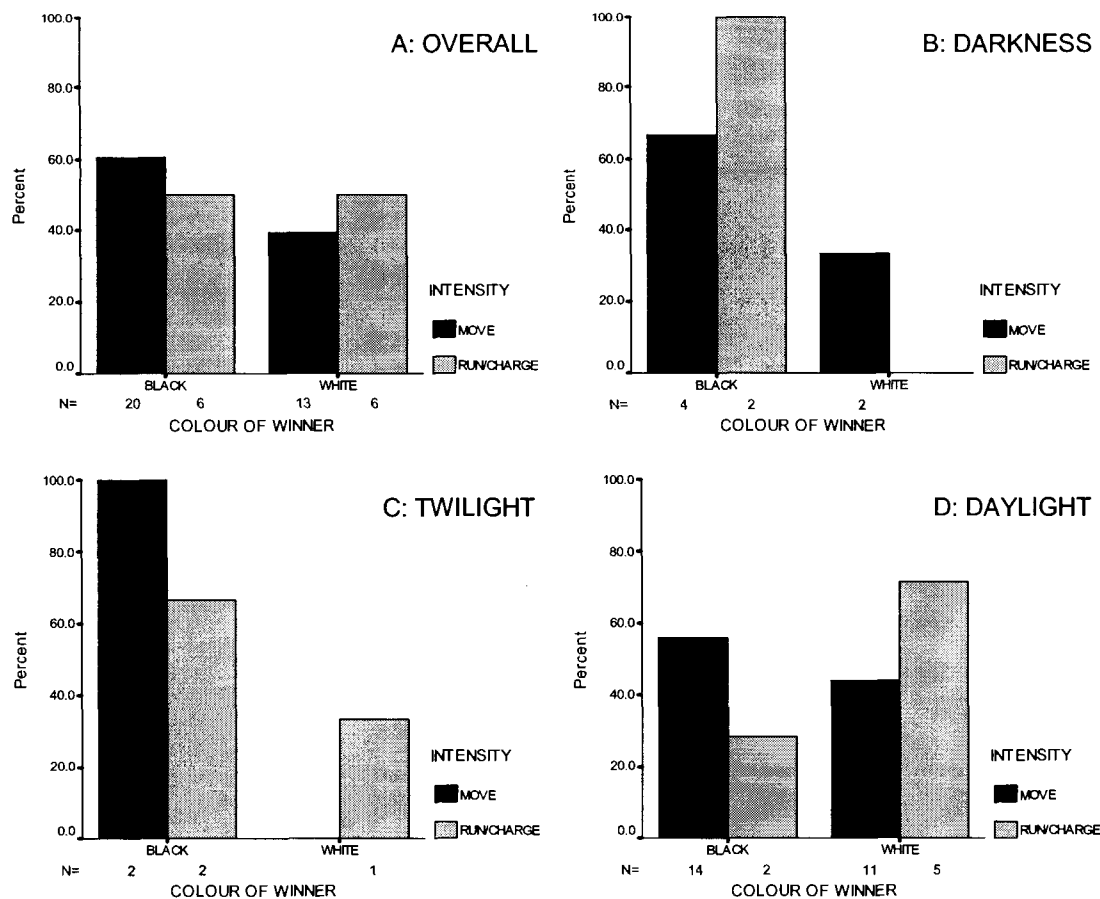


Figure 57. Light level and intensity effects on frequencies of dominance for black (B) and white (W) bears within black-white (B-W) dyads on Gribbell Island during the falls of 2000-2002. Displayed are medium and high level interaction intensities. **A)** Displays overall frequencies of dominance for both colour morphs within B-W dyads. **B)** Displays frequencies of dominance for both colour morphs within B-W dyads during darkness. **C)** Displays frequencies of dominance for both colour morphs within B-W dyads during twilight. **D)** Displays frequencies of dominance for both colour morphs within B-W dyads during daylight.

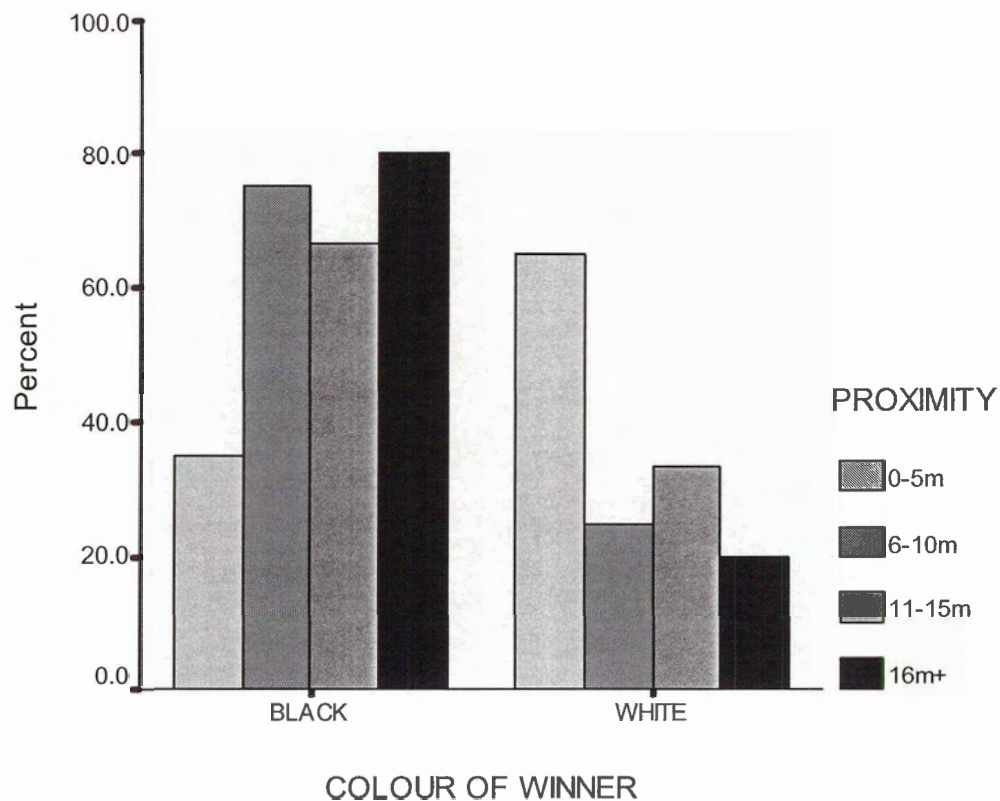


Figure 58. Proximity effects on dominance frequencies for black (B) and white (W) bears within black-white (B-W) dyads within 0-5m, 6-10m, 11-15m, 16m+ on Gribbell Island during the falls of 2000-2002. Displayed are medium and high level interaction intensities.

## 7.4

## Discussion

In the majority of interactions, bears ignored each other with no detectable response (low intensity), while charging and running (high intensity) were relatively rare. In apparent contrast, during his one year study of black bear-salmon dynamics, Frame (1974) reported observing 29 bear interactions where there was a “general tendency” for bears to approach to within several meters before one of the bears ran away. These interactions would be classified as high intensity during my study. However, he also observed interactions where bears would lay down to within 1m of each other with no apparent agonistic response, and such interactions would be classified as low intensity during my study.

### 7.4.1 Light level effects on interaction intensity

Low intensity interactions where bears ignored each other or showed no detectable response were the most common outcome of bear interactions in darkness, twilight and daylight. This was unexpected as it contrasts with Reimchen’s (1998b) observations of black bear behaviour on Haida Gwaii (formerly Queen Charlotte Islands) where he reported that the majority of bear interactions during daylight were of high intensity, with bears immediately running away from one another upon visual contact, while the same bears tolerated proximal conspecifics during darkness. Based on these observations, Reimchen interpreted that the availability of visual cues was an important factor governing bear interactions, supporting similar interpretations found elsewhere (Stonorov and Stokes 1972, Egbert and Stokes 1976, Latour 1981a, Latour 1981b).

