The effect of spawning salmon subsidies on reproduction and territoriality of an avian insectivore

by

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Abstract

Resource subsidies link marine, freshwater and terrestrial ecosystems. The movement of marine-derived nutrients from spawning salmon into riparian forests through multiple trophic pathways provides an important subsidy to recipient terrestrial ecosystems. Studies have established links between salmon subsidies and higher densities of indirect consumers, such as insectivorous birds. However, the mechanisms supporting these higher densities remain largely unexamined as studies have focused on patterns rather than processes. This thesis examines the mechanisms and trade-offs supporting higher densities of Pacific wrens (*Troglodytes pacificus*), a species of avian insectivore, along salmon streams. I found that salmon subsidies mediate habitat selection and reduce territory sizes of adult male wrens along riparian forests. I then examine the effect of salmon subsidies on reproductive success and effort. Thus, not only do salmon subsidies shape spatial occurrence of adult wrens, they also impact breeding behaviour and effort, leading to higher wren reproductive success on salmon streams.

Keywords: marine-derived nutrients; salmon; Pacific wren; habitat selection; reproductive success

This thesis is dedicated to my furtive feathery friends, the Pacific wrens.

Particularly to those that evaded capture.

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Chapter 1.

Introduction

Nutrient subsidies

In the past two decades there has been a growing body of evidence supporting the complex role of resource subsidies on recipient community structure and dynamics (Polis et al. 1997). Resource subsidies are organisms or material derived from one habitat and transferred into another ecosystem, which either directly or indirectly stimulates recipient system productivity (Kelly et al. 2014, Richardson and Sato 2015). The definition of a subsidy can encompass diverse systems, from the passive wave deposition of marine-nutrient filled seaweed on coastal beaches stimulating inland plant growth (Orr et al. 2005, Mellbrand et al. 2011) to terrestrial leaf litter promoting stream aquatic insect community assembly (Going and Dudley 2007). Although subsidies have various forms, from detritus to animals, there is evidence that the strongest subsidies are resources which enter at the lowest trophic levels and whose effects propagate up through the food web (Jentsch et al. 2007). Subsidies can support higher densities of consumers either by attracting them to the available resource or by improving growth or reproduction of consumers (Gratton and Denno 2003).

New research is rapidly expanding our understanding of the far-reaching direct and indirect effects of resource subsidies and the connectivity between adjacent ecosystems. Subsidies originating outside the recipient system can have implications for *in situ* population dynamics and productivity not only for those animals that directly consume the resource, but also indirectly through various trophic pathways (Knight et al. 2005, Reimchen 2017). Net ecosystem productivity can be increased through an increase in the biomass of direct consumers such as herbivores and detritivores. These consumers, in turn, support higher densities of predators. For example, emergent aquatic invertebrates subsidized by terrestrial leaf litter can support higher abundances of nearby spider populations, causing them to depress local terrestrial insects (Baxter et al. 2005). Subsidies also affect consumer life histories and competition for resources. Resource subsidies therefore can have important impacts on both community and population dynamics.

Ecosystems rarely receive constant, unvaried inputs of subsidies (Yang 2008). While Polis et al. (1997) briefly touched upon the importance of different temporal and spatial scales of habitat use in their foundational paper, research in the last decade has further explored the impact of how and when subsidies are delivered to systems. Resource pulses are defined as being brief, infrequent and intense periods of heightened resource availability (Ostfeld and Keesing 2000, Yang 2008). These pulse periods may be episodic, such as seasonal inputs of leaf litter to freshwater streams (Fey et al. 2015) or they may be less predictable, such as large-scale synchronous cicada emergence (Nowlin et al. 2007, Yang 2008). Nutrient pulses may even arise from single chaotic events like forest fires (Spencer and Hauer 1991). They can be driven by abiotic events like El Niño years (Ostfeld and Keesing 2000) or annual biotic events such as the annual migration of Pacific salmon into coastal freshwater streams (Childress and McIntyre 2015). The ability to persist in strongly resource pulsed systems may be affected by the organism’s ability to take advantage of a nutrient pulse, either by rapid growth or storage during available periods and reliance on those stores during periods of low availability (Anderson et al. 2008, Holt 2008). Therefore, predictable subsidy pulses can promote stable communities and maintain higher densities of consumers.

The direct and indirect effects of salmon subsidies

Anadromous salmon returning to their natal streams to spawn represent a predictable annual pulse of marine nutrients into adjacent freshwater and terrestrial ecosystems. Marine-derived nutrients from their carcasses are dispersed into recipient ecosystems through various pathways, including direct consumption or leaching from decomposition into soil and water (Gende et al. 2002). Salmon nutrient subsidies can either represent a consumable energetic resource to animals such as bears (Hilderbrand et al. 1999a), wolves (Darimont et al. 2003), gulls (Field and Reynolds 2013) and invertebrates (Hocking et al. 2009) or important chemical products like nitrogen, which are incorporated into plants and soil bacteria (Gende et al. 2002, Reimchen 2017).

The idea that spawning salmon are an important resource is not a new one (Shuman 1950). However, in the last 20 years, scientist have examined and recognized the biological consequences of salmon subsidies for freshwater and terrestrial community and population dynamics (Cederholm et al. 1999, Reimchen 2017). Spawning salmon carcasses import marine-derived nutrients into freshwater streams where they can be exported to terrestrial systems through bear predation (Hilderbrand et al. 1999b) or flooding (Richardson and Sato 2015). Deposited salmon carcasses are then colonized by terrestrial invertebrates (Hocking et al. 2009) which may in turn reciprocally subsidize in-stream juvenile salmon (Allan et al. 2003), or support higher densities of avian insectivores (Christie and Reimchen 2008, Field and Reynolds 2011). However, nitrogen leaching from spawning salmon carcasses also influence growth and community composition of riparian plants which sustain different terrestrial invertebrate communities (Allan et al. 2003, Hocking and Reynolds 2011).

While there is considerable support for salmon influencing densities and abundances of direct and higher-order consumers, there is less evidence of the mechanisms underpinning those patterns of spatial occurrence. Salmon subsidies are often presented as an inherently positive effect, increasing food availability and thereby increasing consumer and higher-order consumer densities, with the notable exception of bioturbation acting as a disturbance to aquatic invertebrates (Weber and Brown 2013). While resource pulses can have variable impacts on recipient communities based on characteristics such as trophic levels and intraspecific interactions (Anderson and Polis 2004), this level of nuance is often missing from studies on the indirect effects of salmon subsidies for higher-order consumers. Here I present a study of the indirect effects of bottom-up resource pulse from salmon subsidies being mediated by density-dependent trade-offs for an avian insectivore, the Pacific wren (*Troglodytes pacificus*).

The Pacific wren as a model organism

Pacific wrens are ubiquitous along the west coast of North America and present an opportunity with which to understand the nuanced impacts on spatial and behavioural effects of salmon subsidies on an indirect consumer. Pacific wrens are a small obligate insectivore, with adults typically weighing eight to ten grams. Spending the vast majority of their time within 5 meters of the forest floor, males sing to defend territories and attract mates throughout the spring and summer breeding season. In the dense forests of the Pacific Northwest, this proximity to the forest floor along with their distinct songs and relatively small territories allows researchers to more easily track their movements. Wrens also reflect *in situ* resource availability as they are a resident songbird along BC's coast and usually remain in the same habitats over the winter (Toews and Irwin 2012).

While Pacific wrens are very conspicuous through their loud songs, they are much more cryptic in their breeding behaviour. Males will often construct multiple closed-cavity nests woven out of moss, twigs, roots and other materials within their territories. They will typically camouflage these nests within the roots of upturned trees, inside moss clumps hanging from branches or even in the banks of creeks. Many nests will remain unused throughout the breeding season, as females will only line the nest in which she chooses to lay eggs. These dummy nests are thought to either represent anti-predator defences or aid in attracting mates (Toews and Irwin 2012) and we often found males courting females at unoccupied nests.

There have been a few studies showing that Pacific wrens appear to respond to salmon subsidies. Willson and Gende (2001) were one of the first to look at densities of Pacific wrens on salmon streams. Since then other studies such as Christie and Reimchen (2008) and Wagner and Reynolds (2019) have demonstrated that Pacific wrens are found in higher densities along salmon streams, particularly along the Central Coast of BC, where this study was conducted. Here, I look to build on these studies, taking the next step from looking at correlations between salmon and densities of wrens to understanding the behavioural and spatial processes underpinning these patterns.

Overview of thesis chapters

In this thesis I examine the role of salmon subsidies in shaping Pacific wren habitat selection (Chapter 2) and impacts on life-history traits, particularly reproductive success, effort and behaviour (Chapter 3). I use 12 small streams along the Central Coast of British Columbia with variable sizes of salmon runs as my model systems, and Pacific wrens as my model organisms throughout both chapters. In the second chapter I ask how fall salmon biomass affects absolute wren densities the following spring, confirming the results of previous studies. I then go on to examine the role of salmon subsidies in shaping male wren territory size and habitat selection and comment on the density-dependent effects of competition at higher subsidy levels (Chapter 2). In the third Chapter, I assess the role of salmon subsidies in changing wren reproductive success and effort along salmon streams, by examining the number of young produced per male, nest feeding rates, and rates of polygyny and double brooding. Finally, in the concluding chapter, I synthesize and examine my findings in the context of ecosystem-based management.

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Chapter 2.

Salmon subsidies predict territory size and habitat selection of an avian insectivore

2.1. Abstract

The annual migration and spawning of Pacific salmon (*Oncorhynchus* spp.) represents an important cross-boundary delivery of marine-derived nutrients from their carcasses into adjacent terrestrial ecosystems. The densities of some passerine species, including Pacific wrens (*Troglodytes pacificus*), have been positively correlated with salmon abundance along streams in Alaska and British Columbia, but mechanisms maintaining these densities remain poorly understood. Riparian areas near salmon streams could provide higher quality habitat for birds through greater food availability and more suitable vegetation structure for foraging and breeding, resulting in wrens maintaining smaller territories. We examined relationships between salmon biomass and Pacific wren territory size, competition, and habitat selection along 11 streams on the coast of British Columbia, Canada. We show that male wren densities increase and territory sizes decrease as salmon-spawning biomass increases. Higher densities result in higher rates of competition as male wrens countersing more frequently to defend their territories along streams with more salmon. Furthermore, wrens were more selective of the habitats they defended along streams with higher salmon biomass; they were 22% less likely to defend habitat with high volumes of western redcedar (*Thuja plicata*) along salmon streams compared with streams that lacked salmon. This suggests a potential trade-off between available high-quality habitat and the cost of competition that structures habitat selection. Thus, the marine-nutrient subsidies provided by salmon carcasses to forests lead to higher densities of wrens while shifting the economics of territorial defence toward smaller territories being defended more vigorously in higher quality habitats.

2.2. Introduction

Many seemingly disparate ecosystems are linked by the movement of species and nutrients across habitat boundaries (Polis et al. 1997). Predictable pulses of subsidies across ecotones can have a wide range of ecological impacts, from increasing local densities of consumers (Anderson et al. 2008, Bentley et al. 2012) to longer-term, comprehensive effects on recipient ecosystem productivity or community structure and stability (Holt and Barfield 2003, Weber and Brown 2013). Nutrient subsidies often enter recipient communities at low trophic levels, but their effects can propagate through multiple trophic levels (Huxel et al. 2002, Bartels et al. 2012, Weber and Brown 2013). They can increase local densities of primary consumers, leading to widespread consequences for food web dynamics (Jefferies 2000, Nakano and Murakami 2001). For example, a study of the effect of a single pulse of nitrogen fertilization showed that a short resource pulse can have lasting effects on abundance of grasses, but also increase the abundance of insect herbivores and their arachnid predators for up to three years (Gratton and Denno 2003). Increasing densities of secondary consumers has implications for structuring community dynamics through top-down effects or intraspecific competition (Ostfeld and Keesing 2000).

Along the North Pacific Rim, the annual migration of spawning salmon into freshwater streams represents one of the most striking examples of a predictable pulse of nutrient subsidies. Nitrogen derived from carcasses of adult salmon can impact the recipient community directly as food and nutrients for consumers, or indirectly through various bottom-up interactions. Nutrients are exported to terrestrial systems through passive deposition, flooding, or transport by bears, wolves, and birds (Darimont et al. 2003, Quinn et al. 2009, Richardson and Sato 2015, Buxton et al. 2015, Andersson and Reynolds 2017). Salmon carcasses are then colonized by terrestrial invertebrates and this subsidy has been shown to increase invertebrate biomass the following spring (Nakano and Murakami 2001, Gende et al. 2002). Salmon carcasses can also influence growth and community composition of riparian plants through the deposition of carbon and nitrogen (Helfield and Naiman 2001, Hocking and Reynolds 2011) which sustain different herbivorous invertebrate communities (Allan et al. 2003).

Marine-derived nitrogen from salmon create bottom-up trophic cascades, cumulating in higher densities of riparian passerine birds along salmon streams (Gende and Willson 2001, Christie and Reimchen 2008, Field and Reynolds 2011, Wagner and Reynolds 2019). Nitrogen subsidies from salmon carcasses may increase habitat quality for passerines through greater food availability and potentially better habitat structure that enhances foraging opportunities and nest site availability (Pearson and Manuwal 2001, De Santo et al. 2003, Uesugi and Murakami 2007). For example, along salmon streams there is higher invertebrate prey availability (Gende et al. 2002) and the riparian plant community composition is more salmonberry-dominated (*Rubus spectabilis*) (Hocking and Reynolds 2011), which produce fruit and have been shown to support higher insect biomass than conifers (Allan et al. 2003). There is also direct evidence of a trophic link between salmon subsidies and Pacific wrens, as isotopic shifts in wren tissues reflect the availability of salmon in invertebrate diets (Christie et al. 2008).

Many studies have examined the indirect effects of subsidies on recipient communities through increases in consumer abundances, biomass, or densities (Marczak et al. 2007). However, there is an increasing awareness of the need to understand the behavioural processes underpinning these outcomes as higher densities of consumers are not always positively correlated with higher resource availability (Van Horne 1983, McLoughlin et al. 2016). In this study, we present one of the first examinations of mechanisms maintaining higher densities of birds through indirect effects of marine-derived salmon subsidies. We show how individuals balance the trade-off between access to high-quality resources and competition, the consequences of which can be seen through habitat occupancy, individual quality, and local density (Jones 2001, Johnson 2007, Jones et al. 2014). As habitat selection is an important component of these processes, territorial species are particularly well suited to understand the mechanisms maintaining higher densities of passerines along salmon streams.

