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Alternative foraging strategies among brown bears (Ursus arctos) fishing for chum salmon (Oncorhynchus keta) at McNeil River, Alaska

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ALTERNATIVE FORAGING STRATEGIES AMONG BROWN
BEARS (<u>URSUS ARCTOS</u>) FISHING FOR CHUM SALMON
(<u>ONCORHYNCHUS KETA</u>) AT MCNEIL RIVER, ALASKA

By

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A Thesis
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Abstract

Previous research on the fishing behavior of bears (*Ursus* spp.) along salmon streams suggests that dominant individuals forage more efficiently than their competitors; specifically, large adult males are the most efficient foragers at a given stream due to their ability to dominate the most productive locations. I tested this hypothesis by observing 26 individual brown bears (*U. arctos*) fishing for chum salmon (*Oncorhynchus keta*) at McNeil River, Alaska, over 33 days during the summer of 2010. In contrast with previous findings I did not observe strong relationships between the foraging efficiency of individual bears and the frequency with which they engaged in dominance-related behaviors (e.g., displacing competitors, stealing fish, using more productive locations). While some individuals seemed to employ dominance as a strategy to achieve high catch rates, other individuals achieved high foraging efficiency by employing alternative foraging strategies that did not involve dominance-related behaviors. My observations suggest that bears at McNeil River employ a variety of fishing strategies, of which dominance-related behavior is but one alternative. I suggest that where foraging efficiency is concerned, an individual bear's ability to develop an effective foraging strategy may be more important than its social dominance. My findings open the door to intriguing questions for future research into which physical or cognitive traits lead to the development of successful foraging strategies among brown bears fishing for salmon.

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Introduction

According to Optimal Foraging Theory (OFT), individual foragers should act to maximize their net energy intake per unit of time (Emlen 1966, MacArthur and Pianka 1966). All else being equal, those individuals that forage more efficiently should be favored by natural selection over those that forage less efficiently. Thus, OFT provides a meaningful context in which to study the foraging behavior of individual animals. At northern latitudes bears (*Ursus* spp.) have a short season in which they must consume enough calories to survive winter hibernation and, in the case of adult females, the birthing of cubs (Glenn and Miller 1980). Migrating salmon are an important source of food for these bear populations (Hilderbrand et al 1999a). During the summer months when salmon are migrating up their natal streams to spawn, bears spend a significant proportion of their time and energy foraging along salmon streams, where they often aggregate in large numbers (Stonorov and Stokes 1972). Research has shown that variations in salmon availability can affect patterns of intraspecific competition, social dominance, and reproductive success in bear populations (Klinka and Reimchen 2002, Ben-David et al. 2004, Gende and Quinn 2004). Given the importance of salmon in the seasonal life history of bears, OFT is a fitting context for the study of their foraging behavior in general and of their foraging efficiency in particular. Factors affecting foraging efficiency in bears might have important implications for the dynamics and viability of bear populations.

In turn, predation by bears exerts an important influence on salmon mortality and

spawning success, while also acting as an agent of natural selection that affects the size distributions, sex ratios and body morphology of some salmon populations (Quinn and Kinnison 1999, Reimchen 2000, Quinn et al. 2001). Recent research has highlighted the broader ecological importance of bear-salmon predation and shown that bears act as a primary vector for the distribution of salmon-borne, marine-derived nutrients from spawning streams into the surrounding landscape (Ben-David et al. 1998, Hilderbrand et al. 1999b, Helfield and Naiman 2002, 2006, Quinn et al. 2009), which can have important implications for the productivity and diversity of coastal ecosystems (e.g., Helfield and Naiman 2001, Bartz and Naiman 2005). Recent research has also suggested that salmon, via predation by bears and other terrestrial predators, act as a keystone species in riparian ecosystems (Lundberg and Moberg 2003, Helfield and Naiman 2006). Direct observations of bears foraging along salmon streams, therefore, can help deepen our understanding of a key ecological interaction.

Previous research on bear-salmon predation suggests that the foraging efficiency of an individual bear is closely related to its social dominance. Luque and Stokes (1976), Egbert and Stokes (1976), and Bledsoe (1987) all report that large adult males were the most efficient individuals among bears fishing on the Alaska Peninsula. These studies suggest that dominant individuals attained high catch rates because they had better access to the most productive fishing locations. Likewise, Chi (1999) and Gende and Quinn (2004) report similar findings among black bears (*U. americanus*) and brown bears (*U. arctos*), respectively, fishing at streams in Southeast Alaska, both concluding that social dominance has more

influence on individual catch rates than prey density. These findings all fit within a conceptual model of bear-salmon predation that I refer to here as the "dominance hypothesis," which states that behavioral traits related to dominance (e.g., size and ability to exclude competitors from preferred locations) strongly influence foraging efficiency for bears along salmon streams. A reasonable prediction based on the dominance hypothesis is that the frequency of behaviors associated with dominance among individual bears will correlate with high catch rates.

I identified four such foraging behaviors: (1) displacement (i.e., causing, in the course of a fishing bout, one or more competitors to move from a fishing location that they would otherwise occupy), (2) theft (i.e., stealing and consuming a fish caught by a competitor), (3) popular location use (i.e., foraging in a location with above-average concurrent competitor density), and (4) productive location use (i.e., foraging in a location with above-average concurrent rates of per capita fish caught per hour). I identified two additional foraging behaviors that are associated with non-dominance in bears: (5) deferral (i.e., being displaced in response to the presence of a competitor during a fishing bout), and (6) fish loss (i.e., loss of a caught fish to theft by a competitor).

If the dominance hypothesis holds true, I predicted that the four behaviors associated with dominance would have strong positive relationships to individual catch rates, and that the two behaviors associated with subdominance would have strong negative relationship to individual catch rates. The goal of this research was to test these predictions, and by extension the dominance hypothesis, using

detailed observations of brown bears fishing for chum salmon (*O. keta*) at McNeil

River, Alaska. In so doing, I aimed to establish the role that social dominance

plays in determining the foraging efficiency of brown bears fishing for salmon,

and to deepen our understanding of this important ecological interaction.

Methods

<u>Study Site</u>

The McNeil River State Game Sanctuary (MRSGS) lies in the southern foothills of the Aleutian Mountains, at the base of the Alaska Peninsula (Figure 1). The uplands of the MRSGS are vegetated primarily by dense willow (*Salix* spp.) and alder (*Alnus* spp.) thickets, while sedges (*Carex* spp.) and mud flats characterize the inter-tidal zone (Schempf and Meehan 2008). The McNeil River flows approximately 30 kilometers from its headwaters in the Aleutian Range before discharging into an inter-tidal lagoon that drains into lower Cook Inlet. The McNeil River supports a population of chum salmon (*Oncorhynchus keta*) that spawns in July, as well as smaller populations of pink (*O. gorbuscha*) and coho salmon (*O. kisutch*) that spawn in August. The Alaska Department of Fish and Game (ADF&G) has set sustainable escapement goals (SEGs) for the McNeil River chum salmon population between 13,750 — 25,750 spawners, as estimated using the area-under-the-curve method (Otis and Szarzi 2007). The McNeil River chum salmon population has exceeded its lower SEG during 13 of the past 19 years, but has exceeded its upper SEG only three times since 1988, despite a lack of commercial fishing effort during that time (Otis and Szarzi 2007). McNeil Falls is a series of waterfalls situated approximately 1 kilometer upstream from the inter-tidal lagoon that acts as a partial barrier the upstream migration of salmon in the river. The cascading nature of McNeil Falls creates several bottlenecks where salmon are vulnerable to predation by bears (Aumiller and Matt 1994). During July the largest known naturally-occurring, seasonal congregation of brown bears

gathers in the MRSGS, where up to 72 bears at once have previously been observed fishing for chum salmon at McNeil Falls (Griffin and Weiss 2011). Since its establishment in 1967, human activity in the MRSGS has been carefully managed by ADF&G to maintain this high bear density and allow for the safe observation of bears in a pristine habitat.

