

# Adaptive coat colour polymorphism in the Kermode bear of coastal British Columbia

DAN R. KLINKA and THOMAS E. REIMCHEN\*

Department of Biology, University of Victoria, PO Box 3020, Victoria, British Columbia, V8W 3N5, Canada

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We investigated potential ecological attributes of the striking coat colour polymorphism in the black bear (*Ursus americanus kermodei* Hornaday) occurring on several small islands off the mid-coast of British Columbia, where a white morph (Kermode), fully recessive to the black morph, reaches 10–25% of the population. During three autumn field seasons (2000–2002; 697 h of observation time), we monitored salmon capture behaviour of individual bears (black,  $N = 37$ ; white,  $N = 4$ ). Both colour morphs foraged on salmon throughout daylight and darkness but with twice the rate during darkness. Log-linear analysis of capture efficiency (success/attempts) and average capture success per bout of the white morph was marginally lower than the black morph during darkness (22.8%,  $N = 158$  versus 25.8%,  $N = 279$  respectively;  $P < 0.04$ ), although it was significantly higher during daylight (34.1%,  $N = 132$  versus 25.3%,  $N = 896$ , respectively,  $P < 0.02$ ), with similar trends in three different pursuit modes. Replicated ( $N = 10$ –14) field experiments involving a colour dimorphic simulated predator (i.e. human in a black or white cloak) showed that salmon were one-half as evasive during darkness than during daylight, with no differences ( $P > 0.4$ ) in response to either the white or black models; however, during daylight, salmon were twice as evasive to the black compared to the white model ( $P < 0.001$ ). The persistence of this coat colour polymorphism may be facilitated by increased salmon accessibility to the Kermode bear and diel foraging differences between morphs. These results are consistent with multi-niche models of adaptive variability. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, 98, 479–488.

**ADDITIONAL KEYWORDS:** conspicuousness – evasive behaviour – genetic variation – multineche – nocturnal foraging – salmon – underwater vision – *Ursus americanus kermodei*.

## INTRODUCTION

The diversity of general coat colours among terrestrial mammals is strongly associated with habitat and is primarily due to selection for camouflage (Caro, 2005). Most species are monomorphic in adult pelage but some rodents and carnivores exhibit conspicuous pale versus dark polymorphic variation controlled by allelic variation in the melanocortin 1 receptor gene (*Mc1r*) (Mundy *et al.*, 2003). Ecological components of this variation are not well known but have been investigated in field mice and are associated with predator-mediated background matching against different rock substrates (Hoekstra, Drumm & Nachman, 2004).

One of the most visually distinctive polymorphisms in a large vertebrate occurs in the coat colour of black bear (*Ursus americanus*). Throughout most of its continent-wide North American distribution, coat colour is uniformly black, occasionally grading to brown or blue and this is associated with general camouflage in the forested and mountain habitats (Rounds, 1987). However, on several small forested islands on the central coast of British Columbia, western Canada, concordant with the distribution of *U. a. kermodei* Hornaday, a white morph or Kermode bear occurs at modest frequencies (10–25%) co-existing with the more common black morph (Cowan & Guiguet, 1956). Genetic studies of this colour polymorphism indicate control at the *Mc1r* locus in which black is fully dominant to white (Ritland, Newton & Marshall, 2001; Marshall & Ritland, 2002).

\*Corresponding author. E-mail: reimchen@uvic.ca

The ecological or evolutionary interpretations for the restricted distribution and persistence of the white bear are not resolved. In the traditional oral history of First Nations from the region, the white morph was suited to the ice-covered landscape of ancient times. Recent mtDNA data of North American bears (Byun, Koop & Reimchen, 1999) is consistent with survival of coastal bears in a large periglacial late Pleistocene refugium postulated for the region (Warner, Mathewes & Clague, 1982; Josenhans *et al.*, 1995; Reimchen & Byun, 2005). If so, the present distribution of the white bear on several islands, which are low elevation and lack ice habitat, might be relictual and persist as a neutral trait due to genetic isolation from the adjacent mainland. Alternatively, the white coat of the bears may be a recent mutation that has achieved high frequencies from genetic drift in the small geographically isolated populations (Marshall & Ritland, 2002). Although these assumptions of a neutral polymorphism and conditions for persistence may be sufficient, we examine here foraging activity of the bears and consider possible direct fitness benefits of the white coat colour as an alternative or a supplemental mechanism for the origin and persistence of the polymorphism. Levene (1953) initially formulated the theoretical basis under which two morphs could approach equilibrium frequencies if fitness of each varied inversely with respect to habitat or niche space.

