

Reports

Ecology, 97(5), 2016, pp. 1091–1098
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Kodiak brown bears surf the salmon red wave: direct evidence from GPS collared individuals

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Abstract. A key constraint faced by consumers is achieving a positive energy balance in the face of temporal variation in foraging opportunities. Recent work has shown that spatial heterogeneity in resource phenology can buffer mobile consumers from this constraint by allowing them to track changes in resource availability across space. For example, salmon populations spawn asynchronously across watersheds, causing high-quality foraging opportunities to propagate across the landscape, prolonging the availability of salmon at the regional scale. However, we know little about how individual consumers integrate across phenological variation or the benefits they receive by doing so. Here, we present direct evidence that individual brown bears track spatial variation in salmon phenology. Data from 40 GPS collared brown bears show that bears visited multiple spawning sites in synchrony with the order of spawning phenology. The number of sites used was correlated with the number of days a bear exploited salmon, suggesting the phenological variation in the study area influenced bear access to salmon, a resource which strongly influences bear fitness. Fisheries managers attempting to maximize harvest while maintaining ecosystem function should strive to protect the population diversity that underlies the phenological variation used by wildlife consumers.

Key words: brown bear; foraging; GPS collar; grizzly bear; Kodiak; landscape; phenological tracking; portfolio effect; resource subsidy; resource wave; salmon; sockeye.

INTRODUCTION

One of the central themes in ecological theory is that biodiversity enhances and stabilizes ecosystem services (Tilman et al. 1996, Kennedy et al. 2002, Hooper et al. 2005). While most biodiversity research and conservation efforts have focused on species diversity, finer levels of biodiversity (i.e., intraspecific diversity) are far more threatened; for example, extinction rates for populations are roughly 1000-times higher than those for species (Hughes et al. 1997). Thus, a critical challenge in ecology is to understand the functional significance of intraspecific diversity.

There has been recent interest in the potential for intraspecific variation to generate “portfolio effects,” in which asynchronous dynamics among populations have emergent properties expressed at higher levels of biological

organization (Schindler et al. 2015). For example, asynchrony in the population dynamics of sockeye salmon (*Oncorhynchus nerka*) dampens levels of temporal variation expressed across the aggregate of populations. This can be seen in sockeye salmon stock complexes where the boom of one population compensates for the bust in another, resulting in more stable commercial fisheries harvests (Schindler et al. 2010). Asynchrony among populations occurs not only in the interannual trends of abundance, but also in the intraannual timing of life-cycle events (i.e., phenology). For example, populations that occur in different habitats may exhibit different seasonal patterns of birth, migration, and reproduction, often due to local adaptation. There is increasing interest in whether phenological asynchrony among populations (or other scales of biological organization) can generate ecologically significant emergent properties. For example, an accumulating body of evidence shows that asynchronous phenology among prey resources can have strong positive effects on wide-ranging consumers by triggering resource waves (Armstrong et al. 2016).

Manuscript received 11 June 2015; revised 1 December 2015; accepted 11 January 2016; final version received 27 February 2016.
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Resource waves are important when a prey species is only available (or is of high quality) during a specific developmental stage and its phenology varies across prey subpopulations (variation at other levels of biological organization may also cause resource waves). For example, migrating ungulates and waterfowl take advantage of spatial variation in the timing of spring vegetation growth (the so called “green wave”) in order to consume high-quality forage for a longer period than is available at a single foraging site (Sawyer and Kauffman 2011, van Wijk et al. 2012). Similarly, surf scoters (*Melanitta perspicillata*) and rainbow trout (*O. mykiss*) track spatial variation in spawning phenology of herring (*Clupea pallasii*) and sockeye salmon (*O. nerka*), respectively, to extend their access to energy-dense eggs (Ruff et al. 2011, Lok et al. 2012). Although there is rapidly increasing interest in this topic, we often lack data to address how individuals track resources. Commonly, tracking is inferred from consumer distributional data (Fryxell et al. 2004, Lok et al. 2012, Schindler et al. 2013) or assumed based on the existence of a resource wave (Coogan et al. 2012). Using these methods, it is difficult to determine whether changes in consumer distribution and abundance are due to individuals aggregating around a local resource (only using a single prey subpopulation) or individuals tracking resources across the landscape (using several prey populations). Individual movement data is needed to provide conclusive evidence of resource tracking and to directly quantify the functional significance of resource waves to consumers.

