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Size Selectivity of Predation by Brown Bears Depends on the Density of Their Sockeye Salmon Prey

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ABSTRACT: Can variation in prey density drive changes in the intensity or direction of selective predation in natural systems? Despite ample evidence of density-dependent selection, the influence of prey density on predatory selection patterns has seldom been investigated empirically. We used 20 years of field data on brown bears (*Ursus arctos*) foraging on sockeye salmon (*Oncorhynchus nerka*) in Alaska, to test the hypothesis that salmon density affects the strength of size-selective predation. Measurements from 41,240 individual salmon were used to calculate variance-standardized selection differentials describing the direction and magnitude of selection. Across the time series, the intensity of predatory selection was inversely correlated with salmon density; greater selection for smaller salmon occurred at low salmon densities as bears' tendency to kill larger-than-average salmon was magnified. This novel connection between density dependence and selective predation runs contrary to some aspects of optimal foraging theory and differs from many observations of density-dependent selection because (1) the direction of selection remains constant while its magnitude changes as a function of density and (2) stronger selection is observed at low abundance. These findings indicate that sockeye salmon may be subject to fishery-induced size selection from both direct mechanisms and latent effects of altered predatory selection patterns on the spawning grounds, resulting from reduced salmon abundance.

Keywords: phenotypic selection, density dependence, salmon, predation, optimal foraging, *Oncorhynchus nerka*, *Ursus arctos*.

Introduction

Selection shapes the phenotypic landscape we observe and the underlying genetic composition of a population through adaptive evolution (Darwin 1874; Rieseberg et al. 2002). While selection may operate on a wide array of morphometric or life-history traits, selection is observed to vary greatly in both direction and magnitude over time (Grant and Grant 2002; Siepielski et al. 2009), often resulting from inherent nonstationarity in environmental

factors influencing selection (Bell 2010). This inconsistency in selection over time may help to maintain genetic and phenotypic diversity across generations (Kingsolver and Diamond 2011). However, variation in the strength and direction of selection may also result from changes in demographic qualities of the population under selection (Siepielski et al. 2011), including sex ratio (Jann et al. 2000; Punzalan et al. 2010; Leftwich et al. 2012) and density (Mueller 1997; Einum et al. 2008).

Density dependence in selection predicts that the fitness of one phenotype relative to another will change with the abundance of conspecifics at any given time. The theoretical basis for this interface between demography and selection comes first from MacArthur (1962), who detailed differences between populations at high and low density and postulated that density itself was dictating selection. While density dependence may be manifest in selection related to sexual (Zeh 1987; Conner 1989; Tomkins and Brown 2004) or mortality (Milner et al. 1999; Sinervo et al. 2000) processes, the underlying criterion is that there is a change in the distribution of fitness across trait values when the population's density changes. The strength of selection for secondary sexual characteristics, including forceps used in courtship and fighting by the male European earwig *Forficula auricularia* (Tomkins and Brown 2004) and size of male pedipalp pincers (chela) associated with combative mate acquisition in pseudoscorpions (Zeh 1987), has been correlated with density. Specifically, high density and increased male-male competition magnify selection for the large phenotype in these appendages. Conversely, selection for an analogous character in the fungus beetle *Bolitotherus cornutus* was strongest under conditions of low abundance, as large horns provided less advantage in mate acquisition at high density (Conner 1989).

