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Influence of Salmon on the Nesting Ecology of American Dippers in Southeastern Alaska

Abstract

Salmon runs influence the ecology of several mammalian species in Southeast Alaska, but little is known about the effect of salmon runs on avian predators. We tested the prediction that reproductive performance of American dippers (*Cinclus mexicanus*) nesting along stream reaches that have seasonal populations of spawning salmon is higher than that of those nesting along stream reaches without salmon runs. Dippers on reaches with salmon near Juneau, Alaska, had heavier fledglings and less brood reduction than dippers on reaches without salmon. Higher fledgling mass and less brood reduction were associated with the occurrence and nutritional value of young salmon in the nestling diet and not with aquatic macroinvertebrate abundance (which decreased during the salmon spawning period).

Introduction

Throughout the North Pacific region, salmon (*Oncorhynchus* spp.) return from the sea to spawn in freshwater streams, with important consequences for wildlife. The seasonal pulse of migratory fish is fed upon by many wildlife species that consume not only adult salmon and carcasses but also salmon eggs and juvenile salmon (Cederholm et al. 1989, 1999; Willson and Halupka 1995). The reproductive biology of several mammals has been linked to seasonal foraging on salmon (Ben-David 1997, Willson et al. 1998), but the effects of salmon runs on avian predators have been little studied.

American dippers (*Cinclus mexicanus*) feed principally on aquatic invertebrates, and salmon carcasses are reported to increase the abundance of aquatic macroinvertebrates (Wipfli et al. 1998, 1999). Dippers also consume salmon eggs, bits of salmon carcasses, and small fish (Sullivan 1973, Ealey 1977, Piorkowski 1995, Campbell et al. 1997, Obermeyer et al. 1999). Streams with salmonids provide important winter habitat for American dippers in British Columbia (Campbell et al. 1997).

Thus, salmon spawning runs might increase food availability either directly (consumption of salmon and eggs) or indirectly (via salmon-enhanced abundance of aquatic invertebrates). Higher prey availability was associated with higher reproductive success (larger broods, faster nestling growth, more second broods) of Eurasian dippers (*C. cinclus*) in Britain (Ormerod et al. 1991, Vickery 1992). Under the hypothesis that reproductive performance is related to prey abundance, we tested the prediction that the reproductive performance of American dippers is greater on stream reaches that support spawning salmon than on stream reaches without salmon, via differences in prey-delivery rates, prey abundance, or prey quality.

Study Area

We monitored dipper nests on stream reaches with and without salmon runs near Juneau, Alaska (58.3°N, 134.7°W) in 1998 and 1999. This area is characterized by cool, wet, maritime conditions. Precipitation in the center of our study area (Juneau International Airport) averages 140 cm annually (National Weather Service, Juneau, AK, unpublished data), but it varies greatly on a local scale, depending on elevation and rain-shadow effects. All 11 streams used in the study had alpine headwaters, including one of glacial origin, but two had flows moderated by lakes.

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These relatively small coastal streams historically have annual mean streamflows less than 225 cubic feet per second (cfs) (<http://nwis.waterdata.usgs.gov/ak/nwis> for gauged streams), and most are considerably smaller. Study nests were located along the streams from near the mouth up to about 11 kilometers upstream, from sea level up to an elevation of about 300 m. Most nest sites were on steep rock walls, two were under bridges, and one was in a century-old wooden dam.

Some reaches of the study streams receive late summer or fall runs of chum, pink, sockeye, and coho salmon (*O. keta*, *O. gorbuscha*, *O. nerka*, and *O. kisutch*, respectively), and one has a spring run of steelhead (*O. gairdneri*). Carcasses of the first four species accumulate in spawning reaches and decompose there, thus providing potential nutrient enrichment. Pink, chum, and sockeye salmon typically spawn from late July into September; coho spawn later in the fall. Their eggs, when poorly buried in the gravels or exhumed by later spawners, then provide an easily accessed food source for egg predators, including dippers (Obermeyer et al. 1999), especially later in the season. Young coho salmon remain in streams for at least a year following hatching (Groot and Margolis 1991) and thus are available for foraging dippers throughout the entire dipper nesting period. Other fishes occur in these streams, including sticklebacks (*Gasterosteus aculeatus*), sculpin (*Cottus aleuticus*), cutthroat trout (*O. clarki*), and Dolly Varden char (*Salvelinus malma*), and are sometimes eaten by dippers, but the principal piscine prey for nesting dippers in this study were young coho salmon.