Indirect effects of salmon-derived nutrients on territoriality can be studied through the lens of food-value theory (Stenger 1958, Marshall and Cooper 2004), which predicts an inverse relationship between food availability and territory size as territories scale to support the energy necessary to live (Adams 2001). However, territory size can also be driven by the trade-off between defending against conspecifics and habitat quality (Marshall and Cooper 2004). There may be more pressure to defend high quality habitat when competitor density is increased, requiring the allocation of more energy and time to maintain a territory. Marine-derived nutrients have been shown to positively influence many indicators of high-quality habitat for insectivorous songbirds including plant community composition and invertebrate availability (Hocking et al. 2009, Hocking and Reynolds 2011). Therefore, the trade-offs between competition and resource use mediated through nutrient subsidies, can determine territory size (Marshall and Cooper 2004).

We studied the Pacific wren (*Troglodytes pacificus*) to test for mechanisms that translate marine-derived salmon subsidies into higher densities of breeding birds. Pacific wrens are resident territorial insectivores that range along the west coast of North America from Alaska to California (Chesser et al. 2010). Male Pacific wrens establish small breeding territories in the early spring and defend them throughout the spring and summer by countersinging with their neighbours (De Santo et al. 2003). Their small territories and year-round close association with riparian areas along streams make them an effective model organism to study the localized effects of salmon nutrient subsidies on habitat use and competition.

The objectives of this study were to determine if salmon nutrient subsidies affect the territorial decisions influencing habitat selection, defence, and territory size, leading to higher wren densities. First, we tested the prediction that streams with a higher input of marine-derived nutrients through higher spawning salmon biomass would have higher wren densities with smaller territory sizes. Second, we predicted that competition with conspecifics would be more intense along streams with high densities of salmon, as manifested by rates of countersinging. Third, we tested whether higher pressures from conspecifics would lead wrens to be more selective in which habitats they defended. Finally, we tested for differences between wren body condition at different densities and territory sizes across salmon streams. Thus, our study tests the overall prediction that nutrients derived from salmon would lead to higher densities of wrens by mediating trade-offs between resource availability and competition.

2.3. Methods

2.3.1. Study sites

Our study was conducted from April to July in 2015 and 2016 on the Central Coast of British Columbia, Canada, within the traditional territory of the Heiltsuk First

Nation (vicinity of 52.1605° N, 128.1456° W). The stream sites were located on coastal islands and mainland inlets within the Coastal Western Hemlock Biogeoclimatic Zone, which is characterized by nutrient-poor soils and high annual precipitation of 3000–4000 mm·year^{-1} (Pojar et al. 1987). Forest cover is dominated by western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), Sitka spruce (*Picea sitchensis*), amabilis fir (*Abies amabilis*), and red alder (*Alnus rubra*). The latter is the only large deciduous tree found at our sites. Riparian plant understory communities are composed of shrubs including salmonberry (*Rubus spectabilis*), stink currant (*Ribes bracteosum*), blueberries (*Vaccinium* ssp.), false azalea (*Menziesia ferruginea*) and salal (*Gaultheria shallon*). Most of our sites were selectively logged for spruce in the 1940s.

We conducted bird and vegetation surveys at 11 stream-side plots, 5 of which were surveyed in 2015 and 6 surveyed in 2016. We established a 9-hectare forest plot centered around each stream-site, beginning at the mouth of the stream and extending 375 m upstream and 125 m upland on either side of the stream. The streams ranged from 5 to 20 m wetted width. We flagged the plots at 50 m by 25 m intervals, creating points to facilitate data collection and to geolocate observations. We determined the Universal Transverse Mercator (UTM) coordinates for all points using hand-held GPS units.

2.3.2. Salmon biomass

Salmon enumeration on each stream was done by collaborative surveys conducted by our research group combined with from data shared by the Department of Fisheries and Oceans and the Heiltsuk Integrated Resource Management Department. Streams were surveyed three times over the course of the salmon spawning season from early September to late October to determine spawning salmon abundance using the area-under-the-curve estimation method (English et al. 1992). When streams had very low salmon abundance or we were constrained by weather to only one or two counts per stream, we used peak counts of live plus dead to estimate salmon abundance. Both methods result in the same mean estimates of run-size (Hocking and Reynolds 2011).

We used salmon biomass as the metric of marine-derived nutrient subsidy, as biomass is more relevant than salmon number for the amount of nutrient input into the ecosystem. Streams were heavily dominated by pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon (>99% of fish by number). Therefore, biomass was calculated as the chum and pink run size multiplied by their respective average weights (3.5 kg for chum and 1.2 kg for pink; Hocking and Reynolds 2011). We calculated a three-year mean of salmon biomass for each stream for the years before we did our bird surveys to account for longer-term effects of salmon. The streams ranged from having no salmon to an average of 46,609 kg spawning salmon annually (Table A1, Appendix A).

2.3.3. Territory mapping and densities

Early in the breeding season, we colour-banded male wrens by catching them in mist nets through targeted playback to aid in individual identification of territorial behaviour. To determine territory size we used spot-mapping, a well-established method for determining habitat use (Odum and Kuenzler 1955, Bibby et al. 1992, Ralph et al. 1993). We initiated spot-mapping one hour after sunrise each day and continued for 1.5 hours. Observers moved through the plot along the geolocated points at a consistent walking pace, recording the locations of singing, countersinging, calling, and visual observations of male wrens against known plot locations. Each stream was visited eight times during the season, from late April until July, in rotating order (one site per day) and for each visit, we began spot mapping at either a different corner of the plot, or by moving in a different direction to ensure adequate coverage throughout the morning chorus.

Territories were delineated in ArcGIS (Version 10.1) by geo-referencing each song or visual observation against known site points and then overlaying each visit to create an overall pattern of territorial observations throughout the season (Fig. 1). Territory boundaries were mapped according to countersinging locations between male wrens. Countersinging occurs when birds sing in response to their neighbour's song by matching or overlaying songs (Hyman 2003). Pacific wrens will often countersing at the edges of defended habitat, allowing us to mark the outer borders of territories.

We measured territory size using 95% minimum convex polygons, with the adehabitat package in R (Calenge 2006), at the outermost territorial observations for each wren. Territories that had more than half of their observations outside the surveyed plot area were excluded from the study as their size may have been underestimated.

Similarly, male wrens that were detected in fewer than three survey visits or that had fewer than three total observations throughout the breeding season were excluded from the analysis as we categorized them as floaters unable to establish a breeding territory.

To calculate absolute male wren densities at each stream we determined the proportion of each male's territory within the surveyed stream-site and divided the sum by the surveyed stream-site area. This gave us male wren densities as number of territorial males per hectare.

2.3.4. Countersinging rate

We first determined the number of countersinging bouts attributed to an individual bird in order to determine countersinging rate per male as a metric of competition. Observations were categorized as countersinging if observers heard two male wrens singing in response to each other by either alternating or overlaying songs. We tallied the number of locations from which each individual bird countersang during our spot-mapping and standardized it by the total number of hours surveyed. Similarly, we calculated the singing rate of each territorial male wren as the total number of singing observations that occurred within a territory, standardized by survey effort (total survey hours at each stream over the season). We then calculated the number of countersinging bouts divided by the total number of singing bouts to get the proportional rate of countersinging to control for the relationship between larger territories and available locations from which to countersing.

2.3.5. Vegetation surveys

We surveyed vegetation plots at each geolocated stream-site point (50 m x 25 m) for a total of 49 plots per stream using a modified BBIRD protocol (Martin 1997). To measure understory characteristics, percent cover was recorded for all shrub and immature tree species (<2.5 cm diameter at 10 cm or <5 m height) and summed across three different height classes (0-50 cm, 50-200 cm, 200-500 cm) within a 5-m radius. We focused on vegetation below five meters in height because our field observations indicated that this was where wrens spent most of their time. Within the 5-m radius vegetation plot we also measured percent cover of logs and stumps and calculated Shannon's Diversity Index of tree and shrub species. To calculate the habitat characteristics for each territory, we averaged the percent cover estimates of shrubs, trees, diversity indices, and large woody debris for all the vegetation plots within a given territory. We divided shrub cover into two categories: nutrient-rich shrub species and other shrub species. Nutrient-rich shrub species at our sites were salmonberry and stink currant, which are associated with riparian borders, categorized as nitrophiles, and therefore indicate nitrogen-rich soil (Hocking and Reynolds 2011).

To determine forest stand characteristics, we recorded each tree species and its diameter at breast height (DBH) within a 11.3 m radius (400 m² area surveyed) of the centre of each vegetation plot (Martin et al. 1997). Tree species that occurred in less than five percent of plots were excluded from analyses. DBH was used to calculate the stand basal area (SBA) of all tree species, including western redcedar, Sitka spruce, and western hemlock, which dominate the forest composition. We determined SBA of tree species at both the 5 m plot level and at the territory level. Territory-level tree volume of each species was calculated by summing the SBA of each individual species from all the vegetation plots within a territory and dividing by the total area of those surveyed plots (expressed as m² hectare^{-1}).

2.3.6. Body condition

When color-banding wrens, we collected morphometric data to calculate scaled mass index (SMI) to characterize adult male wren body condition. SMI is a condition index for estimating individual energy reserves standardized to body size as it accounts for the scaling relationship between mass and length (Peig and Green 2010). We used wing length for our linear measurement as together with body mass, these measurements have been shown to predict percent body fat and fat mass in birds (Peig and Green 2009). We also confirmed that wing measurements correlated strongly with adult wren mass. We calculated SMI as the predicted body mass for each individual when wing length is standardized by the arithmetic mean of the wing length of our measured adult wren population (46.52 mm) to the power of the slope of the regression (Peig and Green 2009).

2.3.7. Data analysis

To model territory size we used linear mixed effect models with stream site as a random effect and year as a two-factor fixed effect in all candidate models. We used parameters of interest from our top habitat selection model to narrow down habitat parameters to use as predictor variables for territory size, including salmon biomass, high-nutrient shrub cover, and coniferous tree volume.

We modeled male proportional countersinging rate (relative to singing rate) as a linear mixed-effect model with stream site as a random effect and year as a two-factor fixed effect. We included male stream-level absolute density, salmon biomass, and stream site as parameters in our global model.

We characterised habitat selected by wrens by first overlaying the vegetation plots and 95% MCPs representing wren territories in order to determine if wrens are more likely to select habitat with specific vegetation characteristics. To model territorial habitat selection, we created a resource selection probability function (RSPF) and competed generalized linear mixed effect models with a binomial response of wren territory presence/absence (if the vegetation plot fell within or outside the 95% MCP) and logit link. We modeled the probability of wren territorial habitat selection as a function of vegetation characteristics, total salmon biomass in the stream, and year as predictors with stream as a random effect (see Appendix A, Table A2 for full candidate model set). Year (2015 and 2016) was included as a two-level factor in all candidate models to account for year-to-year variability, however removing year from the models did not alter any predictions. We then competed 13 RSPF candidate models to determine a top model from which to generate predictions of habitat selection. The candidate models can be classified under four main hypotheses: 1) habitat only models, 2) salmon only models 3) salmon and habitat characteristics models and 4) salmon and habitat interaction models (Appendix A, Table A2). This allowed us to test the hypothesis that salmon biomass and vegetation characteristics would interact to determine habitat selection.

Global models were assessed for violated assumptions using simulated residuals in the Dharma package (Hartig 2018). For our RSPF models, absence of spatial autocorrelation was checked graphically using variograms. Vegetation plots were categorized as being within a wren territory if any part of them fell within the 95% minimum convex polygon of a territory

As we had a limited sample size of banded wrens that we measured and weighed (half of the territorial males, n=27), we were only able to run simplified models to test for correlates of wren body condition. We modeled body condition first as a function of territory size, then separately as a function of territory size relative to others in the same stream, to test whether males with higher body condition had territories that were larger in absolute terms or larger than average within streams. We then competed these models with null models of only stream and year.

All candidate model predictors (including RSPF models and linear-mixed effect models) were checked for multicolinearity using variance inflation factor scores (VIF). None of the predictor variables had VIF scores greater than 2, indicating an acceptable amount of covariance (Zuur et al. 2009) (see Fig.A2 in Appendix A for correlation coefficients). Additionally, we standardized all explanatory variables (mean=0, SD=2) to allow for direct comparisons of fixed effects (Gelman 2008, Schielzeth 2010). Using an information theoretic approach, we evaluated the relative support for each candidate model set and selected our top models using Akaike's Information Criterion (AIC) with a cut-off of delta 2 AIC (Burnham and Anderson 2002). Territory size and countersinging top models were evaluated using delta AICc corrected for small sample size. All of our top models were > 2 AIC or > 2 AICc higher than the next highest ranked models, and were therefore not model averaged (Burnham and Anderson 2002). Wren density was modeled as a simple linear regression of salmon biomass. All statistical analyses were performed in R 3.4.1 (R Core Team 2017).

2.4. Results

We collected territory size and countersigning data from 44 male wrens from 11 streams in 2015 and 2016. This included data for 22 males in 2015, 11 of which were banded, and 22 different males in 2016, of which we successfully banded and collected measurements for 16. Thus, we banded a total of 27 male wrens. We also collected vegetation data at each stream from a total of 554 vegetation plots on which we based our habitat selection models.

We confirmed our expectation that wren densities would be higher along streams with high salmon biomass (Fig. 2). Wren absolute densities ranged from 0.1 to 0.8 wrens per hectare, with the highest salmon biomass stream having over 4 times higher average wren density than streams without salmon ($F_{1,9}$=10.1, p=0.01, r^2= 0.53).

As we predicted, there was a negative relationship between wren territory size and salmon biomass (Fig. 3). A two standard deviation increase in salmon biomass (31,663 kg) corresponded with a 67% (0.77 ± 0.55 hectare) reduction in male territory size. Salmon biomass was the most important predictor of territory size (Table 1). Surprisingly, none of our habitat measurements (e.g. high-nutrient shrub cover), were in the top model for territory size and habitat variables only accounted for a small amount of additional variation compared with salmon biomass alone.

Individual males at streams with higher absolute wren densities had a higher proportional countersinging rate relative to singing rate than males at streams with low wren densities (Fig. 4). On average wrens at the highest density streams countersang at a 5.6 times higher rate than those at the lowest density wren streams (Fig. 4). Wren density proved to be the only important predictor of proportional countersinging rate (Table 1). As territory size and wren density are highly correlated (r^2= 0.53), we chose wren density as a predictor variable to model proportional countersinging rate as it more closely reflects *in situ* competition.

Although habitat characteristics did not predict territory size, they did predict the locations that the birds defended along the streams. Hemlock tree volume, high-nutrient shrub cover, stream-level salmon biomass, and redcedar volume along with their interaction predicted wren habitat selection and were in the top model (Table 2). However, only high-nutrient shrub cover, redcedar volume, and salmon biomass, along with the interaction between salmon biomass and redcedar volume had a statistically significant relationship with probability of occupation with parameter estimates not overlapping zero (Fig. 5). Diversity of shrubs and trees were not important predictors of habitat selection.

