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

D.R. Klinka and T.E. Reimchen

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 1998*a*) 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,

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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, 1998*a*) 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;

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 hand-held 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 × 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 × 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 × 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.
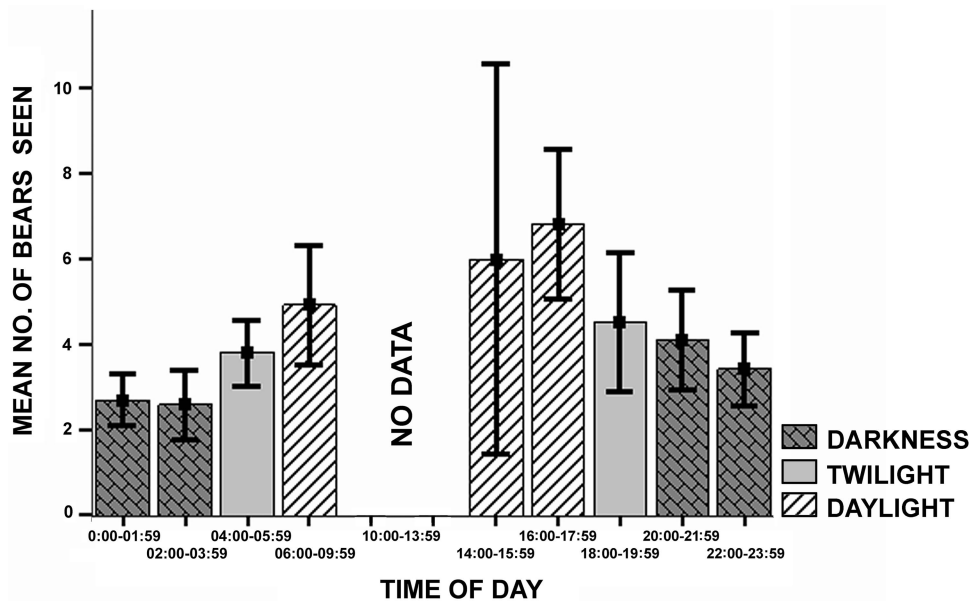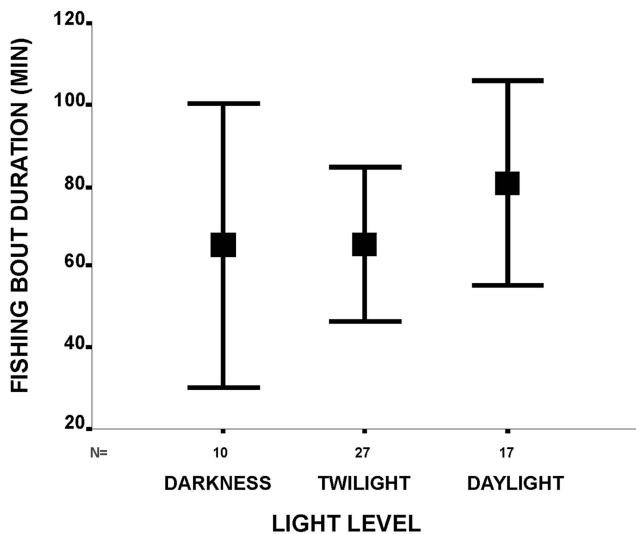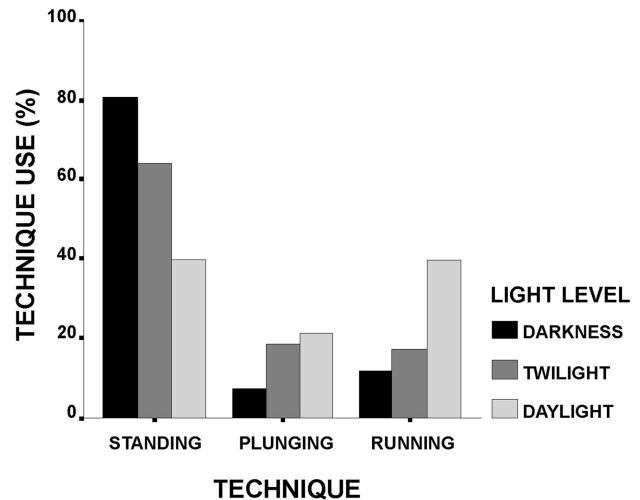

Fig. 2. Fishing-bout durations for brown bears observed within three light regimes. Mean fishing-bout duration did not differ substantially among light levels. Displayed are means and 95% confidence intervals.