Blood (1997) and Marshall & Ritland (2002) considered the Kermode bear to be primarily herbivorous, but multiple studies in coastal British Columbia and Alaska show that a large proportion of the yearly protein requirements of coastal bears are obtained from salmon (Gilbert & Lanner, 1995; Hilderbrand *et al.*, 1999). This diet includes scavenging but primarily active pursuit and capture of salmon during daylight, twilight and darkness (Reimchen, 1998; Klinka & Reimchen, 2009). Salmon are evasive when bears enter the stream but they are particularly evasive during daylight when visual cues are prominent (Reimchen, 1998). Whereas white bears appear to be highly conspicuous in the stream from the human standpoint, this might not be the case from the visual field of a salmon through the water–air interface. Against the down-welling or back-welling light, a white predator can be less conspicuous than that of a dark predator, as has been previously proposed for the white plumage of numerous seabirds and waders (Craik, 1944; Murton, 1971; Cowan, 1972; Mock, 1980). We hypothesize that white bears are less conspicuous to salmon than are black bears and predict that the white morph will have greater salmon capture efficiency during daylight than during darkness and if so, might exhibit increased daylight foraging relative to that of the black morph. To test this,

we monitored individual foraging activity of white and black morphs over three autumn field seasons during daylight, twilight and darkness. We also examine experimentally the evasive responses of salmon to a simulated polymorphic predator during the three photic periods. Our data provide insights to the function and persistence of this exceptional polymorphism.