The resource selection probability function plots further supported our findings that wrens preferred locations with more high-nutrient shrub cover and lower volumes of western redcedar, however wrens were more likely to avoid redcedar at high salmon biomass streams (Fig. 6). Wrens were 46% less likely to select habitat with high volumes of western redcedar at streams with no salmon, however that rose to 68% lower likelihood at streams with high salmon biomass. Additionally, wrens were 32% more likely to select habitat with more high-nutrient shrub cover across all streams.

Wrens were also less likely to defend habitat along streams that had more salmon: the odds of wrens selecting available habitat at a higher salmon biomass stream were less than one third that at a low salmon biomass stream (Fig. 5). We tested this explicitly by analysing the difference between defended and undefended surveyed habitat and found evidence to suggest that as total salmon biomass increases, the amount of undefended habitat also increases in riparian forests ($F_{1,9}$=4.8, p=0.056, r^2= 0.35; Fig. A1 in Appendix A).

We found that neither territory size, nor having a larger territory size relative to others along the same stream, predicted adult male wren body condition (Table 1). Wrens with larger territories both across streams and relative to their neighbours had similar scaled mass indices. The inclusion of territory size or relative territory size as predictor variables did not improve model fit relative to the null model (Table 1).

2.5. Discussion

This study presents the first evidence that nutrients from salmon carcasses shape trade-offs of territoriality for a species that does not directly feed on salmon, leading to higher densities along salmon streams. Specifically, streams with higher salmon biomass during the fall spawning season support higher absolute male Pacific wren densities in the spring and summer (Fig. 2), corresponding with a decrease in wren territory size (Fig. 3). Higher densities of birds and higher salmon biomass led to increased competition between male wrens as shown by rates of countersinging (Fig. 4). As the costs of defending territories were higher, wrens were therefore more selective of what habitat they defended on salmon streams; they were more likely to avoid western redcedar on high salmon biomass streams (Fig 6). There may be a higher cost associated with defending lower quality habitat at streams with high densities of wrens. However, there was no relationship between territory size and changes in adult male body condition (Table 1).

Salmon nutrients may be shaping territory size through several indirect pathways (Reimchen 2017). Salmon streams may provide increased food availability for wrens as the nutrient subsidies from salmon carcasses produce higher insect biomass and affect riparian plant community composition (Bilby et al. 1996, Hocking et al. 2009, Hocking and Reynolds 2011, 2012, Collins and Baxter 2014). Higher food availability has been shown to have an inverse relationship with territory size across many species (Hixon 1980, Dill et al. 1981, Kittle et al. 2015), which may allow higher densities of wrens on salmon streams (Christie and Reimchen 2008). Additionally, higher complexity of habitat structure through foliage density or high shrub density has been shown to correlate with decreased territory sizes of bird species (Conner et al. 1986, Marshall and Cooper 2004). As many animals use food and habitat structure as proximate cues of habitat quality, these measures allow animals to scale their territory sizes with available resources (Odum and Kuenzler 1955, Marshall and Cooper 2004, Tingley et al. 2016).

Although we were correct in our hypothesis that salmon biomass would predict wren territory size, we were surprised that it proved to be the only predictor from the many vegetation characteristics that we measured. Thus, contrary to other studies, no other habitat variables that we measured, including high-nutrient shrub cover, conifer cover or plant species richness was an important influence on wren territory size (Waterhouse 1998, De Santo et al. 2003, Evans Ogden et al. 2012). Vegetation characteristics alone may not be the cues that wrens use to determine territory size. Salmon biomass may influence other measures of habitat quality, including increased food availability (Gende et al. 2002, Hocking et al. 2009). Salmon subsidies may also improve both the quantity and quality of available resources by increasing shrub quality for herbivorous insects, such as caterpillars, which are an important component of wren diet (Van Horne and Bader 1990, Awmack and Leather 2002, Marcarelli et al. 2011).

Our countersinging data indicate that along streams with high wren densities, individual male wrens compete directly with conspecifics more than those in low density habitats (Fig. 4). Competition represents a direct energy cost, as males are able to allocate less time to foraging and provisioning young (Qvarnstrom 1997, Sillett et al. 2004, King et al. 2009). Competition can reduce territory size below habitat saturation levels, which in turn can lead to a reduction in individual fitness (Both and Visser 2008). When competition is reduced experimentally by reducing competitor density, male great tits (*Parus major*) responded by increasing territory size, resulting in higher numbers of second generation recruits (Both and Visser 2008). Indeed, some studies have shown that cost of defense is more important in determining territory characteristics than resource availability (Eason 1992, Adams 2001). We found that despite having higher density of wrens with smaller territories at high salmon biomass streams, there is also more undefended habitat, suggesting competition keeps habitat under saturation levels (Fig. 6, and Fig. A1). Thus, we suggest that the high rate of countersinging necessary to defend territories at high density streams structures trade-offs that affect territorial selection at high salmon biomass streams.

There may be a higher cost of defending low quality habitats at high wren density streams due to greater competition with conspecifics. We found that wrens select habitat based on specific vegetation characteristics across streams, specifically avoiding western redcedar and selecting for high-nutrient shrub cover. However, wrens are more likely to avoid habitat with redcedar on streams with more salmon nutrient input, where wrens achieve higher densities (Fig. 6). Redcedar may represent lower quality vegetation as there are fewer insects on redcedar compared with deciduous shrubs or other trees due to monoterpenes contained in their foliage which deter oviposition and insect herbivory (Alfaro et al. 1981, Allan et al. 2003). Wrens typically forage low in the understory and glean insects from bark and twigs, so redcedar would not be ideal foraging habitat (Holmes and Robinson 1988). Salmonberry and stink currant, conversely, are often used for more camouflaged nest site locations (De Santo et al. 2003) and they are associated with high nitrogen availability (Hocking and Reynolds 2011) which in turn may improve both quality and quantity of insect prey (Hocking and Reimchen 2002, Marcarelli et al. 2011).

Wrens at high densities along high salmon biomass streams do not have higher body condition than those at low salmon biomass streams. Previous studies have found that higher resource availability can increase individual body condition (Kitaysky et al. 1999, Brown and Sherry 2006). However, the benefits associated with higher quality habitat may be balanced by the negative effects of high competition. This trade-off at high salmon streams may result in wrens experiencing a lower realized habitat quality, or the habitat quality the competitor actually experiences (Johnson 2007, Jones et al. 2014). Wrens having equal body condition across heterogeneous habitats suggests that they optimize their territory size to balance different pressures in ecosystems with differing amounts of resources and competition.

In conclusion, this study presents evidence that marine-derived nutrients from salmon carcasses indirectly affect territorial behaviour by an avian insectivore. Along streams with high salmon biomass, there are higher densities of Pacific wrens and males defend smaller territories. This results in increased competition along streams with more salmon, as evidenced by higher rates of countersinging. Increased competition may be responsible for the birds avoiding defence of lower quality habitat. Thus, the nutrient subsidy provided by salmon appears to shift the economics of territorial defence towards smaller, highly-contested territories in high quality habitat, leading to higher densities of wrens.

2.6. Tables

Table 2.1. AICc model selection analysis of linear regressions (models presented: ΔAICc <3) describing Pacific wren territory size, countersinging rate, and body condition response variables predicted by salmon biomass, wren density and environmental metrics. Body condition appears twice as due to limited sample size, we were only able to run simplified models to test for correlates of wren body condition and modeled body condition as a function of territory size and relative territory size separately. K = number of parameters in model, ΔAICc = difference between the model AICc and the top model AICc, w_i = model AICc weight, R^2 = regression coefficient of fitted versus observed values for each analysis, salmon = summed chum and pink salmon biomass, conifer cover = percent cover of all coniferous trees, male density = absolute male wren density per hectare, territory size = male wren territory size in hectares. Year (fixed effect) and stream (random effect) were included as variables in all models but are excluded from the table for clarity.

response	**parameters**	**K**	**ΔAICc**	**w_i**	**R^2**
territory size	salmon	3	0	0.51	0.37
	salmon + conifer cover	4	2.2	0.17	0.45
proportional countersinging rate	male density	3	0	0.53	0.71
	salmon	3	2.4	0.16	0.71
body condition	null	2	0	0.54	0.33
	relative territory size	3	0.4	0.46	0.49
body condition	null	2	0	0.63	0.37
	territory size	3	1.1	0.37	0.54

Table 2.2. **AIC model selection from the logistic regression models for probability of habitat selection by territorial male wrens (models presented: ΔAIC <4). Habitat parameters tested include: salmon = summed chum and pink salmon biomass per stream (kg), redcedar = western redcedar stand basal area ($m^2\ ha^{-1}$), high-nutrient shrub = percent salmonberry and stink currant shrub cover, hemlock = western hemlock stand basal area ($m^2\ ha^{-1}$), and other shrub = percent cover of blueberry, false azalea, and salal. Year (fixed effect) and stream (random effect) were included as variables in all models but are excluded from the table for clarity. K = number of parameters in model, ΔAIC = difference between the model AIC and the top model AIC, w_i = model AIC weights, ER = evidence ratio (relative likelihood of top model compared to given model).**

response	parameters	K	ΔAIC	w_i	ER
probability of habitat selection	salmon * redcedar + high-nutrient shrub + hemlock	7	0	0.61	1.00
	salmon * high-nutrient shrub + other shrub + hemlock	8	2.0	0.23	2.68
	salmon + redcedar + high-nutrient shrub + other shrub + hemlock	7	3.8	0.09	6.75

2.7. Figures

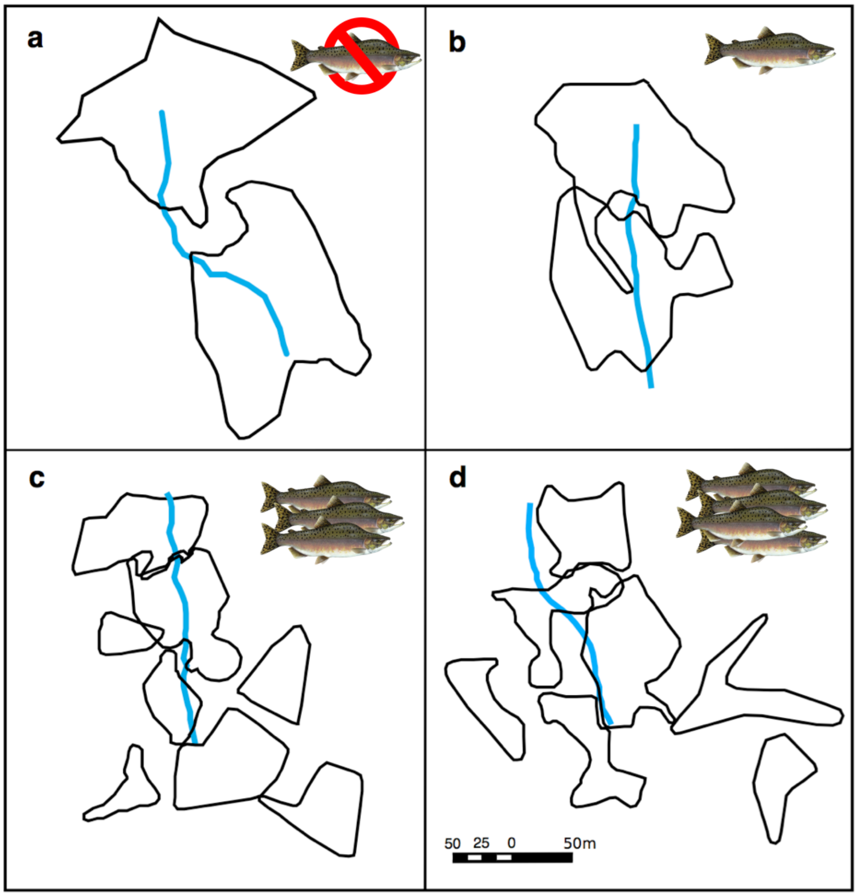

Figure 2.1. Representation of the territories of male Pacific wrens at different streams with different numbers of spawning salmon (A-D). Each polygon represents an individual wren territory along a stream: (a) Ripley with no salmon, (b) Fancy Right with ~2,500 kg, (c) Fannie Left with 32,000 kg, and (d) Clatse with 47,000 kg average annual spawning pink and chum salmon biomass. Blue lines represent the respective streams and the salmon drawing represents amount of salmon biomass.

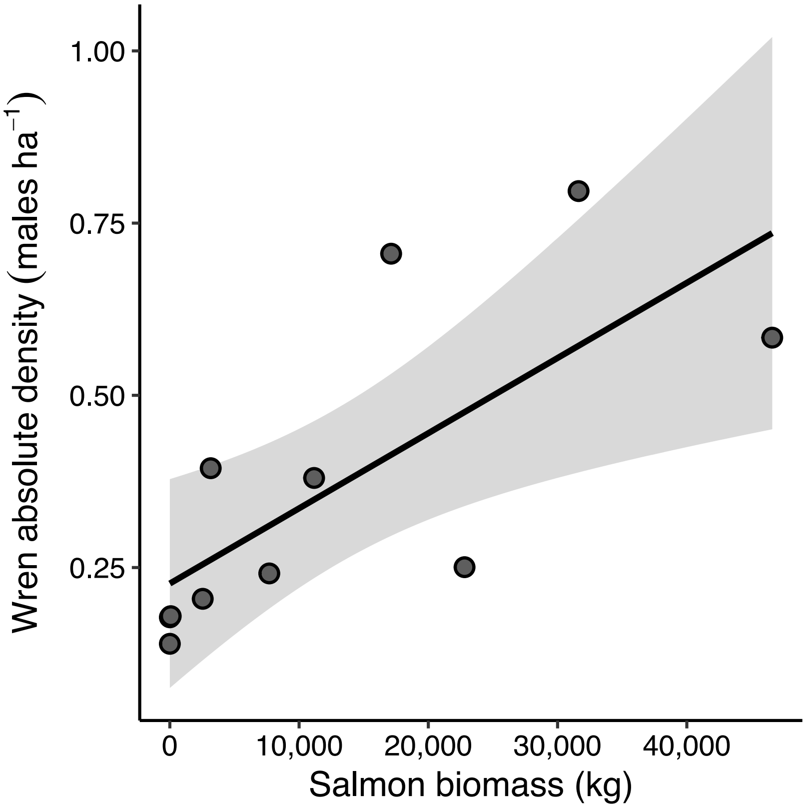

Figure 2.2. **Relationship between salmon biomass per stream and absolute male Pacific wren density in the surrounding forest plot. The dark line represents the best-fit line from the linear model and the band represents the 95% confidence interval.**

