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END OF THE LINE: USING BEHAVIOR AND MOVEMENT TO INFORM CONSERVATION AND MANAGEMENT OF TERRESTRIAL SALMON CONSUMERS IN THE NORTH PACIFIC

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ENVIRONMENTAL STUDIES

by

Rachel E. Wheat

June 2016

The Dissertation of Rachel E. Wheat is approved:

_____
Professor Christopher C. Wilmers, chair

_____
Professor Andrew Szasz

_____
Stephen B. Lewis, MSc

_____
Tyrus Miller
Vice Provost and Dean of Graduate Studies

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END OF THE LINE: USING BEHAVIOR AND MOVEMENT TO INFORM CONSERVATION AND MANAGEMENT OF TERRESTRIAL SALMON CONSUMERS IN THE NORTH PACIFIC

Rachel E. Wheat

ABSTRACT

The inherent conflict between the economic value of Pacific salmon (*Oncorhynchus* spp.) to fisheries and their importance to ecological systems has influenced the development of ecosystem-based fisheries management (EBFM), a new management paradigm that addresses the effects of fisheries on non-target species. However, poor understanding of the impacts of human competition with wildlife consumers of fish has hampered implementation of EBFM. While myriad processes may or may not be included in EBFM, no management endeavors will be achievable without a broader scientific knowledge base regarding cross-boundary salmon ecosystem impacts. This dissertation extends the concept of EBFM in Pacific salmon ecosystems to include consideration of ecosystem components in terrestrial habitats. First, I evaluate the extent of regulatory noncompliance with harvest regulations among subsistence fishers. I find that overharvest is correlated with fishers with low incomes and those providing for large households, as well as Alaska Natives adhering to traditional cultural practices. Second, I examine human disturbance and accessibility of salmon to wildlife by exploring how both habituation to and fear of human activity drive the foraging ecology of brown bears. During a study at a heavily used recreational and ecotourism site, non-habituated bears were

active almost exclusively at night in human-dominated areas, likely leading to suboptimal foraging. Additionally, I test a novel method for microsatellite genotyping via collection of residual bear saliva on partially consumed salmon carcasses, finding it to be an efficient and effective method for monitoring brown bear populations. Finally, I assess the influence of the heterogeneity of anadromous fish systems on the behavior of bald eagles. Using data from 28 individual eagles tracked with GPS transmitters between May 2010 and January 2016, I find evidence of four distinct movement strategies among eagles in the north Pacific. The highly variable anadromous fish system of the north Pacific coast likely contributes to behavioral plasticity in bald eagles in this region and results in a range of movement strategies in the population.

ACKNOWLEDGEMENTS

This work was made possible through financial support from the National Science Foundation, Sam Price Family Foundation, International Association for Bear Research and Management, American Bald Eagle Foundation, Alaska Chilkoot Bear Foundation, Alaska Department of Fish and Game, US Fish and Wildlife Service, the Environmental Studies Department at the University of California Santa Cruz, and 100 individual donors who contributed to a Kickstarter.com crowdfunding campaign.

Thanks to my committee members, Chris Wilmers, Andy Szasz, and Steve Lewis. Chris allowed me a great deal of independence and the freedom to pursue my own ideas, supported my work financially, and helped improved drafts of several of my papers. Andy provided support while I learned to navigate the social sciences, and his feedback on my subsistence fishing work improved the framing, and, I hope, its impact. This work would literally not have been possible without the expertise, guidance, and Master Banding Permit of Steve Lewis. What began as a casual conversation during a Wilmers lab meeting gradually blossomed into a full-blown dissertation project when Steve responded to an email inquiry I sent his way and offered his support. He provided encouragement, assistance with eagle captures, data from additional transmitters, and offered his time for brainstorming sessions, all of which greatly improved the quality of my work.

The text of this dissertation includes contributions from co-authors including Chris Wilmers, Steve Lewis, Taal Levi, Yiwei Wang, Jenn Allen, and Sophie D.L. Miller. Taal's enthusiasm for Haines set me on the path to develop my research there, and Jenn's assistance helping me set and check trail cameras and introducing me to folks during my first year in the field, and then later helping optimize DNA extraction, PCR, and multiplexing protocols, was invaluable.

I gratefully acknowledge the support of many individuals in Alaska who made this work possible, including Marvin Willard, Mike Howard, Anthony Crupi, Scott Ford, Shannon Donahue, Jedediah Blum-Evitts, and Yasaman Shakeri. Thanks to the American Bald Eagle Foundation, especially Dan Hart and Cheryl McRoberts, for providing field interns in the form of Sidney Campbell, Leah Girard, McKenzie Hart, Leia Minch, Emily Warman, and Samantha Wilson. I also thank the many individuals who participated in my subsistence fishing surveys.

Many people provided input that improved the scope of my research. Special thanks to Sara Lewis—without our taqueria lab meetings and her unwavering support, I likely never would have succeeded at social science research, not to mention graduate school itself. Thanks also to my Wilmers labmates: Yiwei Wang, Barry Nickel, Veronica Yovovich, and Justine Smith. Barry's technical expertise made the Ecology Alaska website possible, and he helped to smooth over issues with ArcGIS numerous times. Conversations with Yiwei, Veronica, and Justine were always insightful and helped lend additional depth to my work.

INTRODUCTION

Pacific salmon (*Oncorhynchus* spp.) are species of immense ecological, sociocultural, and economic significance throughout the north Pacific. As anadromous fish, Pacific salmon are born in freshwater and spend some time there before migrating to sea, where they spend their adult lives and accumulate most of their body mass. When they mature, they return to their natal freshwater streams to breed and die. The combination of anadromy and semelparity in salmon lead to very distinct life stages that take place in drastically different environments; as a result, salmon influence food webs and community structure in multiple habitats. Salmon are the dominant prey of both marine (Roffe and Mate 1984, Ford et al. 1998, Nagasawa 1998) and terrestrial (Hilderbrand et al. 1999, Elliott et al. 2011) predators, and senescent carcasses, distributed by flooding events and the feeding behavior of bears, contribute pulses of marine-derived nutrients to terrestrial environments that influence primary producers, invertebrates, and wildlife (Willson and Halupka 1995, Willson et al. 1998, Hilderbrand et al. 2004).

Many cultures throughout the Pacific Northwest, indigenous and otherwise, are closely tied to salmon populations, engaging in subsistence fishing to support their livelihoods (Quinn 2005). Pacific salmon also support a vast commercial fishing industry; in Alaska alone landings exceed 300,000 metric tons annually, valued at more than $260 million USD (Woodby et al. 2005). Industrial-scale fishing efforts exploiting Pacific salmon result in the removal of a significant but variable portion of

salmon biomass from ecosystems, with poorly known consequences for ecosystem integrity (Gresh et al. 2000). The inherent conflict between the economic value of Pacific salmon to fisheries and their importance to ecological systems has stimulated debate about managing salmon for a broader set of objectives that include maintenance of ecosystem processes, rather than to maximize yield for commercial fisheries (Piccolo et al. 2009). This emergent management paradigm is called ecosystem-based fisheries management (EBFM).

At its core EBFM seeks to find trade-offs between a diverse set of ecosystem services and fisheries management objectives (McLeod and Leslie 2009), but current approaches suffer from focus on a limited number of species and species interactions and limited consideration of species whose influence crosses ecosystem boundaries. Further, implementation of EBFM has thus far proved difficult. For salmon ecosystems, EBFM requires a clear conceptual framework for assessing how salmon availability can influence ecosystem processes, but for many regions, the broader impacts of salmon ecosystem services remain poorly understood (Richerson et al. 2010, Hilborn 2011). While myriad processes may or may not be included in EBFM, no management perspectives will be achievable without a broader scientific knowledge base regarding cross-boundary salmon ecosystem impacts.

My motivation for undertaking this dissertation research was to extend the concept of EBFM in Pacific salmon ecosystems to include consideration of ecosystem components in terrestrial habitats. I used novel technologies and a targeted group of study species to increase our understanding of the broader impacts of salmon

ecosystem services on terrestrial consumers, in the hopes that future EBFM can better tailor strategies to benefit a broad diversity of species.

My research focused predominately on three of the primary terrestrial consumers of salmon: humans, brown bears (*Ursus arctos*), and bald eagles (*Haliaeetus leucocephalus*). These terrestrial consumers are the terminal predators of salmon—by feeding on salmon primarily on or just prior to arrival on spawning grounds, salmon are consumed in their final phase of their life history. If salmon abundance is high enough to support terminal consumers, then sufficient salmon numbers should exist to also sustain populations of predators that feed on salmon at earlier stages in their life history, such as seabirds, marine mammals, and marine and freshwater fish (Levi et al. 2012).

The aim of my research was to explore the different ways in which salmon are important to each of these three major consumers in the context of EBFM. Recent approaches to EBFM have suggested using models to compare how departures from status-quo management would impact relative fisheries yield and relative density of a focal wildlife species. A more comprehensive view of EBFM, however, would encompass the broader impacts of salmon ecosystem services, which may affect not only species densities, but also behavior, and might be influenced by non-salmonid interspecies interactions. By monitoring human, bear, and eagle behavior using surveys, motion-detecting trail cameras and DNA, and GPS tracking devices, respectively, my dissertation focuses on how availability of and access to salmon help shape the ecology and behavior of these species.

First, I explore the importance of Pacific salmon to humans, by evaluating harvest behavior of subsistence fishers in a small sockeye salmon (*O. nerka*) fishery. Strategies for increasing escapement to benefit ecosystem processes are unlikely to garner social or political support unless the needs of human fishers are met first. This may be especially true in subsistence areas where individuals depend on fish stocks as a primary component of their livelihood. Chapter one details work to survey subsistence fishers from a range of cultural and economic backgrounds to determine sociodemographic factors most likely to be associated with greater need for salmon and underreporting on harvest permits, which could help direct management efforts to meet both wildlife and residents' needs.

Second, I explore accessibility of salmon for brown bears, the dominant predators on salmon spawning grounds, at a popular recreation and ecotourism site. EBFM efforts that focus on regulating only the biomass of salmon available to wildlife may not be effective. In addition to consumptive uses of fish (e.g. biomass removal by commercial fisheries), which influences availability of salmon to wildlife, human activities can also influence the accessibility of salmon for wildlife (Hilderbrand et al. 2004). Human disturbance, in the form of sport and subsistence fishing, wildlife viewing and photography, and development near streams and rivers may reduce the number of salmon that can be used by wildlife if animals exhibit behavioral avoidance of humans and human activity. Chapter two examines human disturbance and accessibility of salmon to wildlife by exploring how both habituation to and fear of human activity drive the foraging ecology of brown bears. Chapter

three tests a novel method for microsatellite genotyping and monitoring of brown bear populations via collection of residual bear saliva on partially consumed salmon carcasses. In addition to serving as a more effective and efficient method for monitoring brown bears on salmon spawning grounds than scat collection, this method could have future utility in examining individual bears' foraging habits and use of salmon at different spawning aggregations throughout the spawning season.

Finally, I examine the influence of salmon, in addition to other anadromous fish, on a highly mobile predator, the bald eagle. One method to evaluate fisheries-ecosystem tradeoffs for terrestrial consumers of salmon is to investigate how salmon availability drives the behavioral ecology of a focal species. In chapter four, I explore movement strategies of individual bald eagles throughout the anadromous fish system of the north Pacific coast. I use fine-scale location data from 28 bald eagles tagged with GPS transmitters to evaluate the extent of intraspecific variation in movement strategies among eagles. I also identify seasonal areas that attract eagles from throughout the region that are likely disproportionately important to eagles in the population.

Chapter 1: Evaluating behavioral drivers of regulatory noncompliance in fisheries: lessons from a small-scale subsistence salmon fishery

Abstract

Fisheries compliance research has evolved to draw on both rational and normative perspectives, but studies have only recently begun to empirically explore the myriad socioeconomic and demographic variables that might contribute to an understanding of fishers' behavior. Here, a subsistence salmon (*Oncorhynchus* spp.) fishery in Southeast Alaska was used as a case study to explore the prevalence of overharvest in the community and what factors might drive fishers to comply, or not comply, with formal harvest regulations. Anonymous paper-based compliance and sociodemographic surveys were conducted with subsistence fishers in Haines, Alaska in autumn 2014. The survey found 25.2% noncompliance with possession limits, 8.6% noncompliance with annual harvest limits, and 5.1% noncompliance with regulations against the sale of subsistence-caught fish. Results indicate that regulatory awareness and both rational and normative drivers influence fisher behavior, including income, negative perception of management, household size, and ethnicity.

Introduction

Increasing pressure on fisheries has led to widespread decline in stocks, contributing to food security issues worldwide (Pauly et al. 2005). In addition to attempts to replenish stocks, through, for example, establishment of marine reserves,

adherence to conservative harvest limits has become increasingly important. As such, fisheries compliance has been identified as a key factor in sustainable fisheries management. Over the past two decades, fisheries compliance theory has evolved as a means of better understanding fishers' behavior and decision-making in an attempt to develop strategies to enhance compliance with fisheries' harvest limits (Hauck 2009).

Fisheries compliance theory has evolved from two perspectives, one rationalist and one normative (Kuperan and Sutinen 1998, Sutinen and Kuperan 1999, Raakjær-Nielsen 2003). Hardin (1968) would argue that fisheries overharvest is a classical case of the 'tragedy of the commons', with individuals maximizing their harvest, and therefore welfare, at the expense of the welfare of the fishery as a whole. As a result, central governments must intervene to prevent over-exploitation. The rationalist perspective of fisheries compliance follows this line of thought, arguing that external influences, such as economic and personal gains and potential enforcement, encourage individual fishers to act in their own immediate self-interest (Sutinen & Andersen 1985; Anderson & Lee 1986; Nielsen 2003). This approach assumes fishers to "assess opportunities and risks and disobey the law when the anticipated fine and probability of being caught are small in relation to the gains from noncompliance" (Murphy 2004, p. 188).

The perspective that fishers will choose to comply (or not) based on the severity of sanctions has generally led to greater law enforcement efforts to increase deterrence (Hatcher et al. 2000), under the premise that fishers will make the rational choice to comply with harvest limits if deterrents to overharvesting are strong enough

(Hønneland 1999). The reliance on traditional law enforcement as a primary means to enhance compliance, however, ignores the complexity of the socioeconomic and political contexts of fishers' behavior (Berkes 2006, Hauck 2009). The normative perspective of fisheries compliance argues that factors beyond maximization of personal gain shape compliant behavior, including moral and social norms, social pressure, perception of the management authority, and fisher involvement in decision-making (Kuperan and Sutinen 1998, Sutinen and Kuperan 1999, Hatcher et al. 2000, Gezelius 2002, Raakjær-Nielsen 2003, Raakjær-Nielsen and Mathiesen 2003).

Normative theorists believe that moral and social considerations play a vital role in whether individual fishers comply with regulations (Hønneland 1999). For example, social reciprocity can have a greater deterring effect on fishers' noncompliance than traditional "threats of power"—particularly in small communities, adherence to the behavioral norms of the collective community can pressure individuals to conform (Bowles and Gintis 2002). Thus, the normative perspective argues for alternative approaches to rules and laws regarding harvests, such as informal sanctions and participatory management, and while many governments continue to rely on law enforcement strategies to enhance compliance, research suggests that utilizing both rational and normative approaches could improve compliance outcomes (Hatcher et al. 2000, Gezelius 2002, Raakjær-Nielsen and Mathiesen 2003).

Although fisheries compliance research has evolved to draw on both rational and normative perspectives, studies have only recently begun to explore the myriad

socioeconomic and demographic variables that might contribute to an understanding of fishers' behavior (Gezelius 2002, Raakjær-Nielsen and Mathiesen 2003, Roncin et al. 2004, Blank and Gavin 2009), or which types of drivers, normative or rational, might be most important in different types of fisheries. While the need to better understand factors influencing fishers' motivations to overharvest has been recognized, most of this research is still largely theoretical and few empirical studies of the determinants of fishers' compliance behavior exist (Hatcher et al. 2000, Blank and Gavin 2009). Further, perspectives on fisheries compliance have largely evolved from study of large-scale, commercial fisheries; empirical research on small-scale fisheries compliance is lacking.

As a whole, the literature around compliance suggests that different drivers of compliance behavior might be influential in different contexts. In some fisheries, perhaps particularly small fisheries, normative drivers may be more important to compliance. In other fisheries, rational drivers might be key. Here, we set out to test the significance of different types of drivers, both rational and normative, of compliance behavior in a small-scale fishery. We use a subsistence salmon fishery in Southeast Alaska as a case study to explore the prevalence of overharvest in the community and what factors might drive fishers to comply, or not comply, with formal harvest regulations.

Small-scale fisheries can be broadly characterized as those requiring labor-intensive harvesting effort to harvest fishery resources, operating from shore or from small vessels, and generally encompass subsistence, traditional, and artisanal

practices (Hauck 2008). Though commercial fisheries remove biomass far in excess of any subsistence take, small-scale subsistence fisheries are critical to many regions in the Pacific Northwest. Recent surveys in Alaska suggest that between 92 and 100 percent of rural households use wild fish (Wolfe 2010), with hundreds of thousands of salmon harvested annually in some watersheds (Fall et al. 2013). In Southeast Alaska, many salmon streams and run sizes are small (Walker 2009). Small run sizes can create conflict for resource managers, who must decide how fish will be divided among escapement, subsistence, sport, and commercial harvest, leading to harvest limits for subsistence fishers that are often relatively low.

Both Alaska state law (AS 16.05.258) and federal management systems prioritize subsistence among consumptive uses of fish, but these considerations are taken into account only when stock sizes are insufficient to meet both conservation needs and a range of harvest types. When stock levels are adequate to maintain species persistence, subsistence quotas are allocated by region based on "amounts reasonably necessary for subsistence" (ANS) by the Alaska Department of Fish and Game's Board of Fisheries. For ANS, the Board of Fisheries does not distinguish among different types of subsistence users, such as those using fish to supplement diets versus those using fish as a mainstay of livelihood, nor do these quota numbers reflect the ways in which individuals from different cultural backgrounds might choose to allocate their catch. Alaska Natives, who comprise about 55% of the population in rural areas (Wolfe 2010), often have local customs for resource harvest

activities, and share among families and households in a community. Permits for subsistence fishing generally do not recognize these types of activities (Walker 2009).

Economic, social, and cultural drivers can cause fishers to act in unanticipated ways, which can in turn undermine the intent of management actions (Fulton et al. 2011). With low harvest limits and ANS that do not take into account traditional cultural practices, there is high incentive in many cases for subsistence fishers to overharvest salmon. Many residents may engage in subsistence harvest without obtaining a permit, or underreport the total number of fish harvested. There is widespread belief that compliance for subsistence fishing regulations is very low in many parts of Southeast Alaska (Fall et al. 2000). Collection of accurate harvest data is an essential component of effective resource management, and is particularly important in Alaska because of the legal requirement to prioritize subsistence harvest over other (e.g. commercial) uses.

Regulatory noncompliance in Southeast Alaska subsistence fisheries is thought to lead to low subsistence salmon harvest estimates (Brown et al. 2006), which affects perceptions of both subsistence fishers' need for fish and the biomass later available to wildlife on spawning grounds. In order to gain a better understanding of fishers' compliance behavior, it is necessary to understand the extent of compliance within harvest limits as well as the underlying drivers that influence compliance behavior.

The self-reporting methods currently utilized by the Alaska Department of Fish and Game (ADFG) to monitor harvest sizes may be unreliable if records are

frequently falsified (Fall et al. 2000, McCluskey and Lewison 2008), and alternative methods for determining resource use, such as direct questioning of fishers using anonymous surveys, suffer from bias due to the respondents' perception of risk when asked to confess or report illegal behavior (Pitcher et al. 2002). Individuals being interviewed may fear punishment for admitting they have violated harvest limits (Fowler and Mangione 1990). Respondents who fear retribution might provide evasive or dishonest answers to surveyors, introducing bias into the study and resulting in questionable data (Warner 1965, Solomon et al. 2007).

Other common methods for determining compliance levels in fisheries include interviews, use of informants, decision tree analyses, and focus groups (Damania et al. 2003, Solomon et al. 2007). Interview and informant-based methods of determining compliance behavior, however, generally suffer from similar biases as direct questioning, due to the perception of risk among those asked to confess or report overharvesting (Fox and Tracy 1986, Pitcher et al. 2002). Further, biases against authority figures or outsiders may exist, making these methods inappropriate for estimation of compliance behavior by management bodies or independent researchers not originally from the community in question (Mann 1995).

The randomized response technique (RRT) was developed over 50 years ago to counter these problems with response bias by increasing the probability that respondents will provide honest answers to sensitive questions in a survey or interview (Warner 1965). Sensitive questions are those which participants in the study might view as having a cost, either financial or personal (Solomon et al. 2007).

Questions concerning overharvest of fishery resources would be considered sensitive, for example, because individual respondents risk potential retribution for admitting to violating regulations. The responses of interviewees in RRT surveys are anonymous, and respondents have control over the questions, thereby reducing the perceived costs of honesty (Buchman and Tracy 1982). This is accomplished through the design of the method, which allows interviewees to provide information that gives the researcher data only on a probabilistic, not individual, basis (Warner 1965).

A meta-analysis of 37 studies that utilized the randomized response technique "indicated an overall positive effect for RRT across studies compared to other methods", concluding that the technique provides significantly more valid results when compared to other methods, especially as the sensitivity of the question increases (Lensvelt-Mulders et al. 2005, p. 319). Others who have tested RRT have also found it estimates a greater proportion of sensitive behavior than direct questioning and standard survey and interview methods (Warner 1965, Chaloupka 1985, Solomon et al. 2007, Gavin et al. 2010).

Although RRT has been widely used successfully in the social sciences to investigate areas such as sexual behaviors, abortion, gambling, drug use, cheating, and stealing (Fox and Tracy 1986), this method has only recently been employed in studies of natural resource management. RRT has been utilized to investigate noncompliance in freshwater recreational fishing (Schill and Kline 1995) and illegal use of terrestrial (Solomon et al. 2007, St. John et al. 2011, Razafimanahaka et al. 2012) and marine (Blank and Gavin 2009, Arias and Sutton 2013, Lewis 2014)

resources. Here, we use the randomized response technique to investigate different drivers of compliance behavior in a subsistence salmon fishery in the community of Haines, Alaska.

Methods

Study System

The Haines Management Area in Southeast Alaska encompasses multiple communities: the city of Haines and the surrounding Borough, which includes the settlements of Lutak, Mosquito Lake, and Klukwan, a Tlingit Indian village, as well as the city of Skagway at the head of the Chilkoot Inlet. Local Tlingit have had the longest tenure of local residence and involvement with the salmon fishery, but the subsistence fishery in this region is notable for the high rate of non-Native participation (Smith 2003). Subsistence fishing permits for the Haines Management Area, administered by the Alaska Department of Fish and Game, provide open season for sockeye, pink, and chum salmon from June 1 through September 30 each year (Brown et al. 2006). Only one permit is issued per household, but households can request a second permit if the first is filled (Bachman 2014). Harvest is open to all residents of Alaska, but is conducted primarily by residents of Haines and Klukwan and those with familial or other close ties to these communities. Sockeye are the preferred salmon species for consumption in the subsistence fishery, and typically represent more than 80% of the regional harvest (Fall et al. 2013). Since sockeye are

the primary species targeted for subsistence, our survey focused only on questions about sockeye harvests. Limits for sockeye are 25 in possession or 50 annually.

On average, the Haines ADFG office issues upward of 500 subsistence fishing permits each year. Permits list regulations relevant to the fishery, including harvest limits and allowable gear types. Harvest in this area is typically conducted with drift and set gillnets. Permit holders must provide their names and contact numbers, record the number of fish harvested and gear types used, and at the end of the season return the permit to ADFG. Although local managers employ permits only as a quantitative assessment tool to monitor harvest levels, a history of negative interactions between local residents and Alaska Wildlife Troopers, who enforce ADFG regulations, incentivizes individuals to report catches that are lower than or equivalent to harvest limits (Smith 2003). Both managers and subsistence fishers in the region recognize that assessments of subsistence salmon use do not reflect actual harvest levels or fishing activity (Smith 2003), but ADFG does not expand their estimates of total subsistence harvest to include unreturned permits or underreporting on permits (Walker 2009).