Although the presence and quality of visual cues may indeed be important factors governing the dynamics of bear interactions, my data suggest that their presence alone does not predict interaction intensity. In lieu of Reimchen's (1998b) observations, one would have predicted many high intensity interactions (running) to occur during daylight and relatively few during darkness. Yet, in this study, I frequently observed bears within visual range of one another during daylight without displaying evasive behaviours. Furthermore, I was surprised to observe relatively few high level interactions within daylight.

There are many possible reasons why bears on Gribbell Island were so tolerant of one another. The two most commonly addressed motives for agonistic behaviour in bears are limited salmon resources and access to fishing sites (Stonorov and Stokes 1972, Egbert and Stokes 1976). Low levels of agonistic behaviour would be favoured in conditions where resources are not limited and readily available. On this stream, salmon numbers were relatively consistent throughout the spawning period and bears tend to continually move along the stream thereby making available numerous fishing localities on a continual basis. The consistent availability of salmon and fishing areas may have allowed bears to tolerate one another, whereas in Alaska, limited stream localities where successful fishing was possible led to frequent agonistic interactions among bears (Stonorov and Stokes 1972, Frame 1974, Egbert and Stokes 1976).

Another aspect that bears must evaluate is the body size of their opponent. Body size is most often identified as the best cue for gauging resource holding power, or the probability of victory in animal conflicts (Parker 1974). Although I was unable to rigorously evaluate precise sizes of bears in this study, most often they were evenly

matched. Evenly matched opponents make agonistic interactions risky for both participants, and if resources are readily available, the motivation to engage or challenge a similar sized conspecific may be low. However, in cases where there is a size discrepancy, such as between a sub-adult and an adult, or between males and females, the larger bear may seek to escalate the interaction at little risk in order to competitively exclude the conspecific from the area. Benefits incurred could be decreased salmon timidity towards the one bear relative to the higher levels of timidity expressed towards multiple bears. Salmon react unfavourably to multiple black bears and decreased salmon timidity translates to increased salmon vulnerability, and the opportunity for greater fishing success (See Chapter 4: Model Predator).

#### 7.4.2 Proximity effects on interaction intensity

Visual cues which convey information about inter-bear distance (proximity) were strongly associated with interaction intensity. Namely, intensities increased with proximity. This is consistent with Egbert and Stokes's (1976) observations of brown bears increasing the frequency of head-low threats with closer proximities.

The effect of increasing intensities with closer proximities was consistent among light levels. This was interesting in that even in the absence of visual cues (darkness), bears reacted to conspecifics in a similar manner to when they had access to visual cues (daylight). This was surprising as Reimchen (1998b) observed bears to be intolerant towards conspecifics at far distances (>20m but within visual contact) during daylight, then shift to being extremely tolerant of conspecifics (proximities within 5m) during darkness.

The strong effects of proximity during darkness could possibly be due to the increased sensitivity of alternate sensory modes during this time period. A bear that approaches a conspecific on the stream would walk along the bank or within the stream itself, thereby creating acoustic signals perceivable by other bears. Water currents moving past the legs of bears and rock movements would both create noise which differs from background stream noise and alert other bears to the arrival of a conspecific, in the same way that splashing noises made by spawning salmon alerts bears to their location aiding nocturnal foraging efficiency (see Chapter 4; Foraging). Bears could also growl at one another more often during darkness. However, although growling did occur, it was relatively rare during this study. Although stream noise limited my ability to hear interactions occurring more than 30m away, there were numerous instances where I observed interactions with a vantage well within my ability to hear acoustic signalling between individuals, and in the vast majority of these cases, interactions were silent.

Most close proximity encounters did not lead to high intensity interactions suggesting that prior experience with individuals in the bear population may be relevant in accounting for different levels of responses to proximity. Such experience has been found to be a significant factor in other species such as fish (Francis 1983, Beacham and Newman 1987). Over the course of the salmon run, bears may encounter the same bears more than once and subsequently develop an ability to discriminate between individuals based on olfactory cues. By identifying individuals, bears can assess the potential risks of an encounter and act accordingly in order to minimize those risks. However, the usefulness of olfactory systems will vary with proximity and environmental variables such as wind conditions.

### 7.4.3 Interaction intensity

Direct contact (fighting) was extremely rare, and only observed twice during the 3 field seasons. This was consistent with observations by Frame (1974) where he witnessed direct fighting only once. Lack of direct physical contact was predicted as animals possessing formidable weapons tend to avoid direct fighting and settle disputes with alternate methods (Parker 1974). However, not all ursids shy away from high intensity interactions including direct contact and fighting, as brown bears have been reported as having frequent high intensity agonistic interactions between rival males, and between females with cubs and solitary male and female bears (Stonorov and Stokes 1972, Egbert and Stokes 1976).

The elevated frequency of high intensity interactions observed in brown bear populations may be due to the interpretation that brown bears became inherently more 'aggressive' than black bears as a result of selection favouring aggressiveness during their expansion into more open habitats which lack opportunities to evade competitors (Herrero 1972, 1985). This contrasts with the evolutionary history of black bears as they did not expand their habitats into open areas, remaining in forested regions and retained the ability to climb trees to avoid potentially dangerous situations (Herrero 1972, 1985).

It should be noted that Egbert and Stokes (1976) report that the most common agonistic interaction between brown bear dyads consisted of simple avoidance of an *in situ* bear or the withdrawal of one animal at another's approach. Furthermore, Egbert and Stokes (1976) report that "the balance of bear encounters consisted of little more than glancing toward each other... and in some instances bears moved past each other at close range without either making an observable response". This type of interaction would be

classified as low intensity in my study, and is consistent with observations that the majority of bear interactions were of low intensity.

There are other factors which could possibly account for the different rates of agonistic interactions between black bears in this study. One such factor could be the demography of bears fishing on salmon streams. Within this population of black bears, no family groups of mother of cubs were observed and the majority of bears on the stream were large males. This contrasts with the brown bear studies where mothers with cubs were common and were the second most dominant class of bears, second only to the largest males (Stonorov and Stokes 1972, Egbert and Stokes 1976). The physiological demands of lactation may motivate females to seek additional nutrition from salmon tissues (Ben-David 1997), thereby placing them in more frequent contact with other bears.

Assuming that females with cubs are present on the island, then their absence on the stream could be due to them attempting to avoid potentially dangerous agonistic interactions with conspecifics (Egbert and Stokes 1976). The absence of family groups, combined with the high frequency of males observed on the stream during this study eliminates this potential niche overlap. Furthermore, black bear family groups were not seen during any of the three light regimes, suggesting that this avoidance is real and not a consequence of sampling effort (See Chapter 3: Behavioural Activity Patterns). However, assuming that the physiological demands of lactation would be similar for both black and brown bears, it is not clear why black bear family groups tend to avoid overlap with dominant males during all light levels while brown bear family groups do not.

#### 7.4.4 Colour morph and dominance

Colour morphs used similar behaviours during interactions, and this occurred among light levels and interaction intensities. Overall, I did not detect differences among intensities within mixed colour dyads (B-W) relative to all black dyads (B-B), and this was consistent among light levels. Furthermore, where I observed dominance/subordinate relationships between the two morphs, both black and white bears used similar behaviours (intensities), and this was also consistent among light levels. In fact, during interactions where white bears were dominant, half of the interactions were decided by walking away (medium intensity) and half were decided by running (high intensity). Similarly, when black bears were dominant, 60% of the interactions were decided by walking away and 40% were decided by running. This suggests that bears are not adjusting their behaviour towards opponents on the sole basis of coat colour.

There were strong proximity effects where dominance/subordinate relationships were observed between colour morphs. White bears were more dominant in close proximity interactions, while black morphs were more dominant at farther distances. Closer proximities might facilitate the use of olfactory systems to accurately determine the identity of potential opponents and bears may adjust their behaviour according to previous experiences with particular individuals. Furthermore, closer proximities would probably also facilitate visual size assessment of opponents.