Data Collection

I observed predation of chum salmon by brown bears at McNeil Falls daily between the hours of 1600 and 2200, from June 30th to August 1st, 2010 (200 hours total). These dates coincided with the McNeil chum spawning migration. All observations were made from the established ADF&G viewing area on the banks of the McNeil River, which overlooks the falls and is approximately 2 m to 120 m from bears foraging in the river. I divided the area of McNeil Falls into six sections based on the historically common fishing locations of bears (Figure 2). Sections A-E represented discreet locations, while Section F served as a "catch-all" area for bears not currently fishing in one of the other sections, including a deep pool immediately below Section A. I made observations of bears at McNeil Falls at both the population and individual levels.

For population-level observations, I recorded counts of bear abundance in each section of McNeil Falls at the beginning of each hour of observation (6 counts each day), which I then totaled to find the hourly bear abundance at McNeil Falls. I adopted ADF&G's definition of bear abundance (a count of all bears in view from the observation pad) in order to maintain continuity with ADF&G's

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historical data. Additionally, during each hour of observation I recorded the number of chum salmon caught in each section, which I also totaled to find a total hourly catch. From these data I determined the per capita catch rate for each hour (chum caught per hour per bear) by dividing the total number of chum caught each hour by the average number of bears present during that hour.

My data for individual bears are composed of observations of the foraging activity of 26 different brown bears throughout the chum salmon run at McNeil Falls. These focal bears were reliably identifiable by their distinguishing physical features (e.g., scars, missing claws, ear tags), and were classified based on historical ADF&G records by sex, size class (small, medium, and large), and age class (young adult, prime adult, and older adult), as shown in Table 1. Given that I could not anticipate the arrival and departure of individual bears at McNeil Falls on a given day, my data collection was by necessity opportunistic. Since I could only accurately observe up to 5 focal individuals at once, each day I arbitrarily selected an initial subset of five bears to observe from the group of those individuals present upon my arrival at 1600 hours. I then documented the foraging behaviors of each individual during its next 4 consecutive fishing attempts. Each attempt began when an individual approached within 1 meter of the stream. Each attempt ended when a fish was consumed, lost, stolen, or when an individual moved more than 1 meter away from the stream. After each of the first 5 individuals ended its fourth attempt, I stopped observing that individual and began observing the next of the 26 focal individuals to begin a foraging bout. Limiting my daily focal observations of each individual to 4 fish each day allowed me to

cycle through as many of the focal individuals as were present on any given day. An individual was considered present for the day if it was visible from the viewing area at any point during my daily observations.

For each observed fishing attempt, I documented its location and duration and the specific techniques employed. Each fishing attempt was classified based on whether it occurred from the bank of the river, mid-channel, or in the deep pool in Section F. The technique used to catch each fish was classified in one of 5 categories: (1) with mouth alone, (2) with paws, (3) after chase, (4) while plunging underwater, or (5) by theft. The consumption of each fish was classified as occurring in one of the following 4 categories: (1) consumed where caught, pinned to body; (2) consumed where caught, pinned to vertical rock face; (3) consumed where caught, pinned to ground; or (4) consumed elsewhere. Each foraging bout was deemed to have ended when a fish was either consumed, lost or stolen, or when the individual bear moved to a new section or ceased fishing altogether and moved more than 1 meter away from the stream. During each observed fishing attempt, I also recorded the occurrence of any of the dominance-related behaviors defined above.

Data Analysis

From these observations, I calculated the efficiency of each foraging attempt in terms of fish caught per hour spent foraging. Average daily catch rates were then calculated for each of the 26 focal bears for each day based on the fish per hour scores of up to 4 fishing attempts observed for that bear on that day. In cases

where fewer than 4 attempts were observed by a bear in one day, that individual bear's daily average for the day was based on the number of attempts that were observed. To account for potentially confounding variables affecting the success of any given attempt (e.g., salmon abundance, water level, stream turbidity, time of day), I expressed foraging efficiency in terms of relative foraging performance (RFP), calculated by subtracting the concurrent per capita catch rate from each individual's average daily catch rate. For instance, if an individual averaged 2 fish per hour one day and the per capita catch rate at McNeil Falls was 1 fish per hour during the time that individual was fishing, then that individual's RFP score would be 1 (2 fish per hour – 1 fish per hour per capita). Each individual's daily RFP scores were then averaged, and the seasonal mean of each bear's daily RFP scores served as the response variable for correlation analyses.

For each of the 26 focal bears, I also calculated frequency scores for dominance-related behaviors. Displacement frequency was calculated as the proportion of observed fishing attempts during which the focal bear caused one or more competitors to move from a fishing location that they would otherwise occupy. Theft frequency was calculated as the proportion of observed fishing attempts during which the focal bear stole and consumed a fish caught by a competitor. Popular location use was calculated as the proportion of observed fishing attempts that occurred in a section in which the number of bears observed during that attempt exceeded the mean number of bears observed concurrently in all other sections of McNeil Falls. Productive location use was calculated as the proportion of observed fishing attempts that occurred in a section in which the per

capita catch rate (chum caught per hour per bear) during the attempt in question exceeded the mean per capita catch rate observed concurrently in all other sections of McNeil Falls. Deferral frequency was calculated as the proportion of observed fishing attempts during which the focal bear was displaced by a competitor. Fish loss frequency was was calculated as the proportion of observed fishing attempts during which the focal bear lost a fish to theft by a competitor. For each of the 26 focal bears I also calculated an aggregated dominance score (i.e., the proportion of observed fishing attempts that included at least one of the 4 behaviors associated with dominance) and an aggregated non-dominance score (i.e., the proportion of observed fishing attempts that included at least one of the 2 behaviors associated with non-dominance).

To assess the relationship between social dominance and foraging efficiency, I correlated seasonal mean RFP scores with dominance frequency scores. In each correlation each of the 26 focal bears represented a single data point. Since RFP and dominance frequency data violated the assumptions of parametric statistical tests (they were neither normally-distributed nor homoscedastic), I used Spearman's rho, a non-parametric correlation coefficient. Furthermore, given that this research was focused on how foragers compete and interfere with each other in a natural setting, data associated with individual bear behavior were not independent of each other. This interdependence made a classical hypothesis test for significance an inappropriate choice for these correlations. Instead, I calculated a randomized p-value for each correlation, as described by Manly (2007). The null distribution for each test was derived from 9,999 random re-

orderings of each behavioral variable, and the p-values reported herein were calculated as the relative frequency with which values equal to or greater than the observed correlation coefficient occurred in each null distribution (a one-sided test). For instance, if the observed correlation coefficient for a variable was 0.70 and randomization of that variable produced a null distribution that varied from -0.60 to 0.60, then the observed value would be the largest in the distribution (1 in 10,000, p = 0.0001). All analyses were conducted using code developed in version 2.11.1 of R (R Development Core Team 2010).