## MATERIAL AND METHODS

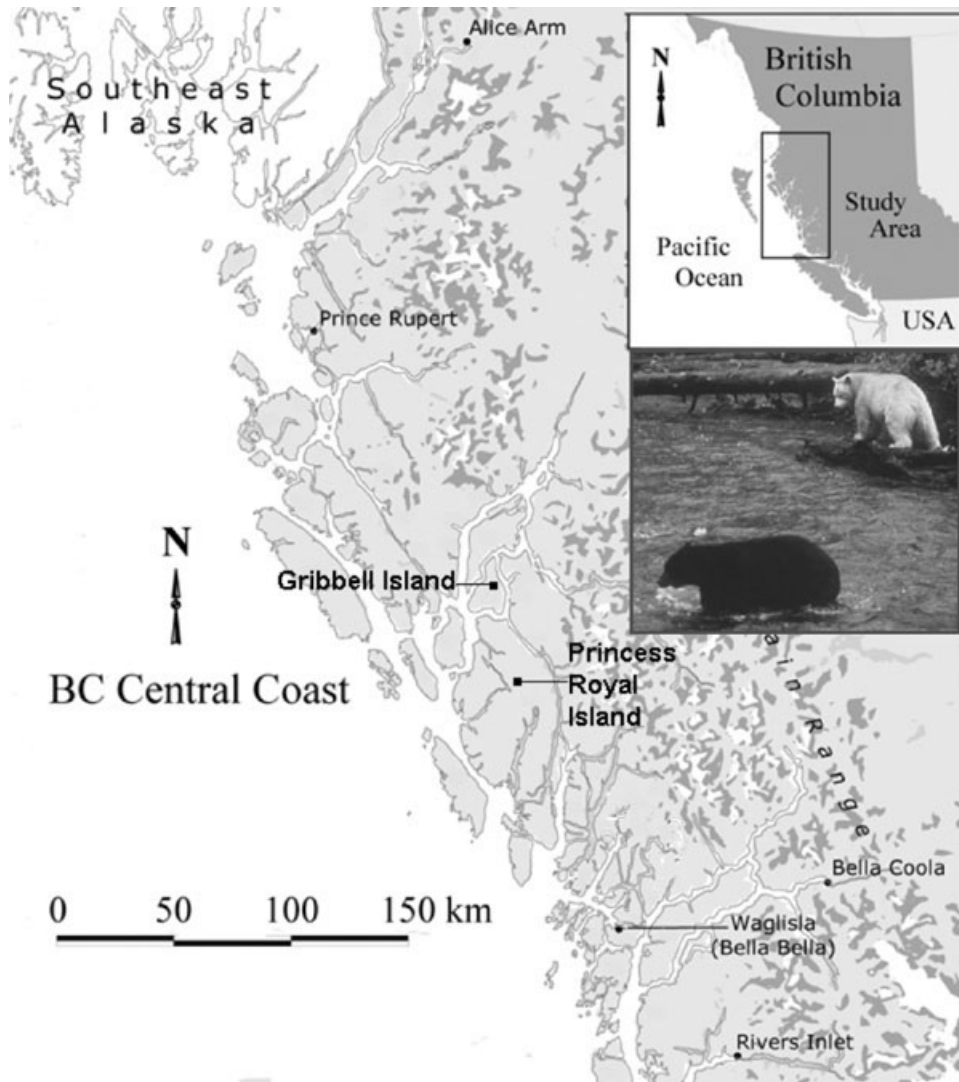
### STUDY AREA

From late August to early October, 2000–2002, we conducted observations of bear–salmon behavioural dynamics along Riordan Creek on Gribbell Island (128°58'16"W, 53°25'26"N), which is separated from the mainland by a 1.5-km wide channel (Fig. 1). Riordan Creek is situated in the very wet hyper-maritime (CWHvh2) subzone of the Coastal Western Hemlock Biogeoclimatic Zone (Green & Klinka, 1994). The climate is cool and wet, with a mean annual temperature of approximately 8 °C, and a mean annual precipitation in excess of 4000 mm (Environment Canada, 1991). On average, the creek is 12 m in width and < 0.4 m in depth.

Riordan Creek supports an annual return of pink salmon (*Oncorhynchus gorbuscha*), along with some chum (*Oncorhynchus keta*) and coho salmon (*Oncorhynchus kisutch*). In the last 10 years, pink, coho, and chum salmon returns on Riordan Creek average 800, 100 and 20 individuals, respectively, which are approximately one-third the numbers counted in the 1950s (Department of Fisheries and Oceans Escape-ment data: 1950–2000, unpub. data). For all species, spawning begins in early September and is complete in October. Bears capture salmon primarily in the lower 2 km of the stream and consume these either in the stream or on the bank.

### FIELD PROTOCOL

During the autumn, spawning runs in 2000–2002 (29–31 days per year; 697 h of observation time), we video-taped and catalogued bear–salmon interactions with a camcorder (DCR-TRV720; Sony). Most observations were taken from a fallen tree spanning the river, primarily during daylight (average 8 h per day), but also during civil twilight (visible horizon, average 1 h per day) and darkness (average 3 h per day). Nocturnal sessions were performed using a hand-held night vision monocular (ITT model CSC-N16140-DX, ×50 000 amplification, 0.95 cycles per milliradian resolution) aided with an infra-red emitter (880 nm) and were tape-recorded for later transcription.



**Figure 1.** General distribution of the Kermode bear (*Ursus americanus kermodei*) in coastal British Columbia. Highest frequencies are found on Gribbell and Princess Royal Island.

We assessed temporal activity patterns of bears by collecting scan samples (Altmann, 1974) every 10 min during stream surveys and recorded the total number of bears visible within daylight, twilight, and darkness. To evaluate differences in diel patterns of stream visitation, we used the Kruskal–Wallis and Wilcoxon signed ranks tests.

We recorded fishing behaviour for all bears, including multiple observations per bear. We classified fishing techniques as three types: Standing, Walking, and Running (Luque & Stokes, 1976; Klinka & Reimchen, 2002). We used coat colour (black versus white) and facial scaring patterns to identify individual bears ( $N_{\text{Black}} = 37$ ,  $N_{\text{White}} = 4$ ). Where possible, age-class (sub-adult, adult) and gender were also assessed, although this population predominantly comprised

adult males. We restricted our analyses to the data involving individually recognizable bears and to those instances where we observed more than three fishing attempts as well as the initiation and termination of fishing bouts. We defined capture efficiency as the probability of a successful capture of salmon (number of captures per total number of attempts) (Klinka & Reimchen, 2009).

We examined differences in foraging efficiencies among bears in relation to fishing technique, light level, and colour morph with nonparametric statistics using SPSS, version 11, *sensu* Norusis (1988). To test for interactions among Technique (Standing, Walking, Running), Light level (Darkness, Twilight, Daylight), Fishing Success (Fail, Success), and Colour (Black, White), we used log-linear models. *Z*-values were

used to assess the relative contributions of cells to the interaction and considered values  $> 1.96$  to be significant at  $\alpha < 0.05$ .

#### EXPERIMENTAL PROTOCOL

We experimentally investigated salmon response to stream disturbance. From previous observations, we noticed that salmon would react to a human entering the stream in a similar way to a bear entering the stream by rapid evasion and gradual return (Reimchen, 1998). Consequently, we measured salmon responses to a simulated dimorphic predator. In an area of the stream where salmon were actively spawning and holding, we set up an observational area (hereafter termed the arena) consisting of two circular rings (2 m and 4 m in radius) delineated by white painted rocks that were clearly visible from above the stream surface and counted the numbers of salmon returning to the arena after a disturbance.