Although the relationship was not statistically significant, it is interesting to note that black bears were more often dominant over white bears during darkness and twilight, while both colours were equally dominant during daylight. This effect did not reach statistical significance most probably due to low sample sizes during darkness and

twilight where only 8 and 5 medium and high intensities were observed, while 32 interactions were observed during daylight, but is suggestive of a light level effect.

Bears exhibit substantive behavioural plasticity during interactions along salmon streams. Although bears largely appear to ignore each other (i.e. low intensity interactions are favoured), high intensity interactions also occur. However, the benefits of fighting are minimal as salmon resources are consistently high during the salmon run yet risk of injury is also high. However, under some conditions, high intensity interactions (chasing) may be useful as it allows for access to favourable fishing sites. Visual cues are important in opponent evaluation and are presumably not useful during darkness. Since I could not accurately compare body sizes among bears, the direct effect of colour remain problematic, but the average effect was small as bears were closely matched in size. In the absence of visual cues, bears may form olfactory identities in order to adjust their behaviour towards recognized individuals.

## General Discussion

### 8.1 Light levels and Sensory modes

Animals react to environmental cues such as ambient light level on a daily basis through the use of available sensory modes. Specialization and reliance on particular sensory modes may occur when animals tend to favor certain light regimes. For instance, diurnally active animals tend to use vision as a primary sensory mode while nocturnal animals tend to utilize non-visual sensory systems (Beers and Culp 1990). However, many animals are also capable of shifting from one sensory mode to another to suit environmental conditions. Examples of this shift are found in many nocturnally active birds (Robert et al. 1989, McMahon and Evans 1992b), fish (Collins and Hinch 1993) and ants (Beugnon and Fourcassie 1988), that switch between diurnal sensory modes such as vision, to alternate modes such as tactile, auditory or chemo-sensory systems during darkness.

Ambient light levels often strongly influence circadian rhythms and activity patterns. For example, light levels can strongly influence when animals forage for food, as prey availability and vulnerability are known to change among light levels. In fact, the effects that changing light levels may have on the behaviour of a particular species may be strong enough to cause shifts in the behaviour of another species to which it has close ecological bonds. For instance, predators will often synchronize their behaviour with the activities of prey in order to increase foraging opportunities, even if it requires activity during periods in which their primary sensory modes are not ideally suited. In fact, some prey may attempt to evade predation by avoiding times when the sensory systems of their

predators are most closely matched with environmental conditions. Examples of this are seals pursuing nocturnally active fish and cephalopods (Harcourt et al. 1995, Thomas and Thorne 2001), fish preying on nocturnally active insects (Beers and Culp 1990), and birds taking advantage of seasonally available nocturnal fishes (Sjoberg 1989).

One of the important changes in salmon behaviour that occurs during the shift from daylight into darkness is the rate of spawning behaviour becomes greatly elevated (Fig. 27). During the day salmon tend to shelter under logs, but during darkness, they venture out into the stream channel and spawn in greater numbers. This may have originated as a consequence of female salmon trying to minimize agonistic interactions with other females among redd sites, or to minimize perceived predation risk (McNeil 1967). However, it sets in motion a series of behavioural consequences that cascade throughout this entire bear-salmon dynamic. One of the consequences of increased nocturnal spawning is that bears completely shift their diurnal diel activity patterns to coincide with the activity patterns of salmon. I observed bears to be completely diurnal before salmon began to enter the stream and commence spawning activities. In fact, stream visitation was rare both before the salmon run had begun, and after it had ended. It was only when salmon began to enter the stream and spawn that bears shifted their stream visitation patterns and adopted a nocturnal visitation regime. This nocturnal visitation pattern remained strong until the salmon run was exhausted. Such diel shifts in behaviour due to the activity patterns and availability of prey are consistent with those observed in birds (Robert et al. 1989, Sjoberg 1989, McMahon and Evans 1992b), fish (Beers and Culp 1990), and other mammals (Harcourt et al. 1995, Lariviere and Messier 1997, Thomas and Thorne 2001).

The nocturnal visitation pattern I observed in this population of bears was especially interesting as bears are typically diurnal but are known to shift activity patterns into darkness when exposed to brown bear activity or human disturbance. These shifts have previously been interpreted as a result of restriction into sub-optimal foraging time periods (Machutchon et al. 1997, Olson et al. 1998). If this was indeed the case, then one would predict that these bears would be primarily diurnal as there are no brown bears on this island and little human activity. My observations of the overwhelming shift of stream visitation patterns into darkness can not be due to restriction into sub optimal foraging time periods and is consistent with observations by Reimchen (1998b). Furthermore, this nocturnal shift also occurs in brown bears (Klinka and Reimchen 2002), and provides additional evidence that this process is not primarily driven by exclusion into sub-optimal time periods, but rather by behavioural shifts in the principal prey of coastal bears: salmon.

Another consequence of increased nocturnal spawning activity is the generation of multiple splash noises. These splashes provide bears with acoustic cues that can enable bears to capture salmon in complete darkness. Yet, is there direct evidence for the use of acoustic cues through a shift in technique use among light levels? Fishing technique used does change among light levels; frequencies of *Running* decrease while the frequencies of *Standing* techniques increase as light levels diminish. I interpret these results to suggest that bears shift from visually-oriented pursuit towards ambush strategies using alternate sensory modes to compensate for the lack of visual cues during darkness. Such shifts in sensory modes are observed in a variety of taxa, as many animals are capable of switching between a primary sensory mode utilized during daylight (vision) to alternate

sensory modes (tactile, auditory or chemo-sensory) during darkness (Beugnon and Fourcassie 1988, Robert et al. 1989, McMahon and Evans 1992b, Collins and Hinch 1993, Randall 1993, Downes and Shine 1998). These sensory shifts enable animals to exploit foraging opportunities and/or reductions in predation risk that are known to differ among light regimes.

Arguably, the most important change in salmon behaviour that occurs during the shift from daylight into darkness is the loss of timidity towards potential predators. My research has clearly demonstrated that salmon are heavily dependent upon their visual systems to detect predators and assess predation risk. During my experimental trials, salmon overwhelmingly reacted to visual cues with high rates of evasive response (high timidity); yet, evasive responses were almost completely absent during darkness (Fig. 17.). Upon losing the ability to visually detect predators, salmon become much more vulnerable to predation. Even during twilight, when visual cues are not altogether absent, bears may have a foraging advantage over salmon as they possess a *tapetum lucida* (Ronald and Lee 1981) while salmon do not (Nicol et al. 1973). The tapetum is a reflective cell layer attached to the retina and functions to reflect light back through the retina, effectively increasing scotopic (low light) sensitivity. As a consequence bears may be able to visually detect and target nearby salmon while the salmon would be oblivious to the associated risk.

Vision is not the only sensory mode available to salmon, as proximate vibrational disturbances are detected by the lateral line system of fishes (Satou et al. 1991, Montgomery and Milton 1993, Satou et al. 1994a). Yet, I was surprised to see such a drop in evasive response during darkness even though the lateral line sensory systems are

active during all light levels. Salmon appeared to be non-responsive to proximate sources of vibrational disturbance as they would often collide with my leg during trials, and not swim away. I speculate that in these instances, salmon mistook my leg for a piece of woody debris, but collisions with the forelegs of bears would not prove so benign. In fact, the higher frequencies of *Standing* fishing techniques I observed during darkness could have been attempts by bears in exploiting this lack of evasive response and frequent collisions with salmon.