Populations of spawning Pacific salmon (*Oncorhynchus* spp.) provide an example of how population diversity can prolong the temporal extent of prey availability across landscapes (Schindler et al. 2010, 2013, Ruff et al. 2011). Salmon breeding phenology is related to freshwater thermal regimes that vary spatially due to heterogeneity in geomorphology and hydrology (Lisi et al. 2013). Across an aggregate of salmon populations, spawning activity often spans several months, however, each individual population may only spawn for as little as two to three weeks (Gende et al. 2004, Carlson et al. 2007, Schindler et al. 2010). These brief periods of salmon spawning are spread across space and through time, creating resource waves that potentially benefit mobile consumers, however, the actual benefit depends on the degree to which mobile consumers can track the shifting mosaic of salmon resources.

Of the large number of predators and scavengers that feed on seasonally available spawning salmon (Shardlow and Hyatt 2013), brown bears (*Ursus arctos*) are perhaps the most iconic and have a well-documented dependence on salmon; fecundity, body size, and population density are all strongly correlated with salmon consumption (Hilderbrand et al. 1999). Given the importance of salmon to bears, their keen sensory abilities, and their mobility, one would expect them to be highly capable of tracking spatiotemporal variation in salmon abundance across landscapes. Schindler et al. (2013) revealed

strongly suggestive evidence that bears surf salmon resource waves and the potential for this behavior to prolong foraging opportunities for bears. However, no direct evidence exists nor do we understand the degree to which individual bears track salmon, or how much individual variation exists in tracking behavior. In this paper, we (1) quantify the salmon resource wave, (2) track individual bear movements in relation to the wave, and (3) quantify the degree to which individual bears extend their foraging opportunities by surfing the resource wave. We provide the first direct evidence of bears tracking salmon phenology and show that salmon phenological diversity prolongs the duration of bear foraging opportunities by an average of 1.7 times.

METHODS

Study site

This work was conducted in southwestern Kodiak Island, in the western Gulf of Alaska (Appendix S1). The Kodiak Archipelago has an estimated population of 3500 brown bears, hundreds of rivers, lake shoals, and streams used by spawning Pacific salmon (*Oncorhynchus* spp.), and limited human activity. The area has a rich history of bear–salmon research (Gard 1971, Barnes 1990, Van Daele et al. 2013). Barnes (1990) showed the home ranges of bears in southwest (SW) Kodiak often overlap multiple drainages and many salmon spawning sites, providing the first evidence that individual bears may exploit multiple salmon populations. The majority of the SW portion of the island is within the Kodiak National Wildlife Refuge, which is managed by the U.S. Fish and Wildlife Service. Human activity in the study area is limited and consists primarily of sport fishers, bear viewers, and hunters. The bears on the Kodiak archipelago are hunted during the fall and spring each year. Approximately 190 bears were harvested annually from 2000–2009.

Although five species of salmon spawn in SW Kodiak waters, sockeye and pink salmon (*Oncorhynchus gorbuscha*) are the most abundant (Van Daele et al. 2013). From 2000–2009, over half of the salmon returns for the Kodiak Archipelago occurred in the SW region, with an average escapement (fish remaining after harvest) of over 3.2 million. Pink salmon spawn primarily in main stem rivers and estuaries at the mouths of rivers. Sockeye salmon spawn mainly in headwater streams, on lake beaches with interstitial flow of groundwater and in lake-outlet rivers. Most of the stream habitats are narrow (<5 m), shallow (<0.5 m), and flow into lakes, rivers, or directly into the ocean. Sockeye juveniles typically rear in lakes downstream of tributary spawning streams. Four large, salmon-producing, stream–lake systems exist in the study area: Karluk, Red, Akalura, and Frazer. Preliminary results from ongoing genetic studies have detected population genetic differences in spawning sockeye salmon at the

level of habitat types within a watershed (i.e., river, lake shore, tributary stream), but not within a habitat type (e.g., tributary streams within the Karluk watershed; Jeff Olson, *personal communication*).