Results

In general, the mean number of fish caught per hour during each daily observation period followed the general pattern expected of seasonal salmon abundance, increasing early in the season, peaking, and decreasing late in the season. Hourly mean bear abundance appeared to follow a similar pattern, lagging behind by 1 day (Figure 3). Per capita catch rates and the average hourly catch rates of the 26 focal individuals as a group both seemed to follow a similar seasonal pattern, peaking around mid-season (Figure 4). The vast majority (92%) of fish were caught in the mouths of bears fishing in mid-channel (84%). I recorded up to 74 individual bears present at once at McNeil Falls, and the daily mean of hourly bear abundance counts ranged from 2 to 65 individuals. In all, I recorded 8,696 chum salmon caught by bears at McNeil Falls. Of those, 1,084 were caught by the 26 focal individuals during observational bouts. The variation in the relative foraging performances of each individual are described in Figure 5. Distributions for each of the dominance-related behaviors among all 26 focal individuals are shown in Figure 6.

None of the dominance-related behaviors correlated strongly with an individual's seasonal mean RFP score (Table 2). Similarly, neither aggregated dominance score nor aggregated non-dominance score showed a strong relationship with seasonal mean RFP. There was, however, a strong relationship between RFP and the frequency of an individual's daily attendance at McNeil Falls (Figure 6; Rho = 0.72, p = 0.0001).

Given the general lack of correlation between behaviors related to dominance and RFP in these data, I proceeded to examine each individual's behavioral traits. While some individuals did appear to conform to the predictions of the dominance hypothesis, exhibiting both high RFPs and relatively high frequencies of dominant behaviors, other individuals achieved high catch rates without demonstrating foraging behaviors associated with dominance (Table 3). A description of the foraging strategies of the 5 most efficient bears follows.

Bear 411, a large older adult male, had the highest RFP for the season (3.32) and appeared to be the largest bear to visit McNeil Falls in 2010. Bear 411 seemed to conform most closely to the expectations of the dominance hypothesis, displacing other bears during the majority of his fishing attempts (displacer frequency = 0.68) while never deferring to a competitor. However, Bear 411 only fished among above-average competitor density and site productivity less than half the time (popular site use = 0.47, productive site use = 0.29), and lost 10% of his fish to theft by competitors.

Bear 610, a small prime adult female with no cubs in 2010, had the second-highest RFP among bears at McNeil Falls (2.62). Bear 610 was displaced more frequently than any other bear I observed (deferral frequency = 0.47), and she lost almost half of her fish to theft (fish loss frequency = 0.49), neither of which suggests social dominance. However, Bear 610 foraged among above-average competitor densities more than half the time (popular site use = 0.57), and used productive locations almost half the time (productive site use = 0.41). Despite her lack of social dominance, Bear 610 maintained high relative foraging

performance throughout the season.

Bear 412, also a large prime adult male, had the third highest RFP among focal individuals (2.60). Given Bear 412's low attendance (only present during 3 days), one might suspect that his high catch rate could be due to chance; however, Bear 412 employed a unique technique consistent with ADF&G records of his behavior in previous years. Bear 412 foraged exclusively by fully submerging himself in a deep pool in Section F. Bear 412 frequently displaced other bears attempting to fish the deep pool (displacer frequency = 0.70), and he never deferred to a competitor. Since the deep pool was included in Section F (a catch-all section with no boundaries), his popular and productive site use statistics are confounded by counts of unrelated competitors. Bear 412 was the only bear to successfully catch a fish in the deep pool during my observations, and appears to exploit a location rarely fished successfully by other individuals.

Bear 416, a large prime adult male, had the fourth highest relative foraging performance among the focal individuals (2.41). In contrast to Bear 411 and Bear 412, Bear 416 used several different fishing locations, infrequently fishing among above-average competitor density (popular site use = 0.17), or in productive locations (productive site use = 0.12). Interestingly, Bear 416 stole just over a quarter of his total catch (theft frequency = 0.26), yet was also displaced during just over a quarter of his fishing attempts (deferral frequency = 0.28). Bear 416 appears to exploit the success of less dominant individuals, while deferring to more dominant individuals.

Bear 408, a large young adult male, had the fifth highest relative foraging

performance at McNeil Falls (2.09). Like Bear 412, Bear 408 exploited a rarely

used location, mid-channel in Section C. Bear 408's primary technique at this

location involved sitting mid-channel and facing downstream, thus creating an

eddy into which salmon could swim. Historical ADF&G records do not indicate

that any other bear has employed this fishing technique at McNeil Falls since the

inception of the MRSGS (L. Aumiller, personal communication). Given his

unique fishing location, Bear 408's popular and productive site use statistics

mostly reflect his own presence and success.

Discussion

I found limited support for the dominance hypothesis in these data. My analysis found no strong relationships between the frequency of dominance-related behaviors and foraging efficiency across individuals. An examination of the most efficient foragers at McNeil Falls this season reveals that bears that employ alternative foraging strategies unrelated to dominance were very efficient. The strong relationship between RFP and daily attendance suggests that an individual's familiarity with McNeil Falls (e.g., the specific morphological features influencing salmon vulnerability) plays an important role in foraging efficiency. I suggest that a strategy-based view of bear-salmon predation, in which each individual adapts its behavior into a strategy that works at a particular location, may be more applicable than a dominance-based view. Rather than supplanting the dominance hypothesis, this broader conceptual model would acknowledge that while some bears employ dominance to achieve high catch rates along salmon streams, others use alternative strategies to forage with comparable efficiently.

One important caveat to this suggestion relates to this study's lack of data describing differences in energy expenditure associated with each individual's foraging behavior. For the purposes of this study I have used time spent foraging as a surrogate for the overall energetic costs of foraging. Within the context of OFT, however, the true measure of foraging efficiency is the amount of net energy gained per unit of time spent foraging (Emlen 1966, MacArthur and Pianka 1966). It is possible that the alternative foraging strategies that I have

documented are more energy-intensive than those that are dominance-based, which would offset the apparent efficiency of the alternative techniques. Certainly, some individuals are more active than others while foraging (e.g., Bear 412, who dove in a deep pool for fish); however, it is important to note that salmon are plentiful at McNeil Falls and very easy for bears to catch and consume. Since the energy return for bears foraging on salmon is so high (Hilderbrand et al 1999a), it seems likely that the apparent energy expenditures of even the most active foraging strategy are negligible compared to the energy gained from any salmon caught. This would render any differences in energy expended between different foraging strategies insignificant.