Sample Design

Before and throughout the duration of the study, the survey was advertised in local print media and on local radio. Four high-traffic sites within the Haines Borough were selected for soliciting responses to surveys. Surveys were collected over a five-week period during October-November 2014, following the close of the subsistence

fishing season. Survey times were scheduled evenly throughout the week ensuring that individuals were available to administer surveys on both weekdays and weekends, before, during, and after normal business hours. We asked individuals entering and exiting public buildings, "Do you subsistence fish?" If individuals responded in the affirmative, we then asked if they would be willing to participate in a short survey regarding subsistence fishing behavior. Additionally, advertisements in print and radio provided contact information for those looking to participate outside of the scheduled survey dates and times in front of public venues. Since permits are administered to households, rather than individuals, we also asked all participants to confirm that no one else in their household had taken the survey, to avoid repeat sampling. Respondents had no prior knowledge of the survey questions and no identifying information was recorded.

Survey Administration

The survey was composed of four sections: randomized response technique (RRT) questions about compliance with sockeye salmon subsistence fishing regulations, as well as questions related to the respondent's awareness of regulations; questions related to economics and the respondent's perceived need for sockeye salmon (rational drivers); questions related to the respondent's subsistence fishing experience and perceived legitimacy of the management agency (normative drivers); and sociodemographic questions (normative drivers). After participants provided verbal consent to participate, individuals were handed a copy of the survey form on a

clipboard, a coin (US $0.25), a pencil with an eraser, and numbered envelopes containing RRT and innocuous questions. We explained the survey method using a set protocol to ensure all respondents were given the same information about how to self-administer the survey.

Prior to answering each RRT survey question, the respondent performed the same randomizing process by flipping a coin, without revealing the result to anyone. They then randomly selected one of two question cards from a numbered envelope without revealing to anyone else which question was chosen. Each of the envelopes contained one card with the sensitive question (RRT 1-4, Table 1) and one with the unrelated innocuous question pertaining to the outcome of the coin toss (see Table 1). The respondent then recorded their reply of 'yes' or 'no' on the survey form. Once the respondent had completed all RRT questions, they were asked to fill in the remaining sections of the survey form. After completing the survey, respondents deposited survey forms into a clear ballot box. Surveys accumulated in the ballot box until the end of the study, after which all surveys were removed from the box and shuffled before data entry began.

Data Analysis

We used a simple probability equation (Fox and Tracy 1986) to determine the proportion of users X_x who answered 'yes' to a given sensitive question:

$$X_x = \left(\frac{\lambda - (1-p)\,\pi_y}{p} \right)$$

where π_y = known proportion of non-sensitive behavior (= 0.5, i.e. flipping heads in the coin toss), λ = recorded proportion of 'yes' responses, and p = probability of selecting the sensitive questions (=0.5).

We also estimated variance Var(X_x) for the general population with 95% confidence intervals:

$$Var(X_x) = \lambda(1-\lambda)np^2$$

where n = total number of respondents.

Using data from all four sections of the survey, an estimate of the proportion of violators was analyzed against both rational (awareness of regulations) and normative (perceived need and experience and sociodemographics) drivers to find out whether certain segments of the subsistence fishing population were more likely to engage in noncompliant behavior. To determine if a certain segment of the fishing community did not comply with regulations at a significantly higher rate than other segments, we used Mann-Whitney U tests to compare respondents' answers to individual survey questions (e.g. age, ethnicity, experience fishing) to whether they responded 'yes' or 'no' in the RRT portion of the survey.

Further, when examining fisher regulatory awareness, we used Mann-Whitney U tests to explore for any significant differences in the mean regulation awareness of fishers who replied 'yes' versus 'no' to the RRT questions, to determine if awareness of regulations differed between compliant and non-compliant fishers. Additionally, we utilized contingency tables to search for relationships between answering the

regulation awareness questions incorrectly and the likelihood of answering 'yes' to the RRT questions.

Results

We approached 152 subsistence fishers to participate in the survey; the final response rate was 78.2% (119 of 152) and 68% were male. Caucasian fishers were the majority (71%) followed by Alaska Natives (16%). The proportion of survey respondents representing each ethnicity (Table 2) was representative of the population of the region as a whole, based on the most recent data generated by the U.S. Census Bureau (2013). On average, the survey took respondents seven minutes to complete.

RRT results for the entire sample illustrate where noncompliance is greatest overall (Fig. 1). Noncompliance with the possession limit is proportionally most common, with 25.2% of fishers estimated to have violated possession limits in 2014, followed by noncompliance with annual limits (8.6%) and sale of subsistence-caught fish (5.1%) We detected several differences between respondents who provided 'yes' responses and those who responded 'no' in the RRT portion of the survey (Table 2):

Regulatory Awareness

Overall, fishers' awareness of subsistence fishing regulations was relatively high, with 97% of respondents acknowledging the need for permits and 83% and 88% acknowledging there were limits on possession and annual harvest of sockeye, respectively. Although awareness of limits was high, few people were able to recite

limit numbers from memory. When asked about limit numbers, only 21% of respondents correctly listed possession limits, and only 32% of respondents correctly listed annual limits. Additionally, just over half of respondents (52%) reported knowing the general dates during which subsistence fishing is permitted.

For the most part, regulatory awareness had little impact on whether respondents answered 'yes' or 'no' to RRT questions. However, those who did not recite the annual limit number correctly were more likely to have responded 'yes' to the RRT question regarding noncompliance with the annual limit. Similarly, contingency analysis illustrated that individuals who provided an incorrect estimate of the legal annual harvest limit for sockeye were significantly more likely to respond 'yes' to the RRT question asking if they had violated the annual harvest limit that year (RRT 3; $\Phi = 0.206$, $p < 0.05$). Individuals who reported learning about subsistence fishing regulations from sources other than subsistence fishing permits or ADFG officials were also more likely to have answered 'yes' to the RRT question regarding noncompliance with the annual limit.

Rational Drivers

Economics

Individuals reporting a low annual household income (less than $25,000/year) were more likely to have responded 'yes' in regards to RRT 3, the question asking whether fishers had violated the annual limit on sockeye harvests.

Perceived Need

We found no significant difference for number of other species harvested for subsistence purposes. Those who reported that sockeye salmon composed a high percentage of their diet were more likely to have responded 'yes' to RRT 2 (possession limit) and RRT 3 (annual limit), and those who felt that the adequate annual limit for sockeye harvests should be greater than 50 fish were more likely to have responded 'yes' to RRT 3.

Normative Drivers

Experience and Perceived Legitimacy of Management

We found no significant difference in fishing experience (number of years fishing) for any RRT question, and no significant difference in the perception of ADFG's current management for the subsistence fishery for RRT questions regarding permitting or compliance with possession or annual limits. However, individuals who reported having a negative opinion of ADFG's management of the subsistence fishery were more likely to have responded 'yes' to the RRT question asking whether they sold subsistence-caught fish.

Demographics

Area of origin, ethnicity, and household size all had impacts on RRT responses. Individuals who reported household sizes of five or more people, individuals originally from the Haines Borough or elsewhere in Alaska, and Alaska

Natives were all more likely to have responded 'yes' to RRT 2 and RRT 3, questions regarding violation of possession and annual limits.

Discussion

Current regulations guiding most Alaskan fisheries are based on a commercial fisheries model, in which quantitative measures are used to determine appropriate management actions (Smith 2003). Commercial fisheries harvest, however, is fundamentally different from subsistence harvest, and regulations for subsistence fisheries derived from a commercial fisheries model do not take into account normative drivers of behavior, such as adherence to cultural traditions.

Maximization of fish harvest, benefit of harvest to participants in the fishery, and efficiency of harvest all differ greatly between commercial, sport, and subsistence fishing, yet the same quantitative models guide the management strategies of all three harvest types. Meeting the need for subsistence users comes, by law, only second to meeting escapement goals necessary for sustained yields of fish stocks, but in practice it is not common for subsistence needs to be prioritized in regulation at the expense of commercial harvests (Smith 2003).

Indeed, it might seem inequitable to some subsistence fishers that commercial fisheries are allotted such a large percentage of the allocation of fish available for harvest. Other studies have found that small-scale fishers believe that the fishing methods and quantity of catch of legal commercial fisheries far outweigh the negative impacts of small-scale fishers, who may violate harvest limits but who rely on catches for their livelihoods (Hauck et al. 2002). This sentiment is likely true for the Haines

subsistence fishery as well. Subsistence fishers find it difficult to have their interests recognized in the face of the larger, more powerful commercial harvests:

> *-I understand subsistence fishing pays the bills but I'm trying to feed my family. Why is it so hard to let subsistence fishers catch more fish, take a few away from the commercial outfits? It won't cost them that much and it would help me put food on the table.*
>
> *-I think Fish and Game does an okay job for the most part. The only times I have problems with them is when they let commercial fishing get out of hand. Fish and Game will extend fishing for [commercial] gillnetters and they'll bleed it dry, and not many salmon will make it upstream [where subsistence fishing is permitted]. I need fish, too.*

This fundamental difference in harvest outcomes, guided by overarching management objectives used among dissimilar harvest types, creates a rift between the management body and fishers. Regulations are more than just a means to influence fisher behavior; they should reflect the values of the fishers themselves, thereby stimulating a sense of moral obligation to comply (Jentoft 2000). Current ADFG regulations do not appear to encourage compliance in this way.

Noncompliance literature suggests that managers need to examine variables within the fishing community that may be impacting compliance behavior (Hønneland 1999, Sumaila et al. 2006). Drivers of compliance behavior might vary in different contexts. In small-scale fisheries, normative drivers, such as community ties, might affect an individual's perception of risk and their subsequent propensity to

comply with regulations (Furlong 1991), whereas in larger-scale fisheries rational drivers may be more important to compliance behavior. Here, we tested regulatory awareness and the importance of both rational drivers (economics, perceived need for fish) and normative drivers (level of experience, sociodemographic profiles) of small-scale subsistence salmon fishers. Information about the relative importance of these drivers and the sectors of the population least likely to comply with regulations can aid managers in appropriately allocating harvests to those groups that need them most (Kent 1997, McGoodwin 2001).

We found that, although compliance is generally high for those regulations included in our survey, there is still a proportion of the subsistence fishing community that likely does not comply with possession or annual limits or regulations regarding the sale of subsistence-caught fish. The regulations in order of decreasing estimated compliance rates are: adherence to possession limits (25.2% noncompliance); adherence to annual limits (8.6% noncompliance); and sale of subsistence-caught fish (5.1%). The subsistence fishery manager for the region felt that these estimated compliance rates were reasonable (Bachman 2015). It is important to note, however, that while the use of the randomized response technique reduces response bias compared to direct questioning or traditional survey methods, these results are likely still underestimates of actual noncompliance rates within the subsistence fishing population, as some participants will likely still provide evasive responses (Chaloupka 1985).

Compliance behavior can be affected by awareness of regulations and both normative and rational drivers, including the incentives and penalties, both economic and social, associated with noncompliance (Sutinen and Kuperan 1999, Hatcher et al. 2000, Sumaila et al. 2006). From the 18 questions we asked respondents regarding regulatory awareness, perceived need, and sociodemographic factors, we identified lack of awareness and two rational and three normative drivers of behavior that significantly influenced the likelihood of noncompliance in the subsistence fishery. Fishers who were unaware of the annual limit on sockeye harvests, fishers with low annual incomes, fishers who had a high perceived need for sockeye, fishers with a negative opinion of ADFG, fishers with larger household sizes, and Alaska Natives were all less likely to comply with regulations overall compared with other groups (all $p < 0.05$).

Regulatory Awareness

The subsistence fishers we surveyed generally possessed high levels of knowledge regarding sockeye fishing regulations, suggesting that ADFG is successfully conveying information on regulations to the subsistence fishing population. In most cases, we found no significant relationship between awareness and understanding of regulations and RRT responses, indicating that those fishers who knew about regulations regarding sockeye harvests were just as likely to admit to noncompliance with regulations as those who did not know the regulations. However, fishers who were not aware of an annual limit on subsistence sockeye harvests were

significantly more likely to respond that they harvested more than 50 sockeye in the previous year, thus violating the annual harvest limit. Further, we found significant correlation between how individuals reported learning about regulations and violation of harvest limits—those who obtained information on regulations from friends or family members rather than subsistence fishing permits or ADFG officials were more likely to report overharvesting.

Additionally, contingency analysis revealed that Alaska Natives were less likely to know the annual limit on sockeye than other groups ($\Phi = 0.189$, $p < 0.05$). Several Native respondents commented on regulations while participating in the survey:

-*There are no harvest limits for Native households.*

-*You don't need a permit to fish if you live in the [Native] village.*

These results have several management implications. First, and not surprisingly, fishers without knowledge of harvest limits are more likely to violate harvest limits. Second, fishers obtaining information about regulations from unreliable sources are also more likely to violate annual harvest limits. Third, regulatory awareness for this subsistence fishery is generally high, but might not be reaching all sectors of the fisher population equally.

Rational drivers

Economics

Individuals reporting an annual income of less than $25,000 were less likely to comply with annual harvest limits on sockeye. There is wide recognition that small-scale fishers, such as subsistence fishers, are often the poorest members of society (Berkes et al. 2001, Béné 2003). Several case studies have illustrated that low income individuals are less likely to comply with fishing regulations, as the marginal benefit gained from violation is higher for lower- than for higher-income individuals (Furlong 1991, Faasen and Watts 2007).

Additionally, we found that income and ethnicity appear to be linked with regards to compliance behavior. Alaska Natives were significantly more likely to report noncompliance with possession and annual limits on sockeye harvests, but contingency analysis showed that among respondents there were also significantly more low-income Alaska Natives than other ethnic groups ($p < 0.001$). This finding is buoyed by census data, which reports that in the Haines Borough, 23% of Alaska Natives fall below the poverty level, compared to only 5.6% of the white population (U.S. Census Bureau 2013). These results suggest that noncompliance behavior with regard to subsistence sockeye harvests are at least partially attributable to economic standing—those fishers who can least afford the financial costs of market foods are likely more willing to risk enforcement actions to harvest additional salmon.

Perceived Need

Respondents who reported relying more on sockeye for subsistence were less likely to comply with annual limits. Further, those who reported the highest reliance

on sockeye as part of their diets were also more likely to report that the annual harvest limit should be higher than 50 fish ($\Phi = 0.316$, $p < 0.001$). This could suggest that noncompliance in annual limits is derived from a belief that limits are too low. While we list these responses as 'perceived' need, the actual need for subsistence fish could well be legitimate; respondents suggesting the annual harvest limit should be higher than 50 sockeye were more often those with larger household sizes ($p < 0.001$) and lower incomes ($p < 0.05$).

There was some concern within the fishery that salmon is not being allocated appropriately to those with the greatest need. One individual expressed distaste with the idea that harvest limits are equivalent across all income brackets:

> *-Subsistence fishing is hugely important to my community and quality of life here. I am concerned that the upper class is taking just as many fish as those who need it more. People with multi-million dollar homes are subsistence fishing in this community, and they just don't have the need for it.*

Current regulations do not take into account household size or income level when determining harvest limits. Thus, the benefit from overharvesting likely outweighs fear of enforcement for individuals whose need for salmon as a subsistence resource is highest.

Normative Drivers

Perceived Legitimacy of Management

A key aspect of management of common resources is ensuring compliance with regulations. However, the management body that imposes rules must be seen as 'effective and legitimate', or noncompliance with rules may be inevitable (Dietz et al. 2003). During the course of this survey, we identified that fishers who had a poor opinion of the way ADFG currently manages the subsistence fishery were more likely to respond 'yes' to the RRT question about selling subsistence-caught fish. This suggests a link between compliance and the perceived legitimacy of ADFG as a management agency. Many comments from respondents related to poor perception of ADFG and the management of the subsistence fishery.

-ADFG is doing a terrible job. They're ruining our fishery.

Several fishers attributed some years' low subsistence harvests to wildlife management:

-I used to subsistence fish, but I don't anymore. I've been around here a long time. The number of salmon has been dropping since the late 80's. There just aren't as many salmon returning now as there used to be. That's [Alaska Department of] Fish and Game's fault.

Further, many of the subsistence fishers who elected not to take the survey did so on the grounds that they did not want information about their harvest practices shared with ADFG:

-Yeah, I subsistence fish, but I'm not going to tell you about it. You're gonna want to know how many I take…. All you're going to do is get

us to admit we overfish, and then next year ADFG is going to throw in some regulation and take more of our rights away.

Although sale of subsistence-caught fish was the only regulation found to correlate with fishers' opinions of ADFG in this study, these encounters could indicate that mistrust of ADFG's management is a more prevalent problem than identified during the survey, as it is likely that some of the individuals who refused to participate in the study are those who perceive ADFG's management as illegitimate, and thus might also be those less likely to comply with regulations.

Demographics

Sociodemographic variables have been found to influence compliance behavior in fisheries in a variety of contexts (Furlong 1991, Hatcher et al. 2000, Sumaila et al. 2006). For example, Furlong (1991) found that older fishers were more risk-averse, and thus more compliant with regulations, than younger fishers, and Blank & Gavin (2009) found that local fishers were more likely to comply with regulations than visitors. In the present study, we found that household size and ethnicity both influenced survey responses regarding compliance with regulations.

Fishers with large household sizes were less likely to report compliance with possession and annual limits on subsistence-caught sockeye. Household size can be viewed as both a rational and a normative driver, which makes it difficult to categorize in the rational/normative dichotomy of compliance theory. On the one hand, larger families require more food, and thus there is likely some rational self-

interest driving noncompliance from larger households. On the other hand, the need to care for family is a social norm, and this need might outweigh the threat of potential enforcement. Current management regulations do not take into consideration variation in household sizes among fishers. Permits are distributed on a per-household, rather than per-individual basis, and households with single individuals have the same 50-sockeye annual limit as households with multiple individuals. Although individuals can return to the local ADFG office and request a second permit for their household if the first is filled, few fishers were aware their household could obtain a second permit-- only 16% of respondents reported knowing they could return for an additional permit. Further, obtaining a second permit can be difficult, and requests for additional permits are not always granted (Smith 2003). Fishers who are denied an additional permit after harvesting the allotted limit of salmon might simply continue to fish without reporting their additional harvest.

Several respondents expressed frustration at the per-household harvest limits:

> -*Households with one or two people shouldn't have the same harvest limits as households with five or six or more people. It's ridiculous.*
>
> -*Fifty sockeye is more than enough for one person or a couple, but there's no way that many could support my family, especially through the whole winter.*

Many fishers argued that the harvest limits should be subjective, and that limits on a per-household basis should take into consideration household size, as well as how often the members of each household consume fish.

In addition to household size, ethnicity was also correlated with compliance behavior; those who identified as Alaska Natives were less likely to comply with annual harvest limits on sockeye. Alaska Natives might be less likely to comply with regulations as a result of conflict between regulations and customary harvest practices. First, not all Native households harvest salmon. In the Native village of Klukwan there are a few fishers who harvest a considerable number of salmon and then distribute them throughout the community. Cooperative harvest activity is common, as is reciprocal distribution of harvest—even if a fisher has harvested enough salmon to fulfill their household's needs for the year, they might continue fishing on behalf of other community members.

Native harvesters often distribute salmon throughout the community, as well as to friends and family elsewhere in Alaska or the lower 48. One Native fisherman freely admitted to harvesting well in excess above the annual limit, but explained that he provides food to other households and to his extended family:

> *-My kids were raised on salmon. I want to make sure that they can continue to eat it even if they don't live here anymore. I catch and send fish to my kids and my grandkids. I catch fish for my friends. Sometimes I catch fish for my neighbors, too.*

Further, Native fishers often harvest salmon for memorial parties or other types of ceremonial occasions, which traditionally require the distribution of subsistence foods to guests, who often number in the hundreds (Smith 2003).

Current regulations regarding subsistence sockeye harvest do not reflect the widespread distribution of salmon among Native households, or the concentration of harvest in relatively few households in Native communities. In this way, the imposition of a 50-sockeye annual harvest limit is likely problematic for many Native fishers, as the limit does not reflect customary harvest practices and distribution or cultural values of sharing and reciprocity (Smith 2003). While harvest limits exist to protect the fishery as a whole, Alaska Natives are unlikely to comply with regulations that do not align with their cultural values:

> Alaska Natives are not prepared to give up their way of life merely because the federal government or the state has passed an unwelcome law or regulation. When a law stands between the Natives and their resources, when it does not take the basic economic realities into account, when it conflicts with Native principles or beliefs, compliance with the law is low. Natives do not regard such non-compliance as lawlessness; they regard it as adherence to their own cultural traditions. (Berger 1985: 65)

While ethnicity was not a significant variable in the sale of subsistence-caught fish, poor opinion of ADFG's management of the fishery was, with significantly more Alaska Natives having a poor opinion of ADFG than other ethnic groups. Trade and sale of subsistence-caught salmon are generally seen as more egregious offenses by ADFG and Wildlife Troopers than violation of harvest limits (Bachman 2015), but again, these regulations do not reflect the traditional practices of the Native

community. Historically, the economy of the Tlingit people was trade-based, with coastal Tlingit groups trading salmon and fish oil to inland groups for furs, game meats, and other goods (Oswalt 1966, Smith 2003). Although technically against subsistence fishery regulations, this type of trading and the sale of fish are still important parts of Tlingit lifestyles. In addition to monetary exchanges, sockeye salmon are traded with members from other communities in exchange for deer meat, black seaweed, and other types of seafood (e.g. crab, shrimp, halibut), among other items.

Conclusion

In the course of this study, we identified issues with regulatory awareness, two rational, and three normative drivers of behavior that appear to influence compliance with subsistence fishing regulations. To address issues with noncompliance in this fishery, managers first need to address the small sector of the population that are unaware of regulations, particularly the size of possession and annual harvest limits on sockeye. Outreach efforts by ADFG to distribute this information throughout the community, with a particular focus on Native households, might ensure greater awareness of the existence and size of harvest limits. Beyond regulatory awareness, efficacy of policies governing noncompliance in this fishery would likely be improved by taking into account both the rational (low income, high perceived need) and normative (perception of the management as illegitimate, large household sizes, ethnicity) drivers of behavior we identified here.

While noncompliance is not restricted to a single demographic, there appears to be a dichotomy between Native and non-Native fishermen in relation to compliance in this community; the normative drivers of compliance we identified can be used to understand why, in a fishery of this size, these two sectors of the fishing population behave differently. In addition to variables like household size and income, normative drivers surrounding cultural practices greatly influence behavior. Individuals tend to comply with regulations that are perceived to be both legitimate and fair (Sutinen and Kuperan 1999). Given the fact that regulations surrounding harvest limits and sale and trade of subsistence-caught fish do not take into consideration the cultural practices and values of Native participants, it is easy to see why that sector of the fishery is less likely to comply.

> -*Myself, my dad, his dad before him… we've been harvesting fish on this land for years, and never had any problems with it. We know how to fish. We don't waste fish. But we're restricted now. Troopers come and trespass on our land, pull our nets out of the water, fine us, sometimes take our gear. I have no use for Fish and Game.*

Regulations made in favor of long-term sustainability of the fishery must be tempered by socioeconomic and cultural considerations, which might require tradeoffs in favor of social equity (Hauck 2008).

Our study suggests that both rational and normative drivers are influential to fishers' compliance behavior, but the cultural considerations regarding Alaska Natives highlight the particular importance of normative drivers in this small-scale

fishery. If there are no conservation concerns for specific sockeye stocks in a given year, greater compliance with regulations might be observed if harvest limits and other regulations more accurately reflect these normative drivers, such as fisher need and community and cultural practices. Shifting regulations to more closely align with traditional Native values would serve a dual purpose, both to increase compliance with regulations as well as improve relations between fishers and the management agency. One option that has been explored in other Alaskan communities is the establishment and use of community, rather than household-based, harvest limits. The use of such limits in this subsistence fishery would reflect the cultural practice of a few individuals harvesting and distributing fish widely, to ensure all community members' need are met. Further, management might consider increased leniency in the trade or sale of subsistence-caught fish, permitting at the very least trade of subsistence-caught fish for other resources, therefore more closely aligning with the traditional Tlingit economy.

