Complementary use of motion-activated cameras and unbaited wire snares for DNA sampling reveals diel and seasonal activity patterns of brown bears (*Ursus arctos*) foraging on adult sockeye salmon (*Oncorhynchus nerka*)

Thomas P. Quinn, Aaron J. Wirsing, Brendan Smith, Curry J. Cunningham, and Jason Ching

**Abstract:** The seasonal and diel movements of predators to take advantage of shifts in prey availability are fundamental elements of their foraging ecology, and also have consequences for the prey populations. In this study, we used complementary noninvasive techniques (motion-activated cameras and hair snares) to investigate seasonal and diel activity of brown bears (*Ursus arctos*, 1758) along six proximate streams supporting spawning populations of sockeye salmon (*Oncorhynchus nerka*) in southwestern Alaska. Camera records over 3 years showed a rapid increase in bear activity around the time salmon arrived in the streams, with differences among streams corresponding to differences in salmon phenology. Bears were active throughout the day and night, but there were clear crepuscular peaks when camera data were pooled. When wire snares (to collect hair samples) were paired with cameras, the data showed similar seasonal patterns, but each technique detected bears missed by the other. Roughly equal numbers of bears left hair but no camera image, and images but no hair, at paired sites. Taken together, the results indicated a close correspondence between bear activity and salmon timing, differences in diel timing among streams, and the complementarity of data obtained by motion-activated cameras and hair snares.

**Key words:** brown bear, *Ursus arctos*, sockeye salmon, *Oncorhynchus nerka*, timing, movement, sampling techniques.


**Introduction**

Studies of foraging dynamics are crucial to understanding the influence of ephemeral resources and mechanisms of coexistence in ecological communities (Kronfeld-Schor and Dayan 2003; Holt 2008; Verspoor et al. 2011). Moreover, when focused on predators, they can offer insights into patterns of antipredator behavior (Lima and Bednekoff 1999) and numerical trends (Krebs et al. 2001) of prey, the maintenance of variation in prey populations (Reimchen and Nosil 2002), and the role of top-down forcing in community structuring (Navarrete 1996). However, despite its ecological importance, temporal heterogeneity in foraging is poorly understood for many large-bodied predators, primarily because these species tend to be sparsely distributed, wide-ranging, elusive, and therefore difficult to observe (Nifong et al. 2014; Ripple et al. 2014). In cases where direct observation and telemetry are precluded or impractical, recent advances in noninvasive sampling methods—notably fecal or hair capture for genetic analysis and camera trapping—can provide cost-effective and tractable alternatives for studying predator behavior (Cutler and Swann 1999; Long et al. 2008; Clevering and Sawaya 2010; Wasser et al. 2011). For many large carnivore species, however, the efficacy of these techniques for behavioral research, and in particular for exploring temporal variability in foraging, has not been evaluated (McCallum 2013).

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During the Pacific Rim, predation by brown bears (Ursus arctos L., 1758) and black bears (Ursus americanus Pallas, 1780) on adult anadromous Pacific salmon (genus Oncorhynchus Suckley, 1861) is a key component in stream and riparian ecosystems, as bears not only affect the salmon themselves but also direct the flow of nutrients from aquatic to terrestrial pathways (Hilderbrand et al. 1999a; Meehan et al. 2005; Helfield and Naiman 2006; Hocking and Reimchen 2009). Bears can kill a substantial fraction of the salmon in small streams (Quinn et al. 2001), especially in years when salmon are scarce (Quinn et al. 2003), and the salmon are a very important component of the bears’ diets (Hilderbrand et al. 1999b; Mowat and Heard 2006). The timing of salmon runs is highly predictable (Ricker 1972; Hodgson and Quinn 2002), though abundance varies greatly from year to year, so bears can move from stream to stream to take advantage of the temporal and spatial variation in salmon as a food resource. However, social status (Gende and Quinn 2004), risk of infanticide within species (Ben-David et al. 2004), and competition between black and brown bears (Jacoby et al. 1999) may reduce access to salmon. Thus, consumption of salmon can vary considerably among individual bears.

Despite widespread appreciation of the importance of the bear-salmon relationship for prey, predator, and the ecosystem, behavioral studies have been largely limited to places where bears congregate to capture migrating salmon such as the waterfalls on the McNeil and Brooks rivers in Alaska (Sellers and Aumiller 1994; Olson et al. 1997; Gill and Helfield 2012). These sites do not represent the smaller spawning streams where most predation occurs; observations on such streams are time consuming and often limited to one (Frame 1974; Reimchen 2000) or a very few streams (Gende and Quinn 2004). In addition, bears can be active at night (Klinka and Reimchen 2002, 2009), further complicating observational studies. Telemetry provides an effective way to gather information on bear movements (Mace and Weller 1997) but is expensive, requires the skills and permits, and necessitates the capture and handling of the animals, with possible effects on short-term behavior (Apps et al. 2004), as well as longer term impacts on fitness (Cattet et al. 2008). The use of noninvasive, passive techniques for enumerating bears and assessing their activity patterns and movements between streams would greatly advance our capacity to study the complex bear-salmon ecological relationship and, by extension, similar systems involving other species.