Another important consideration is that my selection of focal individuals was an opportunistic (non-random) sample of possible individuals, based on my ability to visually identify them throughout the season. It is possible that unobserved individuals were both more efficient and more dominant than the focal individuals, skewing these data. I consider this to be unlikely, however, given that the average daily catch rate of the 26 focal individuals was consistently higher than the daily per capita catch rate for all bears at McNeil Falls (Figure 4). In fact, it stands to reason that our sample is likely biased toward those bears that are most familiar with McNeil Falls (given that they are well-documented historically and familiar to ADF&G staff), and hence the most successful foragers.

Analyses of size as a factor influencing foraging efficiency proved inconclusive due to the fact that the group of focal individuals was heavily skewed toward large adult male bears (23 of 26). While this demographic bias is representative of

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the current population of bears that frequent McNeil Falls, this was not the case in the 1970s, when the population had a more balanced sexual composition (Griffin and Weiss 2011). This demographic change may help explain the discrepancy between my findings and those of previous studies at McNeil Falls (Luque and Stokes 1976, Egbert and Stokes 1976, Bledsoe 1987) and elsewhere (Chi 1999, Gende and Quinn 2004). The success of alternative foraging strategies may be frequency-dependent. That is, alternative strategies may prove more successful at sites where many dominant individuals forage and less so at sites with few dominant foragers. This is analogous to recent findings regarding the success of alternative reproductive strategies among salmonid fishes, where small-bodied, sexually-precocious males (i.e., jacks) have been shown to be more successful when they comprise a smaller proportion of the population, relative to large-bodied adult males (Berejikian et al. 2010). It is possible that the success of alternate foraging strategies among bears is similarly frequency-dependent.

In conclusion, my research suggests that dominance does not always play an important a role in the foraging efficiency of brown bears fishing at salmon streams. Non-dominant bears can forage with comparable efficiency by developing alternative foraging strategies that are adapted to specific locations. This finding makes room for a strategy-based conceptual model of bear-salmon predation, where social dominance is one among many possible strategies that an individual can employ. A strategy-based view of bear-salmon predation suggests intriguing possibilities for future research into which traits contribute to development of successful foraging strategies. While comparative studies at other

salmon streams where bears congregate to fish would shed light on the breadth of

foraging strategies and where they are applied, longitudinal studies of individual

bears (e.g., observations of cubs across consecutive seasons or family groups

across multiple generations) could investigate how bears learn and develop

specific foraging strategies. Future research could elucidate, for instance, whether

physical traits (e.g., eyesight or reaction times) or cognitive traits (e.g., learning

and cognition) contribute more to the development of efficient foraging strategies

among brown bears. For now, it seems clear that social dominance is only one

among several alternative strategies that brown bears employ to forage for salmon

efficiently.

Table 1: Demographic information and foraging performance of 26 focal brown bears observed at McNeil Falls. Sex, Size Class, and Age Class were determined using visual cues or were based on known histories from ADF&G bear identification records. Relative foraging performance (RFP) is the seasonal mean of each individual's daily foraging efficiency relative to the concurrent per capita catch rate of all other bears at McNeil Falls.

Bear Number	Sex	Size Class	Age Class	RFP
411	Male	Large	Older	3.11
610	Female	Small	Prime	2.62
412	Male	Large	Prime	2.60
416	Male	Large	Prime	2.41
408	Male	Large	Young	2.09
403	Male	Large	Prime	1.82
401	Male	Large	Prime	1.80
424	Male	Medium	Young	1.78
463	Male	Large	Prime	1.75
405	Male	Large	Prime	1.68
413	Male	Large	Prime	1.68
417	Male	Large	Prime	1.60
404	Male	Large	Prime	1.52
419	Male	Large	Prime	1.34
444	Male	Medium	Young	0.94
607	Female	Small	Prime	0.84
429	Male	Large	Prime	0.31
454	Male	Large	Prime	0.19
410	Male	Large	Prime	0.16
629	Female	Small	Young	-0.24
450	Male	Large	Prime	-0.36
466	Male	Large	Prime	-0.44
449	Male	Medium	Young	-0.44
462	Male	Medium	Young	-0.60
451	Male	Medium	Young	-0.65
456	Male	Medium	Young	-1.36

Table 2: Correlations of individual seasonal mean relative foraging performance (RFP) scores and frequencies of dominance-related behaviors for 26 focal bears at McNeil Falls. P-values were calculated based on one-sided randomization tests of 9,999 re-orderings of each behavioral variable.

Behavior	Spearman's rho	p-value
Displacement Frequency	0.12	0.27
Theft Frequency	-0.37	0.97
Popular Site Use	0.25	0.12
Productive Site Use	0.32	0.11
Dominant Aggregate	0.3	0.21
Deferral Frequency	-0.32	0.11
Fish Loss Frequency	0.02	0.53
Nondominant Aggregate	-0.25	0.27
Daily Attendance	0.72	< 0.01

Table 3: Relative foraging performance (RFP) scores and frequencies of six dominance-related behaviors for 26 focal bears at McNeil Falls. Each variable was calculated as the frequency with which an individual's foraging bouts included an instance of each behavior. The aggregate statistics were the frequency with which each individual's foraging bouts included at least one behavior. Daily attendance was calculated as the number of days during which an individual bear was observed at McNeil Falls from June 30 to August 1, 2010.