While enforcement of harvest limits in the Haines subsistence fishery is generally mild, many subsistence fishers in the community feel marginalized by both the management agency and the competing interests of commercial and sport harvesters, and at least a percentage of the fisher population engages in noncompliant behavior, driven by both rational and normative factors. Inaccurate documentation of overharvest could work at the detriment to subsistence fishers; if actual needs beyond established harvest limits are not recorded for fear of retribution from the management agency, uses may be further restricted in the event of a decline in stocks,

potentially exposing subsistence fishers to greater legal and economic pressures (Smith 2003). Regulations that more accurately reflect the rational and normative drivers of individual and community needs and values identified here would serve as a first step in improving compliance in this small-scale fishery.

Acknowledgements

Thanks to L. Minch, A. Althauser, S. Campbell, and A. Ling for field assistance. Special thanks to S.G. Lewis for providing help and feedback throughout the study, and to S.G. Lewis and A. Szasz for their thoughtful comments on drafts.

Table 1: Randomized response technique and innocuous questions

Code	*Question*
RRT 1	Did you/your household obtain a subsistence fishing permit for harvesting salmon in 2014?
RRT 2	During 2014, did you/your household ever harvest more than 25 sockeye salmon at one time for subsistence purposes (i.e. have more than 25 sockeye salmon in possession at one time)?
RRT 3	During 2014, did you/your household harvest more than 50 sockeye salmon in total for subsistence purposes?
RRT 4	Did you sell any of the sockeye salmon that you/your household harvested for subsistence purposes in 2014, either fresh or prepared (smoked, jarred, vacuum sealed, etc.)?
Innocuous	Did you get heads on the coin toss?

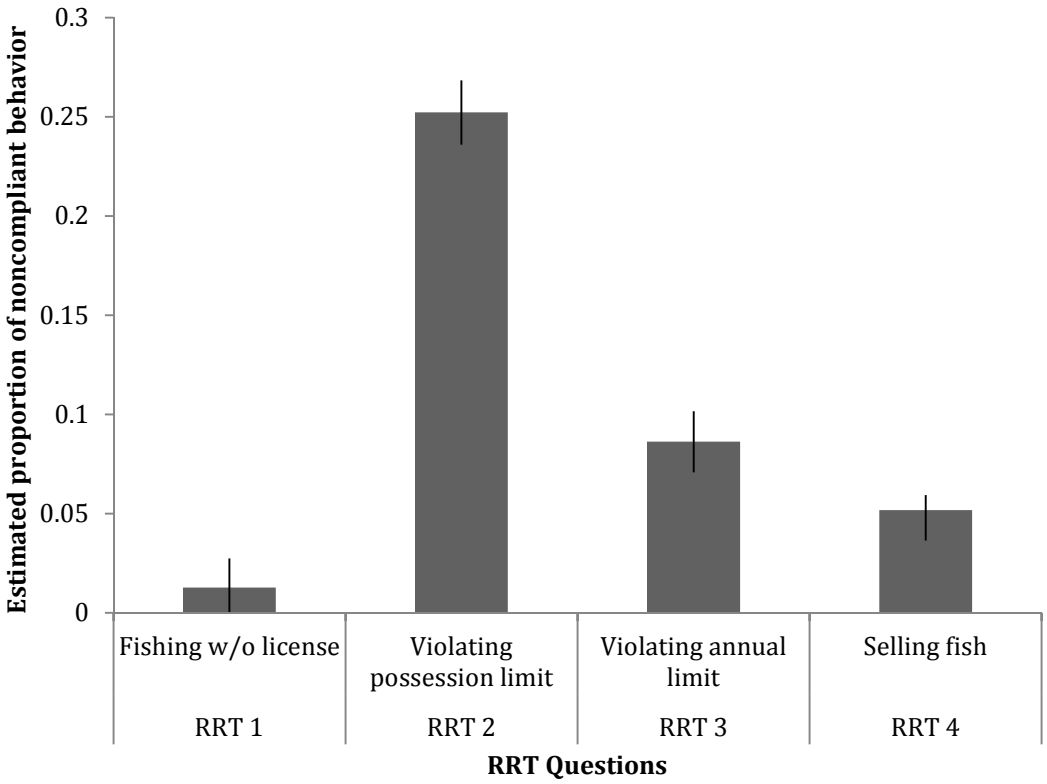
Table 2: Questionnaire items, responses, and comparison between 'yes' versus 'no' responses to the RRT questions

Questions	Responses	*p*-value for comparison of 'yes' versus 'no' responses			
		RRT 1 Fishing w/o license	RRT 2 Violating possession limit	RRT 3 Violating annual limit	RRT 4 Selling fish
Regulatory Awareness					
Do you need a permit to subsistence fish?	73% yes, per household; 24% yes, per individual; 3% no	0.638	0.507	0.282	0.359
During what time(s) of year can you subsistence fish for sockeye?	52% correct dates or dates within one month of actual openings, 32% dates within two months of actual openings, 12% dates greater than two months outside of actual openings, 5% don't know	0.921	0.256	0.139	0.127
Are there subsistence fishing limits for the number of sockeye in possession per household in Haines?	83% yes, 17% no/don't know	0.965	0.099	0.378	0.949
Possession limits are?	79% provided incorrect possession limit, 21% provided correct possession limit (25)	0.096	0.607	0.965	0.812
Are there subsistence fishing limits for the total number of sockeye harvested annually per household in Haines?	88% yes, 12% no/don't know	0.311	0.543	0.217	0.859
Annual limits are?	68% provided incorrect annual limit, 32% provided correct annual limit (50)	0.379	0.277	0.028	0.436
How did you learn about the subsistence fishing regulations?	61% from subsistence fishing permit, 23% from a friend or family	0.540	0.398	0.049	0.859

	member, 14% from another source, 2% from ADFG official				
Perceived Need					
About how much of your yearly diet is composed of sockeye salmon?	34% (average)	0.421	0.017	0.002	0.225
Number of other species harvested for subsistence purposes?	6 (average)	0.604	0.116	0.167	0.288
What do you think is an adequate number of sockeye salmon per household for subsistence needs?	52% 0-50, 20% should depend on household size, 15% 50-150, 13% >150	0.919	0.661	0.007	0.534
Experience and Perception of Management					
How many years have you subsistence fished for sockeye?	21 years (average)	0.520	0.935	0.412	0.987
What is your level of agreement with the following statement? "These days, I think that the Alaska Department of Fish and Game is doing a good job managing our subsistence fishery."	43% agree, 26% neutral, 15% disagree, 10% strongly agree, 6% strongly disagree	0.231	0.145	0.385	0.013
Demographics					
What is your age?	33% 55-64, 18% 35-44, 17% 45-54, 13% 25-34, 12% 65-74, 4% 19-24, 2% +75, 1% 18 or under	0.106	0.876	0.397	0.788
What is your sex?	68% male, 32% female	0.231	0.835	0.248	0.742
What area are you originally from?	55% elsewhere in the US, 26% Haines/Klukwan, 16% elsewhere in Alaska; 3% outside of the US	0.723	0.026	0.006	0.0545

What ethnicity do you most identify with?	71% Caucasian, 16% Alaska Native, 6% other, 5% Asian, 2% Hispanic/Latin American	0.155	0.011	0.0001	0.131
How many people are in your household?	49% 1-2, 33% 3-4, 9% 5-6, 9% >6	0.165	0.032	0.016	0.0719
What is your household's average annual income?	36% $25K-$50K, 33% $0-$25K, 11% $51K-$75K, 10% $76K-$100K, 4% >$150K, 3% $101K-$125K, 3% $125K-$150K	0.632	0.146	0.013	0.494

Figure 1: Estimated proportion (± 0.05) of non-compliance with different sockeye salmon subsistence fishing regulations (see Table 1 for RRT questions).



Chapter 2: Habituation reverses fear-based ecological effects in brown bears (*Ursus arctos*)

Abstract

Fear induced by human activity is increasingly becoming recognized to influence both behavior and population biology of wildlife. Exposure to human activity can cause animals to avoid human-dominated areas or shift temporal activity patterns, but repeated, benign exposure can also result in habituation of individuals. Habituation is typically viewed as a negative potential consequence of human interactions with wildlife, with effects such as increased vulnerability of habituated animals to predation. Concurrently, the advancement of the understanding of the ecology of fear has shown reduced fitness in species because of behavioral changes in responses to fear of predators—including humans. Here we test how habituation and fear drive the foraging ecology of brown bears (*Ursus arctos*) feeding on Pacific salmon (*Oncorhynchus* spp.) in Southeast Alaska, USA. We used motion-detecting trail cameras at salmon spawning areas across a gradient of human disturbance to record human and bear activity at fine spatial and extended temporal scales. Higher human activity was associated with increased nocturnality and suboptimal foraging for non-habituated bears ($P < 0.001$), but had no effect on habituated individuals ($P = 0.49$). For the top 20% of sites for which human activity was greatest, an average of 78.7% of the activity of non-habituated bears was nocturnal, compared with an average of only 10.2% of the activity of habituated individuals. Habituation of brown bears in

this system alleviated perceived risk and avoidance of human activity, allowing habituated individuals to overcome their fear of human presence and maximize foraging opportunities. While habituation may lessen some of the deleterious effects of human activity on large carnivores, the long-term effects of habituation may be negative, as habituated individuals may be at greater risk of depredation. Future research should examine whether habituated bears and their lower perceived risk of human activity ultimately experience smaller population-level effects of human disturbance than non-habituated individuals.

Introduction

The ecology of fear predicts that individuals will avoid forage patches or times of day where the perceived threat of predation is elevated (Bednekoff 2007, Brown and Kotler 2007). This can cause suboptimal foraging, resulting in increased energetic expenditures (Godin and Sproul 1988, Lima and Dill 1990, Cooke et al. 2003), reduced foraging gains (Bednekoff 2007, Jones and Dornhaus 2011, Eccard and Liesenjohann 2014), and reduced pregnancy rates (Fraser and Gilliam 1992, Creel et al. 2007, Travers et al. 2010). Fear induced directly by humans can influence both the behavior (Wilmers et al. 2013) and population biology of animals (Berger 2007) with impacts that can cascade through food webs (Hebblewhite et al. 2005, Wang et al. 2015).

As exposure to human activity increases, animals can respond by avoiding human dominated areas, or shifting temporal patterns of activity to reduce overlap

with human presence (Olson et al. 1998, Frid and Dill 2002, Wang et al. 2015). Some individuals, however, may experience repeated, benign interactions with humans and undergo habituation, leading to some degree of human tolerance (Samia et al. 2015). This is particularly true of animals living in nature-based tourism or ecotourism destinations (Geffroy et al. 2015).

While the advancement of the understanding of the ecology of fear has shown reduced fitness in species because of behavioral changes in responses to fear of humans, habituation may alleviate some of these effects. Habituation is typically viewed as a negative potential consequence of human interactions with wildlife (Higham and Shelton 2011); recent work has indicated that habituation can lead to increased vulnerability of prey animals to predators. For instance, fox squirrels (*Sciurus niger*) habituated to humans were less responsive to predator vocalizations than non-habituated individuals (Mccleery 2009). However, habituation may not be strictly negative if tolerance of humans relieves fear-induced foraging costs, which could potentially benefit species with no natural predators, such as brown bears (*Ursus arctos*).

Here we examine how fear and habituation influence the foraging patterns of brown bears feeding on Pacific salmon (*Oncorhynchus* spp.) in northern Southeast Alaska, USA. By comparing foraging patterns between known habituated and non-habituated bears, we are able to understand two sides of the same coin—the influence of human-induced fear on the foraging behavior of bears, and the degree to which habituation can reduce fear-based effects.

Brown bears, like many other large carnivores, are threatened by human-induced mortality, habitat loss, and habitat fragmentation (e.g. McLellan and Shackleton 1988, Servheen et al. 1990, Paetkau et al. 1998, Proctor et al. 2005, Ordiz et al. 2011). Further, brown bear feeding activities provide an additional source of human-wildlife conflict; in salmon ecosystems throughout the Pacific Northwest, bears' access to Pacific salmon may be impeded by human recreational activities, such as ecotourism, boating, and sport fishing. Previous studies have identified that bears, like other large carnivores, generally avoid human activities throughout their range (Mace et al. 1996, Rode et al. 2006, Nellemann et al. 2007). While brown bears in salmon ecosystems may perceive areas of high human activity as risky and thus alter their behavior to reduce encounters with humans (e.g. by becoming more nocturnal or avoiding areas with high human activity) they may be limited in the extent of their responses because of the need to be close to salmon spawning areas.

Research suggests that brown bears' ability to successfully capture salmon may vary based on environment and visibility. For example, in the clear-water Glendale River in British Columbia, Klinka and Reimchen (2002) found a marginal trend of increased capture efficiency with reduced light levels, which they suggest is due to reduced evasive behavior of salmon at night. Crupi (2003), however, found that in the glacially-turbid Chilkoot watershed in Southeast Alaska, bears had increased capture efficiency with increased light levels, due to better visual detection of salmon during daylight. These findings suggest that in glacially-fed systems where visibility of salmon is poor, nighttime foraging is likely suboptimal. Salmon are an

extremely important resource for brown bears, as bears avoid winter food limitation by storing fat during pulses of spawning salmon and subsequently hibernating during winter. Bears that consume more salmon have been found to have greater body mass, have larger litters, and subsist at higher population densities (Hilderbrand et al. 1999). If human disturbance limits the amount of time bears spend fishing for and consuming salmon or results in bears foraging suboptimally, weight gain could be restricted, potentially limiting survival or reproductive success.

A clear understanding of the forces that influence bear activity patterns is essential for successful management of human recreational activities and to avoid conflicts between brown bears and recreationists. Olsen *et al.* (1998) identified crepuscular patterns of activity in brown bears within Katmai National Park, Alaska, and suggested that this crepuscular pattern may reflect avoidance of humans. Similarly, Martin *et al.* (2010) illustrated that brown bear avoidance of human disturbed areas was most acute during periods of elevated human activity, particularly during daylight hours.

Human-derived shifts in bear activity patterns, however, may occur unevenly across bear populations (Quinn et al. 2014). While some bears may avoid human activity, others may undergo habituation. Habituation of brown bears can have negative consequences. Habituated individuals are at more likely to become food-conditioned, and food-conditioned bears are more likely to be lethally removed from a population than non-habituated, non-food-conditioned individuals (Mattson et al. 1992). Habituated bears are also at higher risk for being injured or killed by motor

vehicles or trains (Benn and Herrero 2002). Additionally, habituated individuals are more likely to be approached by humans, which could result in bear-inflicted injury and lethal removal of the bear. Despite these potential negative consequences, Herrero et al. (2005) suggest that habituated bears might be better able to access resources that exist near centers of human activity. Bear-to-human habituation could benefit bears as habituation lessens unnecessary energy expenditure associated with avoiding human activity (Smith et al. 2005) and could improve feeding opportunities. In this sense, habituated individuals might overcome fear of humans as perceived top predators, but it is unknown the extent to which habituation influences bear activity patterns.

Quantitative data collection on activity patterns of bears using visual observation is difficult because there are few opportunities to observe individuals across large spatial scales for entire 24-hour periods, and visual observation is limited during nighttime hours. Remote, motion-detecting trail cameras operate continuously, can 'capture' bears at all times of a 24-hour day, can be left unattended for long periods of time, and record information about the times of day bears are active, revealing diel activity patterns. Further, identifying marks on bears can be used to distinguish individuals in photographs, which can be used to compare activity patterns among bears.

Here, we use motion-detecting cameras at salmon spawning areas across a gradient of human disturbance in the Chilkoot watershed in Southeast Alaska to test how habituation and fear drive the foraging ecology of brown bears. We predicted

that: (i) fear-based effects of human presence on foraging will be present in non-habituated bears, leading non-habituated individuals to forage suboptimally by becoming increasingly nocturnal as human activity increases, and (ii) fear-based effects of human presence on foraging will be reduced in habituated bears, leading to greater temporal overlap between habituated individuals and human activity and more optimal foraging.

Study Site

We conducted our study in the Chilkoot Valley, located 12 km northwest of the community of Haines, Alaska (Fig. 1A). Chilkoot Lake is a glacially turbid lake, approximately 6 km long and 2 km wide. The lower Chilkoot River travels just over 2 km before reaching the ocean. The upper Chilkoot River, originating from the Ferebee Glacier, flows approximately 26 km to the point where it enters Chilkoot Lake. The Valley is narrow, bordered closely to the east by an unnamed mountain range and to the west by the Takshanuk Mountains.

More than 130,000 people visit the Chilkoot River each year, largely for fishing and wildlife viewing opportunities between the months of July and September (Crupi 2003). Human activity is primarily concentrated along a narrow access road that borders the lower river, and a boat landing, picnic area, and campground on the south end of the lake. Access to the eastern side of the lake is possible only by watercraft, but the western side of the lake is accessible via an abandoned two-track dirt road that parallels the western lake and upper river.

The lake and both upper and lower river provide spawning substrate for three species of Pacific salmon. Sockeye salmon (*O. nerka*) return midsummer and spawn primarily along the western shore of the lake and two areas of the upper river. Pink salmon (*O. gorbuscha*) spawn in late summer along the lower river, and coho (*O. kisutch*) follow in early autumn, spawning in the upper river and the northeast corner of the lake. Spawning sites in this area occur in discrete patches, and the rugged terrain surrounding the lake and river largely prevents aggregations of multiple bears feeding simultaneously at spawning sites.

Methods

We used motion-detecting cameras to observe human and bear activity patterns at fine spatial and extended temporal scales in the Chilkoot watershed (Fig. 1B). We focused our sampling efforts along the river and lake shorelines from the mouth of the lower river to the upper river approximately 4 km upstream of the inlet into the lake. We placed cameras (Bushnell Trophycam; Bushnell Corp., Overland Park, KS, USA) at 30 sites to monitor activity from June-October 2014 (Fig. 1B). Cameras were deployed at all known spawning areas. Additional cameras were distributed in the study area at sites that were (i) easily accessible via watercraft and/or foot; (ii) along existing game trails; (iii) within 50 m of the lakeshore or river; and (iv) at least 500 m from an adjacent camera. All cameras were set to take three pictures when triggered with a one-minute delay between successive triggers.

Cameras were checked and data downloaded weekly or every other week, depending on the amount of activity at the site.

For each photograph, we recorded the date, time, location, and species. To reduce pseudoreplication, we defined unique bear visitations as visits with a greater than thirty minute delay between the last photograph from one visit and the first photograph of the next at that site or at any adjacent camera. Family groups were counted as one bear, as cub activity is not independent of its parent.

Two unrelated, adult female bears in the study area were classified as habituated, and both had been previously tagged by ADFG as part of a study to assess habitat use and movement, thus allowing us to identify them in camera traps. These bears lacked a flight response to humans when foraging, with an overt reaction distance (ORD; Herrero et al. 2005) that was typically less than 5 m, even when foraging near large groups of tourists. Non-habituated individuals had higher ORD—while we did not encounter every bear in the study area while in the field, we never personally encountered a non-habituated individual with an ORD less than around 15 m. We identified unique human visits manually. Similarly to bear photo captures, if the camera captured two or more individuals in one photograph, we treated this as one human encounter.

We used several metrics to evaluate the differences in responses to human activity between habituated and non-habituated bears. We used the R package 'overlap' for non-parametric kernel density estimation (Ridout and Linkie 2009, Linkie and Ridout 2011) to first examine temporal partitioning between humans and

bears. After converting all time to radians, we used kernel density estimation to generate a probability density distribution of activity patterns for humans, habituated bears, and non-habituated bears based on unique encounters pooled for each sampling site (i.e. camera). We then calculated $\hat{\Delta}$, the overlap term, which is defined as the area under the curve formed by taking the smaller of two density functions at each time point, to compare activity patterns of humans to habituated bears and humans to non-habituated bears (Ridout and Linkie 2009). The overlap term, $\hat{\Delta}$, which ranges from 0 to 1, represents the temporal activity overlap between human and bear activity. If bears and humans share similar activity patterns, we would expect an overlap value ($\hat{\Delta}$) close to 1, whereas dissimilar activity patterns between humans and bears would result in $\hat{\Delta}$ values closer to 0. Ridout and Linkie (2009) outlined three methods for estimating $\hat{\Delta}$, and suggest using $\hat{\Delta}_4$ for larger sample sizes (n > 75), which we follow.

Second, we evaluated whether the foraging activity of bears differed among sites with disparate levels of human activity. Since foraging at night is suboptimal in this system (Crupi 2003), we calculated the degree of nocturnality observed for bear activity at each camera by identifying the proportion of unique encounters that occurred between sunset and sunrise, using sunrise/sunset times specific to each day of the study. We then ranked camera sites based on the observed number of unique human encounters (i.e. the camera that recorded the highest number of unique human encounters was ranked highest, the camera that recorded the second highest number of unique encounters was ranked second highest, etc.) and compared increasing

human presence to the proportion of nighttime encounters observed in bear activity using linear regression, with separate analyses for habituated and for non-habituated bears.

Finally, we assessed differences in diel patterns of bear foraging activity between habituated and non-habituated bears, again using non-parametric kernel density estimation and the coefficient of overlap. We calculated $\hat{\Delta}_4$ for habituated versus non-habituated bears across all camera sites and across the six sites (top 20%) for which human activity was greatest. We obtained 95% confidence intervals for all overlap estimates from 10,000 bootstrap samples.

Results

Cameras operated for 4,116 cumulative trap nights at the 30 sites. We recorded a total of 154 unique encounters of habituated bears and 1,959 unique encounters of non-habituated bears. Human activity was highest along the lower Chilkoot River, boat landing, and campground and decreased sharply toward the north end of the lake and along the upper river (Fig. 1B). Bears were observed at all 30 sites, with the highest numbers of unique encounters occurring at spawning areas along the western shore of the lake and along the lower river.

In accordance with our predictions, temporal partitioning between bear and human activity differed between habituated and non-habituated bears. Overlap between habituated bears and humans was very high (81.3 – 94.3% overlap; Fig. 2A), whereas overlap between non-habituated bears and humans was less than half that of

habituated individuals (40.4 – 47.7% overlap; Fig. 2B). While habituated bears were primarily active during daylight hours, non-habituated bears were active during crepuscular periods or nocturnally, and most overlap between non-habituated bears and humans occurred during evening and morning hours.

Additionally, non-habituated bears had less diurnal activity in areas used more heavily by humans. Linear regression revealed that the proportion of nighttime activity for non-habituated bears increased significantly as human activity increased ($P < 0.001$, $R^2 = 0.85$; Fig. 3); in the area of the Chilkoot watershed that sees the highest levels of human activity, non-habituated bears were almost strictly nocturnal. Conversely, there was no relationship between increases in human activity and the proportion of nighttime activity displayed by habituated individuals ($P = 0.49$, $R^2 = 0.07$; Fig. 3).

Overall, the diel patterns of activity of habituated bears differed greatly from diel patterns of non-habituated bears. Particularly in the most human-disturbed areas of the Chilkoot, habituated individuals were primarily diurnal, with activity peaking mid-morning and mid-evening, while the activity patterns of non-habituated bears peaked mid-night. Across all cameras, overlap between habituated and non-habituated bears was low (42.1 – 54.4% overlap; Fig. 4A), with non-habituated bears consistently displaying more nocturnal activity patterns than habituated individuals. Across the 20% of sites for which human activity was greatest, the overlap between habituated bears and non-habituated bears was even lower, with only 31.5 – 52.6% overlap (Fig. 4B).

Discussion

Consistent with our predictions, we found that higher human activity was associated with increased nocturnality for non-habituated bears, which could result in suboptimal foraging, but had no effect on habituated individuals. Habituated bears showed no significant response to differing levels of human disturbance throughout the watershed. Instead, diel patterns of activity for habituated individuals were almost strictly diurnal, suggesting that habituation alleviates fear-based effects in these bears. The two habituated bears in the Chilkoot watershed, with diel activity patterns that were largely diurnal, may benefit from increased daylight during foraging (Crupi 2003), as well as reduced intra-specific competition (Mattson 1990). While previous work has illustrated that habituation of species can either shield animals from predation (Hebblewhite et al. 2005, Berger 2007, Atickem et al. 2014) or make them more vulnerable to predation (Geffroy et al. 2015, Chan et al. 2010), here we have habituation of a predator alleviating perceived risk and avoidance of human activity, allowing habituated individuals to maximize their foraging opportunities.