Hair sampling for DNA analysis and individual identification is often accomplished with barbed wire surrounding bait (Wood et al. 1999; Shardlow and Hyatt 2013), but samples can also be obtained from unbaited snares in areas regularly travelled by bears (Beier et al. 2005; Haroldson et al. 2005; Clevenger and Sawaya 2010) and from trees against which bears rub (Boulanger et al. 2008). While many samples can be obtained in this manner, information on when the bear was present depends on the frequency with which the snare is checked, and this requirement typically precludes fine-scale analysis. In addition, the efficiency of unbaited snaring is not clear; how often do bears pass by without leaving hair samples? On the other hand, cameras activated by the presence of the bear (Mace et al. 1994; MacHutchon et al. 1998; Shardlow and Hyatt 2013) can record the time when the image was taken, revealing diel activity periods and seasonal patterns of bear presence if the cameras are left unattended for long periods. Bear activity can be affected by the presence of humans, and some bears are more affected than others (MacHutchon et al. 1998; Olson et al. 1998), so noninvasive sampling that indicates diel period can be important. However, the cameras do not always obtain sufficiently good images to distinguish individuals and their capture efficiency is also unclear. Thus, there are more or less off-setting limitations associated with the use of hair sampling and cameras for the study of animals in the field in general, and bears as an example.

In this study, we pursued behavioral and methodological goals related to bear activity in streams during the salmon spawning period. First, we used cameras during the summers of 2011–2013 to document the seasonal and diel activity patterns of brown bears along six small streams used by sockeye salmon (Oncorhynchus nerka (Walbaum in Artedi, 1792)) for spawning. The streams were selected for their proximity to each other and the predictable variation in salmon spawning timing and abundance. We sought to distinguish between several possible patterns of seasonal use by bears. The bears might simply shift from stream to stream in sequence, avoiding the streams in which salmon spawn late in the early part of the season. Alternatively, they might “survey” the streams in which salmon spawn late at the beginning of the season but not return until later. Finally, the streams are near enough to each other that bears might visit them all repeatedly throughout the period when salmon are available. In addition to determining the seasonal patterns in foraging, we sought to determine the diel foraging patterns of the bears. Unlike bears preying on migratory salmon, which may themselves have diel patterns (Keeler et al. 2013), these bears are preying on salmon already in the spawning streams, facilitating determination of whether bears forage at night, in the day, or in crepuscular periods. Finally, the varying levels of human activity among the six study streams allowed us to compare bear diel activity patterns on nearby streams with daily and much less frequent human activity.

In 2013, we again set up the cameras but paired one with a barbed wire on each stream to collect hair and left another camera by itself. This study design allowed us to estimate the efficiency of each method (i.e., how often was a photo taken but no hair sample obtained, and vice versa), and it also allowed us to determine whether the additional human activity and scent associated with the camera reduced the frequency of obtaining a hair sample. The hair samples were collected to determine the number of bears on each stream and the extent of their movements between streams, but analysis of those samples is not included in this paper.

**Materials and methods**

**Site description**

Six streams flowing into Lake Aleknagik in the Wood River system of Bristol Bay, Alaska, were selected for study based on generally similar size (Table 1) and proximity to each other (Fig. 1). All are used for spawning by sockeye salmon and virtually no other species of salmon spawn there (<1% of the counts of sockeye salmon, based on annual surveys; Pess et al. 2014), so analysis of bear activity can be related to sockeye salmon without complications from other salmon species. Three streams flow into each side of the lake, and in each of these two sets of three, one stream is occupied by salmon later than the other two, facilitating comparisons regarding the timing of bear use. Happy, Hansen, and Eagle creeks are on the northeast side of the lake (approximately 4 km across) and Yako, Bear, and Whitefish creeks are on the southwest side. Previous studies in Alaska have shown that brown bears can move considerable distances during the salmon spawning season (10s of kilometres; e.g., Glenn and Miller 1980; Barnes 1990; Rode et al. 2007). Yet, we considered travel from one set of streams to the other during the season to be unlikely because, to do so, a bear would have to either swim across the lake or walk to the lake’s southern end and back up, covering a distance of roughly 11 km, passing through several areas of human development, and swimming across the Wood River. However, movement among the three streams on each side was easy (paired distances between adjacent mouths ranged from 0.8 to 4.6 km, mean = 2.0 km). All streams were accessible to bears and have well-documented annual sockeye salmon runs (Table 1) and predation by bears, determined by foot surveys during the season (Quinn et al. 2001, 2003). Of the six streams, Hansen Creek has received much heavier human use than the others, as it has been the focus of ongoing research on bear predation and salmon ecology. Every
Table 1. Length accessible to spawning sockeye salmon (*Oncorhynchus nerka*) mean width, mean depth, peak period of salmon occupancy, and median and range of index counts from 1990 to 2013 for six streams where cameras and wire were used to sample brown bears (*Ursus arctos*), as well as the side of Lake Aleknagik, Alaska, where they are located (northeast (NE) or southwest (SW)).