Salmon distribution was confined to the lower reaches of stream systems because of barriers to salmon migration typically composed of vertical cascades of 4.5-30 meters in height. In contrast, nesting dipper territories were distributed widely throughout stream systems, both above and below barriers, and therefore some pairs had access to salmon and others did not.

Methods

Nest Monitoring

Measures of reproductive performance included nest timing, clutch size, nestling mass, brood reduction and nestling survival, nest success (at least one chick fledged), and frequency of second

broods. We monitored nests every 2-4 days to determine approximate egg-laying, hatching, and fledging dates, as well as clutch and brood sizes. In both years, we banded nestlings with numbered USFWS aluminum bands and plastic color bands. In 1998, we weighed nestlings only at the time of banding and no data are available for number of fledglings per nest. In 1999, we weighed nestlings several times between ages 7-19 days; we felt that collection of nestling mass data either before or after this time period was potentially disruptive to natural nesting patterns of dippers.

In general, we observed selected nests using binoculars (8 or 10X) at close range (<20m), for 1-3 hour periods at different times of day, every 2-4 days throughout the nestling period. We determined composition and number of prey items delivered to nests in order to estimate prey and energy delivery rates, classifying invertebrate prey by size, (Yoerg 1998)(Table 1). Altogether, we classified 2240 prey items delivered to 18 nests (6 non-salmon nests, 12 salmon nests) during 72 nest-observation periods.

Aquatic Invertebrate Sampling

We sampled macroinvertebrates on six streams using a stratified time-constrained search method (Corn and Bury 1990, Bury and Corn 1991) in habitats we observed to be heavily used by foraging dippers. To examine the effects of spawning salmon on macroinvertebrates, we took ten samples at 20-m intervals both above and below barriers to salmon migration, and both before (June) and after (August) pink and chum salmon spawning runs. During 2-minute sampling periods, we examined rock substrates (>5 cm length) typically used by benthic invertebrates in riffle and stream margin sites where water was less than 0.4 meters in depth. We counted the number of macroinvertebrates of all taxa combined, classifying them as small (<0.5 cm length), medium (0.5-1.5 cm), or large (>1.5 cm). These size categories corresponded to size classes of invertebrates that could be reliably identified during subsequent dipper foraging observations (following Yoerg 1998).

We determined energy content of samples of dipper prey types (dried for 24 hr at 100° C in an Ehret VTS 70 drying oven) using a Parr model 1271 bomb calorimeter (Parr Manual 1994), and multiplied that result (joules per gram) by the average dry mass of each class of prey to estimate

TABLE 1. Energy and nutrient content of prey items fed to dipper nestlings on streams near Juneau, AK.

Prey type	Length	Common Examples	Dry mass (g)	% protein	% crude fat	% P	% Ca	Average joules/item
Fish	--	coho salmon	0.066	76	10	1.4	1.5	1414
Salmon egg	--	chum salmon pink salmon	0.135 0.053	73	20	0.8	0.2	3602 1418
Large invertebrate	>bill length	Ephemereillidae ^a Limnephilidae ^b	0.016	--	--	--	--	787
Medium invertebrate	0.5-1.0x bill length	Heptageniidae ^a Nemouridae ^c	0.011	--	--	--	--	264
Small invertebrate	<0.5x bill length	Chironomidae ^d Baetidae ^a	0.003	--	--	--	--	71
All invertebrates (Pooled)			0.010	61	14	0.9	0.3	234

^a Ephemeroptera; ^b Trichoptera; ^c Plecoptera; ^d Diptera

the average energy content of prey. The University of Alaska Plant and Soil Test Lab in Palmer, Alaska conducted the nutrient analyses (percent protein, phosphorous, calcium, and crude fat) of selected dipper prey (mixed aquatic invertebrates, coho salmon fry, and salmon eggs). The mixed aquatic invertebrate sample was composed of all sizes of mayflies (Ephemeroptera), caddisflies (Trichoptera), and stoneflies (Plecoptera).