In addition to salmon, bears routinely consume several species of berries, including red elderberry (*Sambucus racemosa* L.), salmonberry (*Rubus spectabilis* Pursh), crowberry (*Empetrum nigrum* L.), and blueberry (*Vaccinium* spp.) and many species of grasses, sedges, and forbs (Van Daele et al. 2013).

Variation in timing of salmon availability for bears

We used the Alaska Anadromous Streams Catalog (AASC) and field observations to identify the water bodies in SW Kodiak where bears have access to salmon (Fig. 1). We found seven rivers and 68 streams listed in the AASC as salmon spawning habitat. The AASC does not list beach spawning sites; we identified 19 beach sites where sockeye salmon spawn through weekly aerial surveys. In addition to spawning sites, we included one site where a salmon-passable cataract called Dog Salmon Falls makes migrating salmon vulnerable to bear predation. These 95 sites include all of the sites where bears can access salmon within the study area, however, bear telemetry data suggests only a subset of these sites are regularly visited by bears. We characterized the average spawning phenology at 32 of these sites using 9 yr of aerial, boat, and ground observations (William Leacock, *unpublished data*). The order of salmon availability we observed among habitat types (the falls, lake-tributary streams, lake-outlet rivers, lake beaches) matched the patterns documented in similar systems driven by water temperature variation (Doctor et al. 2010, Schindler et al. 2010).

Bear movements in relation to salmon abundance

A challenge in many behavioral studies is to infer foraging behavior from movement and habitat use when data on trophic resources are not available across the entire landscape. Although we could not determine the timing of salmon availability at every site across the landscape, we characterized salmon phenology data across a large number of spawning sites ($n = 32$; 34% of all sites). Inferring bear foraging opportunity from movement behavior would be problematic if bears resided at salmon spawning sites for purposes other than salmon foraging. To test whether this was the case, we monitored streams with remote cameras and evaluated how bear presence responded to salmon abundance. In 2013, we deployed one to three time-lapse trail cameras (PC800, Reconyx, Holmen, WI, USA) along six streams in the study area. The cameras were programmed to take a photo every 5 min, 24 h/d from June through September. We counted the number of bears in each time-lapse frame, counting sows with cubs as a single independent bear. Similar to the results of Schindler et al. (2013) and Quinn et al. (2014), the peak spawning date at each site was positively

correlated with the median date of bear detections ($R^2 = 0.33$, Appendix S2). This indicated that SW Kodiak bears responded to seasonal changes in salmon availability. Most importantly, bears were virtually absent (0.6 ± 1.8 bear detections \cdot d $^{-1}$ \cdot stream $^{-1}$; mean \pm SD) when salmon were not spawning, but became ephemerally super abundant (36.6 ± 66.8 detections \cdot d $^{-1}$ \cdot stream $^{-1}$) during the salmon run. These data, in addition to prior studies (Schindler et al. 2013, Shardlow and Hyatt 2013) confirm that it is reasonable to assume that (1) bears present at spawning salmon sites were foraging on salmon and (2) the number of days spent at salmon sites accurately reflected the duration of salmon foraging opportunities for bears. To account for the occasional use of salmon spawning habitats as movement corridors, we differentiated between bear passage and residence by considering individuals to be exploiting salmon only when they exhibited GPS locations within 50 m of a salmon spawning site at least twice a day for at least 5 d in a year. For each bear, we calculated the number of salmon spawning sites attended and the total number of days spent foraging on salmon.