<table>
<thead>
<tr>
<th>Stream</th>
<th>Length (km)</th>
<th>Mean width (m)</th>
<th>Mean depth (cm)</th>
<th>Spawning period</th>
<th>Median and range of index count of salmon (1,987 – 29,788)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Happy Creek (NE)</td>
<td>6.4</td>
<td>4.7</td>
<td>22.6</td>
<td>Mid-July to late Aug.</td>
<td>3,301.5 – 7,899</td>
</tr>
<tr>
<td>Hansen Creek (NE)</td>
<td>2.1</td>
<td>2.4</td>
<td>9.8</td>
<td>Mid-July to late Aug.</td>
<td>691 – 10,276</td>
</tr>
<tr>
<td>Eagle Creek (NE)</td>
<td>2.0</td>
<td>2.4</td>
<td>12.6</td>
<td>Mid-July to late Aug.</td>
<td>1,121 – 12,714</td>
</tr>
<tr>
<td>Yako Creek (SW)</td>
<td>5.6</td>
<td>3.2</td>
<td>11.4</td>
<td>Early July to late Aug.</td>
<td>5,993 – 10,276</td>
</tr>
<tr>
<td>Bear Creek (SW)</td>
<td>3.2</td>
<td>5.1</td>
<td>19.3</td>
<td>Late July to late Aug.</td>
<td>839 – 1,987</td>
</tr>
<tr>
<td>Whitefish Creek (SW)</td>
<td>2.6</td>
<td>4.6</td>
<td>25.2</td>
<td>Late July to late Aug.</td>
<td>2,029 – 5,993</td>
</tr>
</tbody>
</table>

Moreover, the timing of spawning within the season more salmon than does Whitefish Creek, on the other side of the lake’s shore. The cameras we deployed on each stream confirmed that the presence of other humans over the course of our study was limited, consisting only of our activity and that of other researchers.

In addition to the difference in human use that was hypothesized to affect diel activity by bears, these streams were selected for their consistent differences in seasonal use by salmon. Annual surveys (peak counts of live and dead salmon) have shown that Happy and Hansen creeks have higher sockeye salmon populations than does Eagle Creek; similarly, Yako and Bear creeks have more salmon than does Whitefish Creek, on the other side of the lake (Table 1). Moreover, the timing of spawning within the season also varies consistently. Timing is more difficult to quantify than the peak count, but in each survey (1–3 each year since 1990), the numbers of live, bear-killed, and senescent dead salmon were counted. Following the method described previously (Lin et al. 2008), we used the number of senescent dead salmon as a percentage of the number of live salmon plus the number of senescent dead salmon as an index of the seasonal timing of salmon reproduction. The percentage of senescent dead salmon rises from 0% at the beginning to 100% at the end, when all salmon are dead. Averaged for a 10-day period from 30 July to 9 August (Lin et al. 2008), these values showed a clear progression in both sets of streams (Happy (44.0% senescent) vs. Hansen (8.0%) and Eagle (2.8%); Bear (14.1%) vs. Yako (9.7%) and Whitefish (0.9%)). These dates were so early that they incorporated fewer surveys of the late streams than the early ones, so we also calculated the values in a later period (8–18 August). These data showed higher proportions of the salmon dead of senescence in each population but similar sequences among populations (Happy (51.9%), Hansen (20.0%), and Eagle (8.7%); Bear (31.7%), Yako (31.4%), and Whitefish (1.8%)).

**Sampling methods with cameras and wire**

In 2010, cameras (Bushnell Trophy Cam HD) were attached approximately 2 m above the ground to trees at two locations in Hansen Creek as a pilot study and then, in 2011–2013, cameras were placed at one location along each of the six streams and directed to detect motion along the stream corridor. We affixed the cameras to trees with either hose clamps or nylon straps and positioned them such that the entire wire was in view (confirmed using initial photos of the researchers). The cameras used infrared motion sensors to trigger image capture, were equipped with an infrared flash allowing nighttime photography, and were programmed to take photographs of moving objects every 10 s. The cameras were checked about once a week, repositioned on the rare occasions that they had been dislodged by bears, and the images were downloaded to computers. Occasional gaps in the record occurred owing to malfunction, loss of battery power, poor visibility conditions, or other problems, but overall, the cameras operated throughout their periods of deployment. Data from all years were used for analysis of diel activity, but seasonal patterns were assessed using only the data from the 3 years for which data were collected in all six streams.