Statistical Analyses

We used multi-factor analysis of variance (ANOVA) to determine if the abundance of aquatic invertebrates differed between salmon and non-salmon reaches of study streams both before and after salmon spawning activity began. We used analysis of covariance (ANCOVA) to compare the effect of nest location (salmon vs. non-salmon), while accounting for the effect of nestling age, on energy delivery rates and (in a separate analysis) nestling masses, with post-hoc comparisons of means (Tukey HSD) to test for differences between treatment categories (Zar 1999). We used simple linear regression to determine slope for comparisons involving independent variables (nestling weight and energy delivery rate) and nestling age. T-tests evaluated differences between salmon and non-salmon reaches in mean clutch size, mean clutch initiation date of first broods, and prey delivery rates. We used non-parametric, Mann-Whitney U tests to determine if egg-laying dates differed between nests on salmon and non-salmon streams.

Results

Nesting Phenology and Clutch Size

First-brood nestlings in the Juneau area commonly hatched between late April and early June, and second broods, when they occurred, hatched from late June to mid-July. Mean egg-laying dates did not differ significantly between nests on salmon and non-salmon reaches (Julian dates, 1998: salmon, 114; non-salmon, 111; 1999: salmon, 130; non-salmon, 125; Mann-Whitney U = 6, $P > 0.7$, both years combined). Clutch sizes did not differ significantly between salmon (mean = 4.2 ± 0.5 SE, N = 21) and non-salmon nests (mean = 4.6 ± 0.3 , N = 11) ($t = 1.72$, $P = 0.41$). The frequency of second broods was higher in 1998 (8 of 12 territories) than in 1999 (1 of 16 territories), and was slightly higher on salmon reaches than on nonsalmon reaches, but data from subsequent years showed that the frequency of second broods was similar on both kinds of reaches (MFW, unpublished data).

Diet Composition, Prey Delivery Rates, and Nestling Mass

Prey delivery rates (number of trips per hour) were not significantly different between salmon (mean = 14.6 ± 2.7 , N = 59 observation periods) and non-salmon nests (mean = 16.0 ± 3.9 , N = 16 observation periods) ($t = 1.192$, $P = 0.21$), although the estimated number of items delivered per hour was greater on non-salmon reaches (mean = 27.0 ± 6.6) than salmon reaches (mean 19.9 ± 3.8) (t

TABLE 2. Proportions of prey of nestling dippers, by age category, on salmon and non-salmon streams near Juneau, AK.

Prey type	7-9 days		10-12 days		13-16 days		17-19 days		Total	
	Salmon	Non-salmon	Salmon	Non-salmon	Salmon	Non-salmon	Salmon	Non-salmon	Salmon	Non-salmon
Fish	0.21	0.00	0.32	--	0.42	0.01	0.30	0.00	0.31	0.00
Large invert.	0.24	0.08	0.24	--	0.15	0.37	0.24	0.02	0.22	0.16
Medium invert.	0.28	0.67	0.17	--	0.24	0.29	0.27	0.63	0.24	0.53
Small invert.	0.26	0.25	0.27	--	0.18	0.33	0.18	0.35	0.23	0.31
Total items	331	25	342	--	420	241	627	155	1719	421

= 2.734, $P < 0.01$). Fish, primarily young coho salmon, were delivered only by dippers nesting on salmon reaches (Table 2). On non-salmon reaches, where deliveries of fish were lacking, we observed a corresponding increase in invertebrate prey, principally those of medium, but not large, size. Salmon eggs, in addition to other foods, were fed to chicks in some second broods on salmon reaches, but eggs constituted <1% of items delivered to all nests. Average energy delivery rates (Joules/minute) to salmon and non-salmon nests did not differ significantly ($F_{1,47} = 0.34, P = 0.56$). However, a significant interaction between nestling age and whether a nest was located on salmon or non-salmon reach ($F_{1,47} = 4.16, P = 0.05$) showed that energy delivery rates increased with increasing nestling age on salmon reaches but not on non-salmon reaches (Figure 1). Overall, although nestling body mass increased significantly with age on both reach types ($F_{3,29} = 25.04, P < 0.001$; Figure 2), nestlings were significantly heavier on