Density-dependent selection may also arise from non-sexual processes where mortality rates are linked to individual phenotypic values (Milner et al. 1999). Phenotypes that confer a fitness benefit at high density (K

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selected) or at low density (r selected) should be expected to demonstrate inverse responses in the direction of selection to variation in conspecific density (Pianka 1970; Mueller 1997). Pianka (1970) specifically postulated that (K -selected) traits such as prolonged life span, iteroparity, large size at maturity, and reduced growth rate should be favored at high population density. Sinervo et al. (2000) found that selection for two competing morphs of side-blotched lizard (*Uta stansburiana*) displaying alternative strategies in the trade-off between fecundity and egg size depended on population density. Further evidence suggests that selection for the ability of *Drosophila melanogaster* to persist in suboptimal (cadmium-rich) environments depends on the density of conspecifics inhabiting optimal environments (Bolnick 2001). While numerous examples of density-dependent changes in selection pressure are available from model (Joshi and Mueller 1996) and non-model (Reznick and Endler 1982; Mueller 1997) organisms, most such studies were conducted under laboratory settings or encountered limitations in methodology, including uncontrolled environmental variables in interpopulation comparisons, lack of replication, or the inability to identify the causal mechanism for selection (see Einum et al. 2008 for discussion of Tomkins and Brown 2004). Furthermore, the presence of density dependence in patterns of predatory selection has been scarcely evaluated.

Although selective predation and density-dependent predation rate affect prey survival, few studies have evaluated the interaction between these processes. Here we distinguish between density-dependent selection and frequency-dependent or apostatic selection. Under a frequency-dependent selection regime, the success of a phenotype depends on the relative frequency of that phenotype within the community (Levin et al. 1988; Partridge 1988; Fitzpatrick et al. 2009). Individuals of the rare phenotype may experience lower (Allen and Greenwood 1988; Aditya et al. 2005; Olendorf et al. 2006) or higher (Shigemiyama 2004) risk of predation, representing apostatic and antiapostatic selection, respectively. In contrast, density-dependent predatory selection refers to variation in the magnitude or direction of selection by a predator in response to prey density. Previous research has evaluated the effect of prey density on predatory selectivity at the species level in the form of prey switching in top trophic-level carnivores (Owen-Smith and Mills 2008) and mesocarnivores (Prugh 2005; Randa et al. 2009). However, examples of the interaction between prey density and patterns of phenotypic selection within species by predators are extremely limited (but see Bartell's [1982] report of a positive relationship between zooplankton density and size selectivity by the predator, bluegill sunfish *Lepomis macrochirus*). To evaluate whether predation may become

more or less selective as a function of prey density, we quantified patterns of size-selective predation by brown bears (*Ursus arctos*) on mature sockeye salmon (*Oncorhynchus nerka*) in a fully natural setting.

For several reasons, adult Pacific salmon (*Oncorhynchus* spp.) are ideal for quantitatively testing the hypothesis that the strength of predatory selection is directly affected by prey density. First, Pacific salmon are semelparous, completing their life cycle and inevitably dying after reentering freshwater to spawn (Quinn 2005). This distinctive life history permits extensive sampling of an entire population of mature individuals, including those killed by predators and those escaping predation and dying of senescence within a given year, allowing selection differentials to be calculated. Second, Pacific salmon cease feeding upon freshwater entry (Gilhousen 1980; Gende et al. 2004), with no somatic growth occurring during the time period when predatory selection is operating. Thus, salmon can be measured for body size throughout the breeding season with no need to correct for daily growth, which would otherwise introduce some error. Third, the primary predators of mature salmon are typically brown bears and black bears (*Ursus americanus*), and the cause of death can be easily and consistently determined from visual analysis of remains for conspicuous bite marks and tissue consumption (Reimchen 2000; Quinn and Buck 2001). Finally, salmon reliably home to natal streams and seldom move among streams after initial entry. This site fidelity permits replicate sampling of a single population across years, without the confounding factors affecting the interpopulation comparisons often used for evaluating density dependence in selection (Einum et al. 2008).