To simulate a dimorphic spectral disturbance, the researchers draped themselves in either a black or white linen costume. The fabric costume covered the entire body of the researcher except for small eye openings. The fabric did not break the surface of the water, typically stopping a few centimetres above the water surface. Because the present study was concerned with salmon response to above water visual stimuli, green rubber boots were worn during all trials, thus standardizing below water visual stimuli.

We used five different model stimuli (treatments). Two were of individual models: individual black (B), individual white (W). Three treatments involved paired models: two black (BB), two white (WW), and one mixed treatment consisting of one white one black costume (BW). We conducted 38 trial sets and shifted the trial order for each set over a 4-week period in September 2002 during the salmon migration within three light regimes: darkness, twilight, and daylight. Each trial was assigned a number (B = 1, W = 2, BB = 3, etc.) and each trial sequence ran consecutively (1, 2, 3, etc.) but the starting number was advanced a single place each day (1, 2, 3 . . . 2, 3, 4 . . . 3, 4, 5, etc.). Nocturnal trials were made with night vision monocular and infrared light emitters. In all trials, we counted the number of salmon returning to each zone within the arena per time interval. In our analysis, we used total counts because the majority of fish (88%) occurred in the 2–4-m zone. The stream substrate (small rocks, pebbles, and sand) and depth (20–40 cm) were similar over the entire arena. Occasionally, during a trial, bears would approach us as we stood in the arena, further disturbing the salmon, at which point the trial was terminated and excluded from subsequent analysis. We could not reliably determine what pro-

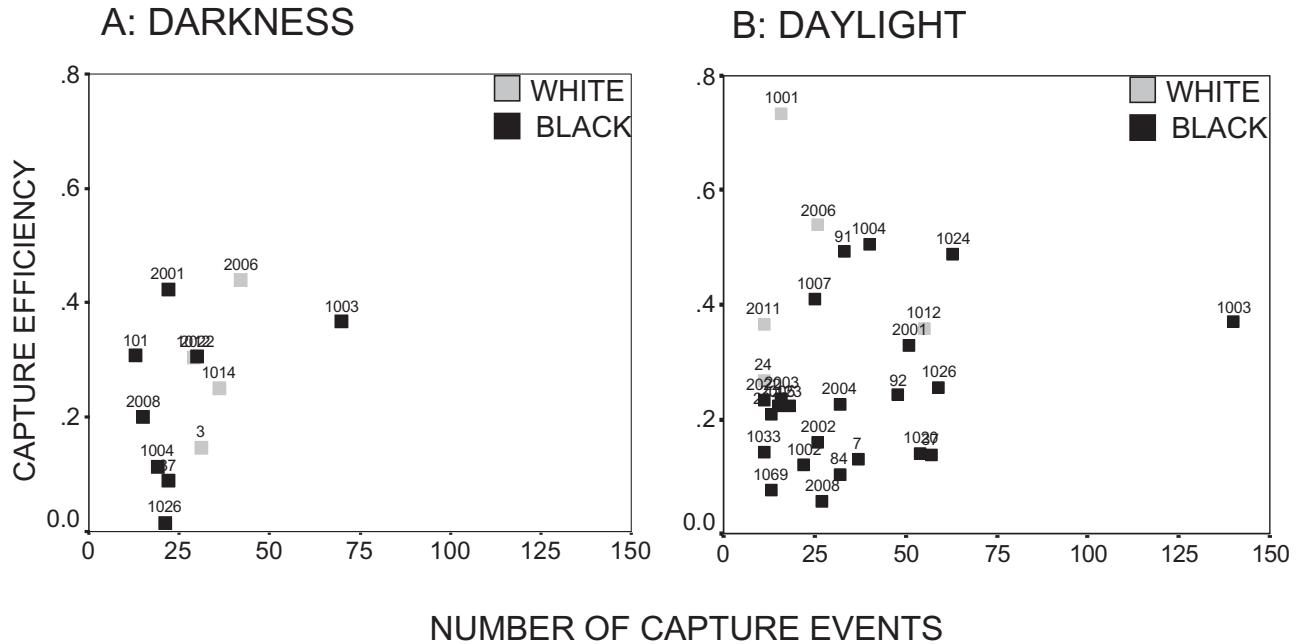
portion of the salmon were repeat visitors among the trials. Salmon occurred throughout the length of the stream and movement both upstream and downstream occurred regularly. Furthermore, there was considerable dynamic turnover with senescent salmon and bear-captured salmon being lost from the system and replaced with new spawners. As such, we suspect that repeat visitors occurred commonly within any trial period, but were less frequent over sequential days and very uncommon or absent over the 21 days of the experiments.