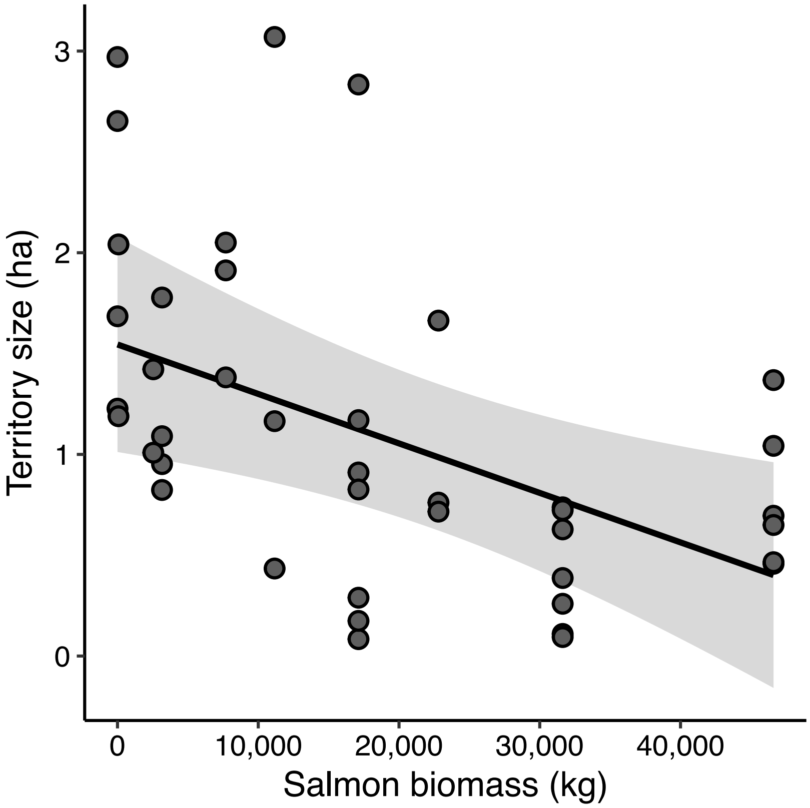

Figure 2.3. **Relationship between the spawning salmon biomass at each stream and male wren territory size in surrounding habitat. The solid line represents the best fit from the top linear mixed-effect model for territory size with all other variables held at their mean. Each point represents an individual male wren's territory size. The band represents the 95% confidence interval.**

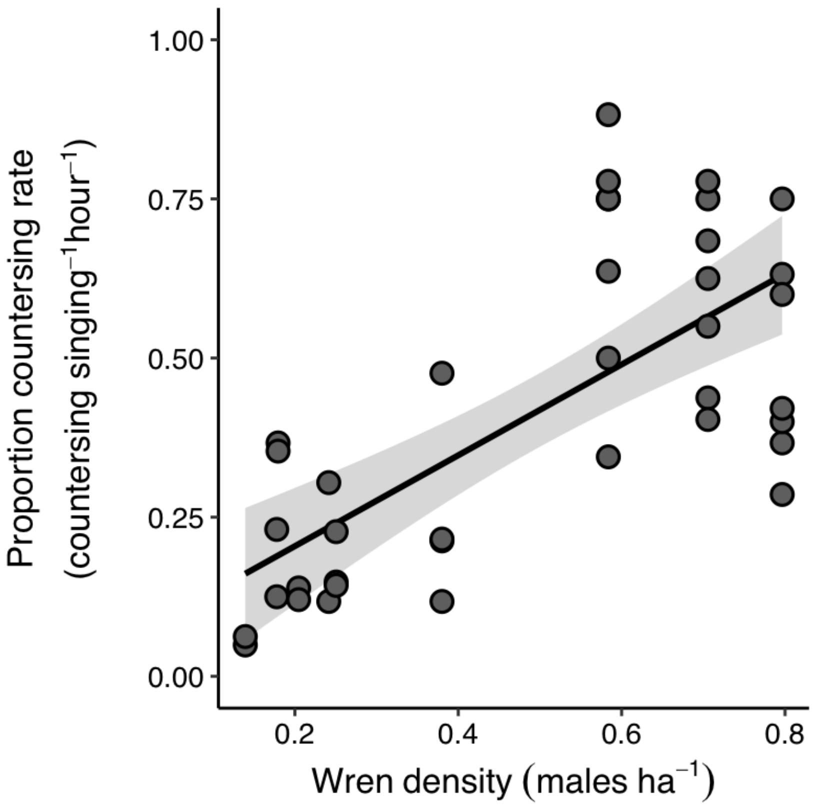

Figure 2.4. **Relationship between absolute male wren density at each stream site and the individual male wren proportional rate of countersinging (countersinging divided by total singing bouts per hour). Wren density was the main predictor variable for the model. The solid line represents the best-fit line from the top model linear regression for proportional countersinging rate and the band represents the 95% confidence interval.**

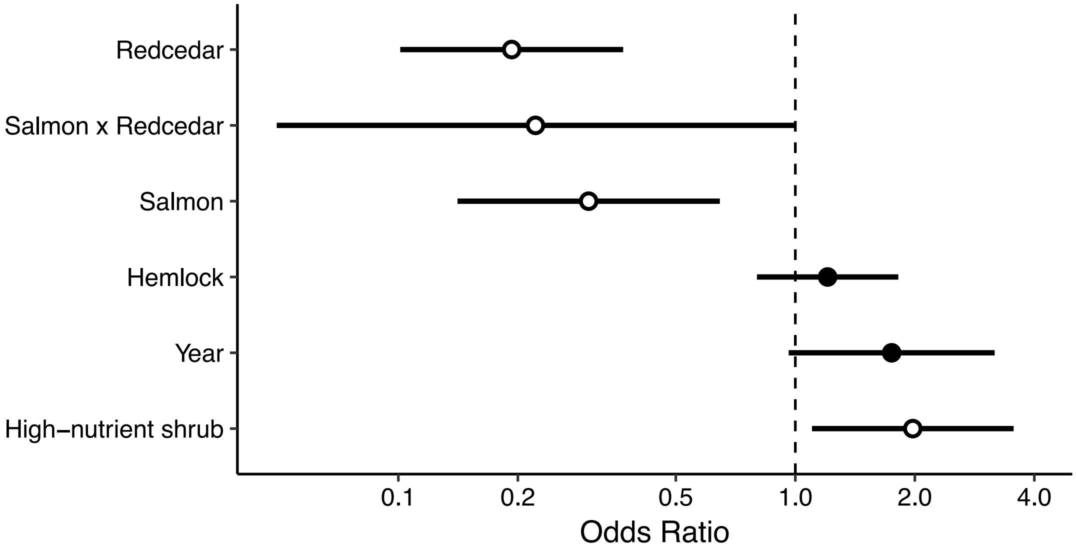

Figure 2.5. **Odds ratio of habitat selection by territorial male wrens compared to habitat vegetation characteristics and stream-level spawning salmon biomass from the top AIC model. The standardized (mean = 0, SD = 2) parameters include redcedar stand basal area (m^2 ha^{-1}), salmon biomass (kg), their interaction, hemlock stand basal area (m^2 ha^{-1}), year, and percent high-nutrient shrub cover (stink currant and salmonberry). Circles show odds ratios for each parameter, with 95% confidence intervals indicated by horizontal lines. The odds ratios significantly different from 1 (95% CI do not overlap 1) are indicated by open circles.**

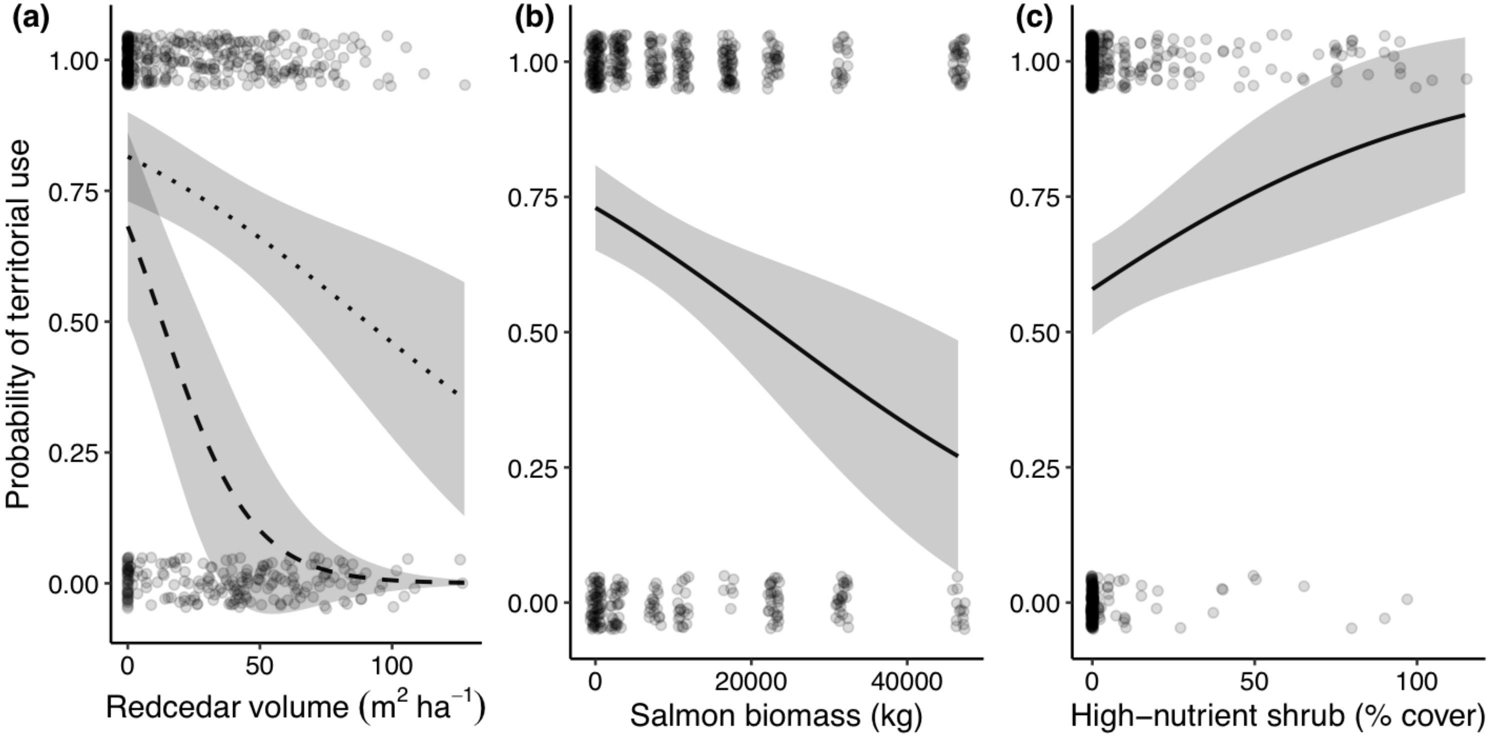

Figure 2.6. **Resource selection probability plots for important predictor variables for the top model of probability of territorial use by male wrens. Lines are predicted probabilities of habitat being included in wren territories against (a) western redcedar stand basal area ($m^2\ ha^{-1}$) at high salmon biomass (47,000 kg, represented by the dashed line) and no salmon (0 kg, represented by the dotted line), (b) spawning salmon biomass (kg) at stream-level, and (c) percent high-nutrient shrub cover, with other variables set to their mean value. Bands are 95% confidence intervals and points are jittered to display the spread of data.**

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Chapter 3.

Salmon subsidies predict territory size and habitat selection of an avian insectivore

3.1. Abstract

Marine-derived nutrients from spawning salmon shape recipient terrestrial communities directly and indirectly through various trophic pathways. While studies have established that higher-order consumers such as insectivorous birds can achieve higher densities along salmon streams, there is still little evidence for the mechanisms maintaining those densities. In this study we examine the role of salmon nutrient subsidies on reproduction by an indirect consumer, the Pacific wren (*Troglodytes pacificus*) across 12 salmon-bearing watersheds. We found that individual male reproductive success was higher at salmon streams, but there was a higher proportion of non-breeding territorial males at salmon streams. This difference in breeding is potentially driven by the density-dependent effects of competition as males with smaller territories did not breed. For those wrens that did breed, salmon subsidies were correlated with a phenological shift towards earlier nest initiation, higher double brooding rates, and lower male nest provisioning rates. However, survival and condition of juveniles was equal across different levels of male investment. This suggests that the bottom-up benefits of resource availability from salmon subsidies are being mediated by density-dependent pressures of competition at high-salmon biomass streams.

3.2. Introduction

The movement of resources and nutrients across ecotones has been shown to subsidize recipient communities, providing increased food or nutrient availability that can structure food webs and impact ecosystem productivity (Polis et al. 1997). Resource subsidies can increase reproductive success (Tylianakis et al. 2004), body condition (Boucek and Rehage 2013), and growth rate (Bentley et al. 2012), change survival (Marczak and Richardson 2008), and advance migration (Jefferies 2000) and breeding phenology (Robb et al. 2008). The bottom-up effects of resource subsidies may also be modulated by strong top-down effects (Ostfeld and Keesing 2000, Yang 2008). Higher densities of consumers may experience deleterious effects of intra-specific competition or attract predators, that can control population dynamics (Hunter and Price 1992) and impact life history traits (Marczak and Richardson 2008).

Along North Pacific coastal regions, anadromous salmon returning to natal streams to spawn provide a predictable nutrient subsidy to recipient terrestrial ecosystems. They have been shown to have bottom-up effects on recipient ecosystems: increasing terrestrial macroinvertebrate biomass (Nakano and Murakami 2001, Baxter et al. 2005, Hocking et al. 2009), shifting plant community composition toward species that benefit from high levels of inorganic nitrogen (Hocking and Reynolds 2011), and increasing densities of direct consumers, such as bears (Helfield and Naiman 2006), wolves (Adams et al. 2010), and gulls (Christie and Reimchen 2005, Field and Reynolds 2013). Salmon marine-nutrient subsidies have also been shown to impact life-history traits of their direct consumers (Gende et al. 2002). For example, increased population productivity of brown bears due to larger litter sizes has been attributed to higher salmon availability (Hilderbrand et al. 1999b). Furthermore, mustelids and plants demonstrate phenology shifts to track the timing of increased resources on salmon streams (Ben-David 1997, Lisi and Schindler 2011).

