

# DARKNESS, TWILIGHT, AND DAYLIGHT FORAGING SUCCESS OF BEARS (*URSUS AMERICANUS*) ON SALMON IN COASTAL BRITISH COLUMBIA

D. R. KLINKA AND T. E. REIMCHEN\*

University of Victoria, Department of Biology, P.O. Box 3020, Victoria, British Columbia V8W 3N5, Canada

We examine foraging behavior of coastal black bears (*Ursus americanus kermodei*) during different light regimes on a salmon stream in British Columbia, Canada (2000–2002). Bears (maximum 7 simultaneously) were primarily active during daylight near the onset of the salmon spawning run and shifted to twilight and darkness as the spawning run progressed. Overall time budget included search and pursuit (58%), handling and ingestion (38%), and agonistic interactions with other bears (4%). Scavenging was greatest during daylight (19%) and lowest during darkness (3%). Bears were most efficient at capturing live salmon when standing (35.4% success) followed by running (20.5%) and walking (15.2%). Highest capture efficiency occurred during twilight (33.6%) compared with daylight (26.5%) and darkness (24.7%). Capture rate ranged from 1 to 3 salmon per hour per bear. Our results suggest that bears increased their total salmon intake by alternate use of visual and auditory cues during daylight and darkness.

Key words: darkness, foraging efficiency, *Oncorhynchus*, sensory modes, twilight, *Ursus*

Mammalian carnivores are highly variable in their foraging periods, ranging from full daylight through to darkness. Presumably, prey detection and capture techniques also will vary from daylight to darkness with respect to the relative contributions of visual, olfactory, and auditory cues. Benefits to daylight foraging could be long-distance visual detectability of prey, whereas in darkness, predators may have closer approach distance and potential for ambush (McMahon and Evans 1992; Reimchen 1998a; Thibault and McNeil 1995).

In most instances, we do not know if predators that are active day and night show variation in foraging techniques or efficiency as light levels vary. Do shifts from visual to nonvisual activities alter the extent of scavenging in opportunistic foragers, and how do predators respond to differences in prey behavior at different light levels? Other than a few examples (Fernandez and Anderson 2000; Fraser and Metcalfe 1997; Klinka and Reimchen 2002; McNeil et al. 1995; Reimchen 1998a), direct comparisons of foraging among light levels have been limited because of the difficulty of observing animals at night. With the development of light-amplifying technologies, the relative importance of vision or alternate senses during nocturnal foraging can be evaluated.

Black bears (*Ursus americanus*) are primarily diurnal throughout North America (Larivière et al. 1994; Machutcheon et al. 1997; Maehr 1997). However, recent studies of bears from coastal British Columbia, Canada, show extensive nocturnal foraging on adult salmon during spawning migration, in part due to reduced competitive interference from other bears as well as elevated capture rates from lowered evasive responses of salmon (Klinka and Reimchen 2002; Reimchen 1998a, 1998b, 2000).

In this paper, we examine daylight, twilight, and darkness foraging patterns of coastal black bears (*Ursus americanus kermodei*) including capture techniques and efficiencies at different light levels and the extent to which these are influenced by salmon activities.

## MATERIALS AND METHODS

From late August to early October, 2000–2002, we observed fishing behavior of bears along Riordan Creek on Gribbell Island, on the northwest coast of British Columbia (53°25'26"N, 128°58'16"W). Riordan Creek is situated in the very wet hypermaritime (CWHvh2) subzone of the Coastal Western Hemlock biogeoclimatic zone (Green and Klinka 1994). During the late 1980s, the watershed was clear-cut up to the streamside in most locations except a portion near the mouth. Riordan Creek averages 12 m in width and depths are typically <40 cm. Fallen logs under which salmon will often pool during daylight hours occasionally collect along the spawning zone. From September to October, there were approximately 800 pink salmon (*Oncorhynchus gorbuscha*)

\* Correspondent: reimchen@uvic.ca

**TABLE 1.**—Ethogram used for study of foraging behavior of black bears (*Ursus americanus kermodei*) at Gribbell Island, British Columbia, Canada, during 2000–2002.

Behavior	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

and 20 chum salmon (*O. keta*) that spawned in the lower 2 km of the river and about 20 coho salmon (*O. kisutch*) that moved above a small waterfall. Activity of bears on the stream increased from August to September concordant with an increase in abundance of salmon and thereafter declined as salmon numbers declined. Brown bears (*U. arctos*) are absent on Gribbell Island.