As salmon begin to enter the stream, bears may be forced to compete for this critical resource which can lead to agonistic interactions between conspecifics as seen in numerous studies in Alaska (Stonorov and Stokes 1972, Frame 1974, Egbert and Stokes 1976). However, in the majority of these studies the consequences of light levels and its effect on the availability of visual cues was not addressed. To my knowledge, Reimchen (1998b) was the only author to observe complete behavioural shifts in the outcomes of interactions between bears among light levels. On Haida Gwaii (formerly Queen Charlotte Islands), the majority of bear interactions during daylight were of high intensity, with bears immediately running away from one another upon visual contact, while the same bears tolerated proximal conspecifics during darkness. Based on these observations, Reimchen interpreted that the availability of visual cues were an important factor governing bear interactions.

Based on the behaviour of bears on Haida Gwaii, I predicted that the intensity of bear interactions would fluctuate among light levels. However, in direct contrast to interactions on Haida Gwaii (Reimchen 1998b), I was surprised to observe that in the majority of interactions in my study, bears ignored each other, and this was consistent

among light levels. This contrast between study sites may suggest that bears are dramatically different between these two sites, visual cues have limited importance as predictors of interaction outcomes, differences in the physical characteristics between study sites can have increased importance, or other predictor variables (such as body size) have increased importance.

I have demonstrated a strong effect of proximity in bear interactions and this occurred among all light levels. This suggests that although the presence and quality of visual cues may indeed be important factors governing the dynamics of bear interactions (Reimchen 1998b), their presence alone does not predict interaction intensity. One possible reason why bears in my study were so tolerant of one another is that salmon resources and fishing localities were not spatially constrained, whereas in Alaska, limited stream localities where successful fishing was possible led to frequent agonistic interactions among bears (Stonorov and Stokes 1972, Frame 1974, Egbert and Stokes 1976).

Yet, most close proximity encounters did not lead to high intensity interactions suggesting that prior experience with individuals in the bear population may be relevant in accounting for different levels of responses to proximity. Over the course of the salmon run, bears may encounter the same bears more than once and subsequently develop an ability to discriminate among individuals with visual, olfactory and perhaps even auditory cues. By identifying individuals, bears can assess the potential risks of an encounter and act accordingly in order to minimize those risks. This is consistent with previous research suggesting the importance of individual recognition and prior assessment of contestants in predicting the outcomes of interactions in a variety of taxa

(Barnard and Burk 1979, Beecher 1989, Drews 1993, Morris et al. 1995, Karavanich and Atema 1998, Neat et al. 1998). However, the usefulness of visual cues to identify individuals will vary with light level and are presumably not useful during darkness, while the utility of olfactory cues will vary with proximity and environmental variables such as wind conditions. Vocalizations are known to be important components of agonistic interactions in deer (Clutton-Brock and Albon 1979) and could potentially be used by bears during darkness, but most of interactions I observed were silent.

Previous studies have interpreted the nocturnal behaviour of black bears to be the result of brown bear activity or human disturbance (Machutcheon et al. 1997, Olson et al. 1998), while others have interpreted that bears may prefer favour nocturnal time regimes because of decreased evasion by salmon and fewer agonistic interactions among conspecifics (Reimchen 1998b, Klinka and Reimchen 2002). However, no studies have investigated the role of salmon spawning patterns and their reliance on visual cues in shaping this association. The results I have presented here support the interpretation that nocturnal foraging by bears is favoured due to decreased evasive responses by salmon but not the role of agonistic interactions. Further efforts to resolve which sensory cues are utilized by bears during nocturnal foraging bouts will contribute to our understanding of how animals shift to alternate sensory modes, and the effectiveness of such shifts.

## 8.2 Polymorphism

Color polymorphism is the occurrence of two or more distinct and heritable phenotypic forms within a single population and occurs in many taxa including gastropods (Cain and Sheppard 1950, Ford 1964, Reimchen 1979, Ekendahl and Johannesson 1997), birds (Rohwer and Paulson 1987, Galeotti et al. 2003), fish (Franck et al. 2001), insects (Kapan 2001, Merilaita 2001), reptiles (Sinervo et al. 2001, Svensson et al. 2001) and mammals (Rounds 1987, Colyn 1993, Gipson et al. 2002, Eizirik et al. 2003). Although polymorphisms are seemingly ubiquitous in nature, the origin and the basic mechanisms maintaining most polymorphisms are not well understood (Jones et al. 1977, Losey et al. 1997). Some hypotheses suggest that colour variations are selectively neutral traits with frequencies dependent on founder effects and random genetic drift (Futuyma 1998). Alternately, colour polymorphisms are maintained by a form of heterozygote advantage (Futuyma 1998), or are functional traits maintained by frequency dependent selection (such as apostatic selection) or multiple-niche partitioning (Levene 1953, Levins and MacArthur 1966, Maynard Smith 1970, Paulson 1973, Smith 1990, Cook 1998). The highly variable colouration patterns and numerous colour polymorphisms observed in carnivores and avian predators may be in part maintained by various forms of resource and niche partitioning (Recher and Recher 1972, Mock 1980, Rohwer 1990, Itoh 1991).

One potentially important form of niche partitioning between colour morphs of this bear population would be differential utilization of important food resources, most notably pacific salmon. It is known that salmon are a critical resource to coastal bear populations (Hilderbrand et al. 1999b, Gende et al. 2001) and greater utilization of this

resource by one morph over the other could translate into higher fitness for that morph. It was in this context that I explored niche segregation between black and white bears with a focus on bear-salmon interactions using a variety of strategies; assessing salmon behaviour, bear activity patterns, foraging performance and social interactions and by reconstructing bear diets using stable isotope analysis. My data suggest a tight correlation between the behaviour of bears and the behavioural attributes of salmon. What is less clear is whether bear colouration affects salmon behaviour, and/or whether morphs react to salmon behaviour in a comparable manner.

My results clearly demonstrate that salmon rely on visual cues to assess predation risk, and it seems logical that with such a strong reliance on visual systems, salmon can discriminate between two different predator morphs. If it is true that salmon can discriminate between colour morphs, does it translate into differences in reaction characteristics towards particular colour morphs? I present strong evidence that this is indeed the case, as salmon are much more timid towards black morph than white morphs (Fig. 31). A differential response by salmon towards the two colour morphs may affect the availability and susceptibility of salmon resources to particular morphs, leading to important consequences in the utilization of this resource.

One possible explanation for this effect is that white morphs tend to appear more camouflaged during daylight as white contrasts less with a bright sky background than black. This explanation has been interpreted for reef herons and foraging seabirds (Murton 1971, Mock 1980, Gotmark et al. 1986, Gotmark 1987). However, this effect of background matching for the white morph should only occur during daylight, as the opposite effect seems more likely during darkness as black would contrast less with a

black sky. While my data support the prediction that this effect background matching for the white morph occurs during daylight, there is no evidence to suggest that salmon react differently towards the two morphs during darkness. On the contrary, salmon appear to react to both morphs in a similar manner during darkness, supporting the interpretation that salmon rely on visual cues to assess predation risk, and when these cues are absent, evasive responses by salmon are minimal or non-existent. This interpretation is supported by direct observations of foraging behaviour of black bears whereby some individuals would stand motionless underneath the underside of a log while visually searching for salmon, and quickly pounce on fish as they approached to within striking distance. I called this technique “shadow fishing” and I believe that the bear is using the log as camouflage to minimize its own contrast with the bright sky. The fact that I never observed white bears fishing in this manner and that I only observed black bears using this technique during daylight further supports this interpretation.

An alternate explanation for the differential response of salmon to black and white morphs is that some form of apostatic selection (frequency dependence) is occurring. In apostatic selection, the rare morph would have a selective advantage by the very virtue of its rarity. Apostatic selection would be facilitated by the rapid turn-over of prey population, in which there are many young and naïve individuals among the prey each year (Paulson 1973). This is indeed the case in salmon, where spawning occurs only once in their lifetime, and adults do not pass learned experiences onto young before they die. As the white morph is relatively rare in the population, naïve salmon may not interpret it as a predator and tend to approach more closely. Although this interpretation has been applied to accounting for the persistence of colour morphs of hawks, such an application

of apostatic selection has been difficult to demonstrate in nature. Furthermore, I don't believe that this form of apostatic selection is occurring in this system as one of its assumptions is that the two morphs are equally conspicuous (Rohwer and Paulson 1987), and I have presented clear evidence that they are not.