In addition to impacts on direct consumers, salmon subsidies can also indirectly support higher trophic consumers through multiple trophic pathways (Reimchen 2017). Salmon subsidies entering in a low trophic position in the food web can increase invertebrate biomass (Nakano and Murakami 2001, Gende et al. 2002) and this marine signature can be traced from invertebrates to insectivorous passerines along salmon streams (Christie and Reimchen 2008, Christie et al. 2008). Many studies have shown that indirect consumers such as birds are supported at higher densities along salmon streams (Wagner and Reynolds 2019, Gende and Willson 2001, Christie and Reimchen 2008, Field and Reynolds 2011). However, there is still little evidence of indirect effects of salmon subsidies on life histories of higher trophic consumers. There have been a handful of studies on the breeding success of indirect consumers (Obermeyer and White 2006) or earlier phenological shifts in plants due to subsidized insect pollinators with higher salmon input (Lisi and Schindler 2011). Tonra et al. (2016) showed available spawning salmon resources increased American dipper (*Cinclus mexicanus*) reproductive success, body condition, breeding effort, and survival along a river above and below a salmon barrier. However, American dippers may be both a direct and higher-order consumer of salmon as their diet consists of both aquatic insects and spawning salmon eggs (Obermeyer and White 2006). Therefore these observed patterns may be driven through direct consumption of salmon. Here we investigate the drivers of reproductive success and effort across multiple salmon-bearing watersheds for an obligate avian insectivore, which does not feed directly on salmon or their eggs, the Pacific wren (*Troglodytes pacificus*). Several of the streams included in our study have already been shown to support higher wren densities (Wagner and Reynolds 2019, Christie and Reimchen 2008).

Pacific wrens are year-round resident songbirds that range along the west coast of North America from Alaska to California. While they are found in many habitats, they have higher densities along riparian forests and higher still along salmon streams, potentially due to increased invertebrate food availability (De Santo et al. 2003, Christie and Reimchen 2008, Evans-Ogden et al. 2012, Wagner and Reynolds 2019). However, higher densities do not necessarily imply higher reproductive success as other processes could be driving these patterns of spatial occurrence (Van Horne 1983). Indeed, if the birds distribute themselves among streams according to an ideal free pattern (Fretwell and Lucas 1972, Tregenza 1995) we may expect them to achieve densities at which reproductive success is similar across streams that vary in salmon subsidies. Wrens defend small territories that reflect *in situ* habitat quality, making them an appropriate model organism with which to study changes in reproductive behaviour and success with marine-derived nutrient availability (Wilcox et al. in review). Wrens can exhibit variation in their breeding effort across habitats as males may be polygynous, with more than one concurrent active nest, or pairs may double brood, with one nest after another successful nest (De Santo et al. 2003, Evans-Ogden et al. 2012). Wrens also exhibit biparental care during nesting, another measure of reproductive effort (Toews and Irwin 2012).

In this study we examine indirect effects of salmon-derived nutrients on reproductive effort and its relationship to reproductive success of Pacific wrens across salmon-bearing watersheds. First, we test whether wrens have higher reproductive success along salmon streams or if they follow the predictions of ideal free theory whereby they would have equal success among streams with and without salmon. Second, we tested whether higher salmon biomass corresponds with reproductive effort, such as polygyny, double brooding and parental care. Finally, we tested whether these differences in reproductive effort and parental care affect offspring condition and survival.

3.3. Methods

3.3.1. Study sites

We conducted breeding and territory surveys over two breeding seasons from April to August of 2015 and 2016. In both years we banded individual wren adults and juveniles, monitored nests, and mapped male territories at 9-hectare plots along 12 streams on coastal islands and mainland inlets on the Central Coast of British Columbia, Canada within the traditional territory of the Heiltsuk First Nation (vicinity of 52.1605° N, 128.1456° W). In 2016 we also monitored rates of nest feeding. The study area was within the Coastal Western Hemlock Biogeoclimatic Zone, which is characterized by nutrient-poor soils and dominated by western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), Sitka spruce (*Picea sitchensis*), amabilis fir (*Abies amabilis*), and red alder (*Alnus rubra*) (Pojar et al. 1987). All of our study streams were accessed by boat. Six of the streams were surveyed in 2015 and six were surveyed in 2016. Chapter 2 provides a detailed description of the study species, study area and general methods.

3.3.2. Salmon biomass

Spawning salmon biomass was determined through a long-term monitoring project by our research group in collaboration with the Department of Fisheries and Oceans and the Heiltsuk Integrated Resource Management Department. Pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon were the dominant salmon species in each stream. As coho (*O. kisutch*) and sockeye (*O. nerka*) salmon made up less than one percent of all counts, they were excluded from the analyses. Streams were surveyed three times each year during the fall spawning season (September to October) during the wren non-breeding season in order to use the area-under-the-curve estimation method to determine spawning abundance (English et al. 1992). When it was not possible to visit streams three times due to poor conditions, we used peak live plus dead counts to determine salmon abundance. This method has been shown to produce similar estimates of mean abundance compared with area-under-the curve estimates (Hocking and Reynolds 2011). To calculate salmon biomass from salmon abundance we multiplied the chum and pink run size by their respective average weights for the region (3.5 kg for chum and 1.2 kg for pink) (Hocking and Reynolds 2011). We used a three-year average of salmon biomass before the spring breeding season to account for longer-term effects of nutrient subsidies through multiple trophic pathways. Streams were selected to represent a wide range of variation in amounts of spawning salmon biomass (Appendix B Table B1). For some analyses we compared salmon and non-salmon streams. We categorized non-salmon streams as streams without an established spawning population within the 9-hectare plot.

3.3.3. Territory mapping

A detailed description of territory mapping methods is provided in Chapter 2. To determine territory size, we used spot-mapping, whereby each stream was visited eight times during the breeding season and the locations of wren territorial observations were recorded (Odum and Kuenzler 1955, Ralph et al. 1993, Bibby et al. 1998). We then overlaid each visit to create a pattern of territorial observations that allowed us to demarcate territory boundaries and size using 95% minimum convex polygons from the adehabitat package in R (Calenge 2006). Males were banded using targeted playback and mist-netting to aid in individual identification.

3.3.4. Breeding Surveys

Male Pacific wrens build cavity nests in a variety of substrates, including moss clumps in trees and shrubs, upturned root masses, and under decaying logs. Nests were usually found by following males during nest-building or courting females, or by following parents that were provisioning young. However, we were sometimes able to follow females to the nest during the pre-laying stage when they were bringing feathers to line it, or during incubation.

Nests were monitored every 5-7 days, and where possible nests were checked for number of eggs or nestlings. However, due to the enclosed construction or the height of the nest, nest stage was instead often determined through 40-min observations of parental behaviour. We used several methods to assess nest stage and success. Active nests contained at least one egg and if a female spent more than 20 min inside a nest, we concluded that she was either laying or incubating. Nests were categorized as successful if: 1) fledglings were seen being fed by the parents within the male's territory, or 2) chicks appeared fully developed at the last visit but the nest was empty at subsequent visits within the appropriate fledgling time period, or 3) camera traps showed young fledging the nest. Nests were determined to have failed if: 1) the nest was obviously disturbed or ripped apart by predators, 2) a predator was caught on the nest camera eating the nestlings (n=3), 3) the nestlings were too young to have fledged but were missing from the nest, or 4) there was no parental activity within the 40-min survey period after being classified as an active nest in previous visits. The number of fledglings was determined either by the number of nestlings in the nest at the last survey visit or by the number of juveniles found being fed by parents within the male's territory 1-7 days after fledging. Juveniles were then banded by flushing them into mist-nets in the post-fledgling period while they were still relatively immobile. Apparent male reproductive success was determined by identifying the banded males near and interacting with a nest or juveniles in their territory. Even if males were not actively feeding at a nest, they were often singing near the nest and interacting with the female. Search efforts for nests were allocated evenly across stream sites and territorial males. To scale productivity up to the stream-level, we summed the total number fledglings produced per male across all males within a given stream, then averaged them across salmon versus non-salmon streams.

We determined both polygyny and double brooding rates for males across streams. We defined polygyny as concurrent active nests that overlapped at any point during the nestling or immediate post-fledging stage (1-7 days). Furthermore, as we did not use genetics to determine paternity, our measures of reproductive behaviour are based on apparent male reproductive success. We defined double brooding as males attempting an additional nest after a successful nesting attempt (produced at least one fledgling). This is defined from a male's perspective as females were too challenging to catch and we were therefore unable to consistently determine female identity. Male seasonal reproductive success was calculated as the number of fledglings produced per male summed across all of his active nests during the breeding season. To compare productivity between salmon and non-salmon streams, we averaged the total number of fledglings produced per male within both salmon (n=9) and non-salmon streams (n=3).

3.3.5. Initiation Date and Nest Fates

Nest fates and stages were determined based on modified BBIRD protocol (Martin et al. 1997). Wrens typically lay 5-7 eggs (one each day), and begin incubation on the day when the final egg is laid. Female wrens incubate for 14-16 days and once the eggs hatch, the nestling period is between 15-19 days (Evans-Ogden et al. 2012). Estimated hatch date was determined by either backdating from fledging date using an average nestling period of 17 days, or by counting forward using the date of the last egg laid and an average incubation period of 15 days, whichever date was most accurate. Similarly, we estimated initiation date (date the first egg was laid) by backdating from hatch date or fledgling date using average incubation and nestling periods, including lay period based on the clutch size. Lay period is equal to the average or known clutch size minus one day (Martin et al. 1997). For analyses, we transformed initiation date into an ordinal date (continuous integer starting January 1st each year).

3.3.6. Feeding Rate

We studied feeding rates during the 2016 breeding season. We conducted feeding surveys on active nests for 40-min observation periods every 5-7 days between 1000 hrs and 1200 hrs to standardize for potential variation in feeding rate with time of day. We recorded time and duration of each visit in addition to the identity of the parent, as nearly all of the males were banded. We were also able to determine the identity of the parent by process of elimination as the male could often be heard singing nearby. However, the configuration of some nests or parental behaviour did not always allow us to determine the sex of the adult and those surveys were excluded from the male proportional feeding rate analyses but included in the total feeding rate analyses (3 out of 23 nests). Once we had determined the fates of the nests, we were able to determine the days-since-hatch or age of the nestlings at the time of the survey. Days-since-hatch was used as a continuous variable in all analyses, but for clarity in the figures we divided feeding rate observations into early and late nestling stages based on the halfway point of the nestling period (usually day 8 from a 15-19 day nestling period).

3.3.7. Body condition

We used scaled mass index (SMI) to determine post-fledging juvenile and adult male body condition. SMI is a body condition index that controls for the scaling relationship between weight and length (Peig and Green 2010). For adults we used wing length as the linear measurement and confirmed that it correlated strongly with mass. For juveniles, we used head plus bill length as the linear measurement as wing length is based on feather development, which varies greatly with age of the fledgling. We calculated SMI as the predicted body mass for each individual when the linear measurement was standardized by the arithmetic linear measurement mean of the population (27.49 mm for mean juvenile head and bill length and 46.52 mm for mean adult wing length) to the power of the slope of the regression (Peig and Green 2009). We then determined mean juvenile condition per nest by averaging the SMI of all juveniles captured from the same nest.

3.3.8. Analyses

All statistical analyses were performed in R 3.4.1 (R Core Team 2017). T-tests were used to compare differences in stream productivity and mean reproductive success between salmon and non-salmon streams for all territorial males and a subset of only breeding males (males with at least one active nest). Simple linear regressions were used to relate stream-level responses such as proportion of males with a nest, to salmon biomass. To model the probability of males breeding based on their territory, we used a generalized linear mixed-effect model with a binomial response of having an active nest (1/0) and logit link with territory size as a predictor variable. Similarly, we modeled the probability of being polygynous or double brooding as a function of ether territory size, male body condition, or salmon biomass. All models had year as a fixed effect and stream as a random effect. To compare the mean rate of double brooding, polygyny, and the mean first nest initiation date between salmon and non-salmon streams we used t-tests. To then test if pairs that double brooded would start their first nest earlier, we used a t-test to compare mean initiation date of male's first nest of the season for single nest attempts and those nests that the pair that would go on to double brood.

We used linear-mixed effect models to test nest-specific responses within streams such as average juvenile body condition per nest, total feeding rate and proportional male feeding rate as responses with stream as a random effect in each model. Total feeding rate and proportional male feeding rate where also modeled with nest identity nested within stream as a random effect in all models to account for nests monitored multiple times. As male wren territory size and salmon biomass were inversely correlated (Pearson's r=0.60), we modeled total feeding rate and male proportional feeding rate first as a function of salmon, days since hatch, and their interaction, then separately as a function of territory size, days since hatch, and their interaction. Due to small sample size (n=24), average juvenile body condition was also modeled separately, first as a function of territory size, then as a function of whether the fledglings came from a polygynous nest or a double brood with year as a fixed effect in all models.

To analyse nest success we used nest daily survival rate (DSR) modeled with the logistic-exposure method to determine if nest survival was influenced by either total feeding rate or proportional male feeding rate (Shaffer 2004). This method of determining nest success controls for the fact that nests discovered at a later stage are more likely to survive (Shaffer 2004). We calculated the probability of DSR as a binomial response of survival given total feeding rate or male proportional feeding rate and the link function defined by Shaffer (2004) with stream as a random effect in all models. Additionally, we tested if DSR was higher on salmon streams compared with non-salmon streams.

All models were checked for violations of assumptions and, when appropriate, multicolinearity using variance inflation factor scores (VIF). None of the predictor variables had VIF scores greater than 2, indicating an acceptable amount of covariance (Zuur et al. 2009). Generalized linear mixed-effects models were checked for violations such as overdispersion and zero inflation using simulated residuals from the Dharma package (Hartig 2018). Alpha was set at 0.05 and model fit was checked using r-squared for simple linear regression or marginal r-squared (variance explained associated with all fixed effects) for mixed-effect models (Nakagawa and Schielzeth 2013).

3.4. Results

At the 12 streams (3 non-salmon and 9 salmon streams) we found and monitored 44 active nests from 34 breeding males and measured territories of a total of 44 male wrens, 27 of which were banded. Additionally, we banded and measured body condition of 36 juveniles from 24 nests. Our parental feeding rate data were collected from 23 active nests in 2016.

3.4.1. Reproductive success

When including all territorial males, there was no difference in mean reproductive success between salmon and non-salmon biomass streams across all territorial males (t= -0.96, p=0.36, Fig. 1). However, male reproductive success was significantly higher on salmon streams (t = -2.65, p = 0.026) when subset by only those males that bred, or those territorial males with an active nest (Fig. 1). Additionally, survival was higher on salmon streams compared with non-salmon streams (1.8 ± 0.95 higher odds, p = 0.03). Scaled up to the stream-level, overall seasonal productivity (fledglings male^{-1} stream^{-1}) was higher on salmon compared with non-salmon streams (t = 7.11, p = 0.024) with an average of 13.6 and 3.3 fledglings produced respectively. However, there was a lower proportion of breeding males, or males with a least one active nest on high salmon biomass streams than on low salmon biomass streams ($p<0.001$, $r^2 = 0.31$). Fewer than half of the males at the highest salmon biomass stream had at least one active nest, in contrast with the lowest salmon biomass streams where all males had at least one active nest (Fig. 2). A male's ability to breed may depend on his territory size. Males with larger territories had a 12.5 times higher odds of having an active nest (from 1.3 - 113.5, p = 0.024). In other words, territories must be at least 0.98 (0.51 - 0.99) hectares in size for a male to have a 75% chance of having at least one active nest (Fig. 3).