We used a combination of facial scaring patterns, size, color, and sex to identify individual bears and recorded fishing behavior and interactions for all bears during the study period, including multiple observations per bear. No cubs were observed on the stream during the study.

We assessed the activity patterns of bears during daylight, twilight, and darkness by collecting scan samples (Altmann 1974) every 10 min during stream surveys. All nocturnal observations were through a handheld night-vision monocular (model CSC-N16140-DX; ITT, Roanoke, Virginia; 50,000× amplification, 0.95 cycles per milliradian resolution) aided with an infrared emitter (880 nm) in extremely low-light conditions. During darkness, we tape-recorded and later transcribed all observations. With night-vision equipment, the ability to detect bears on the stream was generally comparable to that of overcast conditions at midday.

During focal animal sampling we recorded occurrences and durations of different fishing behaviors for all bears. These included standing, walking, running (Klinka and Reimchen 2002; Luque and Stokes 1976), scavenging, feeding on fresh salmon, and capture attempts and successes (Table 1).

When focal sampling in 2001, we recorded behavior every 10 s for the duration of the observation session. Because behaviors are not recorded continuously, there is a risk that rare behaviors of short duration will be omitted (Rose 2000). We identified 2 such behaviors (attempts and successes), and therefore we recorded them independent of the focal sampling time interval. These ad libitum records were incorporated into the overall focal animal sample. During 2002, focal animal sampling was recorded continuously.

For all focal samples we used behavioral analysis software (Blumstein et al. 2000) and SPSS version 11.0 (Norusis 1988) to analyze the number and duration of foraging behaviors among light levels (Kruskal–Wallis and Mann–Whitney *U*-tests). A total of 117 focal samples were included in the anal-

ysis ( $\bar{X} = 26.3 \text{ min} \pm 1.63 \text{ SE}$ ; range 5.7–120.5 min). These samples were distributed among light levels with 29 samples occurring during darkness ( $\bar{X}_{\text{darkness}} = 29.9 \pm 3.4 \text{ min}$ ; range 6–78 min), 16 samples occurring during twilight ( $\bar{X}_{\text{twilight}} = 27.8 \pm 4.7 \text{ min}$ ; range 11–85 min), and 72 samples occurring during daylight ( $\bar{X}_{\text{daylight}} = 24.5 \pm 2.0 \text{ min}$ ; range 6–120 min).

We defined capture efficiency as the probability of a successful salmon 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 (100 m of stream). Capture rate was defined as the number of salmon captured per hour (number of successful captures/length of time foraging in hours).

We examined differences in foraging efficiencies among different bears in relation to fishing technique and light level using nonparametric statistics. To test for interactions among technique (standing, walking, or running), light level (darkness, twilight, or daylight), and fishing success (fail or success), we used log-linear models. 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). We used foraging efficiency data from identifiable bears with  $>3$  fishing attempts, where both initiation and termination of fishing bouts were observed and where foraging bouts were  $>5$  min.

When salmon were excavating redds and spawning (which occurred mostly during darkness), they made multiple splashes audible above background stream noise. Nocturnal bears appeared to use these auditory cues to target their pursuit. We quantified these auditory cues using a digital camcorder (DCR-TRV720; Sony, Toronto, Ontario, Canada). One 5-min audio recording was made during each observation session ( $n = 60$ ). We used analysis of variance to compare the frequency of audible splashes on our recordings made during spawning events among light levels.

## RESULTS

Total number of individual bears on the stream varied among years and among light levels. Based on size and individual markings of bears, we estimated there were 11, 20, and 13 different bears in 2000, 2001, and 2002, respectively, of which at least 3 individuals occurred during all years. Over our 3-year study, there were a maximum of 7 bears on the stream at any single time. Bears showed daily variation in foraging activity on the stream ( $\chi^2 = 128.0$ , *df.* = 11,  $P < 0.001$ ; Fig. 1). Activity of bears was highest during darkness and twilight (1700–0900 h) and lowest during daylight (1000–1600 h).

Foraging activity of bears was related to salmon density. At the start of the salmon run (late August), densities of fish were low and bears were strictly diurnal. However, as salmon densities increased, bears fished more at night, retaining this nocturnal pattern until the salmon run was over (early October), at which time they visited the stream only during daylight hours to scavenge (Fig. 2).