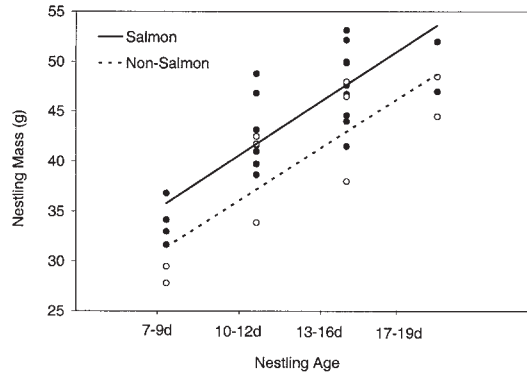


Figure 2. Comparison of nestling mass (grams) at different ages on salmon ($Y = 29.862 + 5.943X, r^2 = 0.634, n = 24, P < 0.001$) and non-salmon ($Y = 25.637 + 5.783, r^2 = 0.691, n = 10, P = 0.003$) reaches; analysis of covariance $r^2 = 0.679, F = 67.445, df = 2, 31, P < 0.001$.

salmon reaches than on non-salmon reaches ($F_{1,29} = 7.56, P = 0.01$);

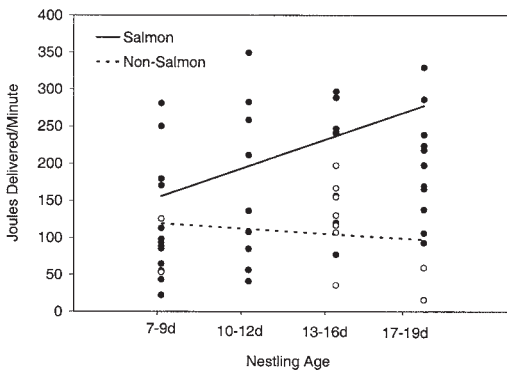


Figure 1. Comparison of energy delivery rates (joules/minute) to nestling dippers at different ages on salmon ($Y = 115.49 + 40.553X, r^2 = 0.10, n = 39, P = 0.062$) and non-salmon ($Y = 126.37 - 7.372X, r^2 = 0.02, n = 11, P = 0.711$) reaches; analysis of covariance $r^2 = 0.174, F = 4.501, df = 2, 47, P = 0.016$.

Nest Failure and Brood Reduction

Overall, 88% of all nests monitored from date of discovery until fledging ($N = 34$) fledged at least one young. Known causes of nest failure included flooding ($n = 3$) and predation ($n = 1$; probably by corvids). We documented an average of 3.3 fledglings per brood in 1999 ($n = 15$). Brood reduction occurred in only two nests, both on non-salmon reaches, with the widest range of nestling masses observed in this study. In each nest, two nestlings were lost; in the first case the smallest two nestlings in the brood were lost, and in the second case smallest and one of the next smallest were lost.

Invertebrate Abundance and Salmon Spawning Activity

Total invertebrate abundance (all size classes combined) differed significantly between sampling

locations (above and below barrier falls; $F_{1,36} = 20.2$, $P < 0.001$) and between periods with and without spawning activity ($F_{1,36} = 10.4$, $P = 0.003$) (Figure 3) in both years, despite a significant annual difference in abundance ($F_{1,36} = 70.9$, $P < 0.001$). In areas below barrier falls, invertebrate abundance was significantly higher before spawning salmon arrived than after their arrival (post-hoc tests: $P = 0.014$), but in areas above barrier falls, invertebrate abundance did not differ before and after the time when salmon arrived below the falls ($P = 0.98$). Invertebrate abundance was similar above and below barriers before salmon spawning ($P = 0.54$), but it was lower below barriers after salmon arrived ($P = 0.001$).

Discussion

Dippers typically build bulky, covered nests of moss with an entrance on the side (Kingery 1996); the nests are generally placed in sites quite inaccessible to most predators. Nest success of dippers tends to be high, as is generally true for cavity nesters (Martin and Li 1992). Our estimate of nest success is “apparent nest success”, which does not take into account when in the nesting cycle the nest was discovered, and therefore can be compared with several previous studies (Table 3). Nest success in our study was at the high end of the observed range. Nest failures were few and often due to flood events, unrelated to presence or absence of salmon. Clutch size in our study was similar to that elsewhere, but the number of fledglings/brood was high compared to most other studies (Table 3).