3.4.2. Reproductive effort

The rate of polygyny was low across all streams, with only 7 out of 44 or 16% of territorial males on three streams having concurrent active nests. The likelihood of polygyny was not predicted by either territory size, male body condition or salmon biomass (Appendix Table B2). However, the three streams that had polygynous males were low to mid salmon biomass streams. Double brooding occurred only at salmon streams and was only ever attempted by one pair at each stream (18% of males). The likelihood of an individual pair double brooding was not predicted by any male attributes (body condition or territory size) or salmon biomass (Appendix Table B2). However, the average overall occurrence of double brooding was higher at salmon streams than non-salmon streams as each salmon stream had one double brooding pair while all non-salmon streams had no double brooding pairs.

3.4.3. Nest Initiation Date

While not significant, there was a trend that initial nests of pairs that went on to double brood on salmon streams were initiated earlier than single attempt nests on non-salmon streams ($F = 3.92$, $p = 0.07$). There was also a tendency for first nests to be initiated earlier on salmon streams (mean = 126.6 ± 2.9 or May 7) than those on non-salmon streams (mean = 141.5 ± 11.8 or May 21, $F = 3.11$, $p = 0.09$, Fig. 4).

3.4.4. Nest feeding

Feeding visits by both parents to nests increased through the nestling period; with each passing day since hatch, the total nestling feeding rate increased by 0.64 (± 0.24) visits per hour (Fig. 5). However, there was no relationship with either territory size or salmon biomass on feeding rate as only the number of days since hatch emerged as a significant predictor in the model (Fig. 6).

Male proportional feeding rate was predicted by days since hatch, salmon biomass and their interaction (Fig. 6). A one-day increase in days-since-hatch corresponded with an 0.19 (± 0.04) increase in proportional male visits per hour. Additionally, a one unit increase in salmon biomass (mean centered and standardized corresponding to 17,698 kg) corresponded with a 0.24 (± 0.09) drop in the proportional feeding effort by males (Fig. 5). Males at low salmon biomass streams contributed on average to about 40% of total nest provisioning visits at late nest stages, compared with males at high salmon biomass streams who accounted for 12% of all visits (Fig. 5). We found no significant relationship between territory size and proportional male feeding rate, as it was not a significant predictor in our model ($p = 0.61$, marginal $R^2 = 0.09$).

3.4.5. Consequences of reproductive effort

We found no relationship between either male proportional feeding rate or total feeding rate and nest daily survival rate (Appendix Table B2). Our sample size was not large enough ($n = 4$) to test juvenile condition as a function of feeding rate, but we found no pattern of average juvenile body condition per nest across the range of salmon biomasses per stream ($p = 0.48$, marginal $R^2 = 0.06$). Average juvenile body condition was also not related to male territory size ($p = 0.39$, marginal $R^2 = 0.04$). Furthermore, there was no difference between average brood body condition among polygynous or monogamous nests or double brooding nests. There was some evidence of a trade-off between number of offspring produced per nest and the average condition of those offspring, but the relationship was not significant ($p = 0.08$, marginal $R^2 = 0.15$).

3.5. Discussion

In this study we found evidence that salmon subsidies impact reproduction behaviour of an indirect consumer, the Pacific wren. We found breeding males produced more fledglings at salmon streams than at non-salmon streams and that overall, salmon streams had higher productivity. However, this was only after accounting for territorial males that did not have an active nest throughout the breeding season (Fig. 1). Therefore, there were proportionally fewer breeding males on high salmon biomass streams, with less than half of males having at least one active nest at the stream with the highest salmon input (Fig. 2). The males that did not breed had small territories under 1 hectare in size (Fig. 3). For the males that did breed, their nests tended to be initiated earlier at salmon streams (Fig. 4), supporting higher double brooding rates and contributing to higher reproductive success. Similarly, polygyny rates were also higher on salmon streams and males contributed less to parental care at high salmon biomass streams (Fig. 5). Together, higher double brooding and polygyny rates along with higher nest survival may contribute to higher reproductive success along salmon streams. Despite differences in male parental care, offspring had equal survival and condition at different levels of salmon biomass.

3.5.1. Breeding success

High salmon biomass streams showed greater male reproductive skew, whereby a small proportion of males monopolized breeding (Johnstone 2000, Fig. 2). Females bore the brunt of reproductive effort at high salmon biomass streams as they raise broods almost independently of males (Fig. 5). As females invest relatively more energy in reproduction (through laying, incubating, and feeding) (Patterson et al. 2011), female choice may drive patterns of reproduction (Kokko and Rankin 2006). Females can choose mates based on territory quality or male attributes (Alatalo et al. 1986, Buchanan and Catchpole 1997), which may explain why males with small territories could not attract a mate. Females may be particularly discriminating against subordinate males with small territories on streams where there are high densities of wrens and higher levels competition among males, as shown by higher rates of countersinging (Wilcox et al. in review). Higher competition at high salmon biomass streams may therefore be driving reproductive skew at high wren densities.

The non-breeding territorial males may be younger birds which remained at high salmon biomass streams instead of dispersing to new habitats. At salmon streams, we found juvenile males that had fledged months before, attempting to establish territories in previously unoccupied habitat at the end of the breeding season in August. Previous work in this study system has shown that there is more available undefended habitat along salmon streams which may represent lower quality resources (Wilcox et al. in review). Juveniles may be retained at high salmon biomass streams, establishing smaller territories the following breeding season, but be outcompeted by older more dominant males for mates. Tonra et al. (2016) showed that American dippers with access to more food provided by salmon were more likely to persist as year-round residents compared to above a salmon barrier where they were more likely to disperse.

3.5.2. Reproductive Effort

Males may be contributing proportionally less (Fig. 5) to feeding nests at high salmon biomass streams because of higher habitat quality. Similar to other birds, we found that wren parental feeding rate increased as days since hatch increased, corresponding with increasing juvenile energetic demands (Steen et al. 2012) (Fig. 5). Male involvement in feeding remained low at higher salmon biomass streams. However, at low salmon biomass streams, the increase in feeding rate as the nestlings aged was divided between parents, with males contributing to about half of total visits. This suggests that adults may have to go further or spend more time searching for food at low salmon biomass streams as there is more time between when each adult visits (Tremblay et al. 2004, Catry et al. 2013). Previous studies have shown that there is higher invertebrate food availability or quality on high salmon biomass streams than streams without salmon (Nakano and Murakami 2001, Baxter et al. 2005a, Tonra et al. 2016). Additionally, parental feeding effort increases to compensate for lower habitat quality and lower food abundance (Tremblay et al. 2004). This suggests that both male and female wrens must both contribute to parental care in order maintain the same feeding rate and to provide the food necessary to successfully rear offspring at lower salmon biomass streams with lower insect biomass. This is supported by the lack of difference in survival and body condition of nestlings across different rates of parental feeding and relative male involvement.

Male wren reproductive effort in terms of polygyny was low overall but higher at higher salmon subsidies and may be partially contributing to higher reproductive success on salmon streams. In high quality habitat with high food availability, birds may be more likely to desert nests to be raised by females in order to maximize their own fitness by breeding again (Zárybnická 2009), as higher food availability allows females to successfully provision nests alone (Tremblay et al. 2004). However, polygyny was generally low and variable across measures of salmon biomass with 7 males in 3 mid salmon biomass streams having polygynous nests. Likelihood of polygyny was not predicted by any male attributes such as territory size or body condition. While the fitness benefits of polygyny are more obvious for males, under the polygynous threshold model females may pay a cost of polygyny unless they are compensated by superior-quality males or territories (Weatherhead and Robertson 1979, Sejberg et al. 2000). Males with territories on streams with high salmon biomass, higher insect biomass

(Hocking et al. 2009), and more high-nutrient shrubs (Wilcox et al. in review) may have higher quality territories, which may explain why polygyny only occurs on salmon streams. However, if the sex ratio is balanced between males and females and there are unmated available males, females will preferentially be monogamous, achieving higher fitness than if she were a secondary mate (Forstmeier et al. 2001). The variation observed in polygyny rates across salmon streams may be driven by different wren sex ratios, not resource availability.

Double brooding, or sequential nesting after a previous successful nest attempt, occurred only on salmon streams but at similarly low rates as polygyny (18% of males double brooded). Double brooding allows adults to increase their reproductive success by attempting to rear a second successful nest (O'Brien and Dawson 2013). However, the costs of reproductive investment means that double brooding is dependent on initial female condition, weather conditions, and early food availability (O'Brien and Dawson 2013, Carro et al. 2014). Not only do salmon streams support higher insect biomass (Nakano and Murakami 2001), they can also shift aquatic insect peak emergence to earlier in the season (Moore and Schindler 2010). We found that first nests at salmon streams tend to have earlier initiation dates, particularly if the pair go on to double brood, however further research is needed to confirm this pattern. Carro et al. (2014) also showed that pairs of Southern house wrens (*Troglodytes musculucs*) with nests started earlier in the breeding season were more likely to initiate a second brood. Breeding wrens may be responding to this shift in phenology of peak food availability by starting nests earlier and thereby increasing the chances of attempting a second brood and contributing to higher reproductive success at salmon streams.

In conclusion, this study indicates that salmon subsidies may mediate density-dependent reproductive effort and success in male Pacific wrens. At low salmon biomass, males have single broods with high parental care while at high salmon biomass streams, breeding males are more likely to have multiple broods with low parental care. However, there is also a density-dependent reproductive skew at salmon streams, resulting in only males with large territories breeding. Ultimately, higher reproductive success is driven by a combination of higher rates of higher nest survival, polygyny and double brooding on salmon streams by breeding males. Thus, salmon subsidies appear to shift the trade-offs between the benefits of resource availability and density-dependent negative effects of competition, structuring reproductive effort and success.

3.6. Figures

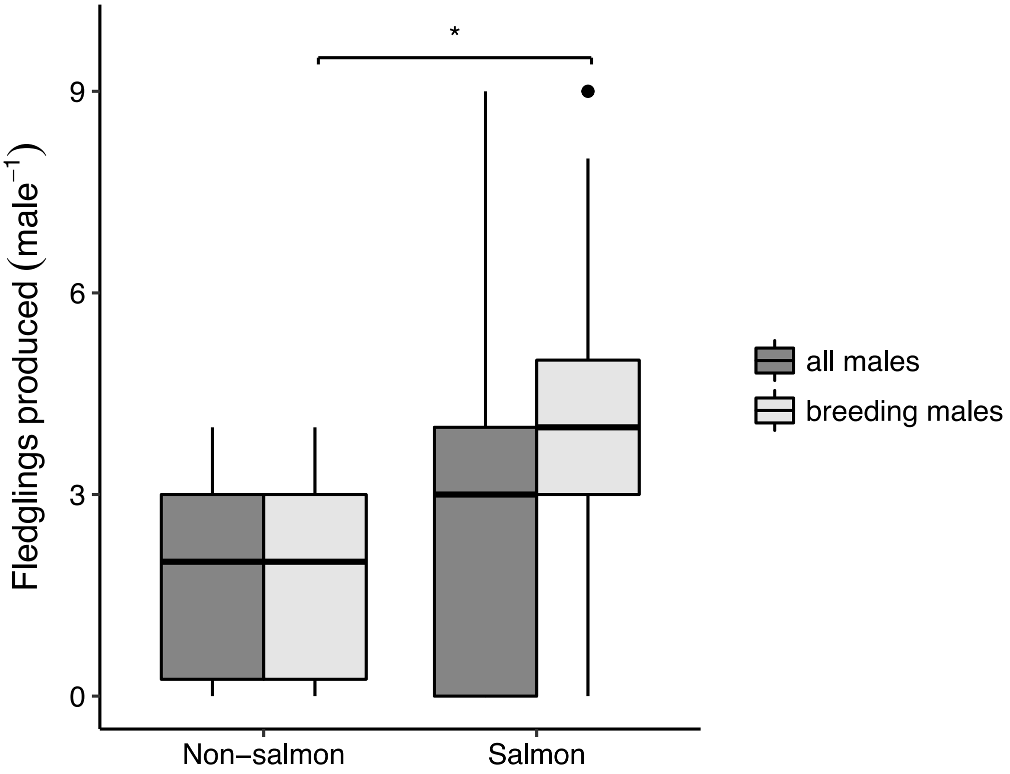

Figure 3.1. Number of fledglings produced per male Pacific wren on salmon (n=9) versus non-salmon (n=3) streams for all males with territories (dark grey) or only those males that have at least one active nest (light grey). The box represents the interquartile range while the median is represented by the dark horizontal line. The asterix denotes significant differences in mean reproductive success between salmon and non-salmon for breeding males, but not all territorial males.

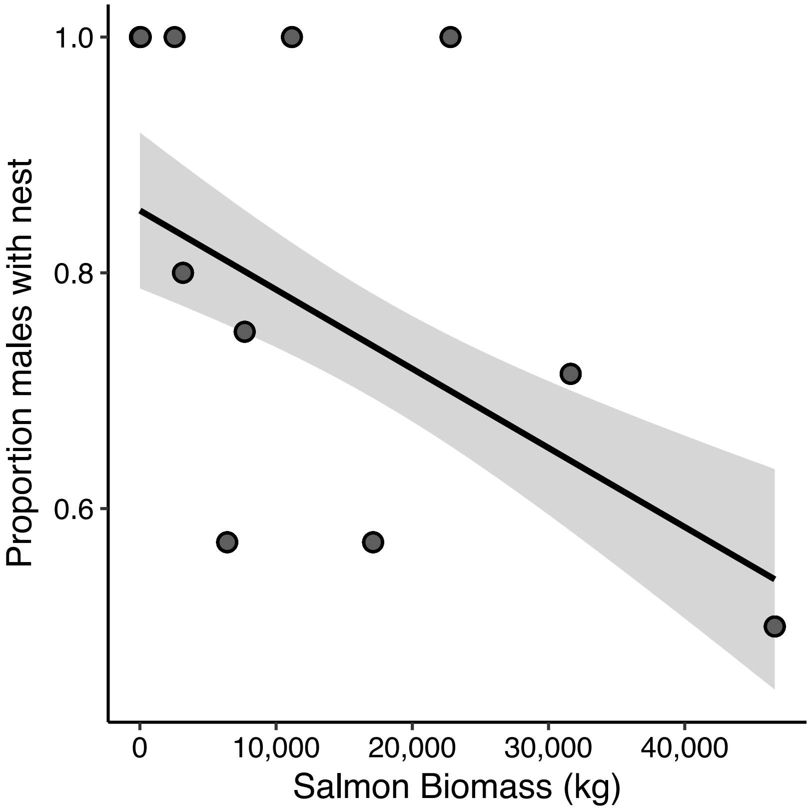

Figure 3.2. **Relationship between stream salmon biomass and proportion of territorial male wrens with at least one active nest. Points represent breeding wrens at each stream and the line represents the simple linear regression with the band representing the 95% confidence interval.**