| Bear Number	RFP	Displacement Frequency	Theft Frequency	Popular Site Use Frequency	Productive Site Use Frequency	Aggregated Dominance	Deferral Frequency	Fish Loss Frequency	Aggregated Non-dominance	Daily Attendance
411	3.11	0.68	0.00	0.47	0.29	0.86	0.00	0.10	0.13	33
610	2.62	0.24	0.00	0.57	0.41	0.73	0.47	0.49	0.73	20
412	2.60	0.70	0.00	0.64	0.39	0.92	0.00	0.00	0.00	3
416	2.41	0.11	0.26	0.17	0.12	0.34	0.28	0.00	0.35	25
408	2.09	0.07	0.00	0.19	0.33	0.40	0.00	0.11	0.14	27
403	1.82	0.20	0.00	0.37	0.27	0.48	0.00	0.09	0.11	27
401	1.80	0.34	0.00	0.52	0.37	0.68	0.00	0.01	0.01	21
424	1.78	0.00	0.00	0.31	0.19	0.37	0.24	0.12	0.33	31
463	1.75	0.10	0.00	0.34	0.21	0.42	0.15	0.00	0.19	21
405	1.68	0.57	0.02	0.07	0.31	0.69	0.14	0.03	0.18	21
413	1.68	0.13	0.00	0.31	0.19	0.39	0.13	0.23	0.32	26
417	1.60	0.72	0.00	0.79	0.56	1.05	0.00	0.00	0.00	14
404	1.52	0.23	0.00	0.07	0.29	0.37	0.00	0.04	0.05	22