For each trial (B or W), the cloaked observer entered the water from the shore and walked directly to the centre of the arena and remained at this central position for the duration of each trial. This disturbance caused the salmon to immediately scatter outside of the arena and gradually return to the arena. Once every minute, the observer rotated 360° and counted the number of salmon within the arena. D.K. performed all the salmon counts for the entire study. From initial trials, we determined that the majority of salmon returned to the arena within 5 min when the observer was present in the water. We therefore set the trial duration at 7 min for each treatment, giving a total of seven counts (one count per min) and these were aggregated into a mean for each treatment. After the last count on any trial, the observer exited the arena and walked onto shore out of sight from the arena. We determined that a 1-min latency period was sufficient for the salmon to return to the arena when the observer was out of the water; thus, we set a 3-min latency period between trials. Each block of trials, encompassing the five treatments took approximately 50–60 min for completion. Trials involving two observers with three cloak configurations (BB, BW, WW) were identical to those involving a single observer (B or W) in all respects, except one of the observers stood at a fixed location at the edge of the 4-m ring delineating the arena boundary. This observer also wore an appropriately coloured costume. At no time during nocturnal trials were visible spectrum flashlights used when in the arena, but the observer at the edge of arena occasionally scanned areas outside the arena with a small flashlight to identify approaching bears during darkness.

We used analysis of variance to test for differences in salmon response between colours (black, white), single versus double models, and among light levels (darkness, twilight, daylight). We tested data distributions for normality with the Kolmogorov–Smirnov test.

#### RESULTS

Each coat colour morph foraged throughout daylight, twilight, and darkness with higher levels of activity



**Figure 2.** Salmon capture efficiency by individual black and white bears within darkness, and daylight on Gribbell Island, coastal British Columbia during the fall of 2000–2002. A, darkness. Salmon capture efficiency during darkness ( $F = 0.12$ , d.f. = 1,  $P = 0.74$ ). B, daylight. Salmon capture efficiency during daylight ( $F = 10.9$ , d.f. = 1,  $P = 0.003$ ).

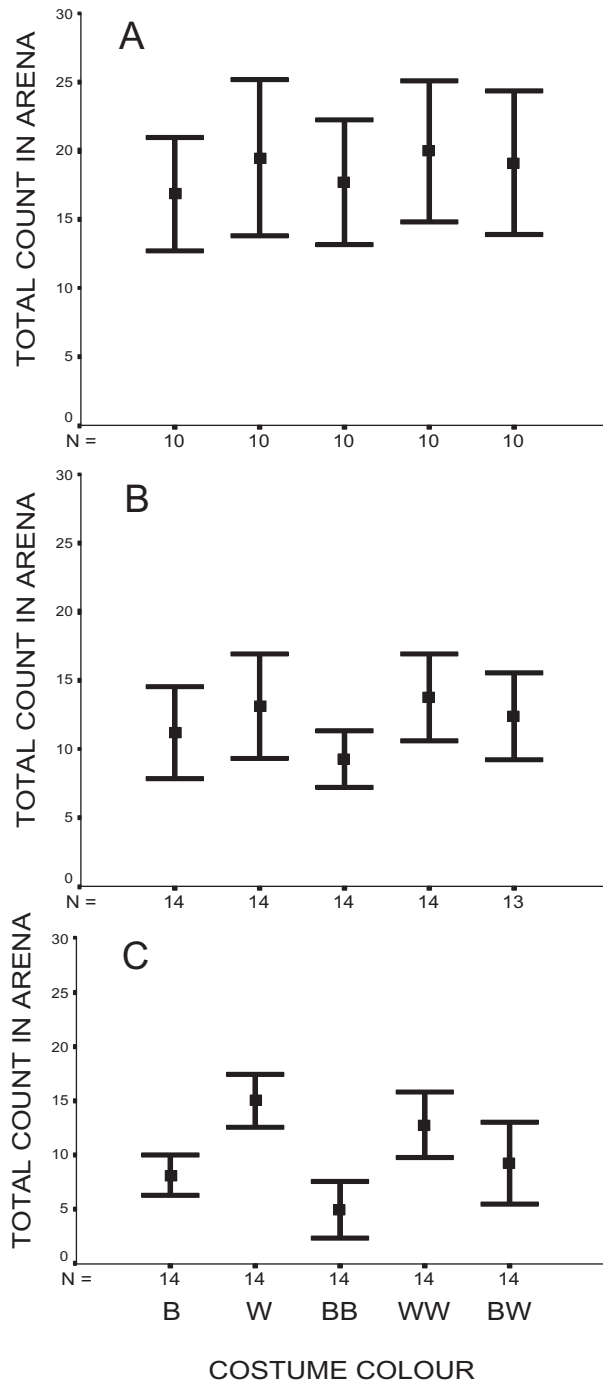
during low light levels (Black:  $\chi^2 = 12.50$ , d.f. = 2,  $P = 0.002$ ; White:  $\chi^2 = 14.00$ , d.f. = 2,  $P = 0.001$ ). Both morphs were similar in their stream visitation patterns within each light level ( $Z = -0.54$ ,  $P = 0.59$ ).