Dippers nesting on salmon reaches in Southeast Alaska had nestlings of higher body mass (at age) and less brood reduction than those nesting on non-salmon streams. These differences in reproductive performance were related to consumption of salmon fry and not to a higher abundance of invertebrates. Although salmon carcasses may increase invertebrate numbers on a small scale and in the short term (Minakawa 1997, Wipfli

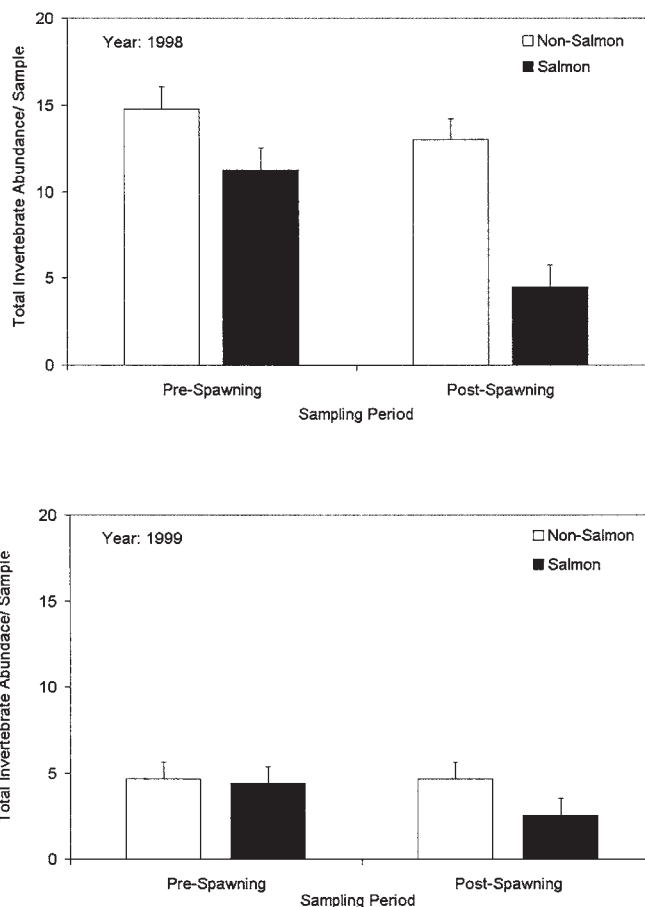


Figure 3. Abundance of aquatic macroinvertebrates in Southeast Alaska streams, above and below barriers to spawning salmon, and before and after spawning runs (a: 1998; b: 1999). Error bars are S. E.

et al. 1998, 1999) and stream productivity in general (Gende et al. 2002), in the streams we studied, invertebrates were less abundant after arrival of adult salmon. The lower abundance of invertebrates in spawning reaches might be due directly to spawning activities (Hildebrand 1971, Field-Dodgson 1987, Minakawa 1997), differentially intensive foraging of the dippers themselves (Harvey and Marti 1993), or invertebrate-eating fish (such as sculpins, perhaps attracted by salmon eggs; McLarney 1967). In some cases, full recovery of the invertebrate standing crop in spawning reaches can be delayed for some time (Hildebrand 1971, Minakawa 1997). However, the effects of spawning salmon may vary among streams (Peterson and Foote 2000, Chaloner et al.

TABLE 3. Comparison of nest productivity of American dippers in Southeast Alaska vs other studies. Most of the data are estimates of “apparent nest success” (except Loegering used the Mayfield method), permitting comparisons with our data.