It was surprising to find such strong differences in salmon reactions, but no differences in stream visitation patterns between morphs (Figures 6 and 7). I would have predicted that white morphs would favour activity during time periods when their camouflage advantage is greatest (daylight), but this was clearly not the case. A possible explanation could be that the overwhelming lack of evasive responses observed in salmon during darkness overshadows the differential response towards the two morphs.

Furthermore, it was surprising to find that although I detected significant fishing technique differences between morphs during daylight and twilight (Fig. 21), the direction of some of the differences between morphs was opposite to what I would have predicted; white bears used *Standing* less often during daylight relative to black bears. If salmon are less timid towards white bears during daylight, it is puzzling why white bears are not exploiting this behavioural characteristic and *Standing* more during time periods when their camouflage advantage is greatest. However, the differences in actual frequencies of technique use between the two morphs were very similar ( $\bar{X}_{\text{Black}} = 46\%$  vs.  $\bar{X}_{\text{White}} = 44\%$ ) and it is difficult to identify ecological and behavioural ramifications for such closely matched frequencies. Yet, other aspects of foraging performance are consistent with what one would expect given the behavioural characteristics of salmon among light levels.

My data indicate that white bears are more efficient at capturing salmon during daylight and twilight but not during darkness (Fig. 24), suggesting that white bears are able to exploit the decreased timidity expressed by salmon towards them during time periods when visual cues are available. A differential in capture efficiency between morphs among light levels suggests that colour polymorphism may be a functional adaptation to foraging on salmon. However, this interpretation is tempered somewhat by my inability to detect differences between the morphs in other foraging attributes, such as capture rate.

The allocation of time to feeding behaviours and movement among fishing sites were similar between morphs among light levels and social interactions between morphs indicated no substantial colour effects although some differences were evident. For instance, white morphs tended to win more interactions at close distances, but black bears tended to win more interactions as proximities increased. Visual cues are important in opponent evaluation and are presumably not useful during darkness, and since I could not accurately compare body sizes among bears, the direct effect of colour remains problematic, but the average effect was small as bears were closely matched in size. In the absence of visual cues, bears may form olfactory identities in order to adjust their behaviour towards recognized individuals but shifts in behaviour towards conspecifics are probably not based solely on pelage colour.

My analysis of the stable isotopes carbon and nitrogen shed light on coastal bear dietary life history as well as provide evidence for niche segregation among colour morphs. Overall stable isotope values were highly variable among bears indicating a broad niche breadth. This is consistent with other studies of bear diets derived from

isotopic analysis (Hilderbrand et al. 1996, Hilderbrand et al. 1999b, Jacoby et al. 1999, Hobson et al. 2000). Yet, even with this high variability, black bears tended to have more variable overall diets than white bears among localities. This was interesting as these bears represented individuals across a broad range of landscapes across the mid-coast of BC. In effect the sampling protocol was a series of individual paired (black versus white) experiments replicated among localities.

Upon expanding the analysis to examine hair segments, it became clear that isotopic analysis of segments indicated seasonal dietary shifts between the two colour morphs among localities and seasons, and provide more detailed evidence for niche segregation among colour morphs. The magnitude and detectability of these dietary shifts highlight the utility of analysing tissue segments in reconstructing diets over finer time scales. Other authors have previously analysed tissue segments to reconstruct the diets of pinnipeds (Hobson and Sease 1998), bovids (Wiedemann et al. 1999), fulmars (Thompson and Furness 1995); in addition to elucidate seasonal shifts in the location of feeding grounds of Bowhead whales (Schell et al. 1989), and to assess the importance of salmon in the diets of wolves (Darimont and Reimchen 2002). This technique has also been applied to the reconstruction of historic salmon abundance, and assess nutrient cycling in the Pacific Northwest through analysis of tree cores from ancient stream-side residents (Reimchen et al. 2002).

There was significant positive relationship between the magnitude of isotopic differentiation between black and white morphs and the frequency of the white coat allele. This is interesting as it indicates that white bears incorporate more MDN into their diets in areas with high frequencies of the allele giving rise to white coat colour.

Although this data set does not provide direct evidence for changes in allelic frequency indicating directional selection favouring the white morph, it does suggest the possibility of niche segregation. Niche segregation may allow the frequency of white alleles to increase, and eventually flow to neighbouring localities. In fact, gene flow from Gribbell island to Princess Royal is speculated as the colonizing agent when the white mutation occurred (Ritland et al. 2001, Marshall and Ritland 2002).

The analysis of stable isotopes found in the tissues of plants and animals is an extremely useful tool that ecologists can use to reconstruct former diets of organisms and elucidate the degree of ecological connectivity among species. Furthermore, stable isotope analysis of tissue, like hair or feathers, holds great promise for studies of niche differentiation in a variety of taxa which exhibit polymorphism.

Variability in pelage colouration is extremely common in mammalian carnivores and birds of prey; with canids, felids and buteos all exhibiting colour polymorphism. This study suggests a working hypothesis for understanding the mechanisms maintaining colour variability within species.

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# Nocturnal and diurnal foraging behaviour of brown bears (*Ursus arctos*) on a salmon stream in coastal British Columbia

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**Abstract:** Brown bears (*Ursus arctos*) have been reported to be primarily diurnal throughout their range in North America. Recent studies of black bears during salmon migration indicate high levels of nocturnal foraging with high capture efficiencies during darkness. We investigated the extent of nocturnal foraging by brown bears during a salmon spawning migration at Knight Inlet in coastal British Columbia, using night-vision goggles. Adult brown bears were observed foraging equally during daylight and darkness, while adult females with cubs, as well as subadults, were most prevalent during daylight and twilight but uncommon during darkness. We observed a marginal trend of increased capture efficiency with reduced light levels (day, 20%; night, 36%) that was probably due to the reduced evasive behaviour of the salmon. Capture rates averaged 3.9 fish/h and differed among photic regimes (daylight, 2.1 fish/h; twilight, 4.3 fish/h; darkness, 8.3 fish/h). These results indicate that brown bears are highly successful during nocturnal foraging and exploit this period during spawning migration to maximize their consumption rates of an ephemeral resource.

**Résumé :** Les ours bruns (*Ursus arctos*) sont généralement reconnus comme des animaux à alimentation surtout diurne dans toute leur aire de répartition. Les résultats d'études récentes sur les ours noirs durant la migration des saumons indiquent qu'ils font une quête de nourriture intense pendant la nuit et que l'efficacité de leurs captures est élevée à l'obscurité. Nous avons étudié l'importance de la quête nocturne de nourriture chez des ours bruns au moyen de jumelles de nuit au cours d'une migration de fraye de saumons, à Knight Inlet, sur la côte de la Colombie-Britannique. Les adultes recherchent leur nourriture aussi bien la nuit que le jour, mais les femelles avec un petit et les individus subadultes se nourrissent surtout durant le jour et au crépuscule, mais rarement durant la nuit. Nous avons observé une tendance marginale vers une efficacité accrue des captures en fonction inverse de l'intensité lumineuse (jour, 20 %; nuit, 36 %), probablement à cause de la diminution du comportement évasif des saumons. Les taux de capture moyens étaient de 3,9 poissons/h et ils variaient selon le régime photique (jour, 2,1 poissons/h; crépuscule, 4,3 poissons/h; nuit, 8,3 poissons/h). Ces résultats indiquent que les ours bruns font une quête active nocturne très profitable et ils exploitent cette période durant la migration de fraye des saumons de façon à maximiser leur taux de consommation d'une ressource éphémère.