419	1.34	0.10	0.00	0.31	0.19	0.39	0.15	0.00	0.19	20
444	0.94	0.10	0.00	0.19	0.17	0.25	0.33	0.00	0.41	27
607	0.84	0.18	0.08	0.65	0.46	0.82	0.36	0.46	0.67	17
429	0.31	0.14	0.10	0.19	0.11	0.25	0.12	0.00	0.15	13
454	0.19	0.20	0.00	0.35	0.21	0.44	0.10	0.00	0.13	9
410	0.16	0.14	0.00	0.27	0.16	0.34	0.06	0.03	0.08	5
629	-0.24	0.00	0.42	0.07	0.10	0.49	0.35	0.10	0.46	7
450	-0.36	0.15	0.00	0.40	0.25	0.50	0.00	0.00	0.00	2
466	-0.44	0.45	0.00	0.37	0.23	0.58	0.10	0.00	0.13	1
449	-0.44	0.00	0.53	0.52	0.37	0.71	0.33	0.00	0.41	9
462	-0.60	0.00	0.00	0.15	0.11	0.18	0.45	0.25	0.63	6
451	-0.65	0.00	0.10	0.04	0.18	0.22	0.10	0.26	0.35	2
456	-1.36	0.00	0.15	0.45	0.32	0.56	0.45	0.15	0.60	3
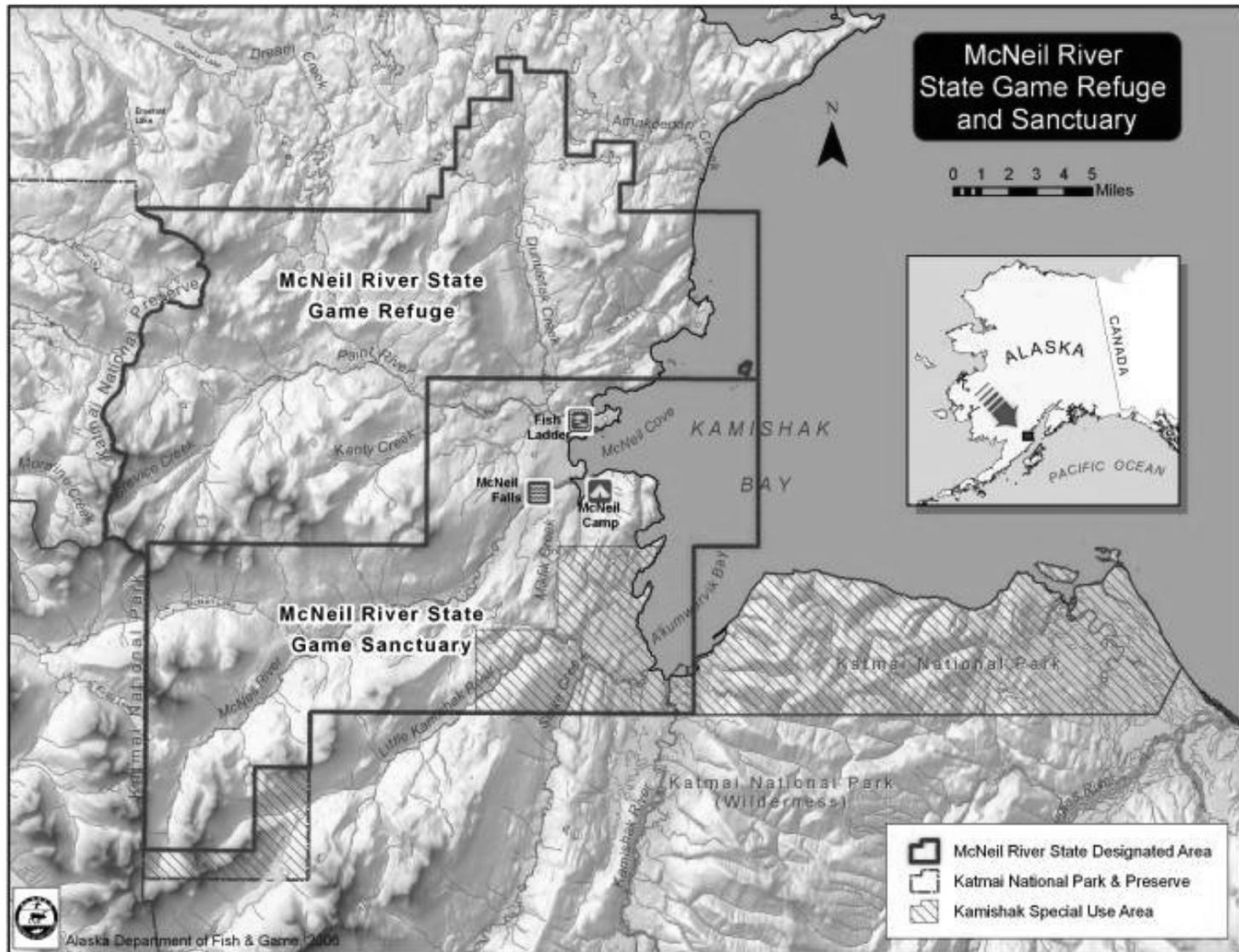
Figure 1: Location of study site, McNeil Falls, in the McNeil River State Game Sanctuary. Map courtesy ADF&G.
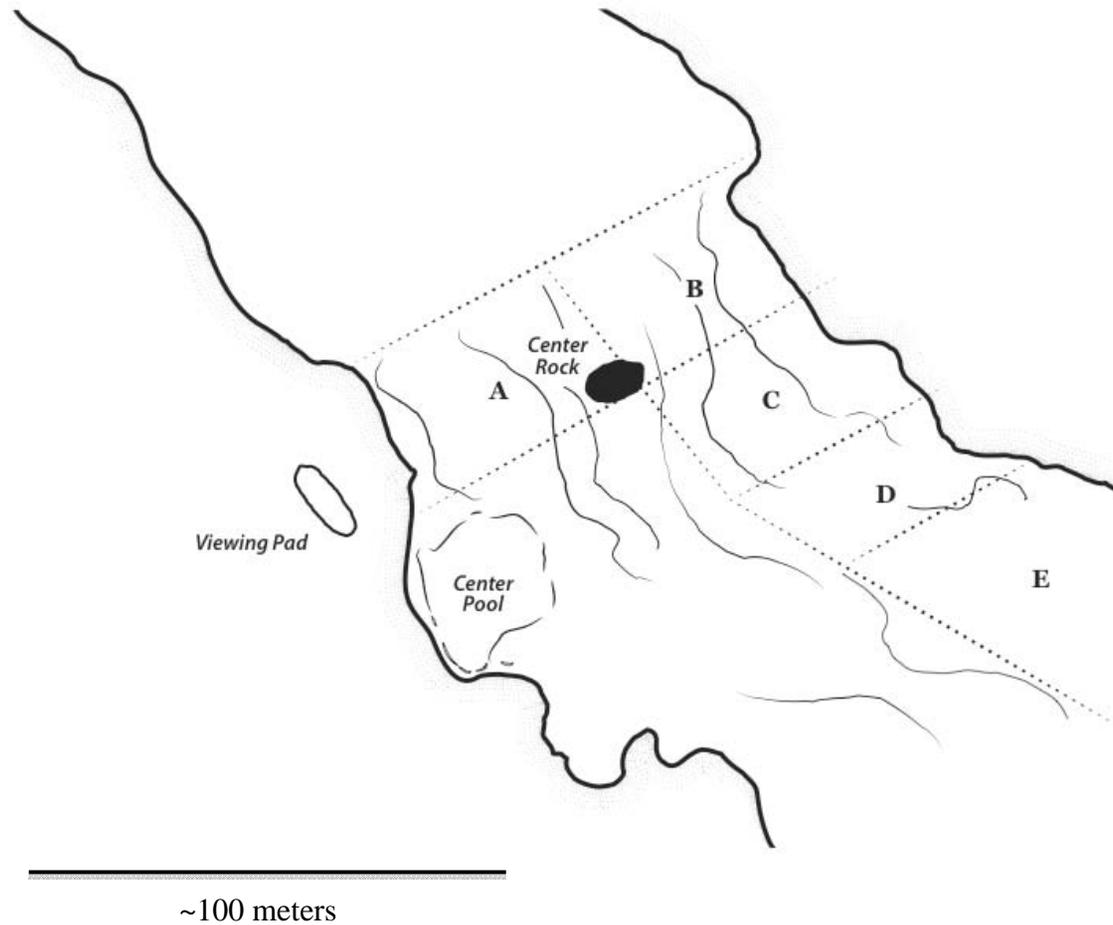