Movements of collared bears

Seasonal changes in bear distribution (Appendix S2) may be due to local bears aggregating at a nearby spawning site (only using a single salmon subpopulation) or individuals tracking salmon spawning phenology across the landscape (using multiple salmon populations). Distributional data cannot distinguish between these scenarios nor quantify the functional significance of salmon resource waves to bears; therefore, we collected movement data from individual bears using GPS collars.

We captured adult female brown bears in the SW region of Kodiak Island, Alaska by firing immobilization darts from a helicopter. We fitted each bear with a GPS radio collar programmed to record a location every hour from early June through mid-November. Collars contained a UHF (ultrahigh frequency) transmitter and were downloaded using an airplane fitted with a UHF receiver. From 2008 to 2014, 143 284 GPS locations were recorded from 43 individuals over 67 bear-years (some bears carried collars for more than 1 yr). We screened GPS locations for accuracy, removing relocations with a positional dilution of precision (PDOP) greater than 10 (Lewis et al. 2007). We excluded bears from the analysis if their collars failed before acquiring at least 1500 relocations in a year. Following these quality-control measures, 133 085 relocations from 52 bear-years and 40 unique bears remained for analysis.

To determine the order of habitat use for each bear, we first produced empirical cumulative distribution functions (ECDF) for each habitat and each bear. Next, we used the median date of each ECDF to determine the first and last habitat used by each of the bear-years where a bear used more than one habitat ($N = 41$ bear-years). Finally, we tabulated these values in a contingency table

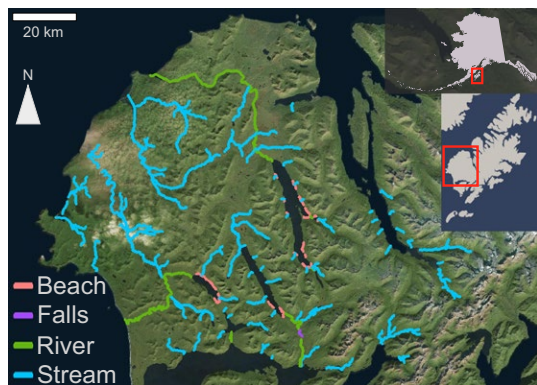


FIG. 1. Map of study area on southwest Kodiak Island, Alaska, USA. There are 95 water bodies in this area used by spawning Pacific salmon (*Oncorhynchus* spp.). These sites are colored by habitat category, each of which corresponds with a different period of salmon availability to bears. Salmon availability in streams, rivers, and lakes occurs during salmon spawning while availability at falls occurs during salmon migration. All of these sites are assumed to be available to bears in the study area.

and used a chi-squared test of independence ($\alpha = 0.05$) to determine whether the pattern of habitat visit order was random (H_0) or not (H_a).

RESULTS

Salmon were available to bears (i.e., on spawning grounds or migrating past the waterfall) at different times in different habitats. Median occupancy date for the waterfall, tributary streams, lake-outlet rivers, and lake beaches was 14 July, 3 August, 23 September, and 23 October, respectively (Fig. 2). Most of the sites visited by bears were salmon spawning grounds, however, salmon availability to bears was further prolonged by point-habitat features that made fish vulnerable to predation. At the Lower Falls of the Dog Salmon River, a small waterfall where bears intercept salmon as they migrate upriver, salmon were available as early as 3 June. Thus, habitat heterogeneity and phenological diversity

of salmon prolonged their duration of availability to bears from approximately 40 d for a single stock, to roughly 150 d for the aggregate.

We documented considerable variation in the number of spawning populations exploited by collared female bears. On average, each female bear exploited 3.1 populations of spawning salmon in a year (median = 3.0, $n = 52$, $SD = 1.5$, Fig. 4A). The maximum used by a single bear was seven sites, while one bear used no salmon sites. In general, the order in which bears visited spawning sites matched the sequence of salmon run timing (Fig. 3A,B); bears tended to visit habitats with early salmon availability first (falls and streams) and habitats with late availability last (river and lake beaches, $\chi^2 = 31.7$, $n = 41$, $P < 0.0001$, Appendix S3). Furthermore, the median date that individual bears used the habitat with the latest availability (lake beaches) was 48 d later than the median date they used the site with earliest salmon availability (the Lower Dog Salmon Falls).