[Traduit par la Rédaction]

## Introduction

Mammalian carnivores such as the canids, ursids, and felids exhibit multiple temporal foraging niches comprising diurnal, crepuscular, and nocturnal periods. During daylight, vision is often relied upon for search and pursuit, while during darkness, nonvisual sensory systems typically have increased importance. Nocturnal foraging can be favoured, owing to increased prey susceptibility and availability (McMahon and Evans 1992; Thibault and McNeil 1995; Reimchen 1998a) and reduced predation risk and competition (Culp et al. 1991). Theoretically, the search for and pursuit of prey during darkness require reliance on different sensory modes and produce different costs and benefits than during daylight. However,

there have been few direct nocturnal observations of foraging behaviour, and the ability of researchers to evaluate sensory modes and capture efficiencies remains limited. In one of the few investigations of nocturnal foraging by a large carnivore, both Schaller (1972) and Stander (1992) observed that African lions were successful in the pursuit and capture of ungulates during darkness, although the sensory modes used by the lions were not determined.

Black bears (*Ursus americanus*) are reported to be primarily diurnal throughout North America (Lariviere et al. 1994; Machutchon et al. 1997; Maehr 1997). However, with the aid of light-amplifying goggles, Reimchen (1994, 1998a) observed that black bears captured the majority of salmon during nocturnal foraging bouts and suggested that nighttime is preferred for foraging because of increased access to high quality feeding areas, reduced evasion by salmon, and high capture rates. Night-fishing black bears appeared to use a combination of tactile, auditory, and visual stimuli to capture salmon.

Brown bears (*Ursus arctos*) also exhibit extensive temporal variability in activity patterns. While they are well known to be diurnally active (Stonorov and Stokes 1972; Luque and Stokes 1976; Craighead et al. 1995; Gilbert and Lanner 1995;

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Gende et al. 2001), crepuscular and nocturnal activity have also been reported (Gard 1971; Roth 1983; Herrero 1985; Phillips 1987; Clevenger et al. 1990; Genov and Wanev 1992). However, relatively little is known about the extent of nocturnal foraging or the behavioural techniques they employ in the search and pursuit of prey.

In this paper we examine diurnal and nocturnal foraging behaviour by coastal brown bears on a salmon stream in British Columbia. We predicted that brown bears would exhibit behaviour comparable with that of black bears on salmon streams, including foraging during the night. Our results, which are consistent with this prediction, suggest that brown bears are capable of substantive behavioural plasticity and that they use multiple sensory modes for nocturnal foraging.

## Methods

For 10 days during September 1999, we observed up to 11 brown bears simultaneously fishing along the Glendale River near Knight Inlet, B.C. (50°40'N, 125°44'W). From late August to late October, 550 000 pink salmon (*Oncorhynchus gorbuscha*) returned to the river to spawn, aggregating at the base of a weir at which bears gathered to forage. These salmon numbers were within the range observed during the previous 10 years on this river (17 500 – 550 000). The weir is located at the entrance of an artificial spawning channel. Human presence in the viewing area consisted of various ecotourism groups, which were present for 2-h observation periods three times a day, and research biologists present both during and between tours. All observations were made from towers erected 10 and 50 m from the weir. Total observation time was 76.5 h within three designated light regimes: darkness, civil twilight, and daylight. We staggered our sessions to ensure similar observation times during all photic regimes. All nocturnal observations were through a handheld night-vision monocular (ITT model CSC-N16140-DX, 50 000× amplification, 0.95 cycles/millirad resolution), aided by an infrared emitter (880 nm) in extremely low light conditions. Daylight observations were recorded manually, whereas nocturnal observations were recorded on tape and later transcribed.

We recorded fishing behaviour for all bears during the study period, including multiple observations per bear. Bears were classified as adult, subadult, or cub; when possible, gender was determined. Discrimination between adults and subadults was based on the overall size of the bear, with larger bears (estimated mass >250 kg) being classified as adults and smaller bears (estimated mass <250 kg) being classified as subadults. Gender was determined by urinary posture, visual assessment of genital region, and the presence of cubs. We classified fishing technique as (i) standing, (ii) plunging, or (iii) running (Luque and Stokes 1976). We defined capture efficiency as the probability of a successful capture (number of successes per number of attempts). We defined capture rate as the number of fish captured per hour (number of successful captures per length of time foraging in hours). We defined fishing-bout duration as the time (in minutes) an individual bear spent actively fishing on the stream. Partial bouts consisted of observations where we did not observe either the initiation or termination of fishing. These observations were not used in subsequent analyses.

For analyses of foraging rates, we initially partitioned the data into two sets, the first consisting of all the bears that were individually recognizable and the second of all the bears that were not. Because capture rates were not substantially different between known and unknown bears ( $P > 0.7$ ), we pooled data for the two types. We also examined differences in foraging efficiencies among different bears. Bears that were not individually identifiable during both daylight and darkness were excluded from these analyses. To test for differences between fishing technique and capture efficiency among light levels, we used log-linear models. We also used log-linear models to test for interactions among technique (standing, plunging, running), light level (darkness, twilight, daylight), and fishing success (fail, success). We used  $Z$  values to assess the relative contributions of cells to the interaction, and considered values  $>1.96$  to be significant at  $\alpha < 0.05$  (Norusis 1988). Distributions of data were tested for normality with the Kolmogorov–Smirnov test. The data tended to be non-normal and, as such, we used Kruskal–Wallis tests to analyze the number of bears seen simultaneously over 24 h and the relationships between foraging-bout duration, number of salmon captured, and salmon-capture rates.

## Results

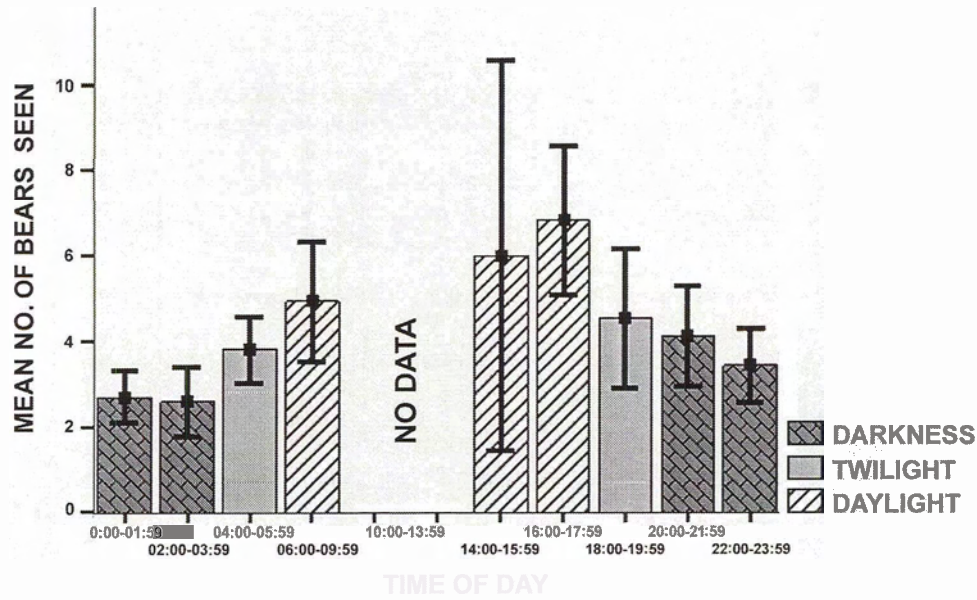
Brown bears were observed foraging in all light regimes, with peak bear numbers occurring in the late afternoon (before 18:00; Fig. 1). Absolute numbers of solitary adults did not differ substantially among light regimes ( $\chi^2 = 0.10$ ,  $df = 2$ ,  $P = 0.95$ ) or time periods ( $\chi^2 = 22.5$ ,  $df = 23$ ,  $P = 0.49$ ). Subadults and females with cubs were more numerous during high light levels, in contrast with solitary adults ( $\chi^2 = 54.8$ ,  $df = 2$ ,  $P < 0.001$ ). Mean fishing-bout duration was approximately 65 min and did not differ substantially among light levels ( $\chi^2 = 1.25$ ,  $df = 2$ ,  $P = 0.535$ ; Fig. 2).