Bears differed in their ability to capture salmon. Overall capture efficiency was similar for both colour morphs (White: 30.0%; Black: 26.5%; Colour  $\times$  Success,  $\chi^2 = 0.55$ , d.f. = 1,  $P = 0.46$ ), but differed among light regimes (Light Level  $\times$  Colour  $\times$  Success,  $\chi^2 = 6.63$ , d.f. = 2,  $P = 0.036$ ). The white morph was less efficient than the black morph during darkness (22.8% and 25.8%, respectively;  $Z = -2.07$ ,  $P = 0.039$ ), but was more efficient than the black morph during daylight (Daylight: 34.1% and 25.3%, respectively;  $Z = 2.33$ ,  $P = 0.020$ ) and this occurred with each fishing technique (Standing: 42.1% versus 35.3%, respectively; Walking: 36.0% versus 10.4%, respectively; Running: 22.4% versus 17.7%, respectively). There were no differences during twilight (Twilight: 37.5% and 32.1%, respectively;  $Z = 0.08$ ,  $P = 0.94$ ).

Because a relatively small number of bears contributed a large amount of foraging data, there is the potential for biases resulting from pseudoreplication within our repeated sampling of individuals within the population. To address this, we computed the mean capture success (efficiency) for each bear with more than ten capture events among all bouts. All of the resultant trends were consistent with our log-linear model based on the complete dataset and

we restrict our analyses to the latter [Darkness:  $\bar{x}_W \pm SE = 28.5 \pm 0.12\%$ ;  $\bar{x}_B \pm SE = 22.8 \pm 0.15\%$ ;  $F = 0.12$ , d.f. = 1,  $P = 0.74$ , analysis of variance (ANOVA); Daylight:  $\bar{x}_W \pm SE = 45.3 \pm 0.19\%$ ;  $\bar{x}_B \pm SE = 24.0 \pm 0.13\%$ ;  $F = 10.9$ , d.f. = 1,  $P = 0.003$ , ANOVA; Fig. 2].

We experimentally evaluated the responsiveness of salmon to black versus white costumed models and found that the numbers of salmon returning to the arena were dependent upon light levels and costume colour (Fig. 3). Highest counts for all costume treatments occurred during darkness ( $\bar{x}_{\text{Darkness}} \pm SE = 18.63 \pm 0.96$ ), lower counts during twilight ( $\bar{x}_{\text{Twilight}} \pm SE = 11.92 \pm 0.66$ ), and lowest counts during daylight ( $\bar{x}_{\text{Daylight}} \pm SE = 10.03 \pm 0.71$ ;  $F = 35.48$ , d.f. = 2,  $P < 0.001$ ). However, the extent of these differences varied with respect to costume colour. For the single model presentation, during darkness and twilight, there were no significant differences in salmon counts for the white (W) costume relative to the black (B) costume (Darkness:  $F = 0.70$ , d.f. = 1,  $P = 0.41$ ; Twilight:  $F = 0.67$ , d.f. = 1,  $P = 0.42$ ). However, during daylight, counts were significantly higher for the white costume ( $\bar{x}_W \pm SE = 15.05 \pm 1.13$ ) than for the black costume ( $\bar{x}_B \pm SE = 8.13 \pm 0.86$ ;  $F = 23.75$ , d.f. = 1,  $P < 0.001$ ). We also evaluated salmon response to paired models and found comparable responses to single predators in both magnitude and direction (Fig. 3). During darkness, there were no significant differences in salmon counts for the WW



**Figure 3.** Number of salmon returning to arena after disturbance to black (B) and white (W) costumes among three light regimes on Gribbell Island, coastal British Columbia during the fall of 2000–2002. Salmon counts differed between costume colours only during daylight. A, number of salmon returning to the arena during darkness ( $F = 0.34$ ,  $P = 0.85$ ). B, number of salmon returning to the arena during twilight ( $F = 1.50$ ,  $P = 0.21$ ). C, number of salmon returning to the arena during daylight ( $F = 9.38$ ,  $P < 0.001$ ). 95% confidence intervals are shown.