The mean number of days each bear exploited salmon was 67 ($n = 52$, $SD = 33.5$), whereas the average spawning population was only available for approximately 40 d. Seventy-three percent of bears spent more than 40 d fishing for salmon. Regression analysis indicates the number of spawning populations exploited was positively correlated with the number of days each bear fished (Fig. 4B, $R^2 = 0.36$, $P < 0.0001$).

DISCUSSION

Although each individual subpopulation spawned for a brief period (~40 d), spawning activity spanned several months across all of the salmon subpopulations. The timing of salmon availability varied by habitat: salmon first appeared while migrating past waterfalls, then while spawning in streams, rivers and, finally, lake beaches. Counts of bears from time-lapse images showed that bears were unlikely to be detected at streams when salmon were not spawning (0.6 detections/d) compared to when they were spawning (31 detections/d). Given this pattern, we used GPS relocations from collared female bears to indicate bear foraging behavior. These data

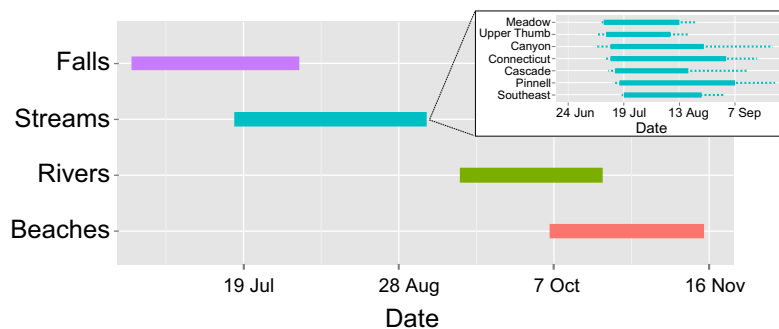


FIG. 2. Dates of salmon availability in four aquatic habitats. Inset shows salmon spawning phenology of seven streams within the study area. Solid lines indicate periods with salmon in all years, while dotted lines indicate less frequent salmon observations. Salmon are available at a single site for approximately 40 d while overall availability spans at least 150 d.