Location	Avg. clutch size (N)	% Nest success (N)	No. fledglings per brood (N)	Reference
Southeast Alaska	4.3 (32)	88 (34)	3.3 (15)	This study
Alberta	4.3 (41)	72 (41)	2.5 (41)	Ealey 1977
British Columbia	4.1 (14)	--	2.97 (36)*	Campbell et al. 1997 Morrissey 2004
	4.3 (99)	59 (99)	2.5 (99)	
Montana	--	80 (48)	2.2-2.8 (51)	Osborn 1999
	4.1 (51)	79 (79)	2.8 (46)	Sullivan 1973
	4.7 (4)	57 (7)	1.9 (7)	Bakus 1959
Oregon	4.2 (??)	87 (77)	2.9 (21)	Loegering 1997
Colorado	3.7-4.6 (68)	50-90 (77)	1.7-2.6 (77)	Price and Bock 1983
entire range	4.1 (99)	--	--	Kingery 1996

* Number of chicks/brood, age not given.

2004), and some of the invertebrates dislodged by spawning activities may be available to predators as ‘drift’ (Peterson and Foote 2000).

Selection of large prey increases the efficiency of prey delivery to nests (Tyler and Ormerod 1994) and adult dippers often select larger prey sizes, especially as nestlings grow (Mitchell 1968, Ealey 1977, Ormerod and Tyler 1991, Agnew and Perry 1993, Ormerod 1996). Selection of small fish, when available, as prey for nestlings is consistent with this observation. Because a significant proportion of prey items delivered on salmon reaches were comprised of fish, overall energy delivery rates increased as nestlings aged on salmon reaches but not on non-salmon reaches. Availability of salmon is likely to affect not only nestlings (via prey delivery returns) but also adults, which then capture and deliver fewer prey items to nests per unit time than adults on nonsalmon reaches and therefore may incur lower foraging costs.

The advantages of salmon as a food source for nestlings may lie partly in its nutritional value (e.g., protein and calcium) in addition to its energy content. Nestlings require protein during early stages of development (Gill 1995), and there is considerable evidence that arthropods do not provide sufficient dietary calcium for egg production and nestling growth for Eurasian dippers (Ormerod et al. 1991) and many other passerines (reviewed in Graveland 1998, Reynolds et al. 2004, Bidwell and Dawson 2005, and others). As a result, salmonid prey is likely to play an important role in dipper reproductive success when protein and calcium, in addition to energy, are important determinants of nestling development. Nestling mass on non-

salmon reaches increased across a 13-day period even though estimated energy delivery rates on non-salmon reaches were constant, suggesting that factors other than energy were at least partially responsible for nestling growth patterns on non-salmon reaches.

Food is often limiting to successful reproduction in birds (Martin 1987). In our study the chief advantages of the availability of fish prey were increased nestling mass and lower brood reduction. If chicks are in good condition at fledging, the probability of juvenile survival often increases (Lack 1966). Juveniles are less proficient foragers than adults in dippers (Yoerg 1994) and many other birds (Wunderle 1991), and young dippers generally capture less rewarding prey (Yoerg 1994, Donnelly and Sullivan 1998). Although nestlings on salmon reaches tended to be heavier than those on non-salmon reaches, as fledglings or juveniles they would encounter lower invertebrate abundances (as long as they remained in a salmon-spawning reach), but the ready availability of poorly buried or drifting salmon eggs might compensate for lower invertebrate abundance. More proficient juveniles can achieve better body condition (Donnelly and Sullivan 1998), and the easily captured eggs could increase the effectiveness of foraging.

In addition, adult dippers nesting on salmon reaches may also benefit from the availability of high-value prey. The estimated daily energy expenditure of adult dippers is high for both parents during the feeding of offspring and for females during egg-laying (Bryant and Tatner 1988), and each nesting effort requires at least 7 weeks of

attention to eggs and chicks (Hann 1950, Price and Bock 1983, Sullivan 1973, Tyler and Ormerod 1994, Kingery 1996). Although prey delivery rates in our study were similar whether or not fish were included in the deliveries, adults might be able to maintain themselves in better condition on reaches with abundant small fish.

In these study streams, pink and chum salmon often spawn in and near the intertidal area, and dippers whose territories includes these areas have access to another source of salmon prey. Pink and chum salmon fry migrate to sea soon after hatching in spring, and from mid-March to early May they are prey available for adult dippers preparing for the nesting season. Males may also deliver such prey to incubating females at early nests (M. F. Willson, pers. obs). The availability to

adults of pink and chum fry in early spring might contribute to better adult body condition in the early part of the nesting season and possibly to higher reproductive performance. This possibility remains to be examined.

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