Conversely, non-habituated bears displayed fear-based avoidance behavior, feeding almost exclusively during nighttime hours in areas of high human activity. While previous studies have documented shifts towards crepuscular behavior in human-impacted areas, we found that on the lower Chilkoot River, where human activity was highest, non-habituated bears were almost strictly nocturnal, with activity levels peaking in the middle of the night (Fig. 5). Further, proportion of nighttime

activity decreased as human activity decreased, suggesting a strong behavioral response by non-habituated bears to human disturbance.

A concurrent genotyping study in the area found that at least 12 out of 25 individual bears identified in the study made regular use of the lower Chilkoot River (R.E. Wheat, unpublished data). Given that only the two habituated individuals were regularly observed feeding diurnally on the lower Chilkoot River, this suggests that a substantial part of the local bear population is being temporally displaced by human activity. Avoidance of human activity could be spatial as well as temporal—at sites in the Chilkoot watershed where human activity was lowest, non-habituated bear activity was distributed more evenly throughout the 24-hour day, with the greatest peak in activity occurring mid-morning (Fig. 5). Increased diurnality at sites farther from human-disturbed areas could indicate that at least some individuals avoid human-disturbed areas during daylight but take advantage of foraging opportunities in areas with low human disturbance during these times.

Temporal displacement of non-habituated bears by humans in salmon spawning areas may limit these bears' foraging opportunities. Bears displaced from spawning grounds by human activity can return at alternative times or move to alternative locations to feed on salmon, but availability of salmon may be limited elsewhere depending on the time of year and the size of returning salmon populations—salmon runs returning to the Chilkoot watershed are somewhat asynchronous, with sockeye salmon returning midseason, followed by a later season run of pink salmon and a late season run of coho, and different salmon species require

different spawning substrates and spawn in different locations throughout the watershed. Habituation to human presence allows bears to overcome this displacement, providing extensive access to spawning areas even when recreational use is high.

Limitation to nocturnal foraging opportunities may influence non-habituated bears' ability to maintain adequate food intake. While one previous study found a marginal trend of increased salmon capture efficiency with reduced daylight levels in a clear-water river (Klinka and Reimchen 2002), a study of bear foraging success on salmon spawning grounds in the glacially turbid Chilkoot watershed between 2000 and 2002 found that bears' capture rates of salmon decreased significantly with diminishing daylight and increased significantly with increasing daylight, likely due to better visual detection of salmon during daylight hours (Crupi 2003). These findings suggest that in this system, temporal displacement of non-habituated bears by human activity may have a detrimental effect on bears' foraging success, while habituation may release bears from fear-based effects of human presence and thus improve foraging opportunities for habituated individuals.

While greater access to spawning salmon and reduced competition for habituated bears may contribute to greater body mass and larger litter sizes (Hilderbrand et al. 1999), the long-term effects of habituation may be negative. In the past 16 years in the Chilkoot watershed, several of the offspring of the two habituated females in this study have been lethally removed as a result of conflicts with local

residents and a lack of wary behavior around humans (A. Crupi, Alaska Dept. of Fish and Game, personal communication).

Habituation, and the ensuing tolerance of human presence that results, represents one potential outcome of low perceived risk of human activity. Here, we illustrated that habituation of individual brown bears alleviated fear of human presence at a popular recreational fishing and wildlife viewing site, likely leading to improved foraging opportunities for these individuals when compared with non-habituated bears. Nature-based tourism and ecotourism are becoming increasingly popular recreational activities (Knight 2009), and as demand for this type of leisure grows, so too will interactions between humans and wildlife in natural landscapes. Our findings suggest that in some cases habituation may alleviate some of the deleterious effects of human activity on large carnivores, as habituated individuals are more tolerant of human activity. Further research should examine population level effects of habituation in areas with high human traffic.

Acknowledgements

We thank Anthony Crupi from Alaska Department of Fish and Game for his expertise, and S. Campbell, L. Girard, M. Hart, L. Minch, E. Warman, S. Wilson, and R. McGee for field assistance. Special thanks to Shannon Donahue for providing lower Chilkoot River data.

Figure 1: A) Chilkoot watershed near Haines, Alaska. B) Locations of camera trapping sites. The relative levels of human activity are indicated by gradient, with the lowest levels of human activity represented by the lightest shades and the highest levels of human activity represented by the darkest shades of grey.

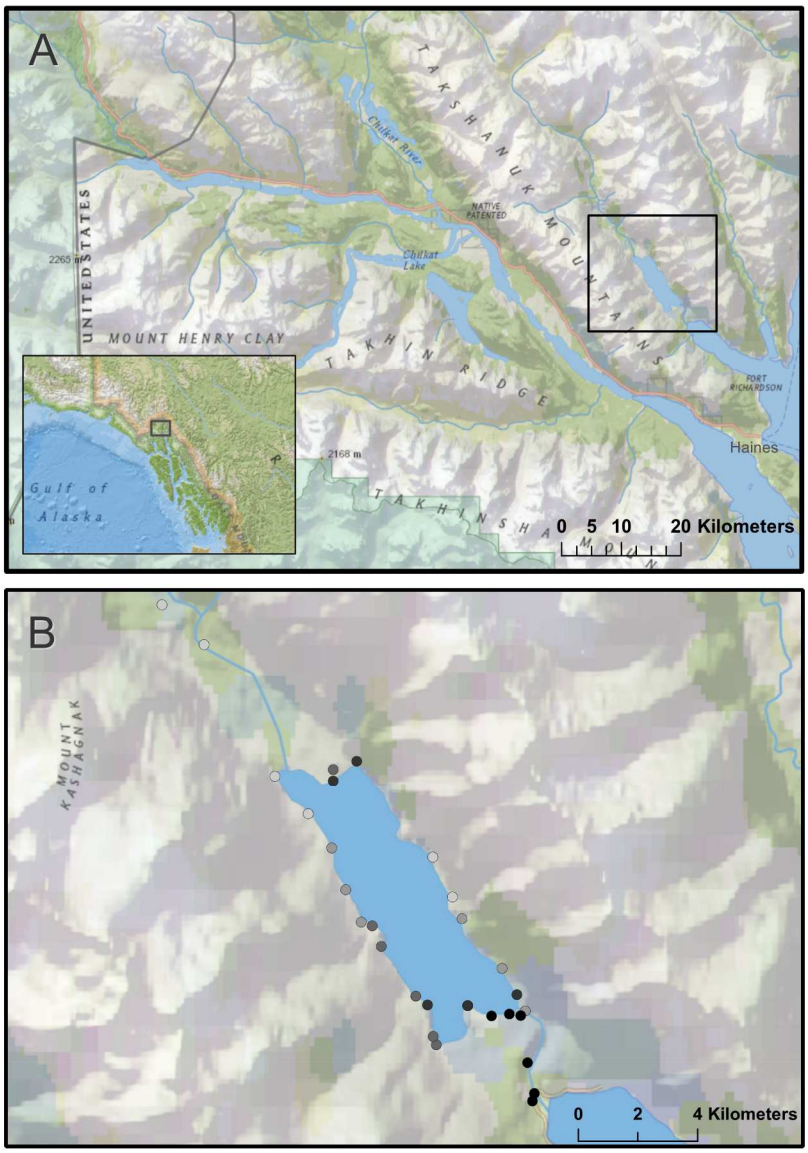


Figure 2: Overlap of A) human activity and activity of habituated bears and B) human activity and activity of non-habituated bears across all camera sites. Grey areas represent periods of time during which both bears and humans are active.

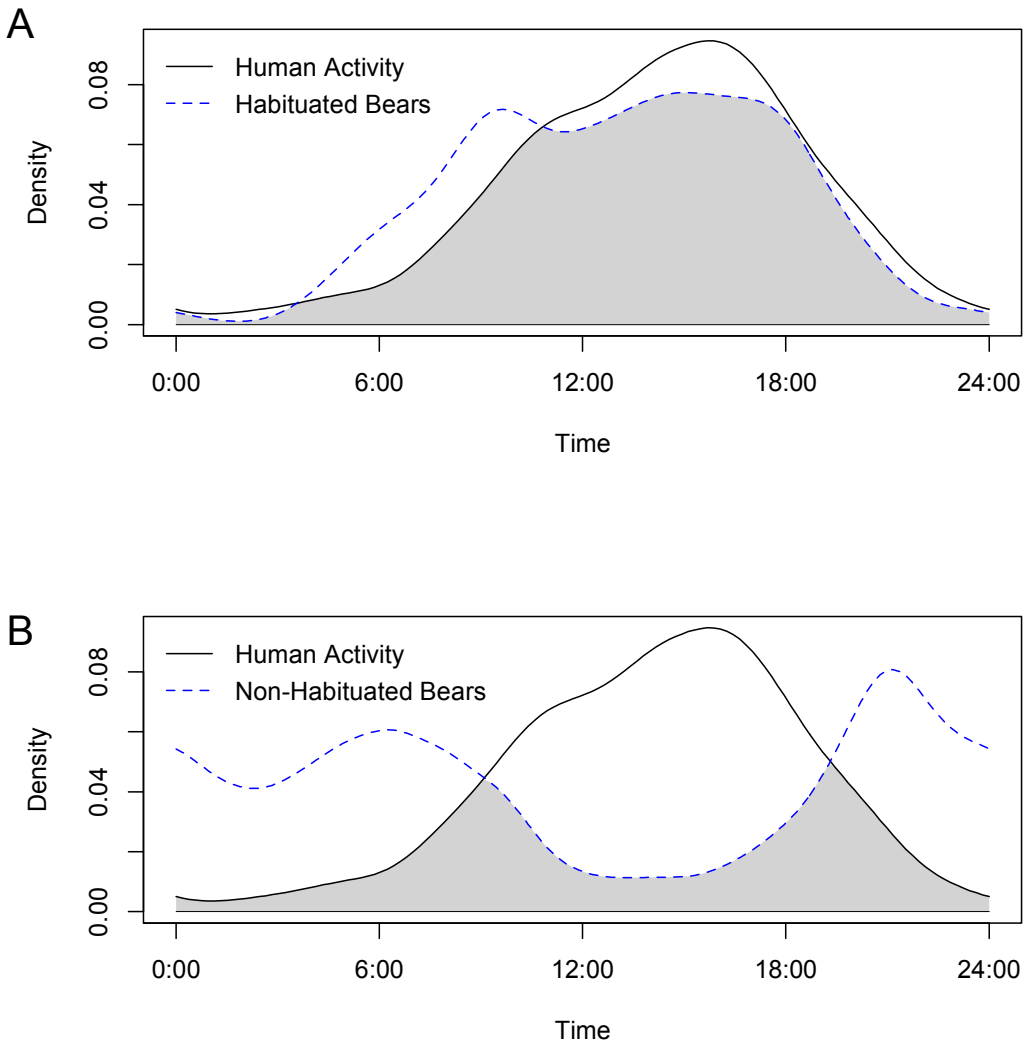


Figure 3: Linear regression comparing the proportion of nighttime activity displayed by non-habituated (solid line) and habituated (dashed line) bears to the level of human disturbance with 95% confidence intervals (shading). Each point is representative of a single camera site. Cameras were ranked based on the number of unique human encounters observed from the lowest (lowest human disturbance rank) to the highest number of unique human encounters observed (highest human disturbance rank). As human disturbance increased, the proportion of nighttime activity displayed by non-habituated bears increased ($P < 0.001$). There was no relationship between human activity and nighttime activity of habituated individuals ($P = 0.49$).

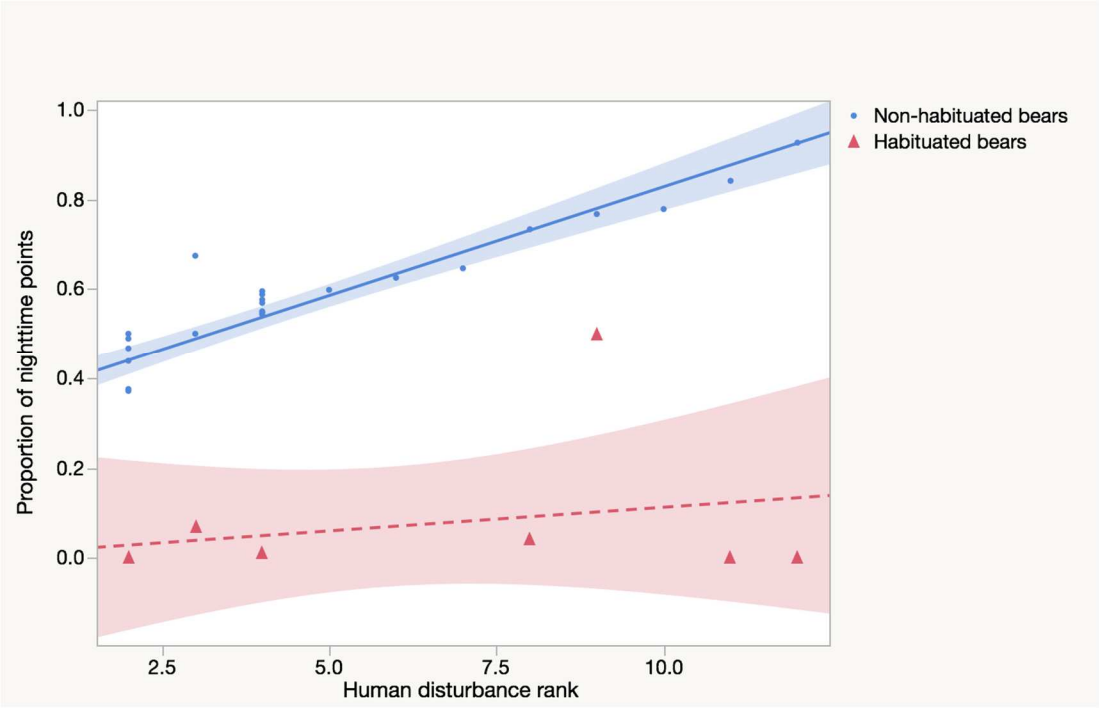


Figure 4: Comparison of diel activity patterns for habituated versus non-habituated bears A) across all camera sites and B) across the 20% of sites (N = 6) at which human activity was greatest. Grey areas represent periods of time during which both habituated and non-habituated bears are active.

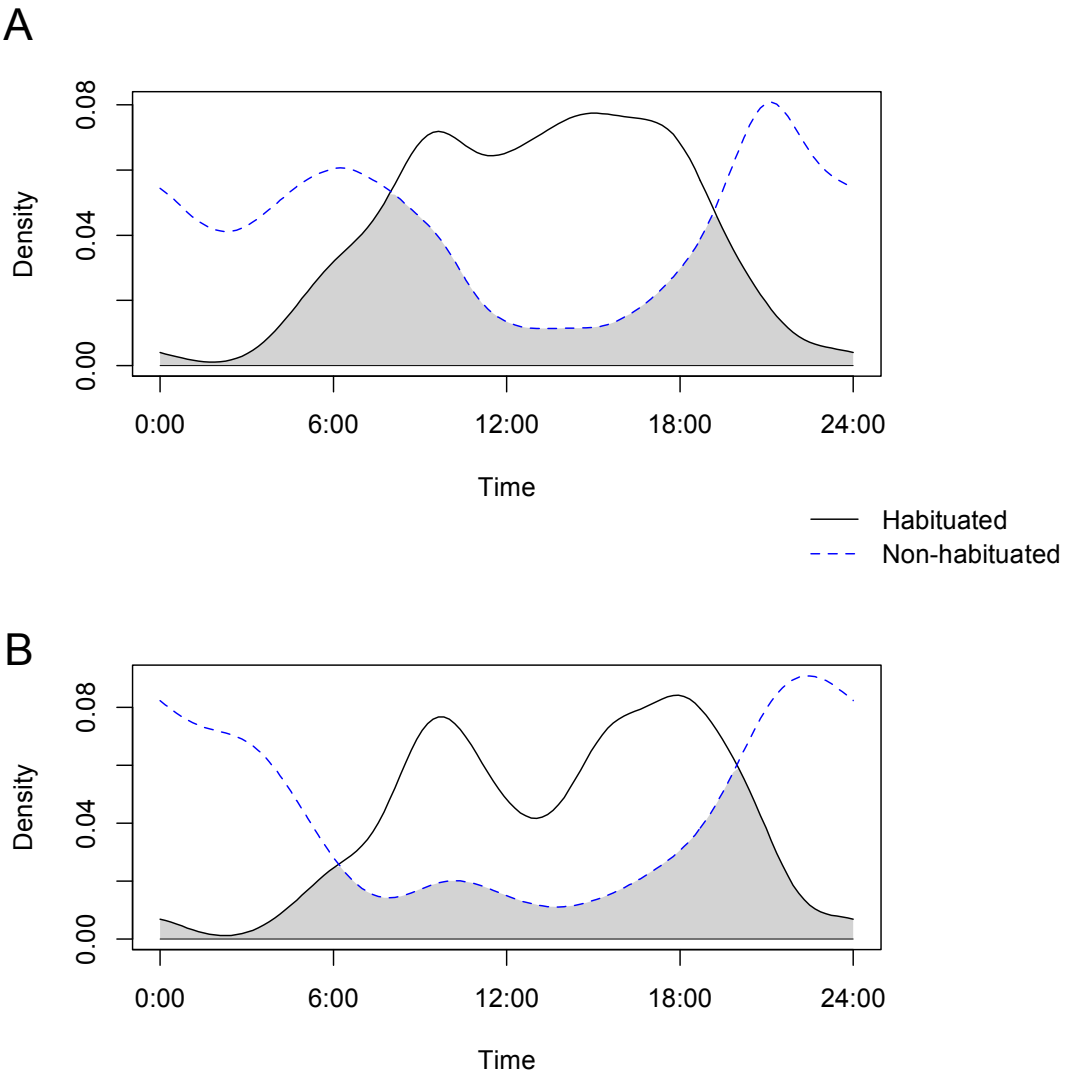
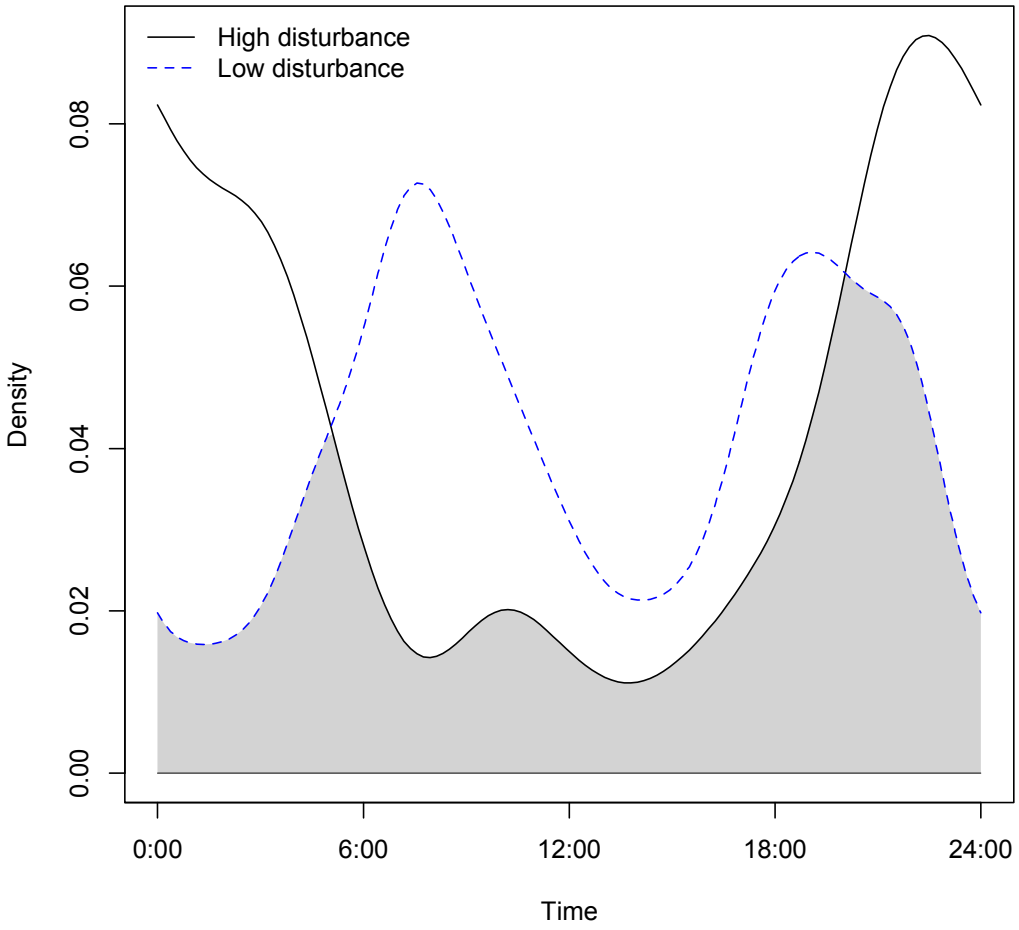


Figure 5: Diel activity patterns for non-habituated bears across the 20% of sites (N = 6) at which human activity was greatest (solid line) and across the 20% of sites (N = 6) at which human activity was lowest (dashed line). At high-disturbance sites, activity of non-habituated bears was almost strictly nocturnal, but at sites with low human presence, bears were active diurnally.



Chapter 3: Environmental DNA from residual saliva for efficient noninvasive genetic monitoring of brown bears (*Ursus arctos*)

Abstract

Environmental DNA (eDNA) allows for the detection of organisms without requiring sampling of living organisms themselves. Noninvasive genetic monitoring of individuals using eDNA has been widely applied in the research and management of brown bears (*Ursus arctos*), typically relying on hair snaring or scat sampling techniques. Hair snaring is labor and cost intensive, however, and scats yield poor quality DNA. Residual saliva from partially-consumed Pacific salmon (*Oncorhynchus* spp.) carcasses represents an additional potential source of noninvasive DNA for monitoring brown bear populations. Salmon carcasses are reliably encountered, often at high density, at spawning aggregations and other stream reaches where salmon are accessible to bears. We compared the efficiency of monitoring brown bear populations with fecal DNA and salivary DNA collected from partially-consumed salmon carcasses in Southeast Alaska. We swabbed a total of 272 scats in good condition and swabbed a range of tissue types from 156 partially-consumed salmon carcasses from a midseason run of lakeshore-spawning sockeye (*O. nerka*) and a late season run of stream-spawning chum (*O. keta*) salmon in 2014. Saliva collected from salmon carcasses had significantly higher genotyping success rates, identified unique individuals more quickly, and required much less labor to locate than scat samples. Salmon carcass swabbing is a promising method for efficient and affordable monitoring of bear populations. Although other carnivores do

not deposit large quantities of partially-consumed prey, systematic baiting and saliva sampling may be an efficient method for monitoring other species, particularly wary species that are difficult to monitor using hair snares.

Introduction

Environmental DNA, or eDNA, has proven to be a comprehensive, noninvasive means of monitoring biodiversity, providing rapid, cost-effective, and efficient insights on species' distribution and abundance (Bohmann et al. 2014, Thomsen and Willerslev 2015). As a tool for applied conservation biology, eDNA is particularly valuable in detection and monitoring of wide-ranging, elusive species (Bohmann et al. 2014). In studies of terrestrial wildlife, hair, scat, and urine are three of the most common sources of eDNA, but buccal cells found in saliva can also provide genetic material (Kelly et al. 2012).

There have been relatively few studies on the success of obtaining carnivore DNA from saliva, and no studies have yet used eDNA from saliva as a tool for density estimation. Williams *et al.* (2003) and Blejwas *et al.* (2006) were able to use microsatellites to identify individual coyotes (*Canis latrans*) from saliva collected from bite wounds on sheep. Similarly, Sundqvist *et al.* (2007) used saliva collected from bite wounds on sheep to show that domestic dogs (*Canis faimiliaris*) were responsible for attacks. More recently, Farley *et al.* (2014) collected brown bear (*Ursus arctos*) saliva from bite wounds on mauling victims and were able to successfully identify individual bears, and van Bleijswijk *et al.* (2014) identified grey

seal (*Halichoerus grypus*) bites on stranded harbour porpoises (*Phocoena phocoena*).