Bears used different fishing techniques upon entering the stream. Of the 706 attempts observed, the most common technique used was standing (58%), followed by running (25%), and then plunging (18%). Standing was most common in darkness and least common during daylight, whereas plunging and running were least common during darkness and most common during daylight. The incidences of standing and running were not substantially different during daylight (light  $\times$  technique,  $\chi^2 = 67.16$ ,  $df = 4$ ,  $P < 0.001$ ; Fig. 3).

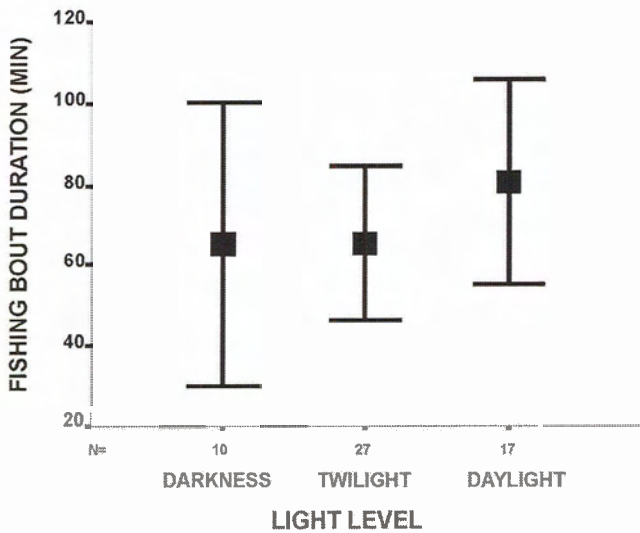
The overall capture efficiency of salmon was 27% ( $N = 706$ ), but this varied among light levels (light  $\times$  success,  $\chi^2 = 10.59$ ,  $df = 2$ ,  $P < 0.006$ ). The highest efficiency occurred during darkness (36%), lower efficiencies occurred during twilight (27%), and the lowest efficiencies occurred during daylight (20%). Relatively low capture efficiency during daylight contributed the greatest effect to the log-linear model ( $Z = -2.23$ ,  $P < 0.05$ ).

There were also interactions between capture efficiency and fishing technique (technique  $\times$  success,  $\chi^2 = 29.35$ ,  $df = 2$ ,  $P < 0.001$ ). Standing ( $Z = 4.38$ ,  $P < 0.05$ ) and running ( $Z = -3.33$ ,  $P < 0.05$ ) contributed most to the log-linear model because of their comparatively high and low capture efficiencies, respectively. Standing was the most efficient technique (43%), while running was the least efficient (26%).

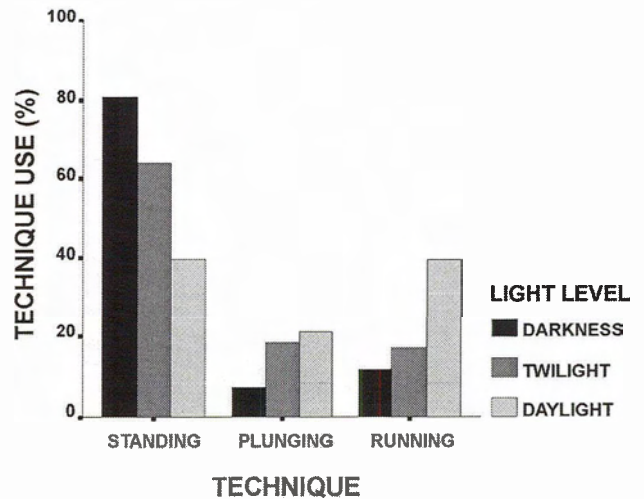
**Fig. 1.** Mean numbers of brown bears observed foraging simultaneously on the Glendale River, British Columbia, in September 1999. Displayed are 95% confidence intervals. The time intervals 6:00–7:59 and 9:00–9:59 were pooled to increase sample size.



**Fig. 2.** Fishing-bout durations for brown bears observed within three light regimes. Mean fishing-bout duration did not differ substantially among light levels. Displayed are means and 95% confidence intervals.



**Fig. 3.** Observed proportions of the three fishing techniques of brown bears within darkness, twilight, and daylight ( $\chi^2 = 67.16$ ,  $P < 0.001$ ).



The efficiencies of standing and plunging tended to decline from darkness to daylight (from 58 to 32% and from 44 to 29%, respectively; Fig. 4). The efficiencies of running varied little (21–27%) among light levels. Overall, the comparatively high efficiencies of running during daylight ( $Z = 1.52$ ) and the comparatively low efficiencies of standing during daylight ( $Z = -1.32$ ) contributed most to the log-linear model. However, none of the three-way interactions were statistically significant (light  $\times$  technique  $\times$  success,  $\chi^2 = 3.53$ ,  $df = 4$ ,  $P = 0.47$ ).

Capture rates varied with length of fishing bout as well as with photic regime. Although total numbers of salmon captured increased with bout length, capture rates decreased

( $P < 0.01$ ; Fig. 5). The extent of this decrease was independent of photic period during shorter fishing bouts (<60 min) but was strongly related for long bouts (Fig. 6). Capture rate was 8.3 fish/h, 4.3 fish/h, and 2.1 fish/h for darkness, twilight, and daylight, respectively ( $P < 0.05$ ; Fig. 6).

**Discussion**

Although brown and black bears are considered to be primarily diurnal throughout their range in North America, crepuscular and nocturnal activity are also present to a lesser extent (Gard 1971; Stonorov and Stokes 1972; Frame 1974; Egbert and Stokes 1976; Roth 1983; Phillips 1987; Reimchen 1998a). Interference from other bears or disruptive human activity may displace bears to suboptimal crepuscular or nocturnal foraging periods and limit individuals to scavenging

Fig. 4. Capture efficiencies of brown bears for three fishing techniques within three light regimes ( $\chi^2 = 3.53$ ,  $P = 0.47$ ).

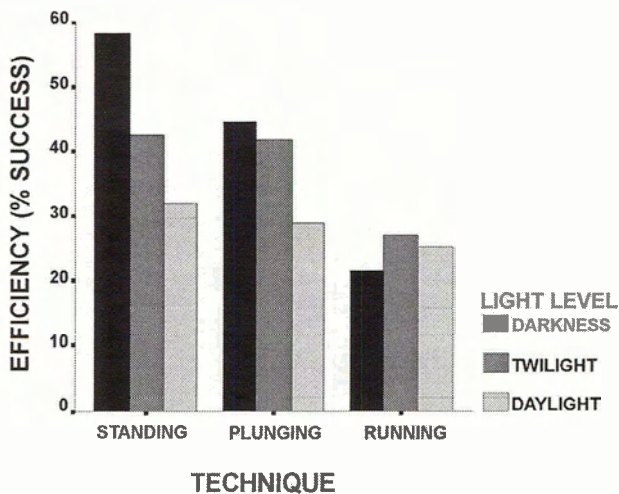
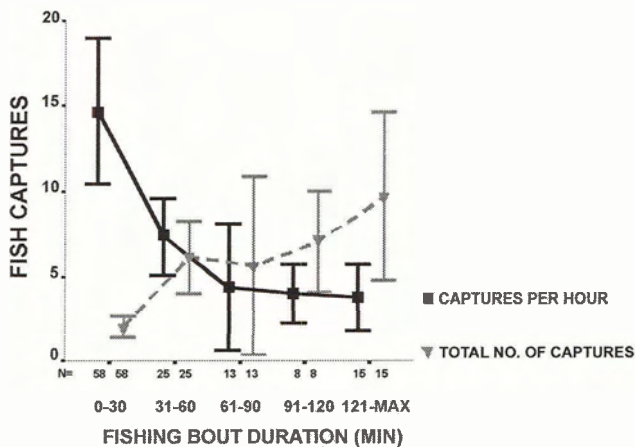
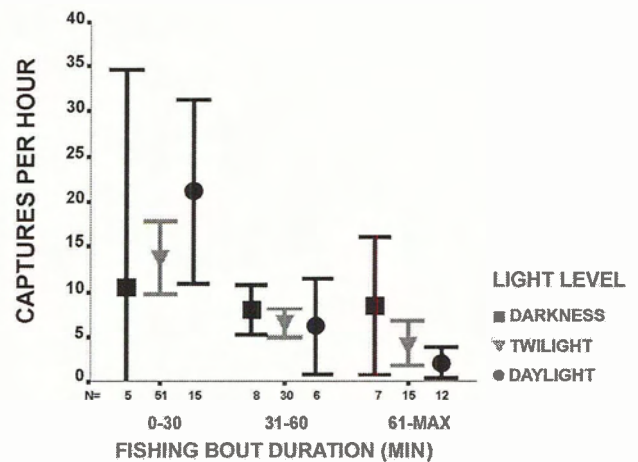