All photos were date and time stamped. Accordingly, when processing photos, we recorded the date, time of day, and number of
bears in each photo, after eliminating images of humans, birds, or other animals. No predators besides brown bears were observed and the only other mammals recorded were moose (Alces alces (L., 1758)). Although bears with distinguishing features (e.g., scars) were occasionally photographed, the cameras typically did not furnish good enough images to allow for individual discrimination and bears were too close to the camera for a clear image. Nevertheless, inspection of the images often revealed cases when multiple pictures were taken in quick succession, apparently of the same animal. To distinguish these from separate encounters (by the same or other bears), we examined the intervals between successive photos (Fig. 2). Many photos were taken <5 min apart and these were treated as a single “encounter” because they were likely to be of the same individual. In contrast, images >5 min apart were treated as separate encounters because individual bears remaining within the cameras’ detection range would have been captured repeatedly. These encounters were binned by day of the year and also hour of the day for analysis of seasonal and diel activity patterns. In total, there were 833 events among the six streams in all years for analysis of diel patterns. Excluding the 2010 data, which were only available at Hansen Creek for a short period, there were 774 events at the six streams in 2011–2013. We restricted analysis to the period from 19 June through 22 August because we had at least one operational camera during that period in each stream in at least 1 year, yielding 731 encounters. The number of operational cameras varied due to battery replacement, malfunction, and other field issues, so we used the mean number of detected encounters per camera-day over the 3 years as the metric for daily bear activity. For example, on 7 August, there was an operational camera on Eagle Creek in each year, but only in 2012 was a bear event recorded, so the mean value for Eagle Creek on 7 August was 0.33. On the same day of the year, the cameras on Hansen Creek detected two events in 2011, one event in 2012, and zero event in 2013, for a mean value of 1.0 event. We used these daily mean values to calculate the median of all the activity during the period of record (19 June–22 August) rather than the sum because on some dates there was not an operational camera in every year on all streams. For example, at Hansen Creek, the sum of all the daily mean values was 71.7 events and the median date was 31 July (Table 2).

In 2013, in addition to the cameras, we deployed one strand of four-pronged barbed wire at two locations, averaging 0.18 km apart on each of the six streams. The wires averaged 8 m long, had a 12 cm barb interval, and were strung directly across the stream and attached to trees on either side using fencing staples. Wires were tightened to parallel the stream’s surface at a height of 50–55 cm above the streambed at mid-channel (Haroldson et al.)
For analysis of diel patterns, inclusion of data from Hansen Creek in 2011 to 2013 were pooled to calculate the seasonal and diel activity patterns. The camera data from 2011 to 2013 were pooled to calculate the mean number of bear detections (encounters, including one or more bears) on each day for each stream from 19 June through 22 August, after which coverage was too irregular for analyses of seasonal patterns, though data were retained for diel activity analysis. The data (676 encounters recorded on 813 operational camera-days) showed very low detection rates in June and early July with a clear increase in mid-late July (Fig. 3). In addition, there was a progression in the median detection among streams, with Happy and Hansen creeks similar to each other and earlier than Eagle Creek on the eastern side of the lake, and Yako Creek earlier than Bear Creek, and both earlier than Whitefish Creek on the other side (Table 2).

For analysis of diel patterns, inclusion of data from Hansen Creek in 2010 and from the operational cameras at the end of the season (i.e., after 22 August) yielded a total of 833 encounters. Bears were recorded by cameras at all hours of the day and night, but Rao’s test of circular uniformity indicated a nonrandom pattern (U = 349.63, P < 0.001). Activity was primarily crepuscular, with peaks near dawn and early morning (0500–0800) and dusk (2100–0100) (Fig. 4). At this time of year (e.g., 1 August) and location, sunrise and sunset occur at about 0620 and 2300 AKDST (Alaska daylight savings time), respectively, off-set from noon and midnight because this region is in the western part of Alaska’s single time zone.

Among the six streams, the crepuscular pattern of activity was most clear in those with more encounters recorded (Bear = 301; Hansen = 234; Happy = 125), and in no stream was there a peak of activity at mid-day (Figs. 5a, 5b). Among the streams with fewer records (Yako = 63; Eagle = 59; Whitefish = 51), Yako Creek showed primarily nocturnal activity (0100–0600) without dusk or dawn peaks, Whitefish Creek showed activity longer into the morning (1100), and Eagle Creek showed the least periodic activity, with a mix of high and low hourly counts during all times of the day. To compare the adjacent streams, we first used Rao’s test of polar vectors, which indicated that none of the six paired comparisons was significantly different (U values ranged from 0.001 to 1.91, P values ranged from 0.99 to 0.16). However, this test is most sensitive to differences in the mean but is less sensitive to differences in pattern around the mean, so that activity concentrated in the middle of the night in one stream will not differ from a bimodal pattern of dawn and dusk activity with a similar circular mean.