In order for saliva to be effective as a noninvasive genetic sampling tool for monitoring carnivore populations, large sample numbers are needed, which may be infeasible if kills are widely dispersed and/or difficult to locate. In ecosystems throughout the Pacific Northwest, however, Pacific salmon (*Oncorhynchus* spp.) provide a reliable, discrete, and highly concentrated food resource for brown bears throughout summer and autumn.

Noninvasive research on population genetics and genetic monitoring of individuals has been widely used in the research and management of brown bears, traditionally relying on hair snaring or scat sampling techniques. This includes the use of barbed wire on natural or artificial rub trees (Kendall et al. 2008b, Karamanlidis et al. 2010) or arranged around bait stations (Woods et al. 1999) for hair collection, or collection of fecal samples along transects or roads and game trails (Taberlet et al. 1997, Wasser et al. 2004). Hair collection, however, can be cost- and labor-intensive (De Barba et al. 2010), and the use of hair corrals might not be appropriate for developed areas (Kendall et al. 2008a). Similarly, fecal DNA samples are often degraded in the wet summers of temperate coastal environments, and scats can be difficult to locate in the large, roadless areas that encompass much of the range of brown bears.

Saliva collection from partially-consumed salmon carcasses provides a potential alternative, or simple augmentation, to hair and scat sampling. Brown bear predation rates on salmon are often high, nearing 50% in some areas (Gende et al.

2004, Quinn et al. 2009), and when run sizes are large, bears may consume as little as 25% of each fish they kill (Quinn et al. 2009). This high-grading behavior results in the deposition of partially-consumed salmon carcasses, and the residual saliva left on these carcasses when bears abandon them could serve as a source of brown bear DNA for noninvasive population monitoring.

We implemented a project during summer and autumn 2014 in northern Southeast Alaska to determine if saliva collection from partially-consumed Pacific salmon carcasses is a feasible, reliable, effective, and cost efficient source of brown bear DNA compared with scat sampling, and to develop a protocol for saliva sample collection that maximized the likelihood of obtaining individual bear identification from salmon carcasses.

Materials and Methods

Study area

We collected saliva samples from partially-consumed Pacific salmon carcasses at two distinct salmon runs: a midseason run of primarily lakeshore-spawning sockeye salmon (*O. nerka*) in the Chilkoot watershed, and a late season run of stream-spawning chum salmon (*O. keta*) at Herman Creek in the Klehini watershed, both near Haines, Alaska (Fig. 1A). We also collected scat samples throughout the Chilkoot watershed, to compare the utility of saliva for monitoring bear populations against this technique.

The Chilkoot watershed is located 12 km NNW of the community of Haines, Alaska. Chilkoot Lake is a glacially turbid lake, approximately 6 km long and 2 km wide. The lower Chilkoot River travels just over 2 km before reaching the ocean. The upper Chilkoot River, originating from the Ferebee Glacier, flows approximately 26 km to the point where it enters Chilkoot Lake. The Chilkoot Valley is narrow, bordered closely to the east by an unnamed mountain range and to the west by the Takshanuk Mountains. A midseason run of sockeye salmon spawns in patches along the western shore of the lake and in the upper river, beginning in early July and extending through early September. Our sampling efforts targeted an abandoned two-track dirt road that parallels the western lake and upper river, and existing game trails that surround the lake, the lower Chilkoot River, and a 6 km reach of the Upper Chilkoot River.

Herman Creek, part of the Klehini watershed, is located approximately 40 km NW of the community of Haines. Two artificial spawning channels along Herman Creek, near where it empties into the Klehini River, serve as part of a wildstock chum salmon enhancement project overseen by the Northern Southeast Regional Aquaculture Association. These channels are currently where the majority of chum salmon returning to Herman Creek spawn. Spawning occurs across several weeks beginning mid-September. We focused our sampling efforts along the banks of both spawning channels.

Field methods

We collected 272 scat samples and 108 saliva samples in the Chilkoot valley from June through September 2014. We divided the study area into five separate sampling regions each visited once weekly (Fig. 1B). Scat samples were collected by walking systematically along an established system of roads and game trails in one region per day. We graded scats based on condition, diameter, and estimated age. Scats in good condition were selected for sampling. We lightly swabbed the surface of each scat with a single sterile cotton swab, and stored swabs in individual 2mL microtubes in 100% ethanol.

We collected saliva from carcasses by visiting known, distinct spawning grounds (Fig. 1B) throughout the study area, and we opportunistically sampled carcasses found elsewhere. Carcasses were swabbed with sterile cotton swabs using a variety of techniques based on the amount and type of tissues consumed: high-graded carcasses, from which only the brain of the fish was eaten, were swabbed along the edges of the braincase; high-graded carcasses with distinct bite holes were swabbed inside of bite holes; carcasses from which strips of skin were removed were swabbed diffusely over exposed muscle tissue or along the torn margins of the skin; fish that had been largely consumed were swabbed along remaining parts, typically the braincase, gill plates, or mandible; some largely intact individuals were diffusely swabbed all along the length of the fish. We kept detailed records of the estimated age of the carcass, swabbing method (e.g. bite marks swabbed individually, diffuse swabbing across exposed muscle tissue, etc.) and the condition of each carcass sampled, and collected photographic evidence of each swabbed carcass. As with scat

samples, saliva swabs were stored in individual 2ml microtubes in 100% ethanol. We removed both scat piles and carcasses from the study area following swabbing to avoid repeat sampling. All collected samples were stored at -20°C until extraction.

We collected 80 additional saliva samples for analysis from 48 partially-consumed chum salmon carcasses in the Klehini watershed along Herman Creek in late September 2014. Chum salmon, which spawn at high density in Herman Creek, are more accessible to bears than the lakeshore-spawning sockeye at Chilkoot. Lakeshore spawners are difficult for bears to access (Quinn et al. 2001), as salmon can escape predation by temporarily moving into deeper waters. As bears expend less energy to capture salmon in shallow streams, high-grading behavior is usually more prevalent. Sampling chum salmon at Herman Creek thus allowed us to compare the effectiveness of swabbing salmon in areas with and without high levels of high-grading behavior. We again swabbed carcasses based on unconsumed tissues. High-grading of chum at Herman Creek also permitted us to swab a single carcass multiple times to compare saliva collection methods within a single sample. For example, both bite holes through the skin and exposed muscle tissue might be present in different areas of one carcass, in which case two different swabs would be taken. Swabs were stored individually in microtubes of 100% ethanol at -20°C.

Genetic methods

We extracted DNA from all samples using AquaGenomic™ (MultiTarget Pharmaceuticals LLC, Colorado Springs, CO, USA), according to a modified

protocol developed from the manufacturer's instructions (see Appendix). Samples were genotyped at seven microsatellite loci: G1A, G1D, G10B, G10H, G10J, G10M, and G10X (Paetkau et al. 1998). SRY (Bellemain and Taberlet 2004) was used for sex determination. We amplified all loci in multiplex PCRs using the Qiagen Multiplex PCR kit (Qiagen, USA). Fluorescence-based detection and sizing of fragments was performed on an ABI 3730 Genetic Analyzer (Applied Biosystems, Foster City, California, USA) at the Oregon State University Center for Genome Research and Biocomputing, and we manually scored alleles using GeneMapper software package, version 4.1 (Applied Biosystems, USA). Genotypes of each sample were replicated a minimum of three times to serve as reliable references. Individuals missing up to two loci (e.g. failed PCR, poor-quality DNA extract) were amplified an additional three times; samples missing more than two loci were excluded from our data set. We followed guidelines in Paetkau (2003) and Waits and Paetkau (2005) for ensuring microsatellite genotyping data quality. Genotyping error was estimated by directly counting error rate per allele.

We identified unique genotypes using the R package 'allelematch' (Galpern et al. 2012), which assigns composite genotypes to unique individuals based on an estimated maximum threshold number of mismatching loci. The package uses a metric of the Hamming distance (Hamming 1950) to find similarities between samples, and uses hierarchical clustering and a dynamic method for identifying clusters on a dendrogram with the Dynamic Tree Cut package for R (Langfelder et al. 2008). Multiple observations of a unique genotype were used as an additional

measure of genotyping reliability; single observations of unique genotypes were not accepted as new individuals unless alleles for all seven loci and the sex marker matched across all amplifications.

Population estimates for samples collected at Chilkoot were generated with the single-session approach of the R package CAPWIRE (Pennell et al. 2013), developed specifically for noninvasive genetic samples (Miller et al. 2005). Data from both saliva and scat collection were overdispersed, with one or two bears captured far more than other individuals. We used the PART algorithm in CAPWIRE to partition the data and fit a two innate rates model (max. population 80) to count data in the lower partition, then added individuals from the upper partition to the maximum likelihood estimate of population size *post hoc*. We performed a parametric bootstrap (1,000 bootstraps) to obtain confidence intervals around our population size estimates (Pennell et al. 2013).

We examined the effectiveness of scat versus saliva sampling techniques using the following criteria: genotyping success, genotyping error rate, number of bears identified, and size of the population estimate and confidence intervals. Pairwise differences in the genotyping success rates of scat versus saliva samples were examined by using the *z* test for proportions. The *z* test for proportions was also used to compare the proportional genotyping success rates of each saliva swabbing technique. We generated population size estimates and confidence intervals for scat and saliva samples separately and combined. Additionally, we assessed the efficiency of sampling methods by comparing search effort and costs needed for scat versus

saliva sampling. Cost per sample, cost per genotyped sample, and cost per unique bear identified were calculated by summing estimates of field labor costs required to collect each sample, lab labor costs for processing each sample, and costs for DNA extraction, multiplex PCR, and genotyping for each sample, excluding consumables.

Results

We sampled a total of 272 scats and 156 partially-consumed salmon carcasses between June and September 2014 (Table 1). After microsatellite PCR screening for sample quality we excluded 42.3% of scat samples and 13.8% of saliva samples. Of the remaining samples, 190 total were successfully amplified at 7-8 loci (including the SRY sex locus), and 87 scat and 74 saliva samples were assigned to individuals. Variability of the selected microsatellite loci was high, with $H_o = 0.74$ and three to seven alleles per locus. P_{ID} ($1.41e^{-6}$) and $P_{ID(sib)}$ ($3.14e^{-3}$) were low; the $P_{ID(sib)}$ threshold for accepting a genotype was 0.05. All PCR replicates of the sex marker SRY gave consistent results. We identified 34 unique genotypes, 20 female and 14 male. Multiple observations of a genotype were recorded for all but five individuals.

Evaluation of swabbing techniques for carcasses

We collected a total of 188 saliva swabs from 156 partially-consumed salmon carcasses at Chilkoot (N = 108) and Herman Creek (N = 80). We generally found that a wide range of carcass types produced DNA. Swabbing technique was broken up into eight categories based on unconsumed tissues (Fig. 2, Table 2). Braincases, from

both high-graded and mostly consumed fish, were the most common areas swabbed (N = 88), followed by bite holes (N = 34). Margins of torn skin had the highest amplification rate at 71% compared to other swabbing techniques (Table 2), but these types of carcasses were encountered infrequently (N = 7). Braincase swabs amplified at a rate of 48%, followed by bite holes at 38%. Amplification success rates were lower for swabs taken from gill plates (25%), mandibles (23%), and exposed muscle (21%), as well as swabs swiped diffusely all over the surface of the length of the fish (22%). Proportional amplification success rates for braincase swabs were significantly higher than all other swabbing techniques ($z = -1.99$, $P < 0.05$; Figure 3).

High-grading was far more prevalent at Herman Creek than at Chilkoot, which allowed us to take multiple swabs from single carcasses. Out of 48 carcasses sampled at Herman Creek, we collected between two and four swabs from 21 fish. Bite holes were the most common swabbing location (N = 22), followed by braincases (N = 19) and exposed muscle (N = 7); in most cases the braincase of the carcass was swabbed in addition to one or more bite holes. Of carcasses swabbed in multiple locations, braincase samples were most likely to successfully amplify—57.9% of braincase swabs from carcasses sampled multiple times were assigned to individual, compared to 31.8% of swabs of bite hole(s) and 28.6% of swabs of exposed muscle tissue.

Evaluation of scat versus saliva sampling

Effectiveness: Genotyping success and population estimation

The genotyping success rate for all saliva samples was 41.7%. Genotyping success rates were highest overall (56%) at Herman Creek, where high-grading behavior was prevalent. At Chilkoot, where high-grading behavior was uncommon and salmon carcasses were sparse, the genotyping success rate was 32%. The genotyping success rate for saliva collected from high-graded carcasses at Herman Creek was significantly higher than for saliva collected at Chilkoot (z = -2.46, P < 0.05).

The genotyping success rate for scat samples was 35%. This value is likely biased in favor of greater success because we sampled only those scats in good condition. Even given this bias, when compared to saliva, genotyping success rates were significantly higher for saliva than for scat samples (z = -2.01, P < 0.05). Additionally, our calculated genotyping error rate was slightly lower for saliva than for scat samples. Per-locus error rates for scat samples averaged 10% across all loci for scat samples, while error rates for saliva averaged 8.6%.

Neither scat nor saliva samples collected at Chilkoot detected all bears, but 24 out of 25 individuals were identified from 87 of 272 scat samples that successfully genotyped, and 12 individuals were detected using saliva from 38 of 108 sockeye salmon carcasses that successfully genotyped. Detection frequency varied among individuals and with different techniques (Fig. 4). Individuals were detected from 1 to 26 times throughout the sampling season, with an average of 2.9 saliva samples per bear and 3.6 scat samples per bear. Combining scat and saliva detections increased

detection frequencies, with individual bears sampled an average of 5.0 different times.

Population size estimates for Chilkoot varied based on sample type, but confidence intervals for all three population estimates overlapped (Table 3). The population size estimate for saliva samples alone was the lowest at 21 individual bears, with 95% confidence intervals of 14-36. The population size estimate generated using scats alone was the highest overall at 28, with slightly narrower confidence intervals (24-35) than saliva alone, though fewer saliva than scat samples were collected at Chilkoot. Combining scat and saliva samples increased the number of detections per bear, resulting in a population estimate of 27 bears and reducing confidence intervals to 25-31.

Efficiency: Cost and labor

Cost per sample, cost per genotype, and cost per unique bear identified were higher for scat than saliva (Table 4). Costs per sample averaged $39 for scat versus $28 for saliva. Cost per genotype averaged $123 for scat and $72 for saliva. Cost per unique bear averaged $447 needed to identify each unique individual using scats, versus $253 needed to identify each unique individual bear using saliva. In general, laboratory expenses for processing and genotyping samples were similar for scat and saliva samples, but field labor costs were substantially higher for sampling scat, at an average of $18 per sample, than saliva, at an average of just over $4 per sample. This discrepancy stems from the number of search hours required to locate salmon

carcasses versus scats. Many more search hours were required per sample and per unique bear for scat than for saliva (Fig. 5). On average, only 0.22 search hours were required to locate each sockeye salmon carcass, and 0.13 search hours required to locate each chum salmon carcass, compared to an average of 0.90 hours required to locate each scat. Additionally, it took an average of 10 hours of searching and sampling scat at Chilkoot to identify each unique individual bear, a much higher rate than that for sampling saliva from sockeye carcasses, at 1.92 search hours/unique bear. Saliva samples obtained from high-graded carcasses required the lowest search effort overall—on average it took just 0.56 hours of search time at Herman Creek to identify each unique bear.

Discussion

Our findings support the application of eDNA from residual saliva as a low-effort, cost-effective tool to monitor brown bear populations. Residual saliva collected from partially-consumed salmon carcasses provided large sample quantities in discrete geographic locations, detected multiple individual bears of both sexes and multiple age classes, and resulted in multiple observations of unique genotypes. Combining scat and saliva samples collected at Chilkoot Lake increased the number of detections per bear and greatly decreased the confidence intervals associated with our population estimate. When collected opportunistically during the course of hair snaring or scat collection projects, saliva samples from salmon carcasses could

increase the number of detections, and possibly the number of unique bears identified, with very little additional effort.

In regions where black bears (*Ursus americanus*) consume salmon, saliva sampling should be suitable for simultaneously monitoring both species because black bears share many of the same microsatellite loci with brown bears (Paetkau 2003). Although brown and black bears are sympatric in Haines, Alaska, we did not obtain DNA from any black bears, which is consistent with previous research suggesting that black bears are locally excluded from salmon in this system by brown bears (Levi et al. 2015).

The reduced labor and cost associated with monitoring bear populations by sampling saliva from salmon carcasses could prove particularly advantageous in locales where infrastructure is lacking. In remote or protected areas where vehicular traffic is restricted, such as most of Southeast Alaska and coastal British Columbia, salmon swabbing could serve as a feasible alternative to hair snaring or scat collection, as many spawning areas are easily accessible by boat. We envision this method being particularly useful in ecosystems with large runs of stream-spawning salmon such as chum and pink (*O. gorbuscha*) salmon, where high-grading behavior by bears is prevalent.

Evaluation of scat versus saliva sampling

Although fewer saliva samples were obtained at Chilkoot and scat collection was biased in favor of scats in good condition, genotyping success rates were higher,

and per-locus error rates lower, for saliva than for scat samples. Further, search hours necessary to locate carcasses were much lower for saliva than for scat samples, with the effect of greatly reducing labor, and subsequently costs, for saliva sample collection compared to scat. Search effort was lowest overall, and genotyping success rate highest, at Herman Creek, where dense aggregates of spawning salmon in a relatively shallow streambed led to high predation rates by bears and frequent high-grading behavior. At Herman Creek, we collected samples identifying nine individual bears in four sampling bouts that spanned fewer than six hours total. Regular, brief visits to spawning areas, particularly during salmon runs when high-grading of carcasses is prevalent, could effectively sample a substantial proportion of the local bear population with very little effort.

When compared to scat sampling, saliva samples from Chilkoot detected fewer bears, and population size estimates generated using scats alone were higher and had smaller 95% confidence intervals than estimations generated with saliva alone. However, we spent more than 200 additional hours searching for scat than for saliva, and we collected more than one and a half times more scat than saliva samples at Chilkoot. Although the sockeye salmon run at Chilkoot Lake in 2014 surpassed the 10-year average for the region (ADFG 2014), lakeshore spawners are difficult for bears to access (Quinn et al. 2001), resulting in fewer high-graded carcasses.

Evaluation of swabbing methods for carcasses

Braincase removal was by far the most common consumption type we encountered; even in cases where the majority of the salmon was consumed, bears would often leave the de-brained skull and gill plates of the fish. Further, braincase swabs had the highest proportional success rate in terms of amplification and assignment to individual. Individual bite holes were also frequently encountered in abandoned carcasses, particularly in high-graded carcasses, and had an only slightly lower amplification success rate than braincase swabs.

Although braincase and bite hole swabs were generally the most useful, we found a wide range of carcass types and conditions to successfully amplify bear DNA (Fig. 2). While we recommend that those looking to adopt this technique in their own work target braincases and individual bite holes when swabbing for saliva, we suggest that researchers keep in mind the relative low costs of collection, DNA extraction, and PCR screening for DNA quality—the margins of any area of a salmon that has been consumed are potential reservoirs for usable bear DNA. Additionally, while we were able to successfully obtain and amplify DNA using dry sterile cotton swabs rolled or swiped along the surface of a carcass, we encourage exploration of alternative collection protocols. For example, swabbing surfaces very lightly or spraying swabs with deionizied water prior to swabbing might increase amplification success.

Limitations

Our results demonstrate that residual saliva collected from partially-consumed salmon carcasses is a feasible noninvasive genetic sampling tool. We believe this technique could be implemented broadly throughout both the Pacific Northwest and coastal Asia in areas where bears consistently feed on spawning salmon. As the first test of an entirely new technique for sampling bear DNA, we recognize that this method may have limitations. First, although genotyping success rates for saliva samples were as high as 56%, this number is relatively low when compared with some bear population studies using hair snares (Beier et al. 2005, Kendall et al. 2008a, 2009). Research has illustrated that amplification rates of noninvasive samples decrease and genotyping error rates increase with increasing precipitation (Piggott 2004, Murphy et al. 2007). Our genotyping success rates were probably negatively influence by an extremely wet summer. The summer of 2014 was the wettest summer in nearly a century in Haines, with record-breaking rainfall nearly every month of the study. Given the difficult field conditions and intense precipitation, we expect greater amplification success could be expected for both scat and saliva samples in drier years.

Second, swabs of partially-consumed salmon carcasses also sample salmon DNA, sometimes in large quantities, in addition to bear DNA. We had to discount two microsatellites (G10C and Mu59) when testing loci to use for our study as a result of apparent amplification of salmon DNA within the region of the bear marker. Scat samples tested using these markers amplified normally, and although some saliva samples produced identifiable alleles, the majority were consistently obscured.

(Murphy et al. 2003) found fecal samples from captive brown bears fed diets of Atlantic salmon (*Salmo* spp.) had very low amplification success rates, and suggested this might be a result of interference with salmonid by-products. Limitations with these markers could be overcome by swabbing carcasses less intensively (i.e. lessening the quantity of salmon tissue picked up on the swab), by additional optimization of DNA extraction, or PCR amplification methods, such as the use of salmon-blocking oligonucleotides.

Third, because of the nature of bear feeding behavior, it is possible for carcasses to become contaminated with DNA from a second individual bear if scavenging occurs following the initial consumption event. To ensure genotyping quality, we did not accept unique genotypes as new individuals unless they were associated with multiple detections or alleles for all seven loci and the sex marker matched across all amplifications. As a result, we discarded many genotypes that were only detected once. Although only five of the scat samples that amplified failed to meet these criteria, we discarded a total of 23 saliva samples, and we postulate that many of these single-detection unique genotypes from salmon carcasses were actually amalgams of two other individual bears. We saw direct evidence of this in the field when we observed two known individuals feeding on the same salmon carcass within a short timeframe of one another. The saliva collected afterward produced an unusable, unique genotype that amplified alleles from both bears at different loci (Table 5). These considerations aside, saliva is a promising new source for bear DNA in salmon ecosystems.

Utility of eDNA from residual saliva for population monitoring

We found residual saliva collected from partially-consumed salmon carcasses to be a successful, labor- and cost-effective way to sample brown bear populations. As far as we are aware, this study is the first to use noninvasively collected saliva to estimate the population density of any species of wildlife. Although salmon carcasses provide a readily available source of saliva to monitor bear populations, baited saliva sampling should be easily generalizable to systematic surveys of carnivores if appropriate baits can be identified and tested. As an eDNA source, salivary DNA can replace or complement alternative sampling methods, particularly when these methods are inefficient, prohibitively expensive, or difficult to implement. For example, some elusive small carnivore species might be more easily tempted to deposit saliva on a bait rather than enter a hair collection tube or trap. Large canids and felids are particularly difficult to survey when scats are not available because researchers typically rely on scented and barbed pads or boards to illicit rubbing behavior in the hope of obtaining hair samples for genetic monitoring. Rub boards could be easily paired with durable baits that might prompt an animal to deposit saliva even when that animal is not provoked to rub on a board or pad. eDNA from saliva for noninvasive genetic monitoring has the potential to be an important general tool for the conservation and management of wildlife populations.

Acknowledgements

We thank Anthony Crupi from Alaska Department of Fish and Game for his expertise, and S. Campbell, L. Girard, M. Hart, L. Minch, E. Warman, S. Wilson, and R. McGee for field assistance.