Previous research showed that the per capita predation rate by brown bears on sockeye salmon was density dependent (Quinn et al. 2003) and bears tended to kill larger-than-average salmon within the population (Quinn and Kinnison 1999; Ruggerone et al. 2000; Quinn and Buck 2001; for similar results with different salmon and bear species, see also Reimchen 2000), but the interaction between these processes has not been evaluated. In this study, we used 20 years of data on predation rate and selection for length in a population of sockeye salmon to test the null hypothesis (that density does not affect the magnitude or direction of size selection) against two alternative hypotheses. First, when salmon density is high, bear predation is more selective because bears have more potential prey among which to choose, whereas at low densities, bears might kill salmon indiscriminately with respect to size because even a small salmon is a valuable prey item. The later hypothesis would be consistent with observations indicating that bears consume a larger fraction of the tissue from each salmon carcass when salmon are more difficult to capture (Gende et al. 2001). Alternatively, bear pre-

dation might be more size selective at low salmon densities. Bears might choose larger, more energetically rewarding prey when the salmon are scarce and harder to catch or because low prey density permits size variation among salmon to be more easily discerned.

Methods

Patterns of selection were evaluated in a population of sockeye salmon spawning in Hansen Creek, a small (2-km) tributary of the Wood River system in southwest Alaska (reference map in Carlson and Quinn 2007). This stream is fed by a beaver pond and series of springs, resulting in stable flows and clear water that facilitate accurate visual surveys. Sockeye salmon is the only salmon species spawning in the stream, further simplifying analysis of density, predation, and selection. Sockeye salmon congregate in Lake Aleknagik at the stream mouth in mid-July and begin entering about July 20, and by August 20 the breeding season is complete and virtually all salmon have died.

In each of 20 years, 1990–1993 and 1997–2012 (inclusive), total salmon density and length distributions were estimated from daily visual surveys of live and dead salmon within the stream. All dead salmon were counted and identified to sex and their cause of death was recorded. Our analysis was restricted to salmon that entered the stream and excluded those found at the mouth of the stream below the spawning areas (Carlson and Quinn 2007). Data from both tagging (1990–1993) and complete (1997–2012) surveys were analyzed in the same manner, with male and female observations pooled in each year. Density in a specific year was calculated as the sum of all individuals found dead in Hansen Creek during daily surveys and the number still alive on the final survey that year (average, <6%).

The length distributions of individuals killed by bears and those dying of senescence were compared in each year. Length was measured to the nearest millimeter from the middle of the eye to the posterior boundary of the hypural plate. This measurement avoids the bias caused by the presence of secondary sexual features, including elongated jaws in males, and error associated with estimating the length of females whose tails become frayed during nest construction. Mode of death was determined from visual inspection, with puncture wounds and partial consumption indicating that mortality was due to bear predation and frayed fins, gaunt appearance, and degradation of scales indicating that mortality was due to senescence after spawning (see Quinn and Buck 2001). During the early years (1990–1993), salmon were measured prior to stream entry and individually marked (see Ruggerone et al. 2000).

The eventual mode of death for these marked individuals was subsequently recorded. From 1997 onward, regular stream surveys were conducted throughout the spawning season (July–August), during which all observed dead within the stream and surrounding riparian area were categorized by source of mortality, and a subset was measured. In total, 41,240 salmon length measurements were included in this analysis of selection. Individual length measurements were weighted to account for daily differences in the fraction of dead individuals measured. For each sampling day, an individual length observation was multiplied by the inverse of the number of fish measured divided by the number of observed dead, for each mortality category (senescent or bear killed). Weighting individual length observations in this way accounts for intraseasonal variation in sampling effort, which could lead to bias, given the tendency for larger fish to arrive earlier in the season than smaller fish (Hendry et al. 1999; Doctor and Quinn 2009):

$$\text{SSD} = \frac{\bar{X}_{\text{post}} - \bar{X}_{\text{pre}}}{\sqrt{v_{\text{pre}}}} \quad (1)$$