We evaluated the extent of spawning activity among light levels. Salmon spawning activity differed among light levels ( $F = 23.6$ , *df.* = 2, 60,  $P < 0.001$ ; Fig. 3). In both 2001 and

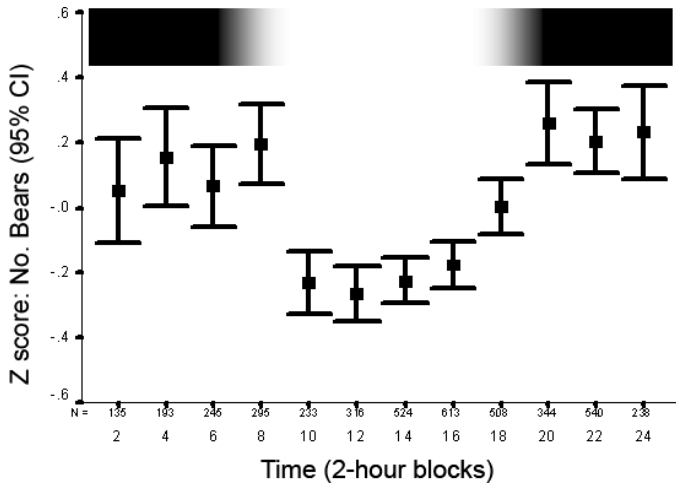


FIG. 1.—Stream visitation by bears (*Ursus americanus kermodei*) within 2-h time periods on Gribbell Island, coastal British Columbia, Canada, during the autumns of 2000–2020. Light level is represented by a horizontal bar where black is darkness and daylight is white. Error bars display 95% confidence interval.

2002, salmon spawning activity was greatest during darkness, followed by twilight, and was lowest during daylight.

Activities of the bears on the streams included search, pursuit, handling, and social interactions. The major activities were search and pursuit ( $\bar{X} = 58\% \pm 0.02\% SE$ ), handling and ingestion ( $\bar{X} = 38\% \pm 0.02\%$ ), and social interactions that occurred during these activities ( $\bar{X} = 4\% \pm 0.02\%$ ). Bears spent approximately 30% more time feeding on freshly captured salmon than scavenging (Fig. 4). Although the proportion of time spent consuming freshly captured salmon was similar among light levels ( $\chi^2 = 5.03, df = 2, P = 0.08$ ), the time spent scavenging was greatest during daylight and twilight and lowest during darkness.

We examined the frequencies of the dominant salmon capture techniques. Overall, the most common was standing (47%), followed by running (32%) then walking (21%).

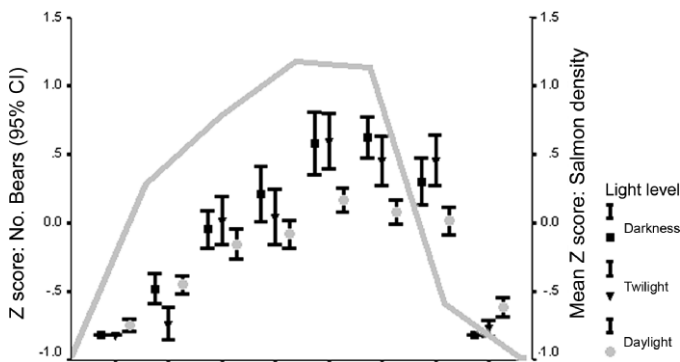


FIG. 2.—Stream visitation by bears (*Ursus americanus kermodei*) within darkness twilight and daylight, and abundance of salmon during the 8 weeks spanning the salmon run on Gribbell Island, coastal British Columbia, Canada, during the falls of 2000–2020. Error bars show 95% confidence interval of Z-scores of relative abundance of bears, whereas mean Z-score of relative abundance of salmon is indicated by the grey line.