Table 1: Results by sample type

Sample Type	Samples Collected	Successfully Genotyped	Unique Bears Identified
Scat	272	87	24
Saliva	188	74	21
-Sockeye	108	38	12
-Chum	80	36	9
Combined	460	161	34

Table 2: Saliva swabbing techniques and results

Area Swabbed	Description	No. Sampled	Proportion amplified
Braincase	A high-graded salmon where only the brain and eyes of the fish have been removed, or a largely consumed carcass where only the braincase and possibly the mandible of the salmon remain. Swab rolled along the edges of the braincase.	88	0.48
Bite hole(s)	A high-graded salmon where distinct bite hole(s) are present penetrating the skin of the fish. Swab inserted into cavity made by tooth.	34	0.38
Mandible	Salmon almost entirely consumed; only one or both halves of the mandible remain. Swab rolled along both interior and exterior of mandible.	26	0.23
Exposed muscle	A high-graded salmon where a portion of skin has been removed and some muscle tissue has been consumed. Swab wiped diffusely over exposed muscle, targeting areas where consumption has occurred.	14	0.21
All over	A carcass that is largely untouched or a high-graded salmon where only the brain and eyes have been removed. Swab swiped diffusely over the surface of the skin along the entire length of the fish.	9	0.22
Gill plate(s)	Salmon almost entirely consumed; only one or both gill plates remain. Swab rolled along both interior and exterior of gill plate(s)	8	0.25
Margins of torn skin	A high-graded salmon where a portion of skin has been removed and muscle tissue appears largely untouched. Swab rolled along margins of torn skin, targeting areas where bite likely originated.	7	0.71

Table 3: Population estimates for Chilkoot valley by sample type

Sample Type	No. Samples	Population Size Estimate	95% Confidence Intervals
Scat	87	28	24-35
Saliva	38	21	14-36
Combined	125	27	25-31

Table 4: Cost (USD) by sample type

Sample Type	Cost per sample	Cost per genotype	Cost per unique bear
Scat	39	123	447
Saliva	28	72	253
Overall	35	99	356

Table 5: Example of contamination resulting from two individual bears (Bear 443F and Bear 235F) both feeding on the same salmon carcass (Carc 9). We directly observed both of these known individuals feeding on Carc 9 within a short timeframe of one another. The saliva sample taken from the carcass produced an unusable, unique genotype that amplified alleles from both Bear 443F (white) and Bear 235F (grey).

	Marker							
Sample	**G1A**	**G1D**	**G10B**	**G10H**	**G10J**	**G10M**	**G10X**	**SRY**
Bear 443F	120/120	174/180	144/156	248/250	92/92	194/194	146/146	F
Bear 235F	110/120	176/176	150/150	248/258	82/88	194/202	136/138	F
Carc 9	110/120	174/176	150/150	248/258	82/92	194/202	146/146	F

Figure 1: A) Chilkoot and Klehini watersheds near Haines, Alaska, and locations of Chilkoot Lake and Herman Creek where we sampled scat and saliva from sockeye, and saliva from chum carcasses, respectively. B) We divided the Chilkoot valley into five separate regions, each visited by personnel on a weekly basis. Fish icons mark the locations of known, distinct sockeye salmon spawning areas.

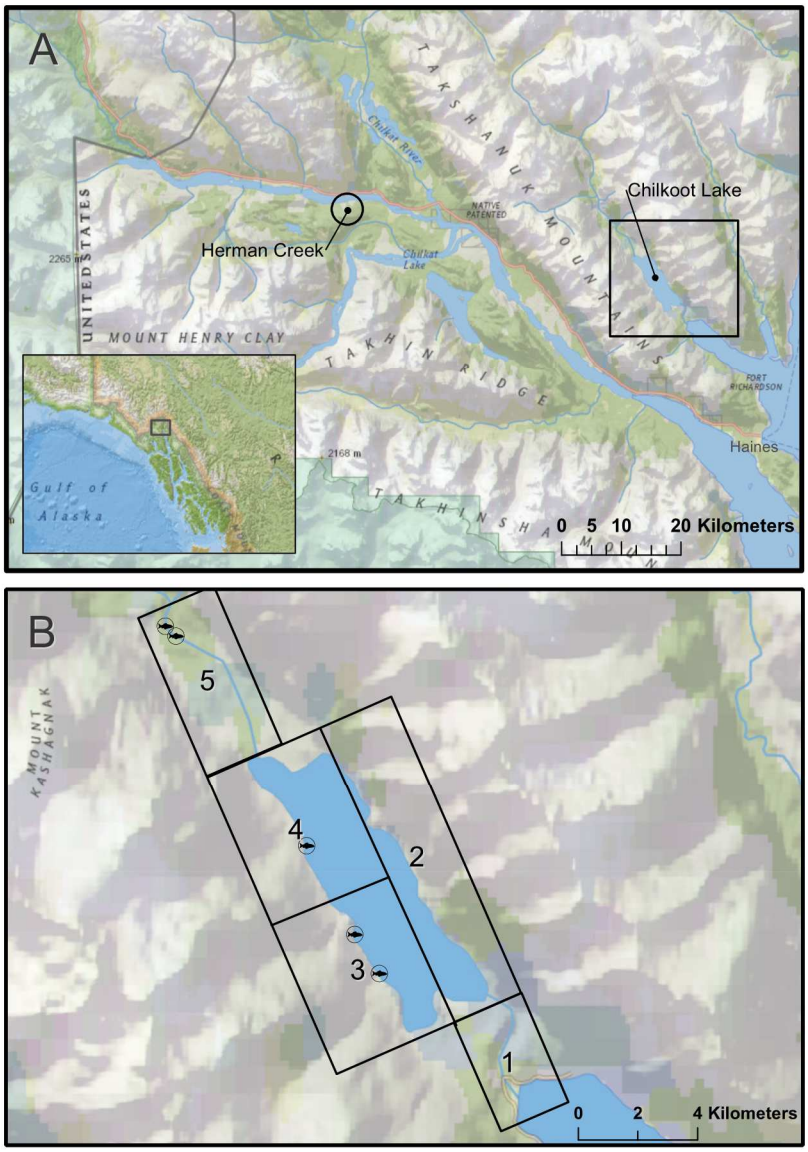


Figure 2: We categorized carcasses based on the type of consumption observed: A) braincase; B) bite holes; C) mandible; D) margins of torn skin; E) exposed muscle tissue; F) gill plates. A wide range of carcass types produced bear DNA that amplified successfully; saliva samples from each of the carcasses pictured were successfully genotyped to individual.

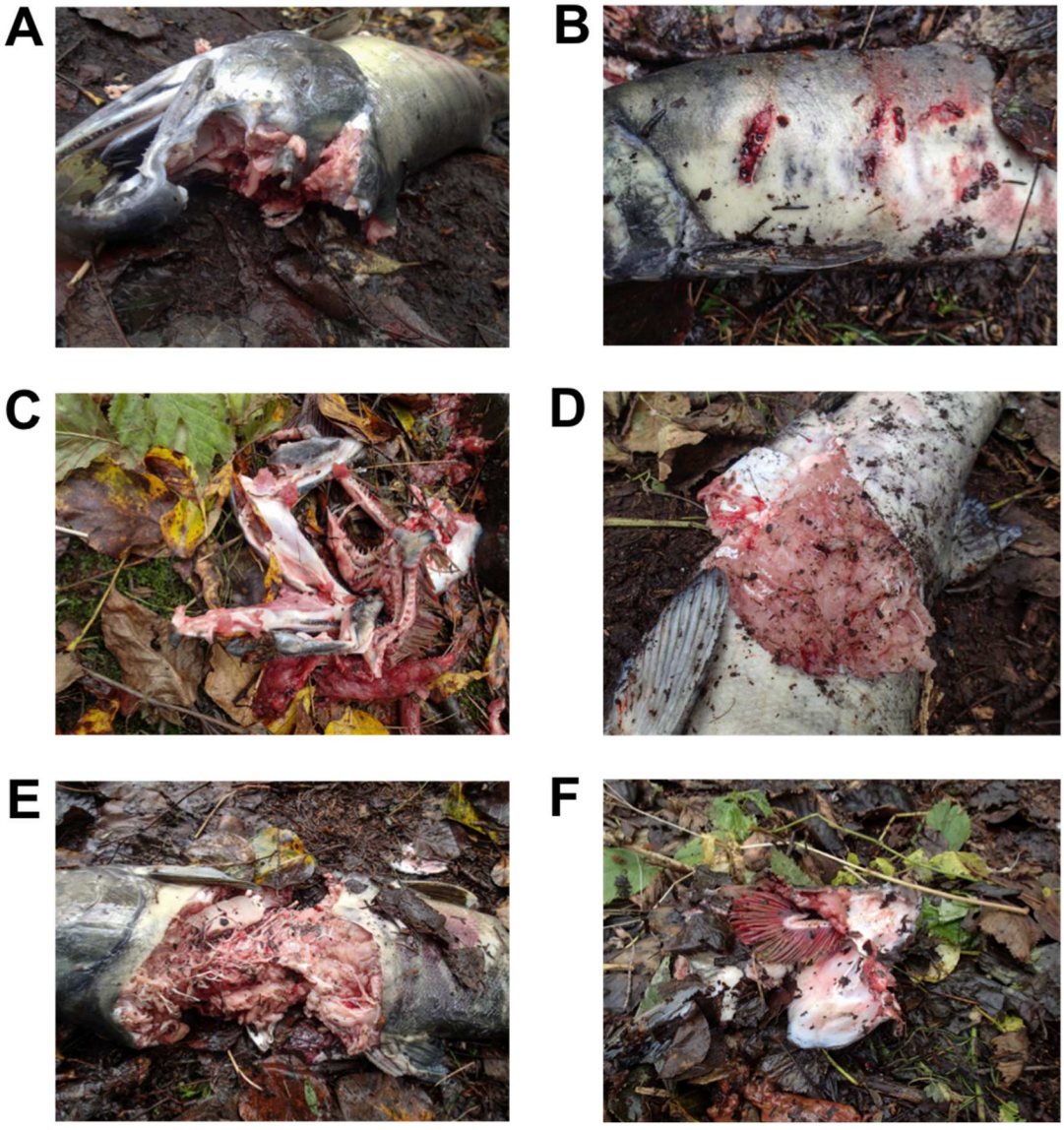


Figure 3: Relative success of different salmon swabbing techniques. Braincases and bite holes were encountered most frequently, and also amplified at proportionally higher rates than other swabbing techniques.

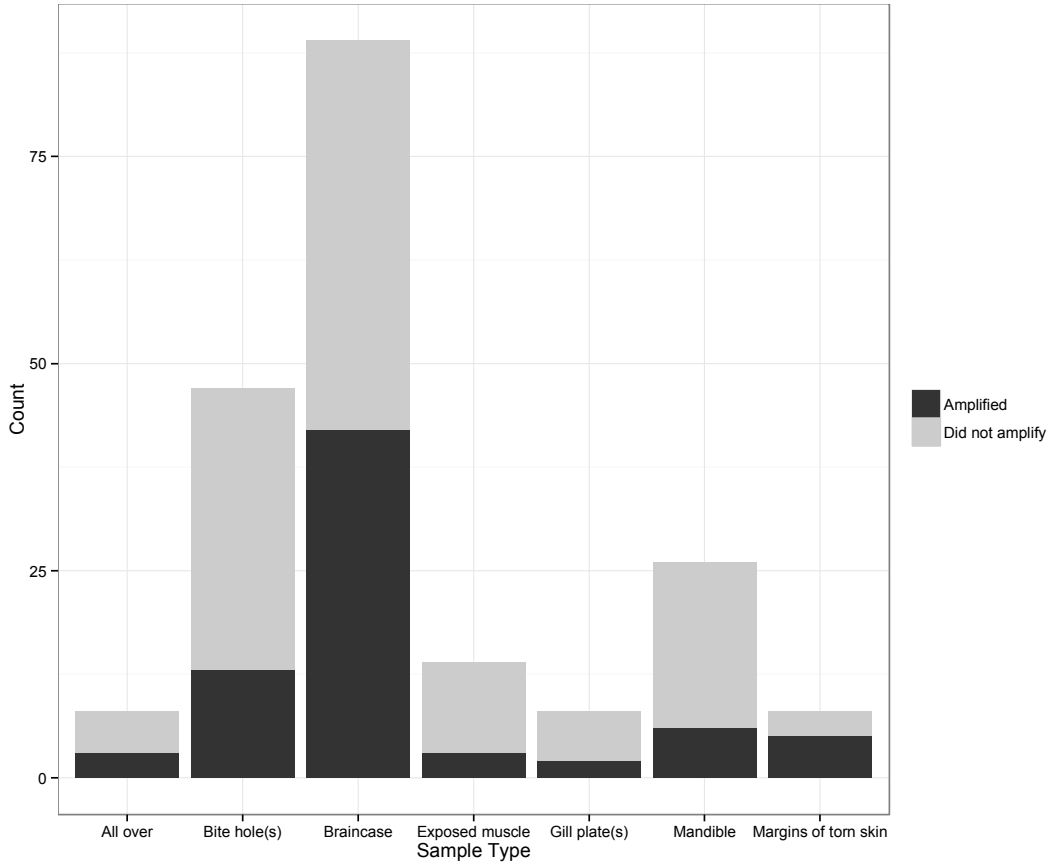


Figure 4: Number of detections by sample type for 25 individual brown bears genotyped from samples collected in the Chilkoot valley near Haines, AK. Age classes, where noted, were determined based on scat diameter (for juveniles) or sightings of known individuals (for immature bears and adults).

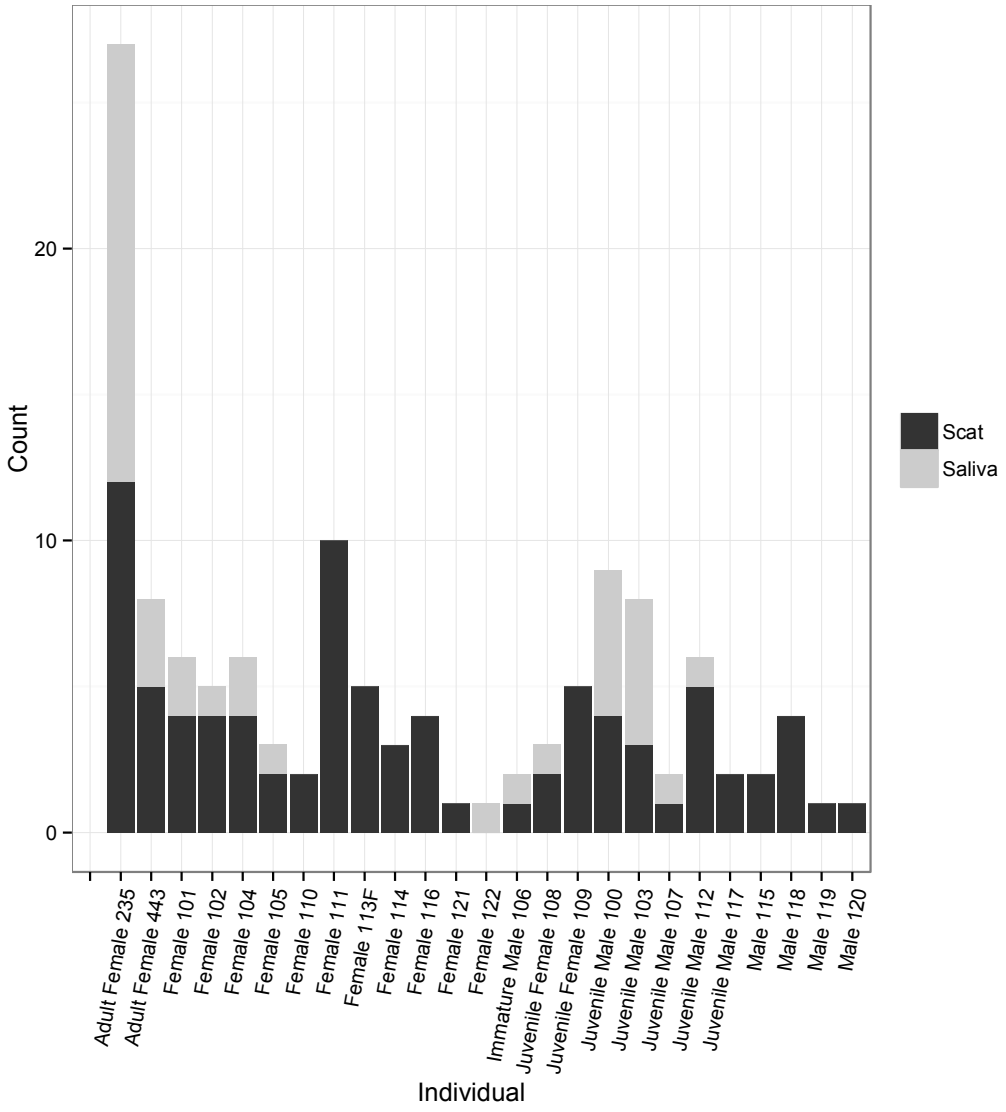
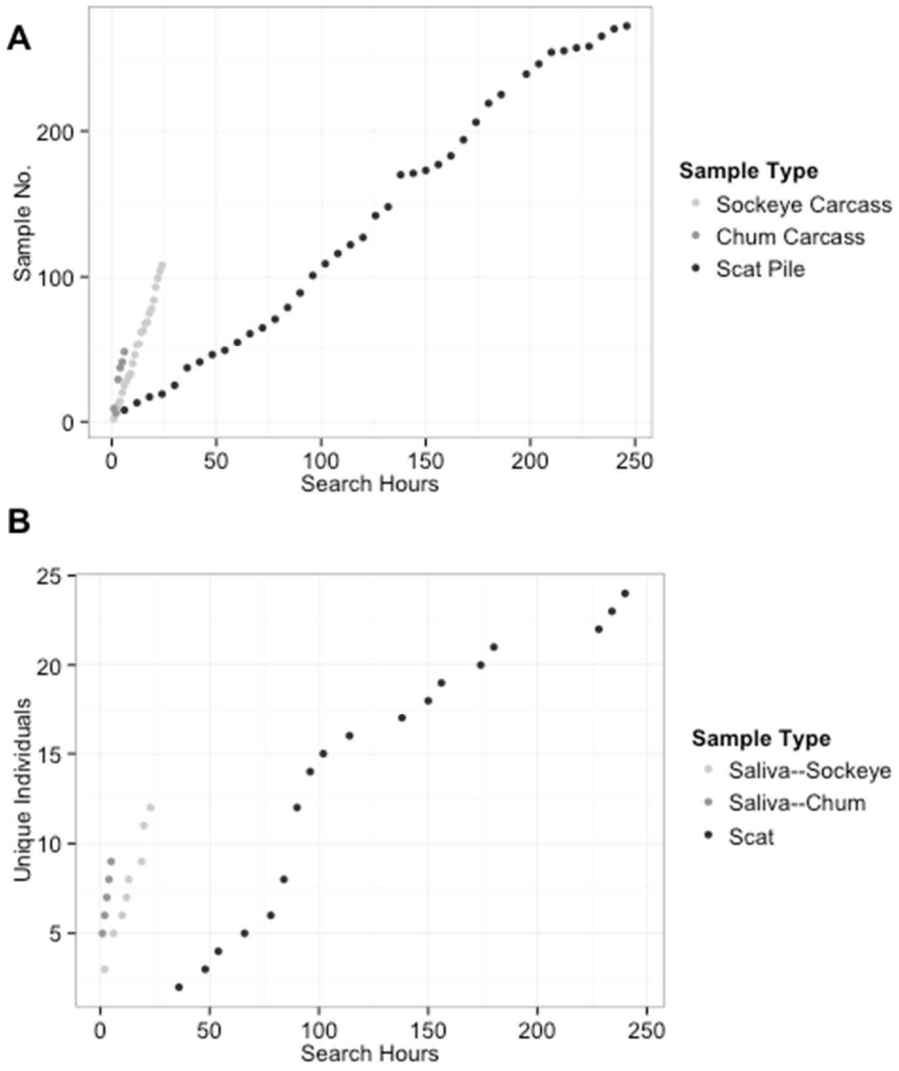


Figure 5: Number of search hours required to locate new samples (A) and unique individual bears (B) based on sample type. Saliva samples from sockeye salmon and scat samples were collected from June through early September in the Chilkoot Valley, while saliva samples from chum salmon carcasses were collected in late September at Herman Creek.



Chapter 4: Intraspecific variation in movement strategies among bald eagles (*Haliaeetus leucocephalus*) in an anadromous fish system

Abstract

While much empirical evidence exists regarding variability of movement strategies among different species, evidence is less prevalent for the extent of variability of movement strategies within species. Intraspecific variation in movement strategies may be particularly prevalent in environments in which resources are highly variable, as individuals that can learn when and where to access the best resources and alter their movement strategies accordingly will be those most likely to survive and reproduce. Here, we explore intraspecific variation in movement strategies of a species in a large-scale, heterogeneous environment, using bald eagles (*Haliaeetus leucocephalus*) in the highly variable anadromous system of the north Pacific coast as a case study. We tracked 28 bald eagles (five immature, 23 adult) using GPS transmitters between May 2010 and January 2016. We found evidence of four distinct movement strategies among bald eagles in Southeast Alaska and western Canada: sedentary breeders who remained on nesting territories year-round, localized individuals who made predominately short-distance movements among sites, migratory individuals who consistently traveled between distinct summer and winter ranges, and nomadic individuals with irregular movement patterns that showed little interannual consistency in terms of departure dates, travel pathways, or sites visited. On average, male eagles traveled more per day than females ($P < 0.001$) and immature eagles traveled farther per day than mature birds ($P < 0.0001$). The highly

variable anadromous fish system of the north Pacific coast likely contributes to behavioral plasticity in bald eagles in this region and results in a range of movement strategies in the population. Effective conservation and management of north Pacific bald eagles will require a framework that recognizes the high variability in movement strategies adopted by individuals in the population.

Introduction

Movement strategies are widely acknowledged to be a critical component of the survival of most organisms (Turchin 1998, Bergman et al. 2000), as food and other important resources can be distributed heterogeneously across both time and space. Theory predicts that animals should minimize the effects of this heterogeneity in resource availability by moving among areas of high resource abundance and limiting time in areas with low resource abundance (Charnov 1976, Arditi and Dacorogna 1988, Zollner and Lima 1999).

Depending on the extent of variability in resource availability in the environment, some movement strategies might prove more effective for resource acquisition than others, and we expect natural selection to favor movement strategies that maximize resource acquisition (Austin et al. 2004). Resources with little variation in spatial heterogeneity, for example, should facilitate a sedentary strategy, whereas resources with predictable seasonal variation should generate migratory movement strategies within populations. If resource heterogeneity is extensive both

spatially and temporally, nomadism should emerge as the favored movement strategy (Mueller and Fagan 2008, Mueller et al. 2011).

While much empirical evidence exists regarding variability of movement strategies among different species, evidence is less prevalent for the extent of variability of movement strategies within a species (Mueller et al. 2011, Singh et al. 2012). Individuals in many species can adapt to varied environments and can adjust behavioral strategies to facilitate resource acquisition through time, by, for example, bypassing low-quality sites or engaging in exploratory behavior to locate new resource patches (Weber et al. 1999). Thus, in some environments it is likely that selection for optimal strategies and behavioral flexibility in individuals is strong.

Intraspecific variation in movement strategies may be particularly prevalent in environments in which resources are highly variable, as individuals that can learn when and where to access the best resources and alter their movement strategies accordingly will be those most likely to survive and reproduce (Komers 1997). Here, we explore intraspecific variation in movement strategies of a highly mobile species in a large-scale, heterogeneous environment, using bald eagles (*Haliaeetus leucocephalus*) in the highly variable anadromous fish system of the north Pacific coast as a case study.

While food resources for almost all animals are variable across time and space, the anadromous fish system is an extreme case in which prey is widely dispersed across the landscape in discrete patches that are asynchronous, but temporally abundant, and are generally predictable (Willson and Halupka 1995). The

north Pacific coast of North America provides spawning habitat for more than 15 species of anadromous fishes. In addition to seven species of Pacific salmon and trout (*Oncorhynchus*; Salmonidae), several species of smelt (Osmeridae), three species of lamprey (Petromyzontidae), and at least one species of charr (*Salvelinus*) spawn in fresh water on the coasts of northern California, Oregon, Washington, British Columbia, and Alaska (Willson and Halupka 1995, Gende et al. 2002). The timing and locations of adult in-migration, spawning, and smolt out-migration varies extensively among species and among populations in different locations, but are generally predictable year to year (Scott and Crossman 1973, Quinn 2005).

Bald eagles are highly mobile consumers prevalent throughout the northwestern United States and western Canada. Although they are considered generalist predators (Buehler 2000), in coastal regions upwards of 90% of eagle diets are comprised of fish (Lincer et al. 1979). Anadromous fish, particularly Pacific salmon, provide a critical food resource to Pacific coast eagles; eagle survival is thought to be limited by salmon availability in winter (Elliott et al. 2011), and individuals with access to salmon are more likely to breed and successfully fledge young than those that do not have access (Hansen 1987).