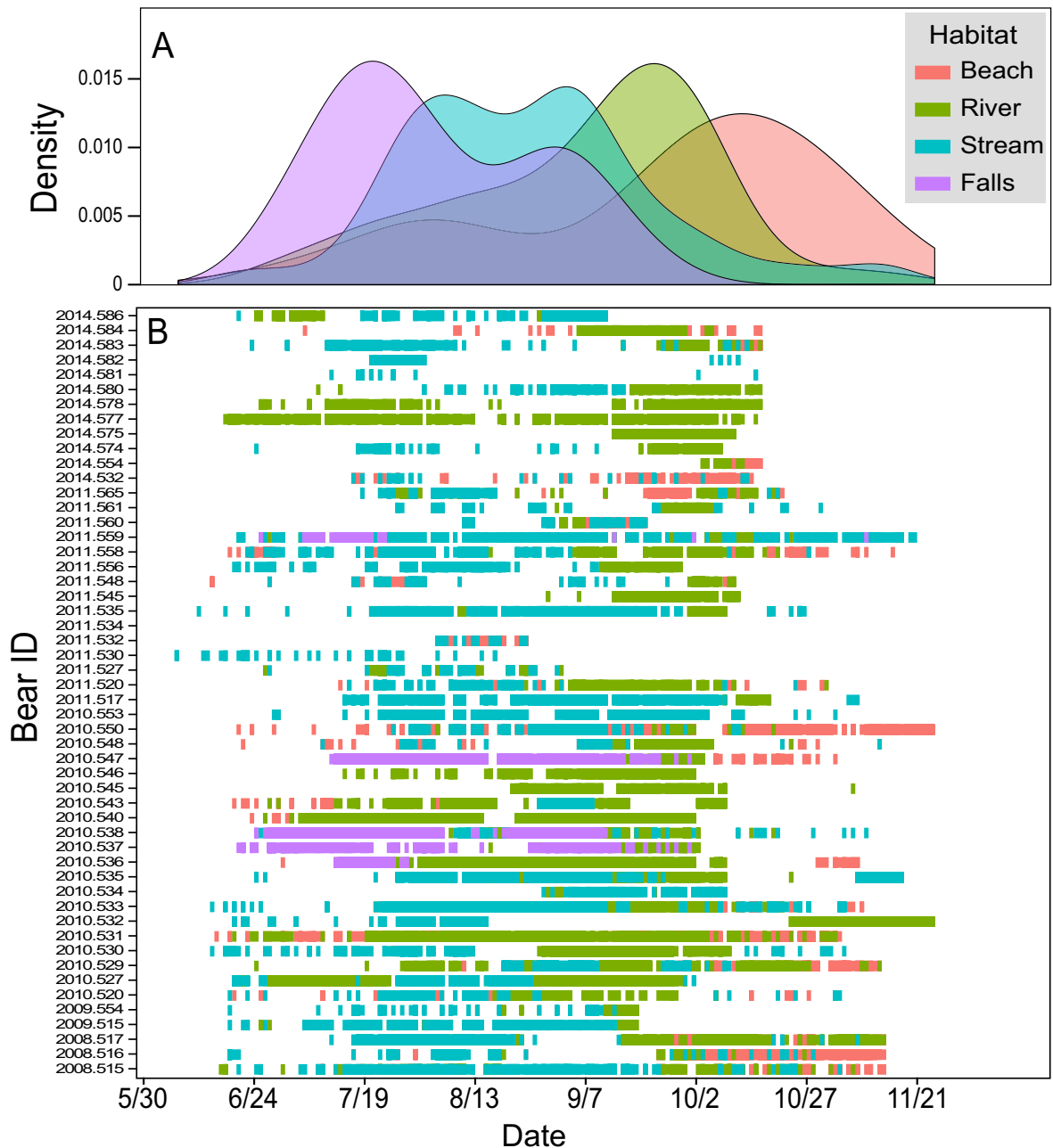


FIG. 3. Seasonal use of salmon spawning/migration sites by GPS-collared bears as a function of habitat type. (A) Location data pooled across individuals and grouped by habitat type. Data were smoothed using a kernel density estimator with a bandwidth of 7.97, which was arbitrarily selected because it highlights the general pattern in bear habitat use (Silverman 1986). (B) Individual timelines of bear use of salmon spawning/migration sites. Each row corresponds to a bear-year. Colors indicate habitat class attended each day, whereas the absence of any marker indicates periods where bears were not attending salmon sites.

showed the number of sites used by bears varied from zero to seven (mean = 3.1, SD = 1.5) and they tended to visit sites in their order of availability, using the falls (available in June/July) an average of 48 d earlier than lake beaches (available September/October). Although spawning salmon were only available at individual sites for ~40 d, bears foraged for an average of 67 d, 1.7×

longer than if there was no variation in run timing. Ruff et al. (2011) documented a similar effect; rainbow trout in their study had access to salmon 1.5× longer due to phenological variation among salmon populations. The degree to which our collared bears moved among sites correlated with their access to salmon: as bears increased the number of sites they attended, they significantly