Figure 2: Aerial view of McNeil Falls showing Sections A-E (Section F was defined as anywhere outside Sections A-E). All data were collected from the Viewing Pad overlooking McNeil Falls. Image created by R. Parry (WWU) from a photo provided by T. Otis (ADF&G).
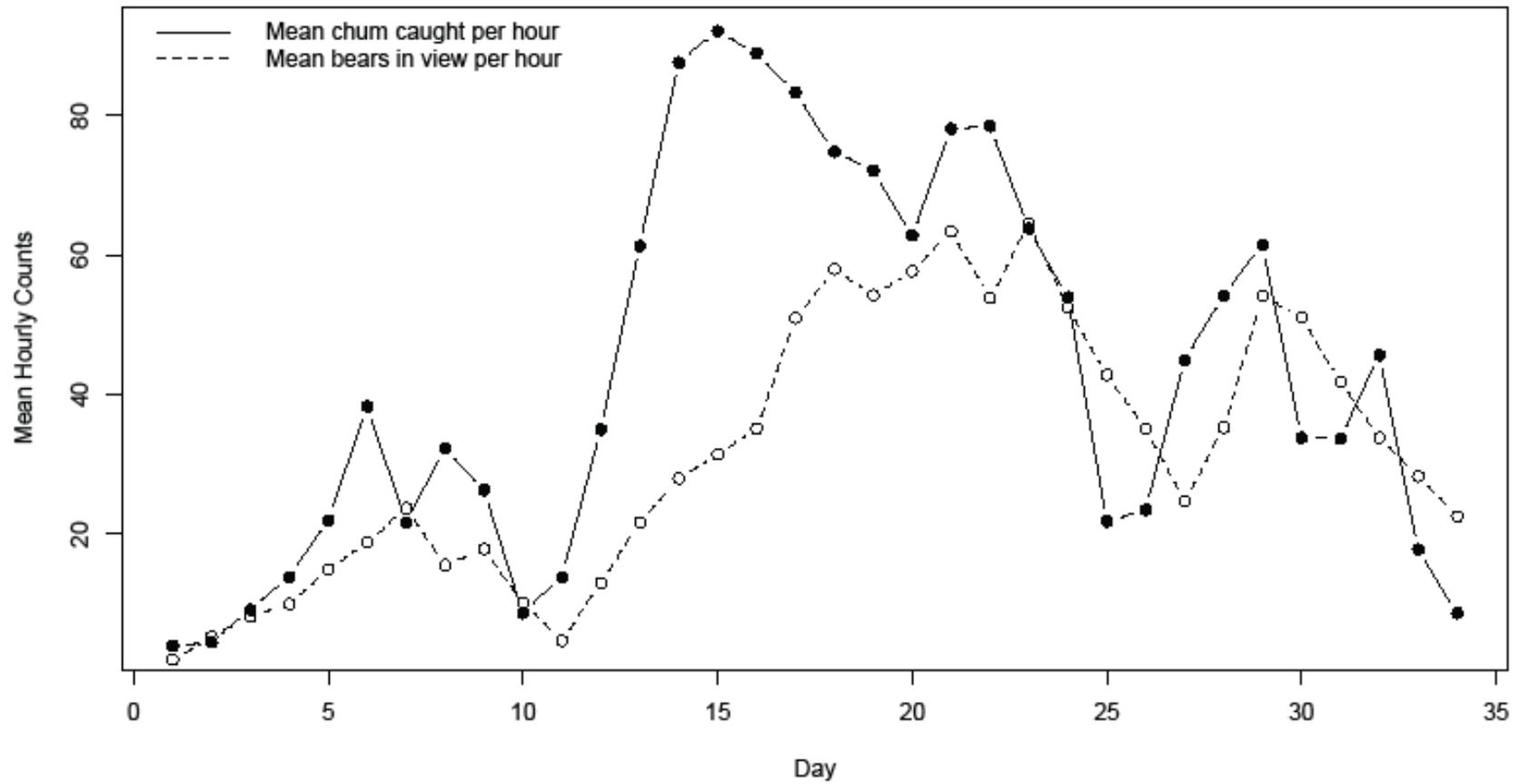
Figure 3: Daily mean hourly counts of bears present and fish caught at McNeil River from June 30 to August 1, 2010. There is a significant correlation between the mean number of fish caught each hour one day and the mean number of bears observed each hour the next day (Spearman's rho = 0.83, randomized p-value = 0.0001).
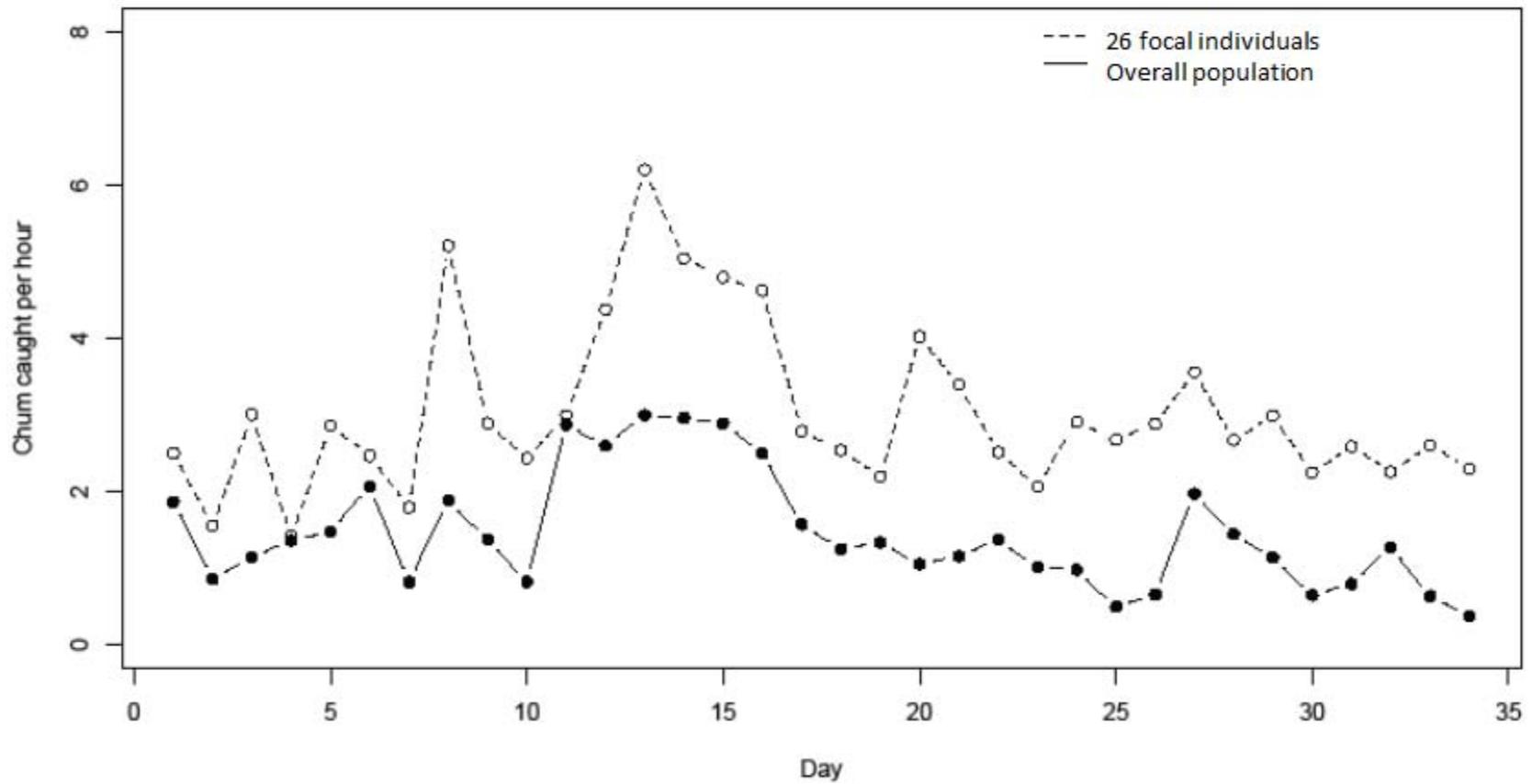
Figure 4: Mean hourly catch rates (chum caught per hour per bear) per day for 26 focal bears and the overall population of bears observed at McNeil Falls from June 28 to August 1, 2010.
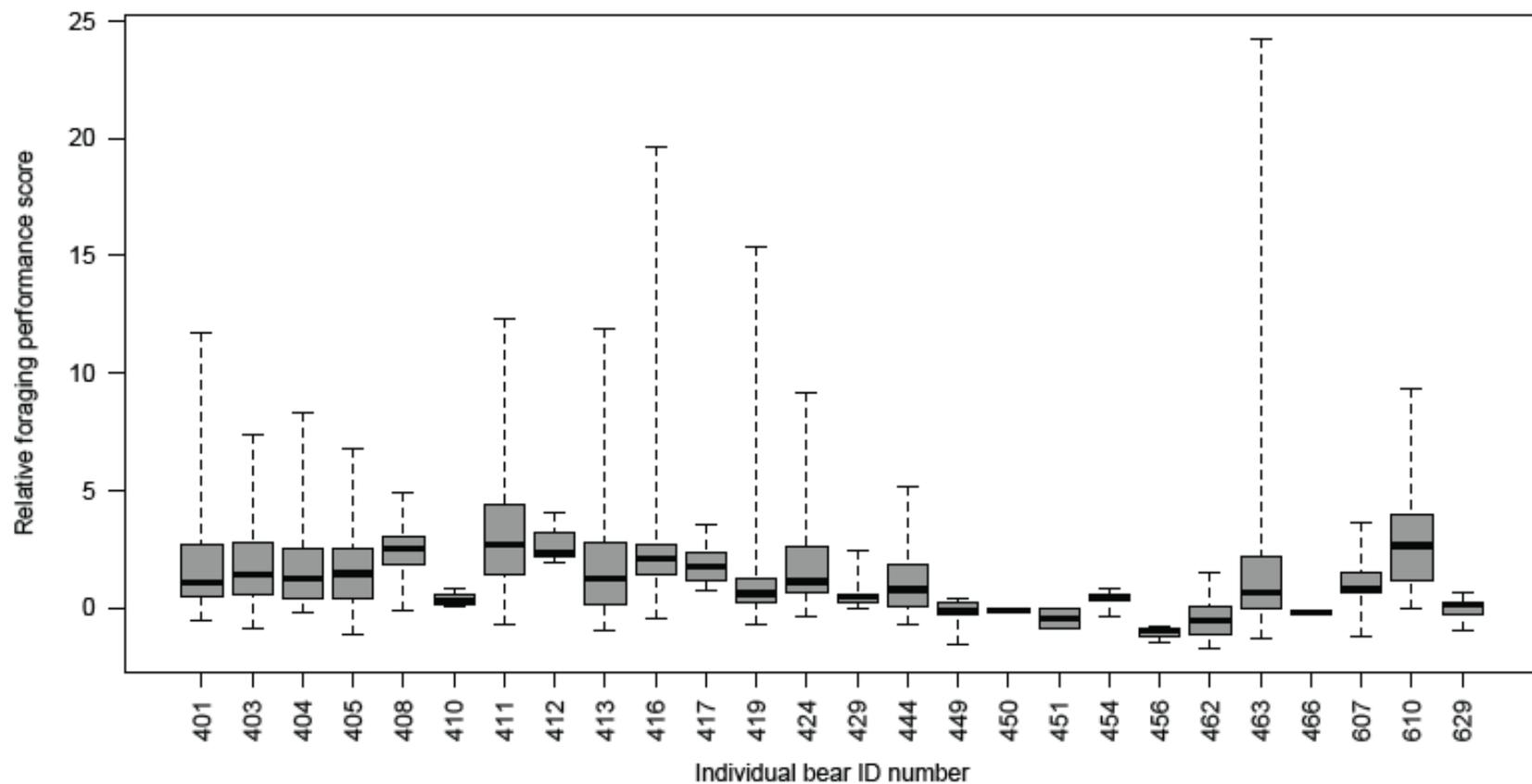