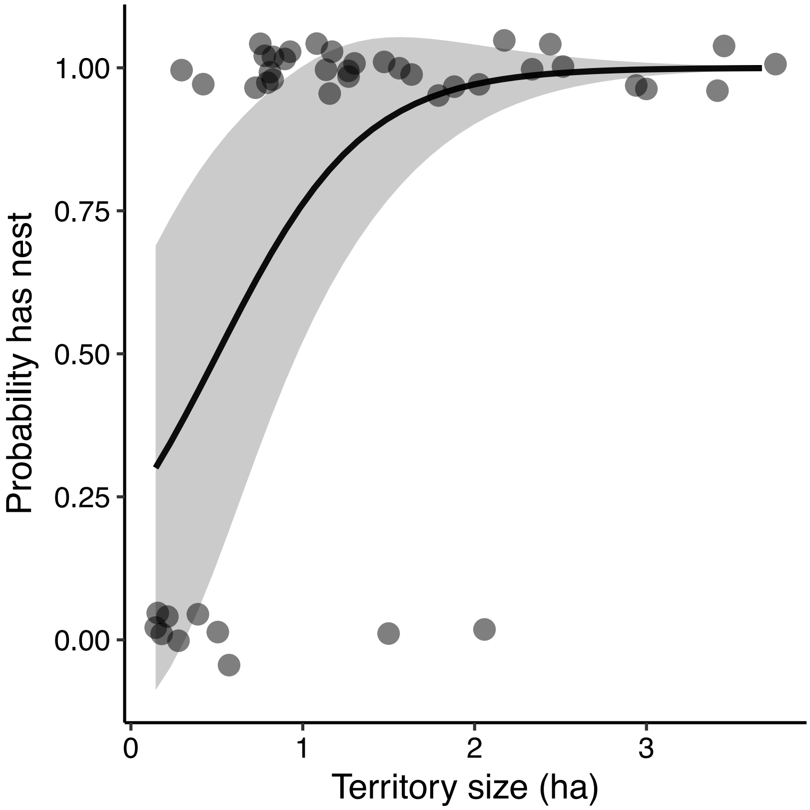

Figure 3.3. **Probability of a male wren having at least one active nest based on its territory size. Each point indicates whether or not an individual male has a nest and the line represents the probability from the logistic regression model. Points are jittered vertically to show spread of data and band represents 95% confidence interval.**

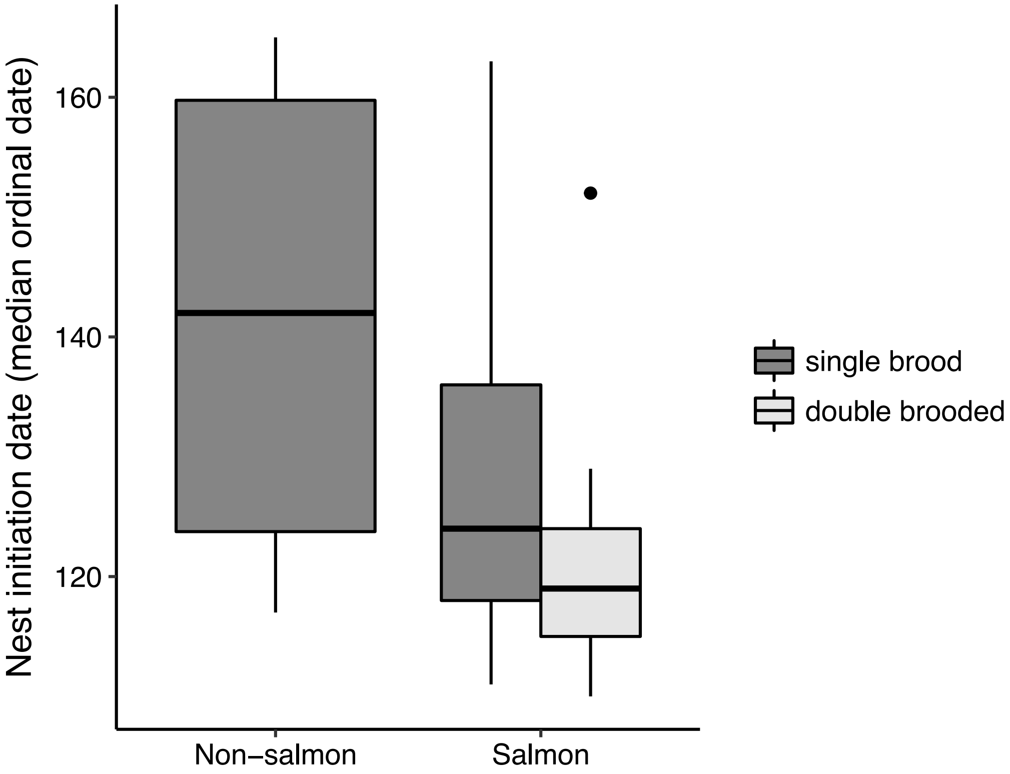

Figure 3.4. First nest initiation date (ordinal date of day first egg laid) for nests on non-salmon (mean = 142 or May 21) and salmon streams (mean = 127 or May 7). The dark grey boxes represent nests that were single nesting attempts, while the light grey boxes represent nests that belonged to pair who would go on to double brood later that season. The box represents the interquartile range and the median is represented by the dark horizontal line.

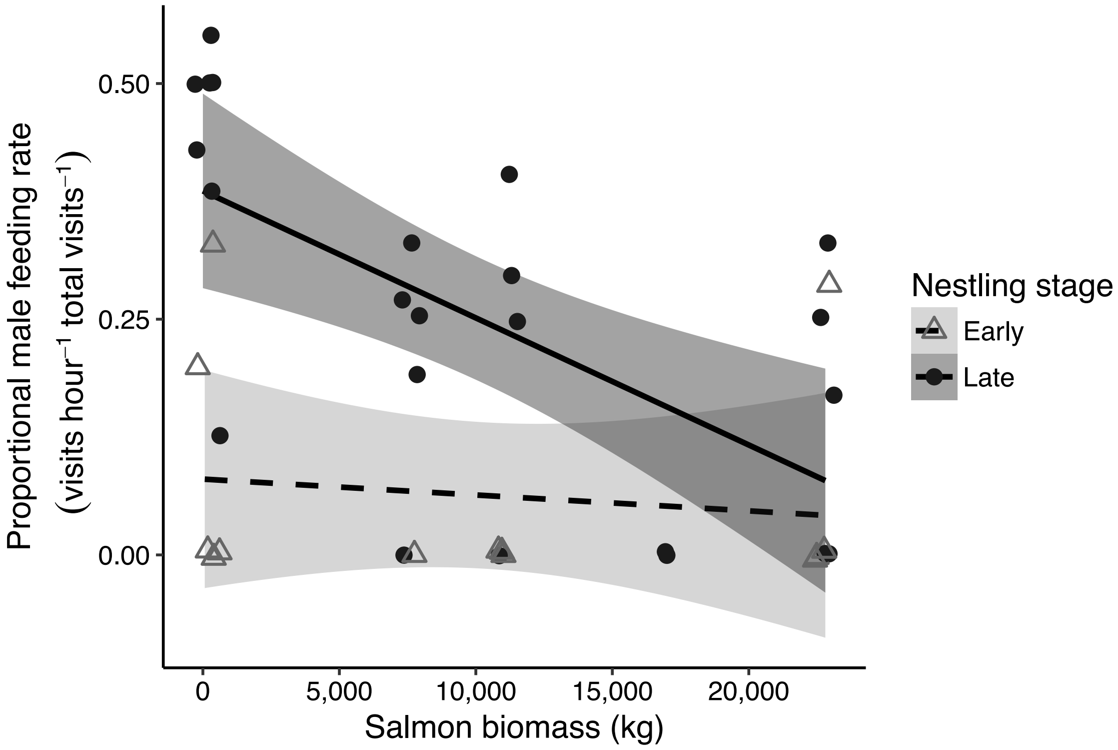

Figure 3.5. Relationship between stream salmon biomass and proportional male feeding rate at different nestling stages (early and late). The dashed line and triangles represent early stage nests (usually < 8 days since hatch) and circles and solid line represent late stage nests (past half of nestling period or usually > 8 days since hatch). Points are horizontally jittered to show the distribution of the data.

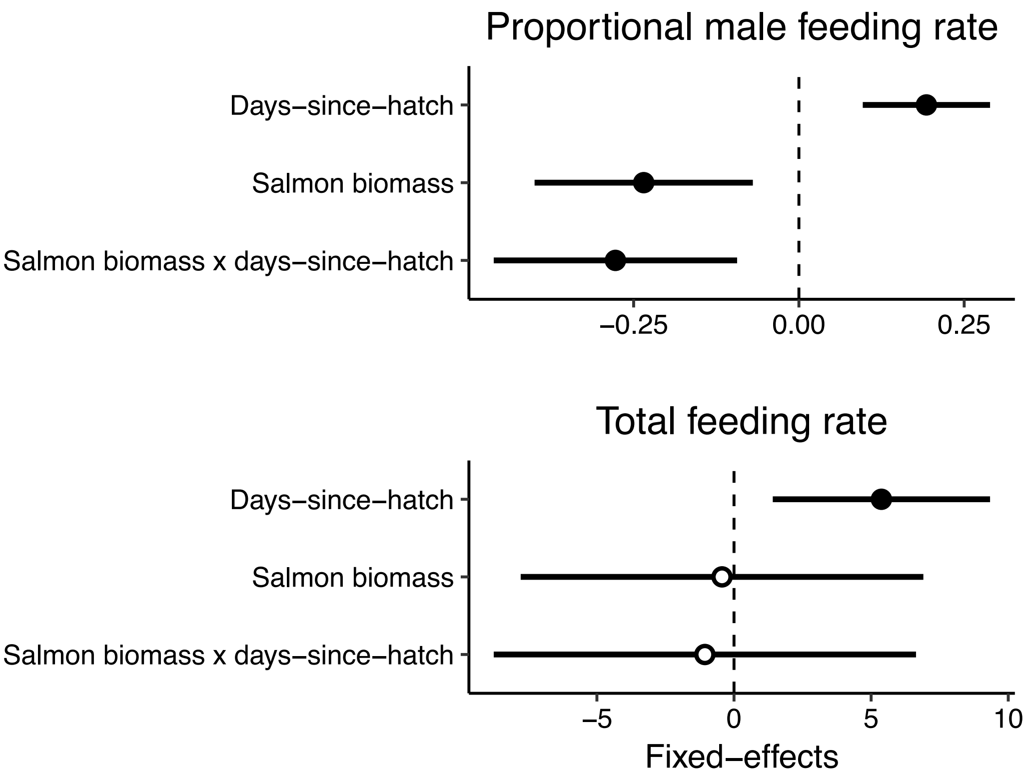

Figure 3.6. **The fixed-effect standardized coefficient estimates of proportional male feeding rate and total feeding rate (both parents) from the linear-regression models. The standardized (mean = 0, SD = 2) parameters in each of the three models include days-since-hatch (ordinal date), salmon biomass (kg), their interaction and a random effect of stream (not shown). Circles show estimates for each parameter, with 95% confidence intervals indicated by horizontal lines. The significant coefficient estimates (95% CI do not overlap 0) are indicated by closed circles.**

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Chapter 4.

General Discussion

While this is not the first study to test whether salmon-derived nutrients impact terrestrial ecosystems, it is one of the first studies to examine the behavioural ecology that underlies the patterns of spatial occurrence of higher-order consumers within highly subsidized riparian ecosystems. While it was no surprise that wren densities were higher with higher salmon subsidies, corresponding with smaller territories, I did uncover some surprises. At first it seemed counterintuitive that despite there being higher densities of wrens there was also more available space on salmon streams. However, this makes sense in the context of my findings that higher competition leads to density-dependent habitat selection, changing the trade-offs of habitat defence.

Not only do salmon support high-density, highly competitive wren populations, but these patterns in turn have implications for their reproductive success and effort. Salmon subsidies increase apparent reproductive success of male wrens. However, not all males reap equal benefits along these streams. Salmon subsidies serve to widen the gap between males, creating reproductive skew where only a few males monopolize breeding. Males with the smallest territories, which are found on highly subsidized streams, lose out on breeding opportunities and cannot attract mates. This was surprising as I assumed that subsidies would operate as an economic stimulus: as a rising tide that lifts all boats. However, just as in any free-market, some individuals profit more than others and not all male wrens benefit equally. Overall, there seems to be little doubt that salmon subsidies improve overall carrying capacity of riparian habitats, supporting higher numbers of wrens and allowing females to raise broods without the help of males. The nuance is in the variation of effect among populations and among males.

What then do these results mean in the broader context of community and conservation biology? Wild salmon populations, including those that feed these terrestrial landscapes, are in decline and at risk of environmental stochasticity driven by climate change (Hsieh et al. 2005), where fluctuating weather events like rainfall become increasingly unpredictable leading to extremes such as droughts and flooding (Chezik et al. 2017). While there have been increases in pink and chum salmon abundance in the North Pacific, which are the two species that dominate the spawning runs at the streams we surveyed, those increases are largely driven by the increased abundance of hatchery and ocean ranched fish (Waples et al. 2007, Ruggerone and Irvine 2018). Those fish do not return to small natal streams for spawning, so they do not subsidize freshwater and terrestrial ecosystems such as those studied here.

Additionally, the stochasticity of weather events, such as delayed rains or severe storms may disrupt the evenness and predictability of nutrient pulses as either low water prevents salmon from accessing the streams, or flooding events flush the carcasses out of the system. Small streams in particular are at risk of stochasticity as they may not be buffered against climate variability by the dampening effect of a large catchment area with diverse sources (Chezik et al. 2017). While predictable pulses of nutrients usually stabilize recipient ecosystems, changes in timing of subsidy or decreased subsidy availability may decouple these trophic interactions, destabilizing these trophic food webs (Weber and Brown 2013). If male wrens are playing the waiting game for higher quality territories, they may lose out. Future directions for this research may include looking explicitly at survival and consistency of male wren territory size and reproductive success, timing, and investment. Are wrens able to rapidly shift in response to environmental changes and large fluctuations in resource availability?