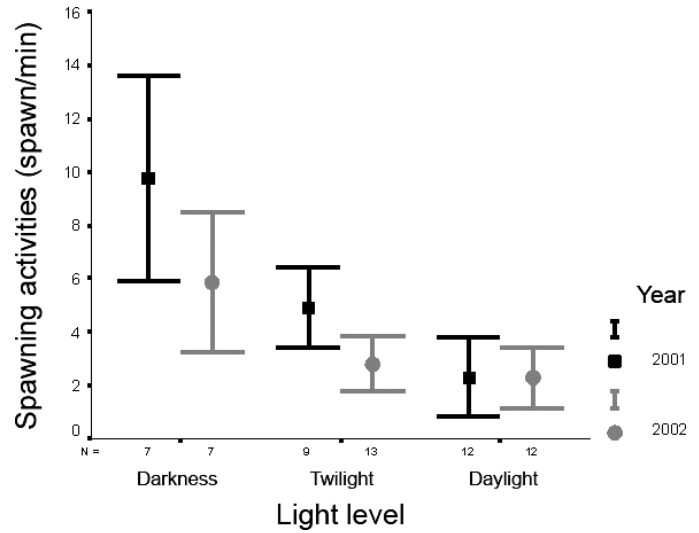


FIG. 3.—Salmon activity observed within 3 light regimes on Gribbell Island, coastal British Columbia, Canada. Spawning activity was variable between years but consistently greatest during darkness and lowest during daylight ( $P < 0.001$ ; Tukey honestly significant difference post hoc test).

Furthermore, these techniques were associated with light levels (light  $\times$  technique:  $\chi^2 = 29.2, df = 4, P < 0.001$ ; Fig. 5). Standing was most common in darkness and least common during twilight, whereas 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 log-linear model.

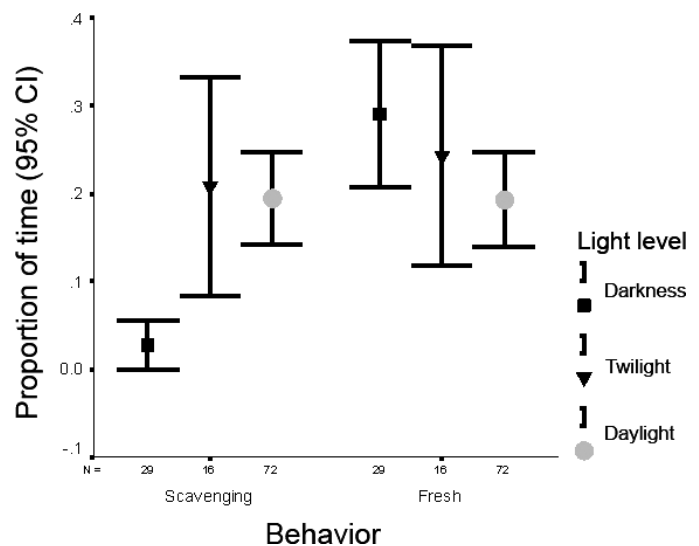


FIG. 4.—Overall proportions of time spent feeding on freshly caught and scavenged carcasses within darkness, twilight, and daylight by bears (*Ursus americanus kermodei*) on Gribbell Island, coastal British Columbia, Canada, during the falls of 2000–2020. Error bars display 95% confidence interval.  $\bar{X}_{\text{fresh}} = 22\% \pm 0.02\% SE$ ;  $\bar{X}_{\text{scavenger}} = 16\% \pm 0.02\% SE$ ;  $Z = -2.07, P = 0.038$ .

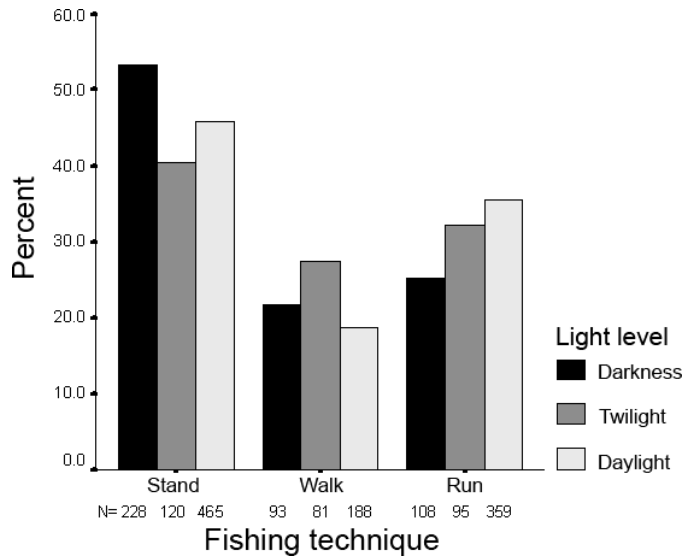


FIG. 5.—Observed proportions of the 3 fishing techniques (running, walking, and standing) used by all known bears on Gribbell Island, coastal British Columbia, Canada, within darkness, twilight, and daylight. Note the reduction of running during darkness.