We therefore then used Rao’s test of equality of dispersions and vectors, which indicated that none of the six paired comparisons was significantly different (U values ranged from 0.001 to 1.91, P values ranged from 0.99 to 0.16). However, this test is most sensitive to differences in the mean but is less sensitive to differences in pattern around the mean, so that activity concentrated in the middle of the night in one stream will not differ from a bimodal pattern of dawn and dusk activity with a similar circular mean. We therefore then used Rao’s test for equality of dispersions and vectors, which indicated that none of the six paired comparisons was significantly different (U values ranged from 0.001 to 1.91, P values ranged from 0.99 to 0.16). However, this test is most sensitive to differences in the mean but is less sensitive to differences in pattern around the mean, so that activity concentrated in the middle of the night in one stream will not differ from a bimodal pattern of dawn and dusk activity with a similar circular mean. We therefore then used Rao’s test for equality of dispersions and vectors, which indicated that none of the six paired comparisons was significantly different (U values ranged from 0.001 to 1.91, P values ranged from 0.99 to 0.16). However, this test is most sensitive to differences in the mean but is less sensitive to differences in pattern around the mean, so that activity concentrated in the middle of the night in one stream will not differ from a bimodal pattern of dawn and dusk activity with a similar circular mean. We therefore then used Rao’s test for equality of dispersions and vectors, which indicated that none of the six paired comparisons was significantly different (U values ranged from 0.001 to 1.91, P values ranged from 0.99 to 0.16). However, this test is most sensitive to differences in the mean but is less sensitive to differences in pattern around the mean, so that activity concentrated in the middle of the night in one stream will not differ from a bimodal pattern of dawn and dusk activity with a similar circular mean.

### Table 2. For each of six streams, arranged on the northeast (Happy, Hansen, and Eagle creeks) and southwest (Yako, Bear, and Whitefish creeks) sides of Lake Aleknagik, Alaska, the number of days between 19 June and 22 August in 2011–2013 that cameras were operational (camera-days), the total number of encounters with brown bears (Ursus arctos) detected (encounters), the mean number of encounters recorded each day summed over the 65-day period (mean count), and the date by which half the total had been recorded (median).

<table>
<thead>
<tr>
<th>Stream</th>
<th>Camera-days</th>
<th>Encounters</th>
<th>Mean count</th>
<th>Median</th>
</tr>
</thead>
<tbody>
<tr>
<td>Happy Creek</td>
<td>140</td>
<td>125</td>
<td>42.7</td>
<td>31 July</td>
</tr>
<tr>
<td>Hansen Creek</td>
<td>175</td>
<td>120</td>
<td>71.7</td>
<td>31 July</td>
</tr>
<tr>
<td>Eagle Creek</td>
<td>131</td>
<td>59</td>
<td>21.8</td>
<td>7 Aug.</td>
</tr>
<tr>
<td>Yako Creek</td>
<td>78</td>
<td>63</td>
<td>44.0</td>
<td>27 July</td>
</tr>
<tr>
<td>Bear Creek</td>
<td>170</td>
<td>265</td>
<td>71.9</td>
<td>9 Aug.</td>
</tr>
<tr>
<td>Whitefish Creek</td>
<td>119</td>
<td>44</td>
<td>24.2</td>
<td>13 Aug.</td>
</tr>
</tbody>
</table>

2005; Long et al. 2008). As bears moved up and down the streams, they encountered the wires and left small tufts of hair on bars.

Wires were checked throughout the salmon-spawning season, usually every other day, between 14 July and 18 August 2013. However, Hansen Creek was selected for closer study and was surveyed daily. A crew checked each wire for the presence of hair, collected any hair present, sterilized the wire using a butane torch, repaired any damage incurred to the wire, and collected camera memory cards. Location of the hair sample on the wire was noted, as one bear “encounter” could leave samples on multiple bars; however, for the present analyses, any wire that had at least one sample was considered to have detected a bear. Subsequent DNA analysis indicated that all samples were from brown bears (17 males and 27 females) rather than other animals or black bears (A.J. Wirsing, L.P. Waits, and T.P. Quinn, unpublished data).
Fig. 5. Diel patterns of brown bear (*Ursus arctos*) encounters recorded by cameras on six streams used for spawning by sockeye salmon (*Oncorhynchus nerka*) separated into the trios of streams on each side of Lake Aleknagik, Alaska: (a) Bear Creek, Yako, and Whitefish creeks; (b) Hansen, Happy, and Eagle creeks.

Comparison of hair and camera sampling

In 2013, a total of 417 individual hair samples were collected on 97 different combinations of stream and day. In addition, 560 photos were taken resulting in a total of 217 bear encounters, when grouped into photo events >5 min apart. Over the sampling period, 49% of the 97 sample days resulted in both hair samples and photo events, 14% resulted in photographs but no hair samples, 13% resulted in hair samples but no photographs, and 23% resulted in neither hair samples nor photographs (Table 3). Contrary to the prediction that the increased human activity associated with the camera might reduce bear use of the site, the efficiency of hair sample collection at wires paired with cameras was slightly higher than at wires without cameras (61.4% vs 52.5%; Table 4).

Table 3. Comparison of the efficiency of barbed wire and cameras for detecting the presence of brown bears (*Ursus arctos*) by tallying the numbers of sampling days on which each method detected a bear on each of six streams.