costumes relative to the BB costumes. ( $F = 0.55$ , d.f. = 1,  $P = 0.47$ ). However, during twilight and daylight, counts were significantly higher for the WW costumes than for the BB costumes (Twilight:  $\bar{x}_{WW} \pm SE = 13.76 \pm 1.45$ ;  $\bar{x}_{BB} \pm SE = 9.26 \pm 0.96$ ;  $F = 6.69$ , d.f. = 1,  $P = 0.016$ ; Daylight:  $\bar{x}_{WW} \pm SE = 12.78 \pm 1.38$ ;  $\bar{x}_{BB} \pm SE = 4.94 \pm 1.21$ ;  $F = 18.23$ , d.f. = 1,  $P < 0.001$ ). The BW treatment revealed intermediate effects during this time period.

## DISCUSSION

Throughout the continent-wide distribution of black bear in North America, the Kermode bear, a recessive white coat colour morph of this species, is largely restricted to watersheds of coastal British Columbia and, within this large area, is only common on several small adjacent islands, including Gribbell Island and Princess Royal Island, which are separated by a narrow channel from the mainland. The long-term historical stability of this polymorphism on these islands is unknown, although Gribbell Island was known for the concentration of white bears in the late 19th Century (Cowan & Guiguet, 1956) and it has an important role in the oral history of First Nations from the region. Such a geographically limited but apparently stable and conspicuous polymorphism in a large carnivore with low population numbers is exceptionally uncommon, but has been reported in several tropical forest felids (Caro, 2005). Small populations will tend towards monomorphism from lineage sorting, particularly if the traits are neutral in fitness (Frankham, 1996, 1997); thus, the presence of both morphs in the islands could be maintained by gene flow from the adjacent mainland where the black morph predominates (Marshall & Ritland, 2002). Long-term persistence of the white bear could be achieved if there was superior physiological fitness of the black heterozygote (Ford, 1964) because this retains both homozygotes at frequencies proportional to their relative fitness reduction (Futuyma, 1998). If so, this predicts an excess of heterozygotes from Hardy–Weinberg equilibrium, yet the two islands with higher frequencies of the white morph exhibit fewer heterozygotes than predicted (Ritland *et al.*, 2001) and this should tend to destabilize the polymorphism. To account for the deficiency of heterozygotes, Ritland *et al.* (2001) postulate either assortative mating of the morphs or elevated immigration of the dominant homozygotes from the adjacent mainland. It is within this framework that we examined foraging behaviours of coat colour morphs of bears across multiple photic regimes.

We observed nocturnal and diurnal differences in foraging success and prey response between colour morphs. Both black and white morphs are active on

the stream throughout day and night, and each morph prefers low light levels (darkness and twilight) over high light levels (daylight) when foraging on salmon. Such increased use of nocturnal time periods is consistent with previous studies (Reimchen, 1998; Klinka & Reimchen, 2002) and may be the result of reduced evasive responses of salmon during darkness, which allows bears to successfully exploit this time period. Bears modify their pursuit and capture techniques of salmon with respect to foraging periods (Klinka & Reimchen, 2009) and the data obtained in the present study indicate that the white morph is more efficient at capturing salmon during daylight but not during darkness. Consistent with our first hypothesis, our experimental results showed greatly increased evasive responses of salmon to stream disturbance in daylight relative to twilight and darkness and more evasion towards a black model relative to a white model during daylight but not darkness. Extrapolating our experimental results to bears in the stream suggests that this difference in salmon evasion results in an approximate doubling of the availability of salmon to the white morph during daylight. Concurrent studies of the stable isotope signatures of hair shafts from white and black bears on this stream indicate a disproportionate enrichment of marine nutrients in the white bear relative to that of the black morph (Klinka, 2004; K. Klinka & T. E. Reimchen, unpubl. data), supporting the results obtained in our experimental study, as well as our empirical observations on salmon capture efficiency. These morph-specific niche effects could facilitate the maintenance of the polymorphism consistent with predictions from multi-niche models (Levene, 1953; Adams & Huntingford, 2002; Galeotti *et al.*, 2003; Majerus & Mundy, 2003; Galeotti & Rubolini, 2004; Hoekstra *et al.*, 2004). If true, this would provide an alternative hypothesis or supplement previous suggestions (Marshall & Ritland, 2002) that the polymorphism is maintained by the cumulative effects of isolation, drift, and migration.