Capture efficiencies varied among fishing techniques (technique  $\times$  success:  $\chi^2 = 72.26$ ,  $d.f. = 2$ ,  $P < 0.001$ ). Standing was the most efficient technique (35.4%), whereas 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 log-linear model because of their comparatively high and low capture efficiencies, respectively.

Capture efficiencies also varied among light levels (light  $\times$  success:  $\chi^2 = 11.67$ ,  $d.f. = 2$ ,  $P < 0.01$ ). The highest efficiency occurred during twilight (33.6%), whereas lower efficiencies occurred during daylight (26.5%) and 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 log-linear model. We also looked for interactions between light level, technique, and capture efficiency but there were no unique 3-way interactions (light  $\times$  technique  $\times$  success,  $\chi^2 = 1.55$ ,  $d.f. = 4$ ,  $P = 0.82$ ).

We examined the number of salmon captured for each bear per hour. For fishing bouts  $>60$  min, bears captured approximately 1–3 fish/h (2000:  $0.8$  fish/h  $\pm 0.24$  SE; 2001:  $3.5 \pm 0.53$  fish/h; 2002:  $1.5 \pm 0.33$  fish/h;  $\chi^2 = 14.4$ ,  $d.f. = 2$ ,  $P = 0.001$ ) with no differences among light levels within each year ( $P > 0.05$  for all comparisons).

## DISCUSSION

We evaluated the extent to which a large carnivore modified foraging behavior from daylight to darkness and whether prey-capture efficiencies differed among these light levels. As the salmon spawning run developed, black bears shifted foraging from daylight to twilight and darkness, which included changes

in their time budgets, fishing techniques, and salmon capture efficiencies.

Reimchen (1998a) suggested that salmon were less evasive at night and that bears increased their nocturnal foraging to exploit this vulnerability. Observations by Klinka (2004) in which evasive behavior of salmon was quantified among different light levels are consistent with this hypothesis. Bears may be at an advantage in low light because they possess a tapetum lucida that assists vision in low light (Ronald and Lee 1981). Salmonids (*Oncorhynchus*) lack a tapetum (Nicol et al. 1973) and as a consequence, may be less visually responsive to an approaching bear at low light levels and rely on their lateral line to evade predation. Furthermore, during daylight, salmon tend to shelter under logs, but during darkness they exhibit higher spawning activity in the stream shallows, leading to increased availability and susceptibility. Spawning salmon generate auditory cues that bears can exploit. We repeatedly noticed the rapid response of bears to auditory cues produced by salmon. By shifting from visual to auditory cues, nocturnally foraging bears are able to exploit this period of vulnerability in salmon. Such diel shifts in behavior due to the activity patterns and availability of prey are consistent with those observed in birds (McMahon and Evans 1992; Robert et al. 1989; Sjoberg 1989), fish (Beers and Culp 1990), and other mammals (Harcourt et al. 1995; Larivière and Messier 1997; Thomas and Thorne 2001).

Bears are typically diurnal but are thought to shift activity patterns into suboptimal foraging periods during darkness to avoid brown bears or people (Machutcheon et al. 1997; Olson et al. 1998). Reimchen (1998a, 1998b) observed that during salmon migration, black bears on Haida Gwaii, British Columbia, foraged primarily during darkness even though neither brown bears nor people were present. Reimchen (1998a) hypothesized that this shift was due to increased foraging efficiencies and lower levels of intraspecific agonistic interactions during darkness. Our data on activity periods of coastal black bears are consistent with elevated nocturnal foraging, although Klinka (2004) observed no differences in agonistic behaviour during daylight and darkness. Only when salmon began to spawn did bears begin to forage at night, yet they abandoned this nocturnal activity when the salmon run was exhausted.