<table>
<thead>
<tr>
<th>Stream</th>
<th>With or without photos</th>
<th>Hair sample</th>
<th>No hair sample</th>
</tr>
</thead>
<tbody>
<tr>
<td>Happy Creek (n = 17)</td>
<td>Photo</td>
<td>13</td>
<td>0</td>
</tr>
<tr>
<td>Hansen Creek (n = 24)</td>
<td>No photo</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Eagle Creek (n = 11)</td>
<td>Photo</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Yako Creek (n = 17)</td>
<td>Photo</td>
<td>7</td>
<td>4</td>
</tr>
<tr>
<td>Bear Creek (n = 13)</td>
<td>No photo</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>Whitefish Creek (n = 13)</td>
<td>Photo</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Total (n = 97)</td>
<td>Photo</td>
<td>48</td>
<td>14</td>
</tr>
</tbody>
</table>

Note: For each stream, the sample size (n) is the number of separate dates on which the wires were checked.

Notwithstanding the discrepancies between methods in detecting the presence of bears at specific places and times, the overall patterns were very similar. Median detection dates over the period of record were strongly correlated between methods at the six streams in 2013 (Pearson’s correlation coefficient = 0.987,
terns in streams are not highly synchronous, even if the streams are species. Here, along salmon spawning streams in the Wood River means to unravel the foraging dynamics and ecological roles of these Neira et al. 2006; Quinn et al. 2011) and do not vary greatly among their phenology are under strong genetic control (Sato et al. 2000; protracted, whereas in others it is compressed; these aspects of their basic biology (Ricker 1972; Quinn 2005). In some species and populations, the spawning period is delayed. Similarly, on the lake’s west side, bears arrived first at Happy Creek, where spawning is the most delayed among the streams and we infer that these patterns reflect some combination of learning the patterns of salmon timing, was observed on both sides of the lake for hair sampling and photos, respectively (Happy Creek (both on 22 July), Hansen Creek (29 and 30 July), Eagle Creek (11 and 12 August); Yako Creek (25 and 27 July), Bear Creek (31 July and 4 August), Whitefish Creek (9 and 12 August)) (Fig. 6).

Discussion

Recent improvements in tracking technology have greatly expanded our ability to examine the behavior of free-ranging animals in their natural environments (Cooke et al. 2004), but patterns of foraging by many large carnivores remain poorly understood, in large part because these species are challenging to monitor (Ripple et al. 2014). Thus, there remains need for inexpensive and tractable means to unravel the foraging dynamics and ecological roles of these species. Here, along salmon spawning streams in the Wood River system of Alaska, we used two noninvasive approaches in an attempt to characterize bear foraging activity—camera trapping and hair snaring. In terms of bear behavior, our results revealed a progressive increase in bear presence on streams near the onset of salmon spawning, sequential seasonal use of salmon streams by bears corresponding to the timing of salmon presence, primarily crepuscular activity by bears, and slight variation among streams in diel timing of activity. We also conducted a cross-validation assessment by deploying both cameras and hair snares (wires) at one location per stream and found that the two approaches detected seasonal bear activity with similar efficacy but that each technique missed about the same number of bear encounters. The regular patterns of salmon migration and spawning timing are an integral feature of their basic biology (Ricker 1972; Quinn 2005). In some species and populations, the spawning period is protracted, whereas in others it is compressed; these aspects of their phenology are under strong genetic control (Sato et al. 2000; Neira et al. 2006; Quinn et al. 2011) and do not vary greatly among years. The sockeye salmon populations that we have been studying are especially regular in timing; the arrival of the first fish varies by no more than a few days among years, and the peak and termination of the spawning period are also very regular. However, the abundance of salmon is much more variable among years; 5-fold variation is common and 10-fold variation is not uncommon (Table 1). Despite general influences of climate on salmon population dynamics (Hilborn et al. 2003; Peterman and Dorner 2012), the patterns in streams are not highly synchronous, even if the streams are in close proximity (Rogers and Schindler 2008; Quinn et al. 2012b).

The consequence of variation in salmon abundance for bears and other predators such as wolves (Canis lupus L., 1758) (Darimont et al. 2003) and scavengers such as Bald Eagles (Haliaeetus leucocephalus (L., 1766)) (Stalmaster and Kaiser 1997; Restani et al. 2000; Elliott et al. 2011; Field and Reynolds 2013) is a mix of predictable and unpredictable aspects. To illustrate this, we calculated the Pearson correlation coefficients among all combinations of the six streams from 1990 to 2013 using the peak salmon counts. All correlations were positive but averaged only 0.36 (range: 0.09–0.71). The positive correlations are not surprising given the common environmental conditions in freshwater and marine life-history stages and the commercial fishery to which they are all exposed. However, the ability to move among streams is important to bears and other animals that take advantage of the seasonal food resource provided by the arrival, spawning, and death of salmon. Species exploiting salmon include fishes that must move within and among streams to maximize foraging opportunities (Denton et al. 2009; Ruff et al. 2011), as well as terrestrial mammals and birds. The blend of aquatic habitat occupied by salmon and the terrestrial and aquatic habitats occupied by the species foraging on them introduces some interesting variation with respect to access and guidance clues. Fishes use olfaction to detect the presence of salmon eggs (Dittman et al. 1998; Quinn et al. 2012a) and then vision for consumption, so the directional flow of streams affects the detection process, and both the salmon and the fishes feeding on their eggs are constrained to the water. In contrast, bears and other terrestrial or avian species foraging on salmon can move overland or fly and thus quickly assess and take advantage of the local variation in timing and abundance, with only occasional surveys needed to determine whether resources are available elsewhere. However, unlike terrestrial prey such as moose, the salmon are constrained to the streams, facilitating the searching process of the bears. Accordingly, there were only sporadic detections of bears at streams prior to the arrival of salmon, but the frequency increased rapidly as salmon arrived, and we infer that these patterns reflect some combination of learning the patterns of salmon timing from year to year and within-season assessment. The areas around the streams are laced with a network of trails used by bears and movement between streams on the order of a few kilometres over the gently rolling terrain would pose no problem for bears. The main constraint is likely to be the presence of other bears, as dominance relationships affect access to fishing areas (Gende and Quinn 2004). The tendency to consume salmon at the edge of the stream or in the forest also depends on salmon density (Quinn et al. 2009), likely because at high salmon densities more subordinate bears are attracted to the stream and competitive interactions with dominant bears increase (Gende and Quinn 2004).