Beyond increasing scientific understanding of the effect of nutrient subsidies, these results may have implications for policy and management of Pacific salmon. Canada’s Policy for the Conservation of Wild Pacific Salmon (Wild Salmon Policy, WSP; DFO 2005)- and more recently, the WSP Implementation Plan (DFO 2018)- outlined strategies to address the declines of wild salmon and their habitats. The third strategy outlined in their plan is the inclusion of ecosystem values and monitoring to address the role that salmon play in freshwater and terrestrial ecosystems (DFO 2005). In other words, this strategy aims to incorporate ecosystem-based management in salmon management. Instead of managing for a single species, ecosystem-based management considers the trophic position of salmon in the food web and takes the salmon required to sustain populations of consumers such as bears and wolves into the equation of management (Levi et al. 2012). However the Wild Salmon Policy states that “few studies provide advice on the numbers of salmon necessary for healthy…ecosystems” (DFO 2005). This is not entirely correct. Many studies demonstrate the effect of numbers, biomass and density of salmon on specific populations (Bilby et al. 1996, Wipfli et al. 2003, Field and Reynolds 2011). There is not, however, one clear defining number for how many salmon are needed to support an entire ecosystem and there is unlikely ever to be one. Ecosystems are too complex and variable to ever be assigned such static numbers. Instead, maybe the conversation should focus on what to prioritize for ecosystem-based management and to define what a healthy ecosystem looks like.

How we prioritize ecosystem-based management is informed by our value system and complicated by the variation between systems and over time. Many ecosystem-based management projects often look to manage for direct consumers, like bears, and orcas (Williams et al. 2011, Levi et al. 2012). Managing for these charismatic megafauna demonstrates our inherent biases in conservation, but they may also act as an umbrella species, representing and protecting other smaller consumers in the ecosystem (Hooker and Gerber 2004). However, I would argue that managing for indirect consumers such as songbirds may better encompasses all trophic levels and processes below them, as indirect consumers rely on what remains from salmon carcasses consumed by bears and other direct consumers. Managing for indirect consumers of salmon would certainly be complicated as it requires a greater understanding of trophic dynamics. However, if the goal of ecosystem-based management is to manage the system holistically not just for certain charismatic species, policy and management must catch up with existing scientific knowledge, incorporating the far-reaching effects of salmon on ecosystem dynamics.

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Appendix A.

Supplementary Material Chapter 2

Table A.1 **Stream characteristics and salmon population data for watersheds (n=11) in this study. Number of pink and chum salmon and salmon biomass are based on a three-year mean (2014-2016). Year refers to the year in which the stream was visited for the bird study.**

Stream	UTM Easting	UTM Northing	Catchment Area (km2)	Spawning length (m)	Bankfull width (m)	Mean No. Pink	Mean No. Chum	Salmon biomass (kg)	No. Territories	No. males banded	Year
Ada	565113	5767615	9.8	435	11.1	155	2145	7,508	3	2	2016
Beales	569502	5782472	6.5	300	10.9	1,444	409	3,163	4	2	2015
Bullock	562736	5806247	3.3	622	10.9	2,524	4,026	17,121	7	5	2016
Clatse	579203	5798981	24.3	900	22.8	27,500	3,888	46,609	7	2	2015
Fancy Right	567421	5767983	9.9	298	4.8	69	703	2,544	2	2	2015
Fannie Left	563991	5766215	16.4	1,500	12.8	8,068	6,270	31,626	7	4	2015
Hooknose	579609	5775529	14.8	1,800	16.9	3,791	1,889	11,162	4	4	2016
Jane	564455	5767042	1.3	500	4.6	0	4	13	2	2	2016
Kunsoot	560151	5777915	4.9	1,500	13.1	13,173	1,999	22,803	3	2	2016
Ripley	575560	5809303	15.7	0	14.7	0	0	0	2	2	2015
Troupe North	566176	5793788	1.6	332	4.4	46	4	68	3	1	2016

Table A.2 **All candidate models from the logistic regression models for probability of habitat selection by territorial male wrens. Habitat parameters tested include: salmon = summed chum and pink salmon biomass per stream (kg), high-nutrient shrubs = percent salmonberry and stink currant shrub cover, other shrubs = percent cover of shrubs blueberry, false azalea, and salal, conifer cover = percent cover of small conifer trees, shrub diversity = Shannon diversity index of all shrub species, hemlock = western hemlock stand basal area (m² ha^{-1}), redcedar = western redcedar stand basal area (m² ha^{-1}), alder = red alder stand basal area (m² ha^{-1}), spruce = Sitka spruce stand basal area (m² ha^{-1}), tree diversity = Shannon diversity index of all tree species, woody debris = percent cover of all logs and stumps. Year (fixed effect) and stream (random effect) were included as variables in all models but are excluded in the table for clarity. K = number of parameters in model, ΔAIC = difference between the model AIC and the top model AIC, w_i = model AIC weights, ER = evidence ratio (likelihood of top model relative to given model).**

response	hypothesis	parameters	K	ΔAIC	w_i	ER
Probability of habitat use	salmon and habitat interactions	salmon * redcedar + high-nutrient shrub + hemlock	7	0	0.607	1
	salmon and habitat interactions	salmon * redcedar + high-nutrient shrub + other shrub + hemlock	8	2.0	0.227	2.68
	salmon and habitat	salmon + redcedar + high-nutrient shrub + other shrub + hemlock	7	3.8	0.090	6.75
	salmon and habitat interactions	salmon * high-nutrient shrub + redcedar + other shrub + hemlock	8	5.8	0.034	17.96
	habitat	redcedar + high-nutrient shrub + other shrub + hemlock	6	6.5	0.024	25.19
	salmon and habitat	salmon + redcedar + high-nutrient shrub + other shrub + hemlock + alder + spruce	9	7.5	0.014	42.45
	global model	salmon + redcedar + high-nutrient shrub + other shrub + hemlock + alder + spruce + conifer shrub + shrub diversity + tree diversity + woody debris	13	11.4	0.002	289.05
	habitat	redcedar + hemlock + alder + spruce	6	11.9	0.002	379.38
	habitat	redcedar + hemlock + alder + spruce + tree diversity	7	13.8	<0.001	>540
	habitat	high-nutrient shrub + other shrub + shrub diversity	5	24.2	<0.001	>540
	habitat	high-nutrient shrub	3	25.2	<0.001	>540
	salmon and habitat interactions	salmon * high-nutrient shrub	5	28.8	<0.001	>540
	habitat	woody debris	3	39.2	<0.001	>540
	salmon	salmon	3	39.6	<0.001	>540

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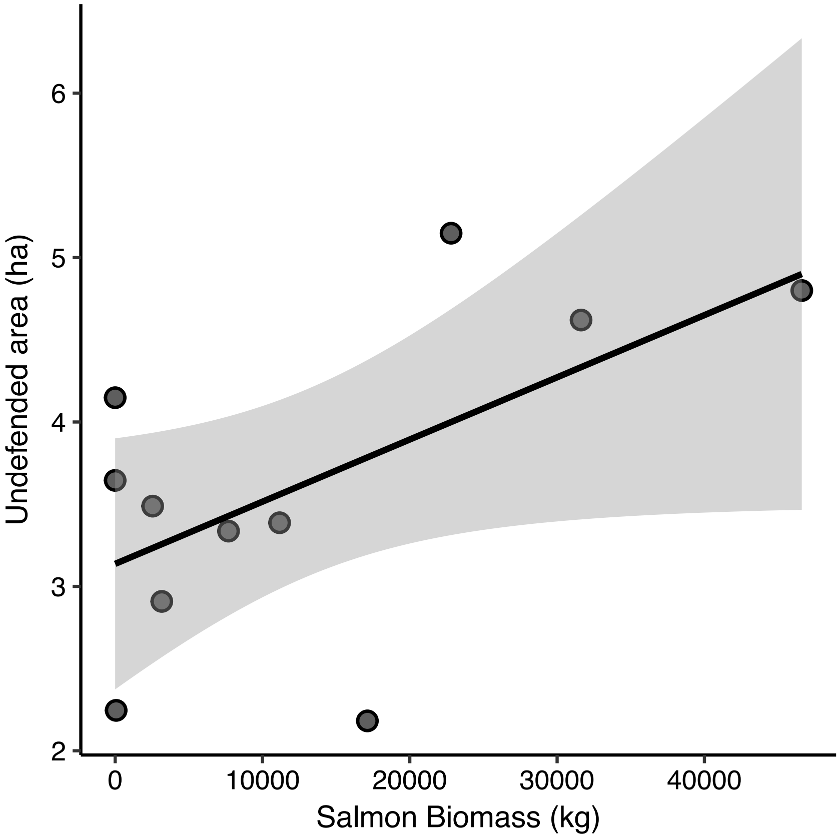

Fig. A.1 **Relationship between salmon biomass per stream and area that was not included within wren territories in the surrounding forest plot (undefended hectares) ($P = 0.056$, $r^2 = 0.35$). The dark line represents the best-fit line and the band represents the 95% confidence interval.**

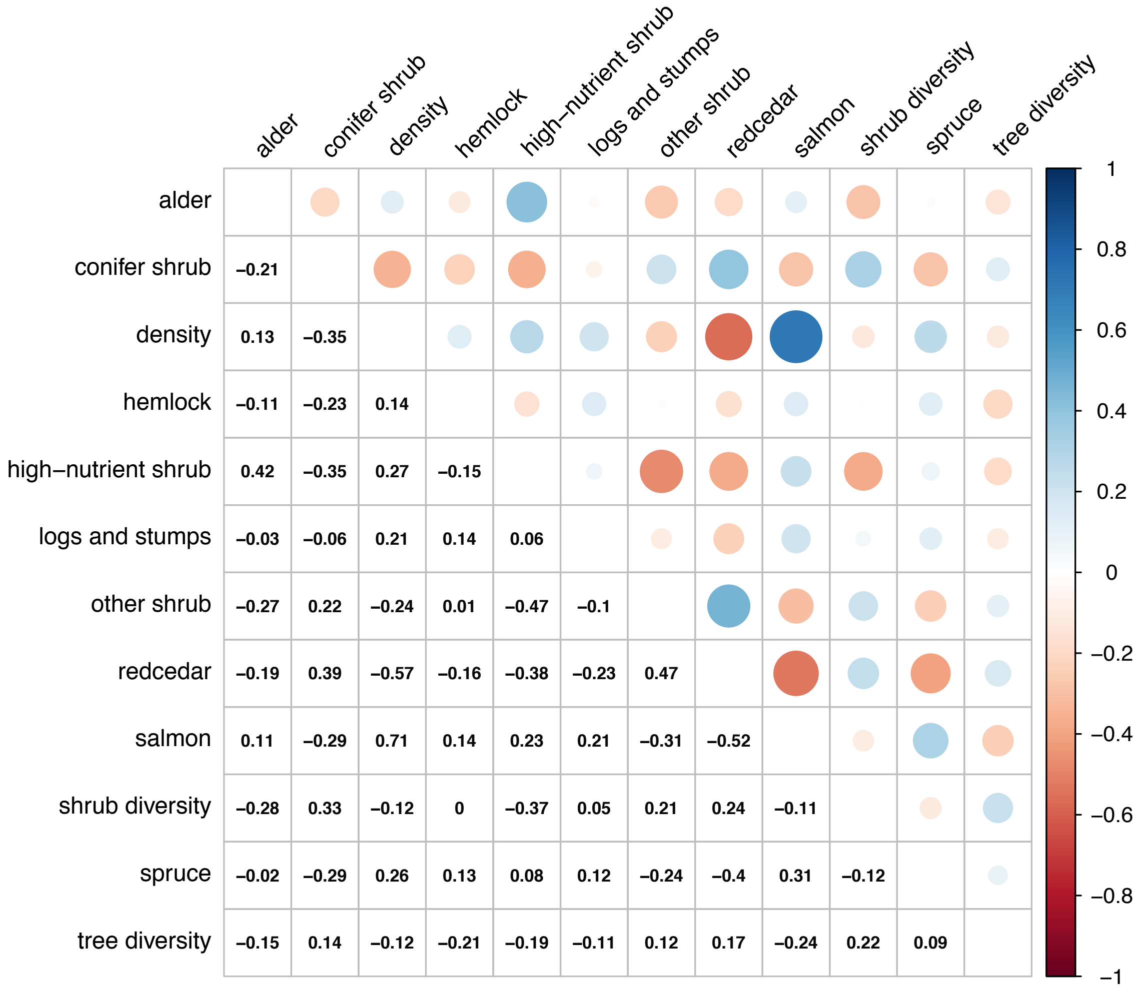

Fig. A.2 Correlation coefficients for all variables used in candidate model sets shown with numbers and represented using colour. Circle size represents strength of correlation and circle colour represents direction (blue = positive, red = negative). Parameters include: alder = red alder stand basal area (m² ha^{-1}), conifer cover = percent cover of small conifer trees, density = male wren density (males ha^{-1}), hemlock = western hemlock stand basal area (m² ha^{-1}), high-nutrient shrubs = percent salmonberry and stink currant shrub cover, logs and stumps = percent cover of all large woody debris, other shrub = percent cover of shrubs blueberry, false azalea , and salal, redcedar = western redcedar stand basal area (m² ha^{-1}), salmon = summed chum and pink salmon biomass per stream (kg), shrub diversity = Shannon diversity index of all shrub species, spruce = Sitka spruce stand basal area (m² ha^{-1}), tree diversity = Shannon diversity index of all tree species.

Appendix B.

Supplementary Material Chapter 3

Table B1. **Salmon biomass (three year mean between 2012-2015) and wren population data for watersheds in this study (n=12)**

Stream	**Jane**	**Ripley**	**Troupe**	**Fancy**	**Beales**	**Ada**	**Hooknose**	**Bullock**	**Kunsoot**	**Fannie**	**Clatse**
Salmon biomass (kg)	0	0	68.0	2,544.5	3,162.7	7,693.9	11,161.5	17,121.4	22,803.3	31,626.2	46,609.2
Number of male with territories	2	2	2	2	5	3	4	7	3	7	8
Number of males without active nest	0	0	0	0	1	1	0	5	0	4	4
Male density (male hectare^{-1})	0.18	0.14	0.18	0.20	0.40	0.24	0.39	0.71	0.26	0.80	0.58
Polygynous males (#)	0	0	0	0	3	0	2	0	2	0	0
Number of double broods	0	0	0	1	1	1	1	1	1	1	1

Table B2. **Binomial linear mixed-effect models for likelihood of polygyny, double brooding and nest survival. Model refers to all the parameter estimates in the model, while estimates include the standard error in grey and R^2 is the marginal r-squared, or the r-squared associated with all fixed-effects. All models include a random effect of stream and the model for survival has a random effect of nest identity nested within stream. Territory = male wren territory size (ha), salmon = stream salmon biomass (kg), male body condition = male SMI, and male feeding rate = proportional male feeding rate per hour out of total nest visits.**

response	model	estimates	p-value	R^2
polygyny (0/1)	territory	0.46 ± 0.41	0.26	0.055
	salmon	-4.67e-5 ± 3.34e-5	0.16	0.14
	male body condition	0.22 ± 0.57	0.70	0.012
double brood (0/1)	territory	-0.05 ± 0.57	0.93	<0.001
	salmon	1.14e-5 ± 3.76e-5	0.76	0.007
	male SMI	0.82 ± 0.73	0.26	0.14
Survival (0/1)	male feeding rate	-3.84 ± 10.10	0.70	