Coastal bears receive 33–94% of their yearly protein from salmon through direct capture of adults as well as scavenging on carcasses (Hilderbrand et al. 1996; Jacoby et al. 1999), making the spawning season a critical time to gather sufficient energy for overwintering. During our study, bears spent about 4 times as long searching for and eating live fish than they did scavenging for carcasses, similar to results from observations on Alaskan black bears (Frame 1974). Greater consumption of live salmon suggests there are higher nutritional benefits to eating fresh fish, despite increased costs in foraging. The energy content of somatic tissues in sockeye salmon (*Oncorhynchus nerka*) declines 41% in females and 29% in males between spawning and senescence (Gende et al. 2001; Hendry and Berg 1999).

We observed that bears scavenge on carcasses more during daylight than during darkness. One might anticipate equal or

greater use of carcasses during darkness because olfactory cues should be comparable but visual cues reduced. We suggest that it is the reduced efficiencies of live capture during daylight (Klinka 2004; Reimchen 1998a) that provide increased benefits to daylight scavenging despite the reduced nutritional value of carcasses.

Bears use similar fishing techniques throughout coastal regions of western North America (Egbert and Stokes 1976; Frame 1974; Klinka and Reimchen 2002; Reimchen 1998a), with differences related to site characteristics such as the amount of tidal flats and barriers that interfere with upstream migration of salmon. We observed that techniques also are related to light levels. Frequencies of running decreased during darkness, whereas standing increased. We suggest that bears shift from visually oriented pursuit during daylight to ambush strategies during darkness using alternate cues, especially the splashing sounds of spawning salmon. In this way, bears can exploit the reduced evasiveness of salmon at night. Such shifts in sensory modes are observed in a variety of taxa where animals switch between a primary sensory mode used during daylight (typically vision) to alternate senses (tactile, auditory, or chemosensory) during darkness to use better foraging opportunities, reductions in predation risk, or both, that differ among light regimes (Beugnon and Fourcassie 1988; Collins and Hinch 1993; Downes and Shine 1998; McMahon and Evans 1992; Randall 1993; Robert et al. 1989).

During this study, overall salmon capture efficiency averaged 27%, which is comparable to data from other geographical areas. Observations of brown bears in Alaska and British Columbia have reported comparable capture efficiencies of 31% and 27%, respectively (Klinka and Reimchen 2002; Luque and Stokes 1976), whereas studies of black bears from Alaska and British Columbia have reported efficiencies of 25% (Frame 1974; Reimchen 1998a). These efficiencies are similar to those observed for other large mammalian predators, including African lions (15–38.5%—Schaller 1972; Stander 1992), hyenas (33–44%—Kruuk and Turner 1967), jackals (33%—Kruuk and Turner 1967), and North American wolves (39%—Darimont et al. 2003).

Capture efficiencies were influenced by light levels and technique. Black bears in our study had the greatest capture efficiencies during twilight (34%) and lower efficiencies during daylight (27%) and darkness (25%). Brown bears had the greatest salmon capture efficiencies during darkness (36%) and lower efficiencies during daylight (20%—Klinka and Reimchen 2002), probably due to the reduced evasiveness of salmon during darkness (Klinka and Reimchen 2002; Reimchen 1998a). These efficiencies also were influenced by capture techniques. Standing was most efficient in each light level and was most frequently used, whereas running was intermediate in efficiency and use and walking was used least often and was the least efficient of all the techniques among each light regime.

Capture rates of salmon by brown and black bears appear to be similar in most coastal areas. Bears in this study area had capture rates ranging from 0.8 to 3.5 fish/h. These rates are comparable to 2.1 fish/h reported for black bears in Alaska

(Frame 1974), and 13 fish/day (roughly 0.5 fish/h) for black bears on Haida Gwaii, British Columbia (Reimchen 2000). The capture rates in this study also are comparable to those reported for brown bears in British Columbia, which caught an average of 4.2 fish/h (Klinka and Reimchen 2002), and to dominant Alaskan brown bears, which caught an average of 1.0–3.4 fish/h (Egbert and Stokes 1976; Luque and Stokes 1976).

In summary, foraging black bears on the Pacific coast exploit daylight, twilight, and darkness during salmon spawning migration. By modifying fishing techniques among light levels, bears are able to capitalize on changes in vulnerability of salmon and maintain high capture rates in a variety of lighting environments. Although salmon are highly evasive during daylight, their elevated spawning activity during darkness provides increased acoustical cues that bears are able to exploit.

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