Bald eagles display delayed maturation, in that most individuals do not reach sexual maturity until their fifth or sixth calendar year (Buehler 2000), and it may take even longer to earn a breeding territory in a likely-saturated breeding population (Hodges et al. 1987). Immature individuals are generally less successful at foraging than adults (Stalmaster and Gessaman 1984, Bennetts and McClelland 1997). Bald

eagles are thought to be partially migratory but may exhibit a complex pattern of migration strategies depending on biotic and abiotic conditions specific to each population (Buehler 2000). Historical research on eagle movements along the north Pacific coast suggests that adults may be resident while immature birds move south as abundant food resources (e.g., salmon runs) are exhausted (Hodges et al. 1987, Kralovec 1994). Counts of eagles along the British Columbia, Canada coast suggest an influx of eagles (presumably from coastal Southeast Alaska) during winter (Elliott et al. 2011).

Despite considerable interest in the species, little is understood about the influence of anadromous fish systems on variability in bald eagle movement strategies. Further, identifying the extent of intraspecific variability in movement strategies among eagles could have important implications for conservation and management. Management plans that fail to account for multiple movement strategies might be limited in their effectiveness and risk reducing behavioral diversity within populations.

Our objectives here were to use fine-scale GPS tracking data and Brownian bridge movement modeling to examine variability in intraspecific movement strategies among individual eagles and to delineate areas of high eagle use along coastal areas in Southeast Alaska and western Canada. We predicted that (i) given the highly variable, but predictable, nature of resource availability across the region, migratory movement strategies should be favored, (ii) immature eagles would be

wider-ranging than mature eagles, and (iii) areas of highest-intensity use would vary seasonally in accordance with resource availability.

Methods

Study Area

Our study area encompassed the north Pacific coast and surrounding region from Vancouver Island, British Columbia north to the top of the Alaskan panhandle, northwest of Yakutat Bay. The area is characterized by steep, rugged topography, numerous islands, coastal fjords, and large tracts of temperate rainforest. The landscape is naturally fragmented by mountainous terrain, wetlands, and various fine-scale disturbances (e.g., wind-throw) as well as varying degrees of anthropogenic disturbance (e.g., clear-cut logging). The forests are dominated by western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) in the north and western hemlock, Douglas fir (*Pseudotsuga menziesii*), and western red cedar (*Thuja plicata*) in the south. A cool and wet maritime climate characterizes the region.

Captures and Tracking

We captured bald eagles in Icy Bay (59°57'55.80"N, 141°25'49.71"W; N = 9) in May 2010, 2011, and 2012, in Juneau (58°21'13.65"N, 134°36'12.04"W; N = 1) in March 2011, in Sitka (57°02'36.58"N, 135°22'50.19"W; N = 5) in March 2011, and on the Chilkat River (59°14'58.20"N, 135°35'25.19"W; N = 13) in November 2012 and 2013. In Icy Bay, Juneau, and Sitka, we captured eagles on near-shore waters of

the ocean using a modified floating-fish snare (Robards 1967, Cain and Hodges 1989). We trapped bald eagles on gravel bars along the Chilkat River using perch snares (Hodges et al. 1987) or a radio-controlled bow net (Superior Bownet & Design, Washington, MD, USA) or rocket net (Coda Enterprises, Mesa, AZ, USA) baited with salmon carcasses. Eagles were outfitted with 70 g solar-powered GPS/PTTs (Microwave Telemetry, Inc., Columbia, MD, USA) using a backpack-style Teflon ribbon harness. All birds were banded and aged based on plumage (McCollough 1989, Clark 2001). A blood sample was taken, and sex was determined by DNA (Zoogen, Inc., Davis, CA, USA). Eagle capture and handling methods were in compliance with Institutional Animal Care and Use Committee protocols at the University of California, Santa Cruz (Wilmc1206) and the U.S. Fish and Wildlife Service (2010004).

GPS units were configured with duty cycles that shifted based on time of year to conserve battery life during shorter days. Units were programmed to gather hourly GPS locations 1 October through 28 February from 08:00 to 17:00, 1 March through 30 April and 1 August through 30 September from 05:00 to 19:00, and 1 May through 31 July from 03:00 to 22:00 AKT. Each GPS unit transmitted to the Argos satellite system (CLS America, Lanham, MD, USA) for four hours every other day during spring and summer and every fourth day during autumn and winter. We parsed data using the manufacturer's software. Units yield locations with a horizontal accuracy of up to ± 18 m (Microwave Telemetry, Inc.). As a result of low battery voltage, likely related to insufficient insolation, signals from some transmitters were intermittent,

lapsing for days or occasionally weeks at a time, particularly mid-winter, when daylight is limited. In our analyses, we include only data that were not affected by such lapses.

Analysis

We plotted data in ArcGIS 10 (ESRI, Redlands, CA, USA) for visual inspection, removal of erroneous data, and data analysis. We recognized four types of movement strategies and grouped individual eagles into one of four movement strategy classes based on interannual movement: breeder, localized, migratory, or nomadic. Eagles classed as breeder were individuals with nesting territories where a breeding attempt was made. Nest sites and breeding attempts were confirmed via aircraft. These eagles were largely residential, remaining near nest sites year-round, with occasional short forays to nearby watersheds for access to seasonal resources. Eagles classed as localized were non-breeding individuals with distinct ranges and largely residential behavior. These individuals had no nesting territories and showed no evidence of breeding, but, much like breeders, engaged only in short-distance travel with occasional forays to nearby watersheds for access to seasonal resources. Individuals classed as migratory had no nesting territories and showed no evidence of breeding. These eagles displayed distinct ranges with localized movements in defined overwintering and summering areas, followed by long-distance, directed travel in late autumn and early spring between winter and summer ranges. Like localized and migratory eagles, individuals classed as nomadic had no nesting territories and

showed no evidence of breeding. Nomadic eagles displayed a range of short- and long-distance, irregular movements among multiple locations throughout the year with little interannual consistency in sites visited, seasonal departure dates, or overwintering or summering areas.

We compared movement strategies, as well as sex and age classes, using average distance traveled per day, home range analyses, and utilization distributions. For each individual, we calculated step length as the straight-line distance between consecutive GPS fixes. To reduce bias towards larger step lengths that may result from lapses in signal and travel occurring between duty cycles, we removed all distance values from fixes that were greater than 15 hours apart, the maximum possible gap between duty cycles. We then calculated average daily distance traveled by month for each individual. We calculated minimum convex polygon (MCP) home range sizes for each eagle using the 'adehabitat' package in R (Calenge 2006). We investigated potential differences in MCPs and average daily distances traveled among movement strategy classes, between males and females, and between adult and immature eagles using Kruskal-Wallis tests, and report means ± SE.

Utilization distributions (UD) allow for the mapping of the intensity of use within a defined area (Worton 1989). Following Watts et al. 2015a and Watts et al. 2015b we used Brownian bridge movement modeling (BBMM; Horne et al. 2007) to develop utilization distributions for each individual eagle using locations (n = 245,865) collected between May 2010 and January 2016. We used the R package 'move' (Kranstauber and Smolla 2014) to produce UD surfaces using the dynamic

Brownian bridge movement model (dBBMM; Kranstauber et al. 2012). We set dBBMM parameters to a window size of 21, margin of 7, location error of 18 m, and a raster cell size of 5 km^2. Widow size of 21 was based on the maximum number of GPS locations received per day for an individual eagle. The margin of 7 was set in proportion to window size. Location error was determined by the transmitter manufacturer as ±18 m. In order to generate the most detailed output for the geographic scale of our study area, we set the cell size to 5 km^2. However, we also produced a limited number of UD with a cell size of 1 km^2 to highlight intensity of use in smaller regions. We exported UDs as rasters and overlaid them across the study area in ArcMap.

We produced independent surfaces for all eagles individually for winter (January through March), spring (April through June), summer (July through September), and autumn (October through December) to reflect seasonal variation in movement. We combined UD surface maps produced for individual eagles by averaging probabilities for each cell to produce UDs for each movement strategy (breeder, localized, migratory, and nomadic) for each season. The number of locations in each movement track varied among individual eagles, so we weighted, combined, and standardized UD surfaces according to the number of locations per track.

For display purposes, we ordinated cell values from highest to lowest and grouped cells within categories that represented 10% of the total eagle utilization, such that the first category was comprised of the cells with the highest utilization. The

first category represents the minimum area to achieve 10% of the total utilization, the second category reflects the minimum area to achieve the next 10% of the total utilization, etc. This presentation thus allows for visualization of the relationship between the intensity of use and area (Watts et al. 2015b).

Results

We tracked 28 individual eagles between May 2010 and January 2016. Tracking periods ranged from 6.8 months to 4.8 years (Appendix). We classified eight individuals as breeders, seven as localized, four as migratory and nine as nomadic (Table 1). Eagles exhibited strongly individualistic movement in terms of travel pathways and locations visited throughout the year, but general movement strategies were consistent within classes (Fig. 1). Migratory and nomadic individuals ranged widely throughout the study area, as far south as Vancouver Island, British Columbia, Canada, and as far north as the Peel River, Yukon Territory, Canada.

Across all movement strategy classes, distances traveled were highest in spring ($P < 0.0001$), at an average of 17.4 ± 1.1 km/day, followed by winter (11.4 ± 0.81 km/day) and autumn (8.1 ± 0.63 km/day), and were lowest in summer months (7.8 ± 0.47 km/day; Fig. 2A). Migratory birds traveled greater daily distances (21.2 ± 1.7 km/day) than any other movement class ($P < 0.001$; Table 1). Nomadic birds traveled significantly farther (10.7 ± 0.67 km/day) than breeders (8.17 ± 0.44 km/day; $P <0.05$). No significant differences existed in daily movement between breeders and localized birds (8.97 ± 0.54 km/day) or between nomadic birds and localized birds.

Migratory eagles also had the largest ranges of any movement class (169,072 ± 74,599 km^2; $P < 0.0001$; Table 1), followed by nomadic eagles (49,107 ± 8,062 km^2), localized eagles (5,522 ± 2,365 km^2), and breeding eagles (1,161 ± 546 km^2).

Across all movement strategy classes and across all months, immature birds traveled significantly farther per day (18.9 ± 1.8 km/day) than adults (10.1 ± 3.7 km/day; $P < 0.0001$; Fig. 2B). Male eagles (13.3 ± 0.69 km/day) traveled significantly farther than females (9.1 ± 0.42 km/day; $P < 0.001$; Fig. 2C).

Intensity of use, as revealed through dBBMM, varied by season and movement strategy (Fig. 3). Breeders remained on or near nesting sites year-round. Localized eagles engaged in short-distance travel, particularly in spring, but use was generally restricted to areas near Sitka, Juneau, and the Chilkat River near their respective locations of capture. Migratory and nomadic eagles used the north Pacific coast much more extensively. Migratory individuals shifted habitat use seasonally, with migratory corridors highlighted in autumn (southward migration) and late winter (northward migration). Nomadic individuals had the highest intensity of use across the greatest area, particularly in spring (Fig. 3).

We processed dBBMM with 1 km^2 raster cell sizes to produce UD to identify areas of the highest-intensity use across both migratory and nomadic individuals, the two movement strategy classes that traveled the most extensively across seasons and throughout the region. The UD for winter for these two movement strategy classes illustrated the highest-intensity use areas at landfills in several communities in British Columbia (Fig. 4A), as well as small sections of the Skeena and Nass Rivers. Spring

high use areas are concentrated around the communities of Hoonah, Sitka, and Juneau, in addition to an intensively utilized migratory corridor between Juneau and Berners Bay (Fig. 4B). The highest-intensity use areas for migratory and nomadic individuals in autumn are located along the Chilkat River (Fig. 4C) and Yakutat Bay.

Discussion

The variability in movement strategies we documented among north Pacific bald eagles has rarely been reported for large mobile predators. While bald eagles have previously been described as partially migratory, our results provide evidence of four distinct movement strategies among bald eagles along the north Pacific coast: breeding individuals that were largely sedentary and remained on nesting territories year-round; localized individuals who made predominately short-distance movements among sites; migratory individuals who consistently traveled between distinct summer and winter ranges; and nomadic individuals with irregular movement strategies that showed little interannual consistency in terms of departure dates, travel pathways, or sites visited. Our study is the first to document this wide range of intraspecific variation in annual movement strategies among bald eagles in the north Pacific.

Understanding the extent of intraspecific variation in movement strategies can provide important insights into population distribution and what factors influence the spatial dynamics of predator populations, and has important consequences for modeling resource and habitat use. Given that anadromous fish systems and other

resources available in the coastal system vary across broad scales but are temporally predictable, we anticipated that migratory movement strategies would be favored, but migratory individuals represented the smallest movement class of the eagles we tracked. Much larger proportions of the non-breeding eagles we followed were either localized or nomadic. However, given that our sample size was only 28 individuals, it is difficult to generalize and it is possible that migratory individuals represent a larger proportion of the total population than is represented here, as is suggested by results from coastal British Columbia, Canada (Elliott et al. 2011).

Though sample sizes were small, some patterns did emerge within movement strategy classes. All breeding and localized individuals were adults. This result confirms that seen by Hodges et al. (1987) and Kralovec (1994) in southeastern Alaska where adults were residents that made small movements to locally abundant food resources at times but remained on one range year-round. However, we were able to differentiate two classes within the resident adults described previously (i.e. breeders and localized). Of the immature eagles captured, four out of five were classed as nomadic. There was a relatively even distribution of the sex classes among breeders, localized, and nomadic individuals, but all of the migratory individuals we captured were male. Since sample sizes were small, it is likely that some female eagles in the region are migratory. However, bald eagles are sexually dimorphic—females weigh around 25% more than males (Buehler 2000). Additionally, larger eagles are more successful than smaller individuals in contests for food (Hansen 1986). It is possible that female eagles are better competitors when food becomes

limiting, and thus males are more likely to adopt alternative movement strategies in search of food. This is supported by our finding that, among all movement strategy classes, males traveled farther per day than females throughout the year.

Intraspecific variation in movement strategies has been observed in other taxa. For example, Singh et al. found evidence of four different movement strategies within moose (*Alces alces*) across seven latitudes in Sweden: migratory, disperser, nomadic, and resident (2012). Similarly, Austin et al. (2004) found that grey seals (*Halichoerus grypus*) near Nova Scotia, Canada could be separated into three different movement groups: residents, seals that moved in a random fashion, and seals that undertook long distance, directed movements. Among birds, many species exhibit partial migration, with distinct migratory and sedentary behavioral morphs. Indeed, many populations of bald eagles are thought to be partially migratory, with a mixture of resident and migratory individuals (Mojica et al. 2008), but no study of the species has yet documented the extent of variation in movement strategies exhibited by eagles here. This difference seems to reflect the greater complexity of the anadromous fish system in the north Pacific compared to the relative spatial and temporal predictability of resource availability throughout other areas of the species' range.

All eagles exhibited seasonal shifts in the extent and intensity of use across the landscape. Across movement strategies, several areas had distinct seasonal significance. Yakutat Bay and the Chilkat River were high use areas for all movement strategy classes in autumn. The Chilkat River sees late runs of chum (*O. keta*) and coho (*O. kisutch*) salmon, and an area called the Council Grounds (Fig. 4C) has

unique geomorphology that prevents the river from freezing well after freeze-up in other regions (Hansen 1986, 1987). Fishing lodges surrounding Yakutat Bay, as well as a fish processing plant, provide access to fish scraps after anadromous fish runs in the area have ended or become inaccessible due to freezing.

Prince Rupert and nearby communities in British Columbia were high use areas for some eagles in winter. Access to landfills in these areas (Fig. 4A), combined with milder temperatures than communities farther north, likely make these appealing overwintering sites. Individuals from all movement strategy classes made use of landfills, but the highest intensity of use was displayed by migratory and nomadic individuals in communities on or near the British Columbian coast, including Prince Rupert, Terrace, and Kitimat (Fig. 4A). These findings are consistent with previous research that suggested bald eagles congregate at landfills (Elliott et al. 2006, Turrin et al. 2015). Turrin et al. (2015) found that landfills were primarily important scavenging sites for hatch-year birds, and found no relationship between landfill use and season. Elliott et al. (2006) found that the proportion of subadults at landfills increased as the winter progressed, suggesting that subadults were learning about potential food concentrations from other birds. Both immature and adult eagles in our study spent extensive time on landfills during winter months and early spring. Eagles visited landfills infrequently other times of year.

Additionally, both the Skeena and Nass rivers in northern British Columbia host late winter (i.e., March) concentrations of spawning eulachon (*Thaleichthys pacificus*) that attract many marine birds (e.g., gulls [*Larus* sp.]) and migratory eagles

(Hay et al. 1997, Holst et al. 2007). Marine predators (including bald eagles) congregate at eulachon runs along the north Pacific coast (Marston et al. 2002, Sigler et al. 2004, Womble et al. 2005); these fish provide a high lipid food source (Van Pelt et al. 1997) during a time of year when most other food sources are lacking. Some of our marked eagles visited both these sites during this time of year.

Across all movement strategies and across both sex and age classes, distance traveled per day was highest in spring. Resource availability is particularly variable in spring—Pacific salmon have not yet begun to spawn and the spawning events of other anadromous and forage fish are short-lived—leading to increased movement among all eagles. Sitka, Yakutat Bay, and a corridor between Juneau and Berners Bay were high use areas for localized, migratory, and nomadic classes in spring (Fig. 4B). Sitka hosts a sizeable spawn of Pacific herring (*Clupea pallasii*), Berners Bay hosts a concentration of spawning eulachon and Pacific herring, and the outside coast south of Yakutat hosts several eulachon concentrations in spring, and it is likely that these resources draw eagles from throughout the region.

Distances traveled by eagles in all movement strategy classes were lowest during summer months. These months coincide with the peak of the spawning season for most populations of Pacific salmon in Southeast Alaska. We suggest that movement during summer months is lowest across all individuals as a result of salmon availability. Regional salmon availability throughout Southeast Alaska is high, and heterogeneity in the dispersion of salmon and the timing of spawning events extends eagles' access to salmon across multiple months (Moore et al. 2010). Thus,

Pacific salmon represent a highly predictable and temporarily widespread food resource for bald eagles.

Within movement strategy classes, breeders generally remained on or near nesting territories year-round, but some individuals made short-distance forays to nearby watersheds. For example, a female breeder near Juneau visited the Chilkat River and a male breeder north of Yakutat visited Yakutat Bay in autumn. This relative immobility could indicate a lack of suitable nesting locations relative to the number of available breeders in the population. There are a high number of non-breeding adult eagles along the north Pacific coast (Hansen and Hodges 1985), and breeding individuals may have to forego access to seasonally abundant resources in distant locations in favor of holding nesting territory outside the breeding season. Favored nest sites might also be located in areas where heterogeneity in resource availability is relatively low. Raptor populations often contain substantial numbers of non-territorial, non-breeding adults known as floaters (Brown 1969, Hunt 1998). The existence of floaters implies that breeding opportunities are limited, allowing us to infer that floaters arise in a population because territorial pairs occupy all suitable nesting habitat (Hunt 1998). Our data support this hypothesis, suggesting that suitable nesting habitat in southeastern Alaska is occupied by breeding bald eagles and supplemental adults may adopt a localized movement strategy to utilize some seasonal resources but remain available to capitalize on openings in the breeding population when available. While localized eagles were not as constrained in their

movements as breeders, most of their travel was short-distance, with occasional longer-distance forays, primarily in spring.

Breeders, localized, and migratory eagles all tended to use sites that had been visited before, often many months prior. This suggests that bald eagles may have a cognitive map that allows them to navigate to previously used locations, as well as a sense of the timing of different anadromous fish runs throughout the year. To a much lesser extent, some nomadic individuals revisited sites as well. Nomadism in animals is generally thought to be associated with unpredictable patchiness of resources (Mueller et al. 2011). Predictability, however, can be defined both by the spatial and temporal consistency of the resource availability and the awareness of the animal of the timing and location of the resource; i.e., a resource that is spatially and temporally predictable may seem unpredictable to an animal with incomplete knowledge of the resource's availability. Given that memory plays a critical role in finding previously used sites and timing revisits to areas to coincide with spawning events, it is possible that nomadic individuals do not yet have the requisite knowledge of the landscape and lack the experience necessary to reliably reencounter resource pulses of anadromous fish on an annual basis. Four out of the five immature eagles we captured adopted a nomadic movement strategy, and across all movement strategies immature eagles moved greater distances than adults throughout the year. It is possible that as these individuals mature and gain familiarity with the timing and spatial location of resources their movement strategies will shift toward migratory or localized strategies.

Future research should examine if and how strategies of movement change within individuals as eagles age. Research on eagle movement strategies would also benefit from modeling linking external variables, such weather patterns, intraspecific competition, fish abundance, and landscape characteristics to eagle movement towards a mechanistic understanding of these varying movement strategies. Accurate measurement of some of these variables, however poses a serious challenge, especially at a meaningful landscape scale. While many Pacific salmon streams are monitored for salmon abundance throughout Southeast Alaska and British Columbia, data for many runs are often collected once a season or infrequently, as opposed to frequent intervals that more closely parallel the time scales on which eagles feed. Additionally, other anadromous species important for eagles and other wildlife, such as eulachon and Pacific lamprey (*Lampetra tridentata*), are not regularly monitored, and little information exists regarding abundance and spawning timing and duration for these species.

Conservation strategies for highly mobile species such as eagles have largely focused on migration, operating on the assumption that animals are making regular, annual movements between distinct seasonal ranges. One consequence of this assumption is that conservation efforts have focused largely on protecting habitats associated with migratory movements. In migratory or partially migratory bird species, these habitats generally include migratory stopover points, overwintering areas, and specific migration corridors. However, in a population with high intraspecific variation in movement strategies, any management plan tailored solely

toward migratory individuals risks reducing behavioral diversity in the population. For example, neither protection of migratory corridors or protection of seasonal ranges will sufficiently account for the movement of nomadic individuals. The presence of nomads in the population makes protection of movement corridors largely infeasible, as nomadic individuals are moving irregularly across the landscape at large spatial scales. Further, protected movement corridors would have little benefit to the largely sedentary breeding individuals, or to localized individuals who engage in primarily short-distance travel.

Effective conservation and management of north Pacific bald eagles will require a framework that recognizes the high variability in movement strategies adopted by individuals in the population. Studies on other highly mobile predators have found that protection of essential foraging grounds may be more important to species conservation than generically protecting habitats. For example, a study on African penguins (*Spheniscus demersus*) used behavioral information on penguin foraging to prioritize protection of a habitat that was heavily affected by anthropogenic disturbance. Creation of a marine protected area rapidly benefited the penguin population (Pichegru et al. 2010).

It is possible that a focus on protecting important regional food resources for north Pacific eagles will sufficiently account for intraspecific variation in movement strategies. Identification of critical resources, however, may be a challenging endeavor given the spatial and temporal heterogeneity of resource availability in anadromous fish systems. Our study identified several areas of seasonal importance

that attracted eagles representing multiple movement classes from throughout the region. Spring runs of Pacific herring in Sitka Sound and eulachon in Berners Bay, autumn runs of coho and chum salmon on the Chilkat River, and landfills in communities in west-central Canada all seem to be disproportionately important to the regional eagle population.

Conclusion

Our results provide evidence of four distinct movement strategies among bald eagles in Southeast Alaska and western Canada: sedentary breeders who remained on nesting territories year-round, localized individuals who made predominately short-distance movements among sites, migratory individuals who consistently traveled between distinct summer and winter ranges, and nomadic individuals with irregular movement strategies that showed little interannual consistency in terms of departure dates, travel pathways, or sites visited. The highly variable anadromous fish system of the north Pacific coast likely contributes to behavioral plasticity in bald eagles in this region and results in a range of movement strategies in the population (Komers 1997). We surmise that younger and inexperienced eagles adopt nomadic movement strategies until resource availability becomes predictable, after which memory and perhaps competitive ability determine whether an eagle becomes migratory or localized or acquires a nesting territory and breeds. Future research will hopefully elucidate whether movement strategies are consistent within individuals throughout time, or whether movement strategies shift as a function of age or other factors.