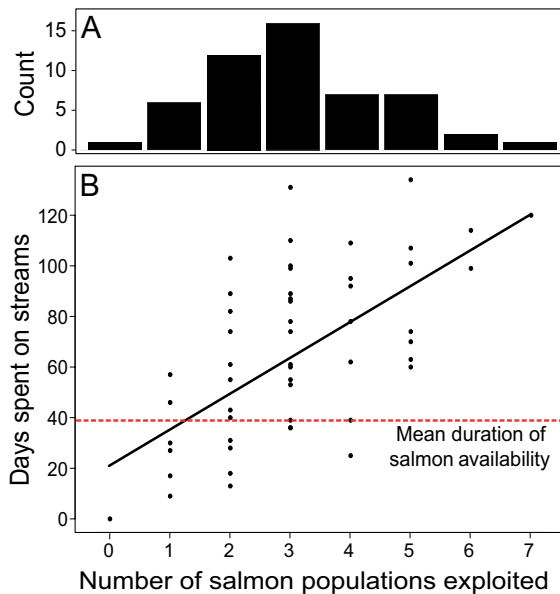


FIG. 4. (A) Histogram of the number of spawning populations exploited by GPS-collared bears. Median = 3.0 populations. (B) Number of days collared female bears ate salmon as a function of the number of salmon populations exploited. Simple linear regression shown; $P < 0.0001$, $R^2 = 0.36$. Red dashed line corresponds with the maximum length of time a bear could eat salmon if there was no phenological variation among salmon populations.

prolonged their access to salmon ($R^2 = 0.36$, $P < 0.0001$). Given that a bear's consumption of abundant prey such as salmon is limited by duration of access (because of digestive constraints on foraging rates) rather than merely abundance, our results strongly suggest that bears directly benefit from salmon life history diversity. Because we only studied the foraging habits of female bears, the results of this study are likely conservative; females have smaller home ranges than males, particularly when they have cubs (Berns et al. 1980), and their smaller body sizes make them less dependent on high calorie foods such as salmon (Welch et al. 1997, Rode et al. 2001).

Population diversity in salmon and the corresponding asynchrony in spawn timing increases the duration of salmon availability for bears. In addition, physical features along salmon migration routes, such as waterfalls or cataracts, can extend the life history phases in which salmon are vulnerable to include not only spawning, but also migration to upstream spawning sites. While point features (e.g., McNeil and Brooks Falls, Alaska) are recognized as important because they make salmon vulnerable to bears in large rivers where they are otherwise inaccessible (Quinn et al. 2001, Peirce et al. 2013), their significance in regards to timing are much less appreciated. In the Karluk system, salmon were available at the Lower Falls of the Dog Salmon River almost a month before spawners in streams.

Loss of life history diversity has the potential to erode the ecosystem services important to humans. Schindler

et al. (2010) simulated the effects of loss of population diversity on the reliability of commercial fishing harvests and found that population homogenization would result in ten times more frequent fisheries closures. Our results indicate that loss of population diversity would also impact wildlife consumers such as bears: the average bear in our study would have 48% less time to consume salmon if all of the salmon in our study area spawned at the same time. A challenge for fisheries management is to conserve diversity at the population level while managing harvest at coarser levels (i.e., watersheds consisting of dozens of populations). Population diversity is not explicitly considered in the maximum sustained yield paradigm of salmon fisheries management, yet it clearly mediates the long-term reliability of fisheries (Hilborn et al. 2003, Schindler et al. 2010) and likely the energy flows from fish to consumer species in freshwater food webs (Ruff et al. 2011, Schindler et al. 2013). Many salmon fisheries are temporally biased, substantially increasing harvest rates once escapement goals are met (Quinn et al. 2007). Given evidence for population-level variation in salmon migration phenology (Boatright et al. 2004, Doctor et al. 2010, McGlauffin et al. 2011), temporally biased fisheries may diminish population diversity by selecting against stocks with late migration phenologies (Quinn et al. 2007), which are likely associated with late spawning phenologies and thus availability to bears (Boatright et al. 2004, Doctor et al. 2010).