In general, brown bear diets are thought to closely track resource phenology (Fortin et al. 2013), including the availability of salmonid fishes. For example, among tributaries of Yellowstone Lake in Yellowstone National Park, the timing and intensity of brown bear foraging mirror cutthroat trout (Oncorhynchus clarkii (Richardson, 1836)) spawning activity (Reinhart and Mattson 1989). Thus, over the course of the salmon spawning season, bears should move sequentially between proximate streams in a manner that corresponds with the timing of spawning. In accordance with this prediction, bear activity in our two focal stream networks corresponded with the arrival of spawning salmon. Specifically, on the eastern side of Lake Aleknagik, bears were detected earlier on Happy and Hansen creeks than on Eagle Creek, where spawning is delayed. Similarly, on the lake’s west side, bears arrived first at Yako Creek, where spawning is earliest, and last at Whitefish Creek, where spawning is the most delayed among the streams that we examined. By inference, bears using our stream networks apparently were able to extend their foraging window by sequentially exploiting staggered salmon runs. It might seem self-evident that mobile predators would follow the temporal patterns of prey availability, but in some cases they do not. For example, harbor

### Table 4. Comparison of the collection of brown bear (Ursus arctos) DNA samples using barbed wire at sites with and without motion-activated cameras, inferred from the percentage of days on which each wire obtained a hair sample on each of six streams.

<table>
<thead>
<tr>
<th>Stream</th>
<th>Camera at wire</th>
<th>% with hair sample</th>
<th>Sample days</th>
</tr>
</thead>
<tbody>
<tr>
<td>Happy Creek</td>
<td>With camera</td>
<td>94.4</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>Without camera</td>
<td>61.1</td>
<td>18</td>
</tr>
<tr>
<td>Hansen Creek</td>
<td>With camera</td>
<td>68.0</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>Without camera</td>
<td>65.2</td>
<td>23</td>
</tr>
<tr>
<td>Eagle Creek</td>
<td>With camera</td>
<td>54.5</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>Without camera</td>
<td>60.0</td>
<td>10</td>
</tr>
<tr>
<td>Yako Creek</td>
<td>With camera</td>
<td>61.1</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>Without camera</td>
<td>55.5</td>
<td>18</td>
</tr>
<tr>
<td>Bear Creek</td>
<td>With camera</td>
<td>37.5</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>Without camera</td>
<td>25.0</td>
<td>16</td>
</tr>
<tr>
<td>Whitefish Creek</td>
<td>With camera</td>
<td>38.5</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>Without camera</td>
<td>42.9</td>
<td>14</td>
</tr>
<tr>
<td>Total</td>
<td>With camera</td>
<td>61.4</td>
<td>101</td>
</tr>
<tr>
<td></td>
<td>Without camera</td>
<td>52.5</td>
<td>99</td>
</tr>
</tbody>
</table>

\(P < 0.001\). The expected progression of bear activity, based on salmon timing, was observed on both sides of the lake for hair sampling and photos, respectively (Happy Creek (both on 22 July), Hansen Creek (29 and 30 July), Eagle Creek (11 and 12 August); Yako Creek (25 and 27 July), Bear Creek (31 July and 4 August), Whitefish Creek (9 and 12 August)) (Fig. 6).
seals (*Phoca vitulina* L., 1758) prey heavily on Pacific herring (*Clupea pallasii pallasii* Valenciennes, 1847), but they did not take advantage of seasonal pulses of adult herring on spawning grounds (Thomas et al. 2011).