Figure 5: Daily relative foraging performance (RFP) scores of 26 focal bears observed at McNeil Falls. Black bars in the box plots represent the median value, while grey boxes represent the middle 50% of observed data points for each individual. Dashed lines extend above and below to represent the upper and lower 25% of observed data points respectively.
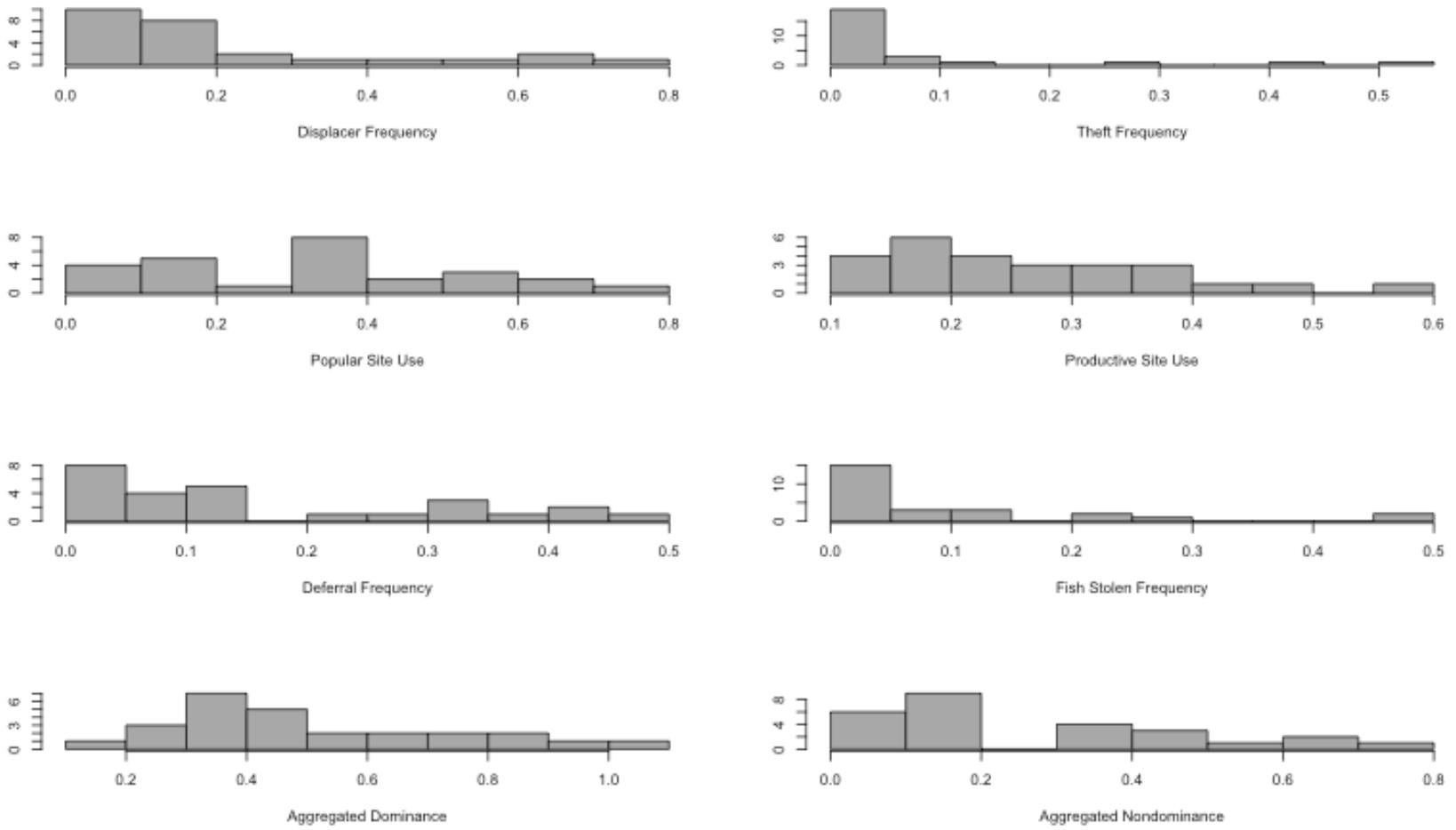
Figure 6: Frequency distributions for dominance-related behaviors among bears observed at McNeil Falls.
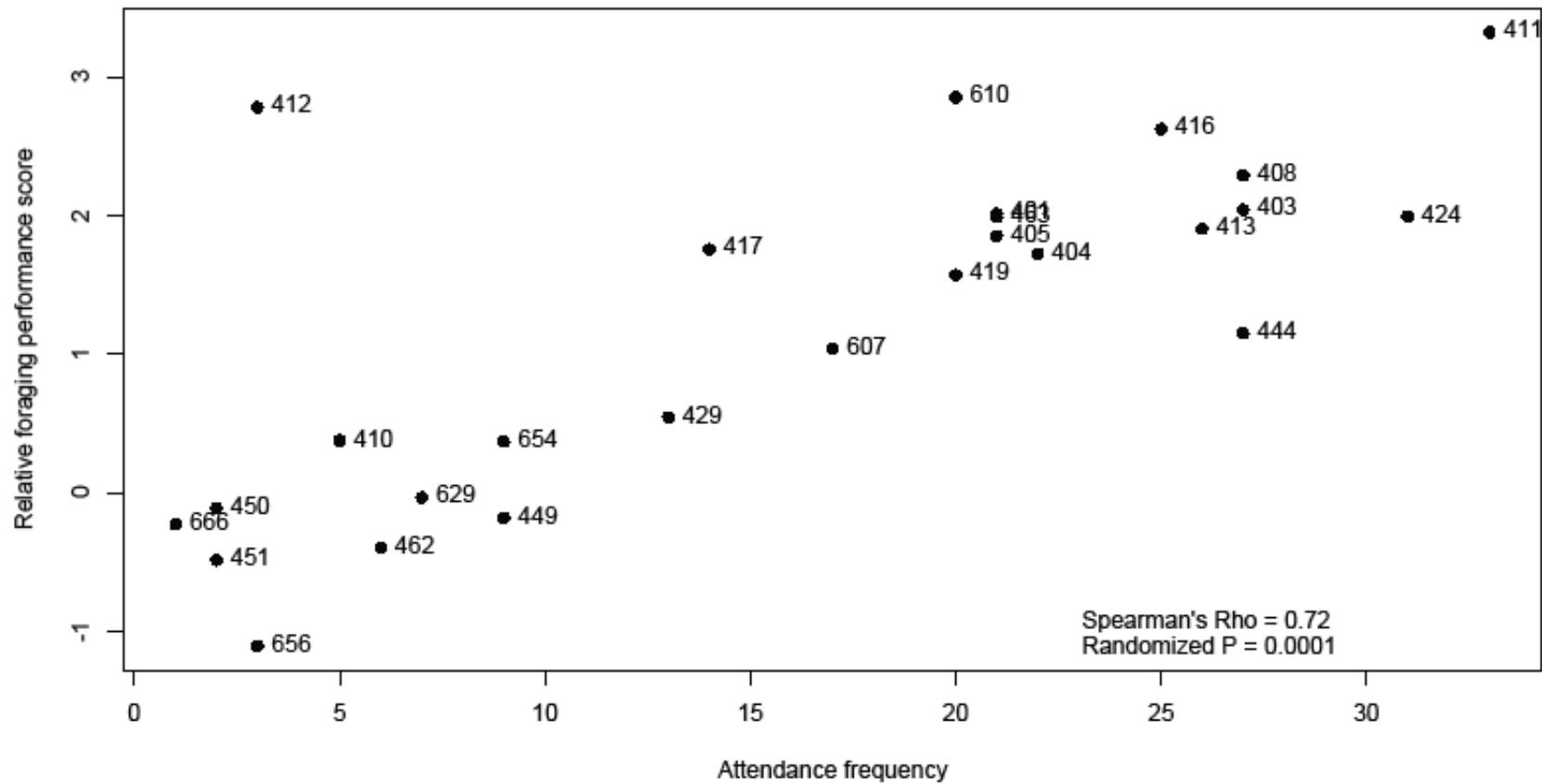
Figure 7: Correlation of individual relative foraging performance (RFP) scores and frequency of daily attendance of 26 focal bears observed at McNeil Falls. Daily attendance was based on whether or not an individual was observed at McNeil Falls on a given day.

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