Given the well-documented benefits of salmon consumption, it is interesting that several bears (23% of bear-years) used salmon for <40 d and one bear was never relocated within 50 m of a salmon site. An earlier study on the Kodiak Archipelago (Van Daele et al. 2013) found that salmon accounted for an average of 48% of assimilated diets of adult female bears and 16% of females had diets consisting of less than 10% salmon (based on stable isotopes and mercury analysis). Some bears may eat few salmon because salmon availability varies across the study area. In some areas, a bear could attend multiple spawning sites with only short movements, while in others the costs of moving among sites are greater. It may also be a result of intraspecific competition at salmon sites; due to higher bear densities, there is a heightened risk of aggressive encounters (Gende and Quinn 2004) and infanticide for sows with cubs (Ben-David et al. 2004). This may cause some bears to eschew salmon for less energy-dense, but less risky, foods such as vegetation or berries.

Researchers have noted the amount of salmon consumed by bears varies by sex, age, and maternal status, with dominant males consuming the most salmon and subdominant bears the least (Van Daele et al. 2013). This may be due to allometric scaling between body mass and nutritional requirements (Welch et al. 1997, Rode et al. 2001), but likely also reflects the tendency for dominant bears to exclude less dominant bears from preferred salmon foraging sites (Gende and Quinn 2004). Although

bears adopt strategies to limit competitive interactions at spawning sites, for example, by partitioning use across space and through time (Nevin and Gilbert 2005), competition may be reduced further when several populations of salmon are spawning at the same time in multiple locations. Thus, while phenological diversity increases the duration of salmon access for bears, this benefit may only be realized by the most dominant bears unless salmon are spawning across a sufficiently large area to limit competition. In this context, it is not surprising that 73% of tracked bears used at least one stream site, while only 10% used the Lower Falls, the site that provides the earliest access to salmon.

The SW Kodiak Island study site has limited human development and recreational activity. In many other parts of Alaska, landscapes face increasing pressure for resource and infrastructure development. Recent evidence suggests that such habitat alteration often results in permeable barriers that may maintain habitat connectivity, yet interfere with the ability of consumers to track resource waves (Sawyer et al. 2013). Bears in the most productive populations often rely on salmon for the majority of their annual energy intake (Hilderbrand et al. 1999). Our results suggest that tracking of phenologically diverse salmon populations plays an important role in allowing bears to acquire energy from ephemeral salmon resources. Human actions that reduce salmon population diversity or inhibit bear movements reduce the potential for bears to eat salmon, which would likely decrease bear population productivity (Hilderbrand et al. 1999). The corollary for salmon restoration efforts is that restoring salmon abundance with homogenous hatchery stocks, in heavily fragmented landscapes, is unlikely to restore the functional link between salmon and culturally, commercially, and ecologically important consumers such as brown bears.

ACKNOWLEDGMENTS

W. Deacy and J. Stanford were supported by the Jessie M. Bierman Professorship, J. Armstrong was supported by the David H. Smith Conservation Research Fellowship, and W. Leacock was supported by the U.S. Fish and Wildlife Service (USFWS). Funding for fieldwork was provided by the USFWS Inventory and Monitoring and Refuge Programs. We appreciate the staff at the Kodiak National Wildlife Refuge and Flathead Lake Biological Station for their committed support and assistance. We thank Mat Sorum, Caroline Cheung, and volunteer field technicians Barbara Svoboda, Alex May, Bill Dunker, Tim Melham, Tyler Tran, Marie Jamison, Louisa Pless, Francesca Cannizzo, Isaac Kelsey, Mark Melham, Jane Murawski, Prescott Weldon, Shelby Flemming, Andy Orlando, and Kristina Hsu for assisting with data collection. We thank helicopter pilot Joe Fieldman and fixed-wing pilots Kurt Rees, Kevin Vanhatten, Kevin Fox, and Issac Beddingfield for their skilled flying during bear captures and aerial telemetry. Thanks also to Marie Kohler for her assistance in preparing and submitting this manuscript. Comments by Mark Hebblewhite, Kate Searle, and one anonymous reviewer improved this manuscript. This work is dedicated to the memory of Tip Leacock, who we miss dearly.

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