To quantify the magnitude and direction of predatory selection in each year, we calculated variance-standardized selection differentials (SSDs), representing the difference in the sockeye salmon length distribution before and after predatory selection (eq. [1]). SSDs are a common metric for the relative strength of selection required to cause an observed shift in a phenotypic distribution (Falconer 1981; Endler 1986; Kingsolver et al. 2001). All individuals who were killed by bears plus those that died of senescence composed the preselection group (\bar{X}_{pre}), and the individuals that died of senescence, thus surviving predatory selection, composed the postselection group (\bar{X}_{post}). Only bear-killed and senescent individuals were included as members of the preselection group because inclusion of the alternative mortality sources would have meant calculating the effect of all selection from all sources and not predation in isolation, thus obscuring our focus on the effect of the primary predator. Selection differentials were divided by the square root of the variance ($(v_{\text{pre}})^{1/2}$) in the preselection phenotypic distribution to standardize the value, permitting comparison across years (Kingsolver et al. 2001). Negative SSD values indicated that smaller fish were less likely to be killed than larger fish, thus having greater expected fitness, and higher absolute values indicated stronger selection.

The relationship between annual densities of sockeye salmon and the corresponding SSDs quantifying length-selective predation was evaluated using weighted least squares regression (Carroll and Ruppert 1988; Ryan 1997). A weighted regression procedure ensured that each data

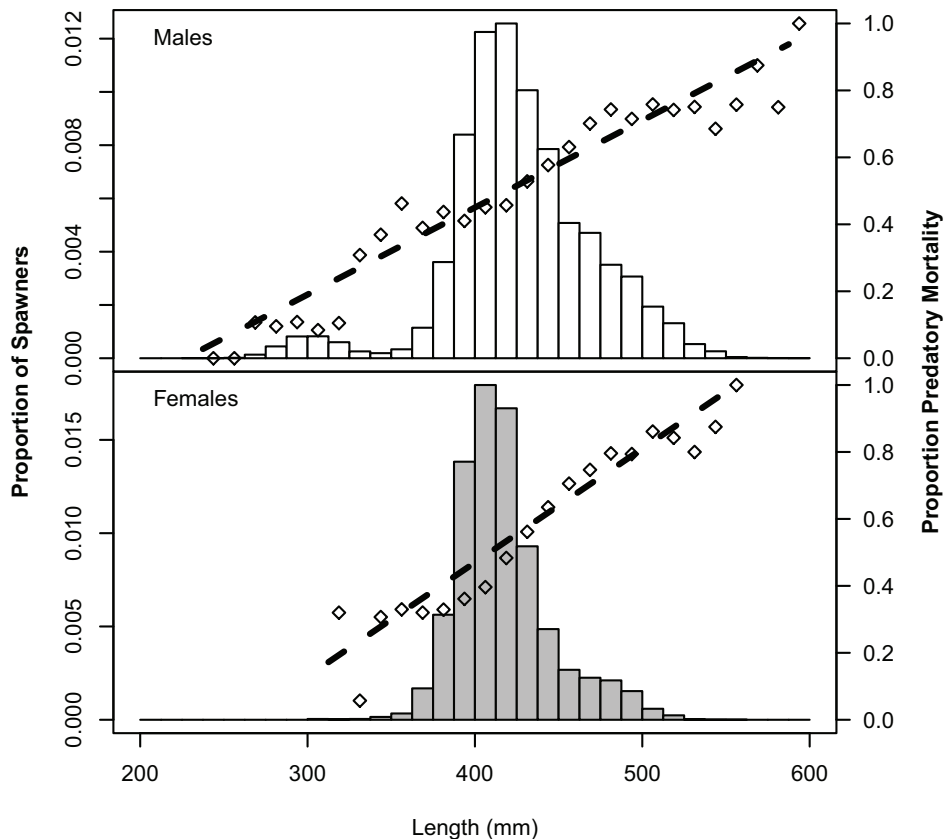


Figure 1: Weighted sex-specific length frequency histograms for all dead salmon measured within Hansen Creek from daily stream surveys 1997–2012. Diamonds represent the percentage of each size category killed by bears. Lengths are in millimeters and have been binned by 12.5-mm increments, with individuals at the upper and lower end of the length distribution (<200 and >600 mm) combined in respective end categories. Dashed lines indicate the least squares regression of the proportion killed by bears on length for males ($R^2 = 0.938$, $P < .001$, $n = 18,235$) and females ($R^2 = 0.926$, $P < .001$, $n = 25,967$).