We predicted, but did not detect, increased foraging activities during daylight by the white morph relative to the black morph given their higher capture success in this time period. Elevated foraging may be present, but was not detectable with the existing sample size and time frame. For example, general observations of social interactions at this site suggest a marginal behavioural dominance of the black morph over the white morph, which could potentially result in partial competitive exclusion of the white bear from preferred fishing localities (Klinka, 2004). As such, the white bear may be foraging at higher rates in daylight in other areas on the stream that we did not monitor. It is also possible that the amount of foraging time in the stream is limited by

other behavioural constraints, such as rest within a 24-h period.

Spatial geometry of predator and prey influences assessment of the photic environment and functionality of animal coloration (Endler, 1978; Reimchen, 1979). In particular, the detection of above surface objects by aquatic animals is influenced by Snell's window, which compresses these objects into a 96° vertical cone (Horvath & Varju, 1991). We observed greatly reduced evasive responsiveness of salmon towards white models relative to black models during daylight but not during darkness. One possibility for this is the relative contrast of the models against the photic background. Although these salmon streams are typically bordered by a riparian forest, white models may be more camouflaged than black models during daylight because white would contrast less with a bright sky background, whereas dark models would contrast less during darkness. Similar interpretations have been made previously for the white plumage of reef herons and numerous seabirds (Craik, 1944; Murton, 1971; Cowan, 1972; Recher & Recher, 1972; Mock, 1980; Gotmark, Winkler & Andersson, 1986; Gotmark, 1987; Rohwer, 1990; Itoh, 1991).

Past encounter rates between salmon and bears, rather than relative coat contrast, may provide an additional explanation for the differential response of salmon to black and white models. The white morph comprises less than 30% of all bears in the immediate region (Ritland *et al.*, 2001) and, as a result, salmon are more likely to have encountered a black morph in estuaries prior to their upstream movement. The reduced evasion of the salmon could result from the failure to recognize the white morph as a predator. Such apostatic or frequency-dependent selection is considered to be an important mechanism in the retention of uncommon but conspicuous phenotypes (Clarke, 1983). This might be applicable for the white bear but, if so, it does not readily account for the lower salmon capture success by the white morph during darkness. This is more consistent with the hypothesis of differential coat contrast rather than frequency dependence.

If our interpretation of a functional advantage to the white coat colour is reasonable, it remains problematic that the white morph is rare or absent elsewhere around the north Pacific given that salmon are the predominant prey for coastal bears (Gilbert & Lanner, 1995; Hilderbrand *et al.*, 1999; Reimchen, 2000). Distinctive streambed spectra of the white bear islands might account for the restricted occurrence, but, from recent stream surveys conducted throughout coastal British Columbia, we observed no obvious spectral attributes of Gribbell and Princess Royal Island streams relative to those on the adjacent main-

land. Possibly, there are additional costs associated with white pelage that are more expressed in other areas. Marshall & Ritland (2002) suggest that the conspicuous white coat colour does not directly influence fitness because bears do not have predators, therefore eliminating the requirement for camouflage. These suggestions, which emerge from those proposed by Blood (1997), are not supported by the available life-history data. In carnivores, including bears, adult males will kill and consume conspecific young (Stonorov & Stokes, 1972; Swenson & Dahle, 2003). In addition, one of the most widely distributed large predators of coastal British Columbia are wolves (*Canis lupis*), which are known to kill and consume adult bears and cubs (Darimont *et al.*, 2004). Furthermore, Grizzly bears (*Ursus arctos*) are present throughout the coastal north Pacific, where they co-exist on the mainland and compete with black bears (Belant *et al.*, 2006) and also constitute their predators (Smith & Follmann, 1993; Boyd & Heger, 2000). Accordingly, it is probable that the coat colour of black bears would influence susceptibility to these predators, each of which hunt with multiple sensory modalities, including vision, and this might contribute to the low frequencies of the white morph on the coastal mainland. Although this is reasonable for the mainland, it is not a satisfactory explanation for Haida Gwaii, a large isolated archipelago 100 km to the west of the Kermode bear islands, where wolves and Grizzly bears are absent (Cowan & Guiguet, 1956), although black bears are common there and salmon are a major component of their diet, yet the white morph is absent (Reimchen, 2000).

In summary, the data obtained in the present study suggest that the white coat colour morph in black bears of coastal British Columbia has elevated salmon capture efficiency relative to that of the black morph during daylight, partly as a result of the differential evasiveness of salmon to the two morphs. Because salmon may be particularly important for the white morph, the ecological persistence of this seasonal resource becomes an essential conservation consideration. Recent and ongoing industrial deforestation of the riparian zones on Gribbell Island and Princess Royal Island, where the white morph reaches its highest frequency, as well as major historical declines in salmon numbers returning to streams of the east Pacific (Gresh, Lichatowich & Schoonmaker, 2000), continue to compromise the integrity of this striking polymorphism.

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