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 × technique × 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 ($\chi^2 = 3.53$, $P = 0.47$).
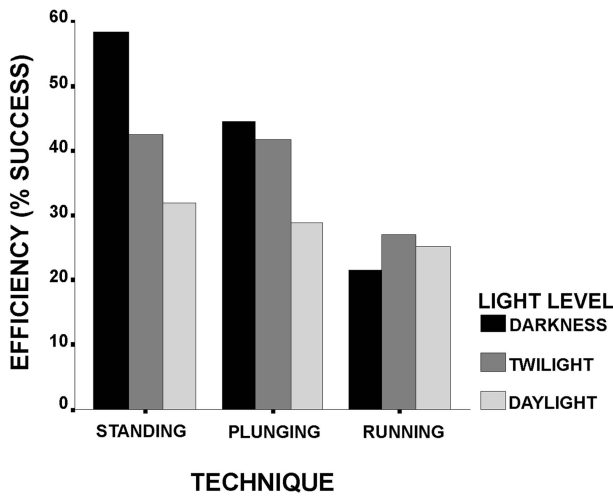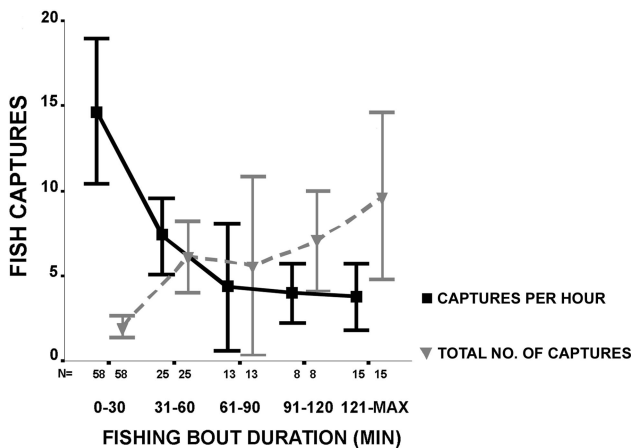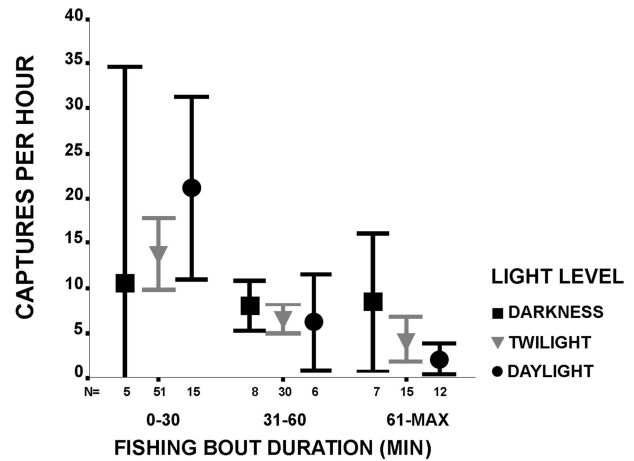

Fig. 5. The relationships between fishing-bout duration and number of fish captured and number of fish captured/h for brown bears. The number of successful captures increases with time spent fishing ($\chi^2 = 42.42$, df = 4, $P < 0.001$), while rate decreases ($\chi^2 = 15.83$, $P < 0.01$).

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, $P = 0.13$).

(Machutchon 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 (Machutchon 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.

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 (1998*a*) 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 then 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 1998*b*), 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.

Acknowledgements

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