Table 1: Summary by movement strategy, sex class, and age class of bald eagles monitored along the north Pacific coast, 2010-2016. Mean 90% MCP ranges and distance traveled per day are reported ± SE.

Movement Strategy	Adult		Immature		Total	MCP (km^2)	Dist/day (km)
	♂	♀	♂	♀			
Breeder	4	4	0	0	8	1,161 ± 546	8.17 ± 0.44
Localized	3	4	0	0	7	5,522 ± 2365	8.97 ± 0.54
Migratory	3	0	1	0	4	169,072 ± 74,599	21.2 ± 1.68
Nomadic	3	2	0	4	9	49,107 ± 8062	10.7 ± 0.67

Figure 1: Examples of the four different strategies of movement observed in bald eagles monitored along the north Pacific coast, 2010-1016. Breeders (A) remained on or near nesting territories year-round. Non-breeding, localized individuals (B) engaged in primarily short-distance movements within a contained area. Non-breeding, migratory individuals (C) had defined overwintering and summering areas, and long-distance, directed moves in autumn and spring between summer and winter ranges. Non-breeding, nomadic individuals (D) displayed irregular movement patterns and engaged in a variety of short- and long-distance moves with little interannual consistency among departure dates, travel pathways, and sites visited.

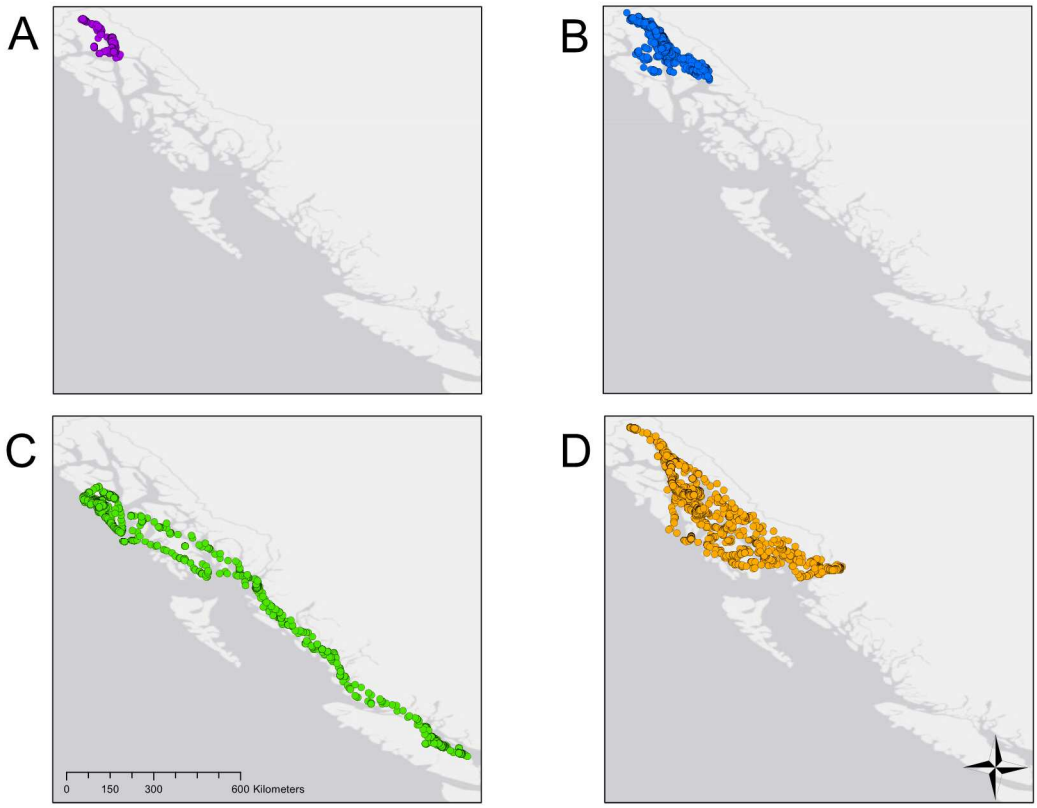


Figure 2: Average distance traveled per day by bald eagles monitored along the north Pacific coast, 2010-2016; data presented by month by A) movement strategy class, B) age class, and C) sex class, ± SE. Migratory birds traveled greater distances per day than any other class ($P < 0.001$). Across all months, immature birds traveled greater distances per day than adults ($P < 0.0001$), and males traveled greater distances per day than females ($P < 0.001$).

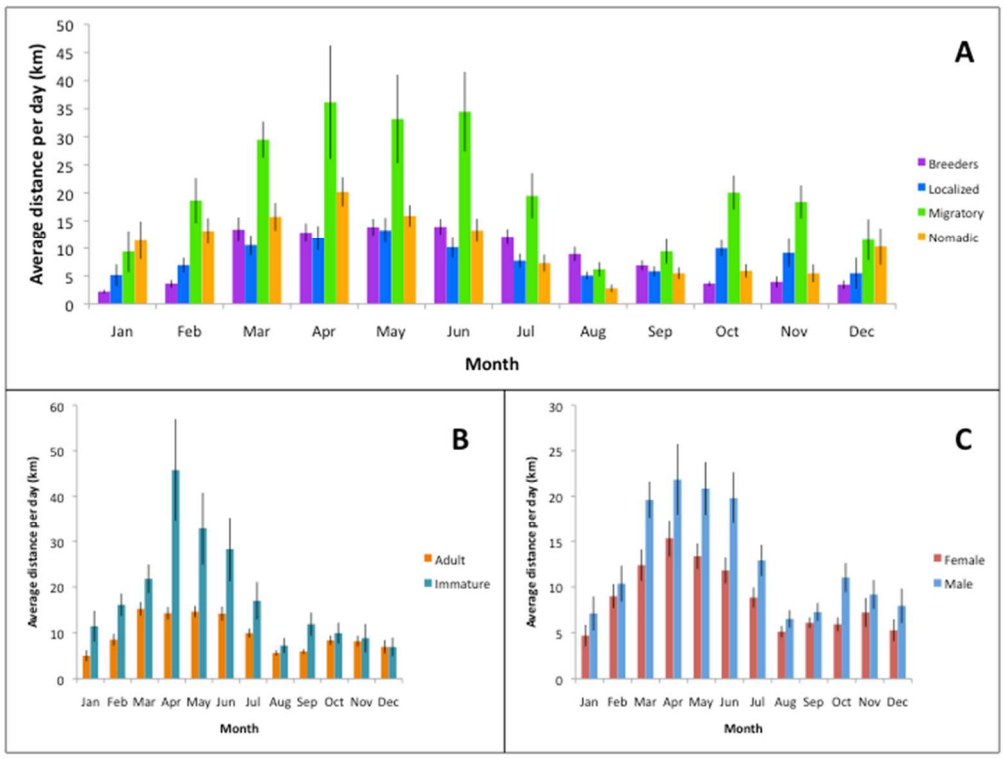


Figure 3: Utilization distribution (5 km^2 raster cell size) from BBMM of breeders (purple), localized (blue), migratory (green), and nomadic (orange) bald eagles monitored along the north Pacific coast, 2010-2016 for each season (Wi = winter, Sp = spring, Su = summer, Au = autumn). For each class, the darkest color represents the minimum area to achieve 10% of the total utilization. YB= Yakutat Bay, CR = Chilkat River, SIT = Sitka, JNU = Juneau, PR = Prince Rupert, VI = Vancouver Island.

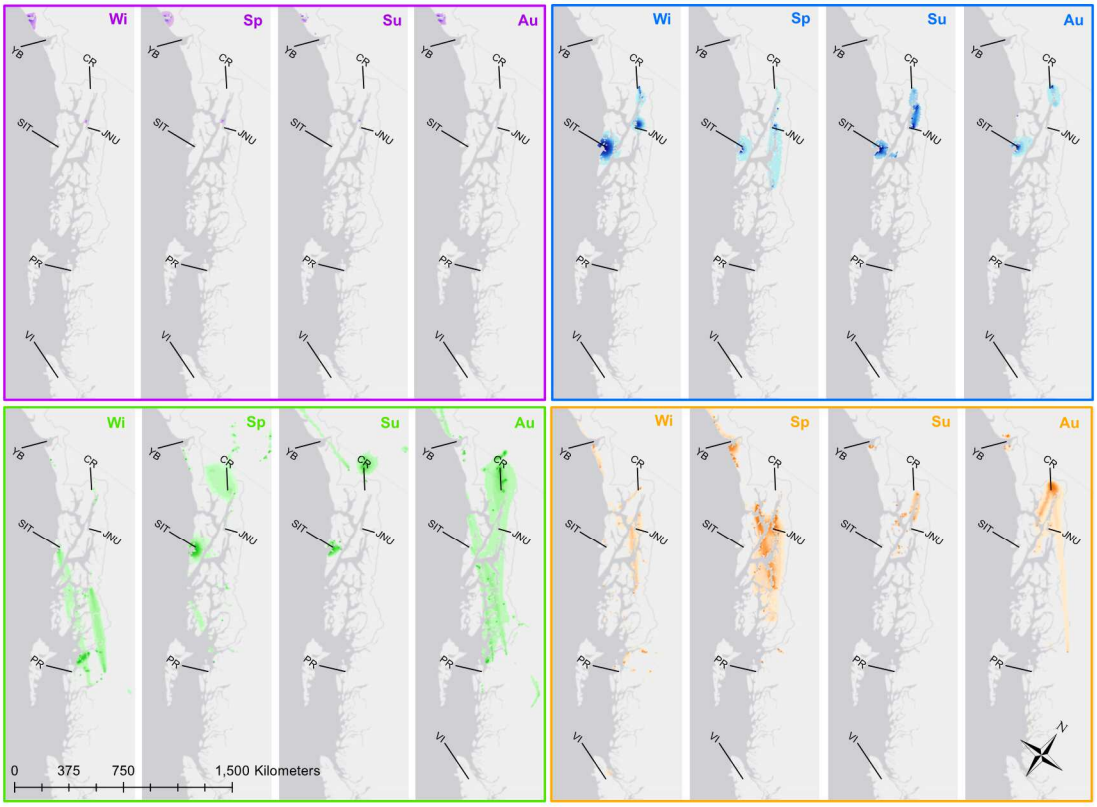
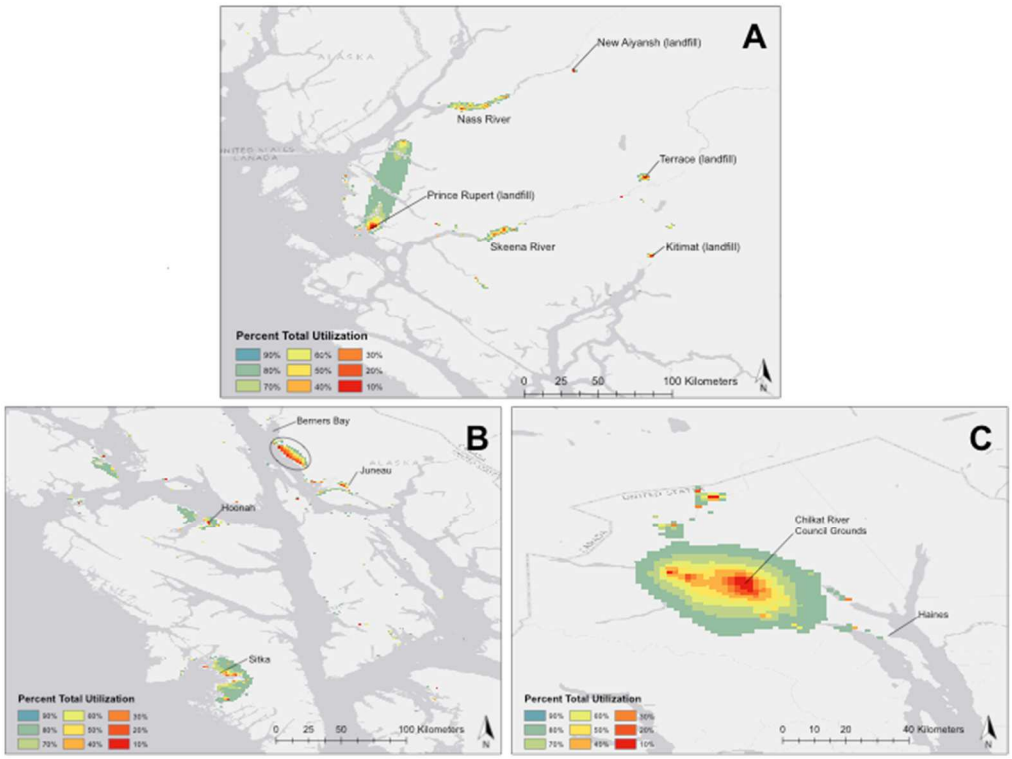


Figure 4: Utilization distribution (1 km^2 raster cell size) from BBMM averaged across all nomadic and migratory bald eagles monitored along the north Pacific coast, 2010-2016 in A) winter, B) spring, and C) autumn. Warmer colors reflect areas with higher utilization density. A) Eagles made frequent use of landfills in winter. B) The ellipse denotes a heavily used migratory corridor for eagles travelling to Berners Bay, the site of a large eulachon spawning event in spring. C) The Chilkat River Council Grounds hosts late runs of chum and coho salmon in an area of unique geomorphology that prevents river freeze-up late into the year.



CONCLUSION

Pacific salmon have disappeared from more than 40% of their historic range in southern British Columbia, Washington, Oregon, and California, largely due to the degradation of freshwater spawning habitats associated with land use changes in the form of damming, housing development, logging, mining, and agriculture (Quinn 2005). Despite this loss, salmon runs in Alaska, including Southeast Alaska, remain relatively unaffected. In Alaska, however, commercial fisheries intercept a large proportion of inbound salmon that would otherwise be available to the aquatic and terrestrial ecosystems they support, resulting in the loss of upwards of two-thirds of the marine-derived nutrients delivered to freshwater spawning grounds (Schindler et al. 2005).

Any departure from current fisheries management will necessarily involve conflict between competing objectives. However, if we wish to preserve salmon stocks and salmon ecosystem linkages, we must consider balancing economic gain with maintenance of ecosystem function. For subsistence fishers, this may mean trade-offs between commercial harvests and subsistence take and subsistence harvest quotas that more accurately reflect income and household size, as well as a subsistence harvest system that adequately takes into account the cultural heritage of Alaska Natives.

For wildlife, determining appropriate trade-offs between commercial harvest and escapement will be a complex undertaking, influenced by a range of factors, including run timing, size of salmon stocks, and stream morphology, as well as

consumer life history. Bears, for example, maximize their annual energy balance by depositing fat during periods of salmon abundance and hibernating when food is scarce, so increasing escapement of one or more local stocks might sufficiently increase bear population densities. Highly mobile salmon consumers, however, including bald eagles, can track asynchronous pulses of salmon on vast spatial scales, meaning that management decisions made locally could fail to impact the regional eagle population, or have measurable impacts on other systems if eagles relocate earlier in the year or more frequently in search of food.

Previous research has shown that increasing escapement could positively impact brown bear densities (Levi et al. 2012); it is possible that relaxing harvests on lower value salmon species, such as pink (*O. gorbuscha*) and chum (*O. keta*) would effectively increase bear population productivity (Levi et al. 2015). However, migration timing, when salmon are available for commercial harvest, and timing of spawning, when salmon are available to terrestrial consumers, do not always closely correspond (Boatright et al. 2004, Doctor et al. 2010), so determining which stocks to focus on for commercial harvest versus increased escapement may be difficult. Further, increased escapement may not necessarily benefit bears if salmon accessibility is influenced by human activity, as was the case with non-habituated individuals feeding in the Chilkoot watershed. Management efforts should focus on both availability and accessibility of salmon to terrestrial consumers, which, in addition to increasing escapement, might involve limiting human presence at high-

density spawning grounds or a focus on improving infrastructure in recreational sites to separate humans and bears, providing bears unrestricted access to foraging areas.

For bald eagles, who travel sometimes thousands of kilometers throughout the north Pacific to access anadromous fish, any ecosystem-based fisheries management intended to benefit eagle population productivity will need to adequately take into account eagles' mobility. Effective conservation and management of north Pacific bald eagles will require a framework that recognizes the high variability in movement strategies adopted by individuals in the population. It is possible that a focus on protecting important regional food resources for north Pacific eagles will sufficiently account for this variation. Identification of critical resources, however, may be a challenging endeavor given the spatial and temporal heterogeneity of resource availability in anadromous fish systems. Promising candidates include spring runs of eulachon in Berners Bay and herring in Sitka Sound, as well as the late run of chum and coho salmon on the Chilkat River. We anticipate that further study will identify additional anadromous fish runs that are disproportionally important to the regional eagle populations, and these regionally important stocks should be the first targets for increased escapement or protection should eagle populations begin to suffer.

Though humans, brown bears, and bald eagles are among the most dominant of terrestrial salmon consumers, there are multitudinous additional species that make use of spawning salmon and senescent carcasses in some fashion. A truly comprehensive ecosystem-based fisheries management plan will need to address the needs of many species with many varied life history strategies. My hope is that the

studies outlined in this dissertation, though limited in scope, will act as a first step for managers to work toward an ecosystem-based fisheries management paradigm that encompasses and enhances the linkages among Pacific salmon and the diversity of species they support.

APPENDICES

Appendix 1: Protocols for DNA extraction, microsatellite PCR, and data analyses used for genotyping noninvasive saliva and scat samples collected for brown bears in Southeast Alaska.

DNA extraction and microsatellite PCR

Prior to extractions, scat and saliva swabs were removed from ethanol and allowed to dry overnight in a sterile environment. We performed all DNA extractions using AquaGenomic. We followed a single extraction protocol for both scat and saliva samples based on the AquaGenomic Stool and Soil Protocol with the following modifications: 1) Swabs were incubated in microfuge tubes with 400µl AquaGenomic for one hour at room temperature to rehydrate; 2) Following rehydration, we added 17.8µl Proteinase K and a small number of 1mm zirconia/silica beads to each microfuge tube; 3) Tubes were then incubated for one hour at 60°C, vortexing every 15 minutes to promote cell disruption, followed by incubation for 15 minutes at 95°C to inactivate the Proteinase K; 4) After pelleting and removal of debris and addition of AquaPrecipi and vortexing, we incubated samples at -20°C for 20 minutes prior to spinning samples down in the centrifuge; and 5) DNA pellets were rinsed three times with 70% ethanol and allowed to air-dry overnight following rinsing.

DNA concentration was not quantified. We avoided contamination by 1) using aerosol resistant pipette tips for critical procedures in DNA extractions and PCR preparations, 2) conducting PCR setup in an appropriate clean hood, 3)

preparing saliva and fecal samples in a separate location from PCR setups with glove changes between samples, and 4) using negative controls. We screened extracted samples by performing a single duplex PCR to exclude samples from non-target species or of poor quality DNA (Paetkau 2003). We examined duplex PCR products on 1% agarose/GelRed visualized with ultraviolet fluorescence, and kept samples for further analyses if a band from at least one of two loci was visible.

To genotype samples, we separated primers into two groups (Table 1) for multiplex PCR. Multiplex PCRs were performed using Qiagen Multiplex PCR kits in 12µl volume, with reactions containing 2X Qiagen master mix, 50mg/ml BSA, 0.1-0.2 mM of each primer, 2µl template DNA, and Milli-Q water to 12µl. Reactions for multiplex group 2 (Table 1) also contained 5X Qiagen Q-solution. The PCR profile was 15 min at 95°C initial denaturation followed by 39 cycles of 30 s for denaturation at 94°C, 90 s for annealing at 56°C, and 60 s for extensions at 72°C, followed by a final extension step of 30 min at 60°C. PCR products were loaded on an ABI 3730 Genetic Analyzer and scored using GeneMapper 4.1.

Samples were first multiplexed for group 1 and were discarded if they did not produce scorable results at ≥ 2 loci. Samples multiplexed for both groups were amplified a minimum of three times to ensure reliable results. Individuals missing two or fewer loci (e.g. failed PCR, poor-quality DNA extract) from both groups were amplified an additional three times; samples missing more than two loci were excluded from our data set.

Protocol for genetic analyses

We identified unique genotypes using the R package 'allelematch' (Galpern et al. 2012), using a mismatch parameter of four alleles. Multiple observations of a genotype were used as an additional measure of genotyping reliability; single observations of unique genotypes were not accepted as new individuals unless alleles for all seven loci and the sex marker matched across all amplifications. We used program GIMLET (Valière 2002) to estimate heterozygosity, number of alleles per locus, and calculate P_{ID} and $P_{ID(sib)}$. We estimated genotyping error rate by directly counting error rate per allele.

Table 1: Sequences (5' – 3') of the microsatellite primers used for genotyping scat and saliva samples collected noninvasively for the brown bear in Southeast Alaska. Loci are listed in multiplex PCR groups.

Locus	Forward Primer	Reverse Primer
Group 1		
G1D	GATCTGTGGGTTTATAGGTTACA	CTACTCTTCCTACTCTTTAAGAG
G10H	CTCTTGCCTTACTTACATGG	ATCAGAGACCACCAAGTAGG
G10J	GATCAGATATTTTCAGCTTT	AACCCCTCACACTCCACTTC
G10M	TTCCCCTCATCGTAGGTTGTA	AATAATTTAAGTGCATCCCAGG
G10X	CCCTGGTAACCACAAATCTCT	TCAGTTATCTGTGAAATCAAAA
Group 2		
G1A	TCCAGTGTCCTCCCTTTCT	AGATTAGTGAAAAAGAAGCAGG
G10B	GCCTTTTAATGTTCTGTTGAATTTG	GACAAATCACAGAAACCTCCATCC
SRY	GAACGCATTCTTGGTGTGGTC	TGATCTCTGAGTTTTGCATTTG

Appendix 2: Tracking information for 30 bald eagles captured in Southeast Alaska

Individual	Sex	Age	Movement	Tracking Period		N Loc
49525	♀	Adult	Breeder	19 Jul 2010	4 Sep 2012	5399
49526	♂	Adult	Breeder	22 May 2011	3 Jan 2016	14433
495271	♀	Adult	Breeder	29 May 2010	29 Jun 2011	4182
495272	♂	Adult	Breeder	19 May 2012	4 Jan 2016	10444
49528	♂	Adult	Breeder	22 Jun 2011	5 Jun 2012	3583
49532	♀	Immature	Nomadic	25 May 2010	3 Sep 2011	5062
49545	♀	Adult	Breeder	23 Jul 2011	5 Nov 2015	11557
49547	♂	Adult	Breeder	16 May 2010	6 Nov 2012	9111
49553	♀	Adult	Breeder	20 Jul 2011	18 Nov 2012	4524
103318	♀	Adult	Nomadic	19 Mar 2011	16 Oct 2015	14323
103319	♀	Adult	Localized	17 Mar 2011	26 Dec 2015	15854
103322	♂	Adult	Localized	18 Mar 2011	8 Jul 2014	8567
103326	♀	Adult	Localized	25 Mar 2011	17 Jan 2014	7140
103327	♀	Adult	Nomadic	4 Nov 2013	10 Oct 2015	6327
103328	♂	Adult	Migratory	19 Mar 2011	30 Apr 2013	5658
103330	♂	Adult	Migratory	17 Mar 2011	8 Nov 2015	13581
107178	♂	Adult	Nomadic	5 Nov 2013	5 Nov 2015	7156
107179	♂	Adult	Nomadic	5 Nov 2013	28 Oct 2015	6876
107180	♂	Adult	Localized	5 Nov 2013	29 May 2014	1731
107181	♂	Adult	Nomadic	5 Nov 2013	27 June 2015	5732
122094	♀	Adult	Localized	5 Nov 2012	3 May 2015	5158
122095	♂	Adult	Migratory	5 Nov 2012	1 Nov 2015	12638
122096	♂	Adult	Breeder	9 Jun 2014	27 Feb 2015	1580
122519	♀	Immature	Nomadic	5 Nov 2012	6 Nov 2015	11611

122795	♂	Immature	Migratory	4 Nov 2012	4 Nov 2015	15184
133480	♀	Immature	Nomadic	4 Nov 2013	3 Oct 2013	4490
133481	♀	Immature	Nomadic	4 Nov 2013	17 May 2015	3385
133482	♀	Adult	Breeder	5 Nov 2013	27 Oct 2015	5148

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