In contrast to the variation among streams in the seasonal timing of bear activity, the variation in diel activity was more subtle. The lowest frequency of detections was in mid-day (only 28% during the 12 h daytime period); there were more in the middle of the night; and the highest frequency was around dawn and dusk (Fig. 4). This pattern of movement peaks around twilight and reduced activity during daylight is commonly seen in brown bears (Kaczensky et al. 2006; Moe et al. 2007; Martin et al. 2010). Comparisons of diel activity of brown bears in streams with high and low human use within Katmai National Park, Alaska, indicated that this crepuscular pattern may reflect in part the avoidance of humans (Olson et al. 1998). In support of this idea, a study in Scandinavia showed avoidance of disturbed areas that was most acute during daytime periods of elevated human activity (Martin et al. 2010). However, some bears (typically subadults) are more tolerant of human presence than others (Olson et al. 1997). Thus, human-driven shifts to crepuscular activity may be manifest unevenly across bear populations and observations during particular periods of the day may not fully represent the abundance or social composition of bear populations. Similarly, diel activity patterns of black bears feeding on salmon in British Columbia varied over the course of the season and among bears (Klinka and Reimchen 2009). Brown bears were very successful in catching salmon at night (Klinka and Reimchen 2002), so crepuscular and nocturnal foraging may also allow bears to optimize energy intake and, if needed, minimize interactions with humans.

Of the streams we surveyed, the overall pattern of crepuscular activity was most evident in Bear Creek (Fig. 5a). At Yako Creek, most proximate to Bear Creek, the activity was largely nocturnal, whereas at Whitefish Creek, most proximate to Yako Creek, there were fewer records and a less distinct pattern, which more closely resembled that on Bear Creek (Fig. 5a). The patterns at Happy and Hansen creeks, adjacent to each other, were similar (both generally crepuscular); data from Eagle Creek showed little diel pattern, but there were fewer records (Fig. 5b). This intercreek variability with respect to diel activity of bears may stem in part from the lower sample sizes on Eagle and Whitefish creeks. Nevertheless, it could also mean that activity patterns on any given stream are a function of the local environment (including stream characteristics) and tendencies of the individual bears foraging there. By implication, patterns of bear activity at any one stream may not apply to other streams in the same system. Overall, our prediction...
that the streams with highest human use (especially Hansen and Bear creeks) would differ in the diel activity of the bears was not supported. Rather, bears may have readily moved among these proximate streams and patterns of activity may have been more a reflection of the individual bears than the streams themselves. Moreover, to the extent that bears move among streams, human influence on bears at one stream may affect their behavior elsewhere. Consistent with this conclusion, another study on different streams in the Wood River system detected generally crepuscular concentrations of activity but less diurnal activity by bears along a stream with heavy human presence compared with distant streams (Bentley et al. 2014). Taken together, these findings further underscore the spatial and temporal heterogeneities that can characterize bear use of salmon spawning streams and, more broadly, the temporal flexibility in foraging by brown bears (Fortin et al. 2013).

Our data on the complementary use of cameras and barbed wire to sample bears indicated that both approaches detected the same general seasonal activity patterns. Not surprisingly, there were cases where bears were detected by the camera but left no hair. In some images, the bear was moving at an angle that would not result in direct contact with the wire. More surprising, however, was the similar frequency of hair samples without camera images. We scrupulously examined every barb of the wire and burned off any residual material after we collected the hair, so it is unlikely that hairs undetected on one day were seen subsequently. The cameras were directed at the wire and so it is unclear why in some cases the bear was not detected. Regardless of the reason, this finding indicates that failure to detect bears or other animals on cameras does not necessarily mean that they were not near the site. Importantly, the presence of the camera did not reduce the frequency of hair samples, as might be the case if the additional scent from human activity deterred the bears from visiting a site. Of course, there was no true control; that is, there was no way of knowing how often bears would have been present had there been neither a camera nor a wire. Nevertheless, it was our general impression that the bears readily moved along the stream corridor, as well as along paths in the forest, and showed no adverse effects of encountering wires. In a number of images the contact with the wire was evident, but there were no indications of avoidance or destruction of the wire setups. We have found bear hair on tree branches overlooking the stream, and the bears seemed to treat the wires as they treated natural obstructions, which they step over or under, depending on the size of the bear, or walk through. Thus, wire sampling without bait in areas routinely used by bears can be an efficient way to obtain samples of hair for DNA or stable isotope analysis without effects on the bears. Although the cameras and barbed wires revealed similar seasonal activity patterns, these two approaches are complimentary rather than redundant. The cameras were inadequate to distinguish between numerous individuals and preliminary DNA analysis indicated that each stream was visited by at least 5 bears (Bear Creek) to at least 19 bears (Hansen Creek) in 2013 (A.J. Wirsing, L.P. Waits, and T.P. Quinn, unpublished data). In these situations, pairing cameras with wires capable of snagging hair can allow for individual identification of pictured bears. On the other hand, barbed wires cannot provide the fine-scale temporal data yielded by cameras (i.e., daily patterns of activity indicated by date and time stamps) and require frequent attention because of DNA degradation (Robinson et al. 2009). Thus, wires alone are not feasible if the timing of detection is required and (or) frequent checking is inhibited.

Finally, the attractiveness of salmon to bears no doubt facilitated the success of the wires in our study. We were able to string wires across small streams and sample hair without the use of bait or other attractant because bears were already concentrating along our study streams to forage on salmon. Our hair sampling approach would likely be less effective at times of the year when bears are more dispersed and in other systems where wires cannot easily be strung across spawning streams or nearby trails.

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