Fig. 5. The relationships between fishing-bout duration and number of fish captured and number of fish captured/h for brown bears. The number of successful captures increases with time spent fishing ( $\chi^2 = 42.42$ ,  $df = 4$ ,  $P < 0.001$ ), while rate decreases ( $\chi^2 = 15.83$ ,  $P < 0.01$ ).



(Machutcheon et al. 1997; Olson et al. 1998). However, Gard (1971) reported that brown bear predation on salmon is greatest at night, while Egbert and Stokes (1976) reported elevated fish capture efficiency and faster capture rates by brown bears late in the day and during the early evening (15:00–22:00). Supporting these findings, Reimchen (1998a) reported preferential nocturnal foraging by black bears that was mostly due to decreased evasion by salmon and fewer aggressive interactions with conspecifics. Our observations of brown bears actively pursuing and capturing live fish during darkness are consistent with observations of black bears. That the capture efficiency was marginally higher during darkness than during daylight suggests that nocturnal foraging by brown bears is not a consequence of restriction into suboptimal foraging periods, which has been assumed to be the case (Machutcheon et al. 1997; Olson et al. 1998). Although our quantitative data are restricted to a single year, we have observed brown bears in the same region over 2 years and suspect that these behaviours have generalized context.

Fig. 6. The relationship between fishing-bout duration, light level, and the number of fish captured/h for brown bears. For fishing bouts in excess of 1 h, capture rates were highest during darkness and lowest during daylight ( $\chi^2 = 7.09$ ,  $df = 2$ ,  $P < 0.05$ ), while for shorter bouts, capture rates did not differ substantially among light regimes ( $\chi^2 = 4.05$ ,  $df = 2$ ,  $P = 0.13$ ).



During this study, capture efficiencies of brown bears averaged 27%, a value comparable with previously reported efficiencies. Luque and Stokes (1976) observed short-term daytime capture efficiencies of 31% by Alaskan brown bears. Frame (1974) also reported a daytime efficiency of 26% by Alaskan black bears, whereas Reimchen (1998a) observed a nocturnal efficiency of 24% by black bears on the Queen Charlotte Islands. These values are similar to those observed for other large carnivores, including African lions (15–38.5%; Schaller 1972; Stander 1992), hyenas (33–44%; Kruuk and Turner 1967), and jackals (33%; Kruuk and Turner 1967). Our reported elevated foraging efficiency by brown bears during darkness compared with daylight (20% efficiency during daylight to 36% efficiency during darkness) is analogous to Schaller's (1972) data on differential foraging efficiencies of lions during daylight (27%) and moonlight (42%). We suspect that the improved foraging efficiency of these carnivores during darkness results from the reduced capability of prey to visually detect approaching predators.

Fishing technique and relative capture efficiencies were variable among light levels during this study. During darkness and twilight, bears favoured standing over running and plunging, whereas during daylight, they used standing and running with nearly equal frequency. Overall, standing was the most efficient of the three foraging techniques, possibly owing to the absence of movement-induced pressure waves in the water that could alert salmon to the approach of a bear. High densities of salmon could also influence fishing technique, as seen among Alaskan brown bears (see Luque and Stokes 1976). The locally high densities of salmon at our study site and their causes (viz. restrictions to upstream movement, shallow water (<30 cm), and a narrow stream channel (<12 m wide)) all functioned to increase bear–salmon proximity, thereby facilitating fish capture without chasing.

Running after the salmon was a more common foraging technique during daylight than during darkness. Although we detected no differences in capture efficiencies for this technique among light levels, we suspect that the more fre-

quent use of this technique during daylight resulted from increased reliance on visual cues to initiate and complete a chase. Reimchen (1998a) suggested that black bears use tactile and acoustical cues to detect salmon during darkness. Brown bears also used touch and hearing but we could not ascertain the relative importance of these senses. Our results suggest that bears shifted from visually oriented pursuit towards ambush strategies using alternative sensory modes. Topographic effects can also influence fishing technique (Luque and Stokes 1976), and the apparent lack of chases by bears during our study could be attributed to the limited space available within the confines of the stream and its banks, resulting in limited opportunities for bears to chase fish without violating the zone of tolerance of proximal conspecifics.

Extending from optimal foraging theory (Krebs 1978), bears should optimize foraging bouts by using the most efficient capture techniques. Congruent with prediction, standing was used most often and was the most efficient, while running was the least common and the least efficient; these results are consistent with those of Luque and Stokes (1976). However, contrary to our prediction, bears used plunging less often than would have been predicted by the efficiency of the technique. Possibly, the plunging technique is ineffective and injurious in shallow water.

During darkness there was a substantive reduction in foraging activity by subadult brown bears and adult females with cubs relative to their observed activity during daylight. We suspect that the prevalence of large solitary bears on the stream during darkness excluded smaller or more risk-averse bears. In Alaska, subadults and adult females with cubs were observed to depart streams prior to darkness (Egbert and Stokes 1976), probably to reduce the risks of intraspecific aggression and infanticide by dominant conspecifics. Such photic-mediated spatial and temporal segregation is not novel to bears and has been observed in other large carnivores. For instance, female cougars (*Puma concolor*) with kittens time feeding bouts in a manner that minimizes encounters with male conspecifics (Pierce et al. 1998). We suggest that visual cues are either difficult or impossible to detect during darkness (Reimchen 1998b), thus decreasing a bear's ability to detect behaviours by conspecifics that indicate potential aggression. Thus, foraging during darkness may increase the risk of potentially fatal aggression by large and aggressive conspecifics towards cubs, causing females with cubs to remove themselves from streams at night. If females with cubs are restricted to daylight time periods, increased disturbance during daylight may reduce their access to salmon resources.

Capture rates of salmon by bears appear to be similar in most coastal areas. Brown bears from our southern British Columbia study area caught an average of 2.1 fish/h during daylight (for fishing bouts in excess of 1 h). This rate is comparable with capture rates by Alaskan brown bears, which ranged from 1.0 to 3.4 fish/h (Egbert and Stokes 1976; Luque and Stokes 1976). We also observed that capture rate was influenced by duration of foraging bout. Capture rates were higher during short fishing bouts than during long ones, and during daylight and twilight than during darkness. This may be a result of bears reducing their effort as they become increasingly satiated during a longer foraging bout.

In summary, our observations of brown bears indicate that they engage in substantive nocturnal foraging activity, with

high capture rates and high efficiencies comparable with those observed during daylight. The use of multiple photic periods and sensory modes provides brown bears with extended access to a food source that is ephemeral but probably critical for over-wintering survival.

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