point (SSD) was attributed an appropriate level of influence; each weight was proportional to the inverse of the pooled variance in the calculated selection differential (eq. [2]) for that year (Endler 1986).

$$\sigma_{\text{pooled}}^2 = \sqrt{\frac{n[(N_{\text{pre}} - 1)\sigma_{\text{pre}}^2 + (N_{\text{post}} - 1)\sigma_{\text{post}}^2]}{(n - 2)N_{\text{post}} \times N_{\text{pre}}}},$$

$$n = N_{\text{post}} + N_{\text{pre}}, \quad (2)$$

$$\text{predatory preference} = \bar{X}_{\text{senescent}} - \bar{X}_{\text{predator killed}}. \quad (3)$$

To further elucidate the mechanisms driving the observed selection patterns, the average difference in length between senescent and predator-killed salmon was calculated annually. Unlike the SSD (eq. [1]), which quantifies the shift in length distribution resulting from predatory selection, this metric for “predatory preference” (eq.

[3]) represents the explicit selective behavior of the predator itself.

Results

The available data from 16 consecutive years of stream surveys (1997–2012) included 107,169 carcasses categorized by mode of death, of which 44,202 were measured for length and 37,820 died of senescence or were killed by bears. In both sexes, the proportion of individuals killed by bears was positively correlated with individual length (fig. 1). The increase in predation risk with length was significant when evaluated by linear regression for males ($R^2 = 0.938$, $P < .001$) and females ($R^2 = 0.926$, $P < .001$); predation rate increased from <20% to >80% across sex-specific length distributions (fig. 1). From an evolutionary perspective, these data indicated that predation by

brown bears favored survival of smaller salmon within the population.

SSDs quantifying the observed change in length distribution resulting from predation for the combined sexes in years with tagging (1990–1993; $n = 3,420$) and survey (1997–2012; $n = 37,820$) data varied among years but were always negative (mean, -0.237 standard deviation units [SDU]), indicating that survivors of predation tended to be shorter than the population mean in all years. SSD values ranged from -0.012 SDU in 2006, when salmon were abundant ($n = 14,952$), representing a minimal impact of predatory selection, to a maximum of -0.574 SDU in 2001, when salmon were scarce ($n = 1,957$).

Yearly salmon densities ranged from 1,320 in 2009 to 16,296 in 1999 (mean \pm SD, $7,505 \pm 4,869$). To investigate the relationship between salmon abundance and selection, linear and curvilinear models describing annual variation in SSD with yearly total in-stream density as the predictor variable were fitted to these data. Various transformations were also explored for the density predictor, and model selection was conducted using Akaike's Information Criterion (Burnham and Anderson 2002). The model with natural log of salmon density as the sole predictor was selected (AIC = -21.18) when compared to a model with untransformed density as the predictor (AIC = -16.84), but the general results were the same in both cases.

Employing the natural log of in-stream density as the predictor for the observed predatory SSD in each year, least squares regression weighted by the reciprocal of the variance in each SSD estimate (eq. [2]) was significant ($R^2 = 0.55$, $P < .001$). Smaller (i.e., more negative) SSD values at low salmon densities indicated that bear predation exerted greater selection favoring the survival of smaller salmon in years when salmon density was low (fig. 2; table 1). A t -test with $n - 2$ df (Endler 1986; Sokal and Rohlf 1981) and $\alpha = 0.05$ indicated that four of the calculated SSD values were not statistically different from 0, and all four of these values occurred in years of high salmon density (fig. 2).

To further examine the selection by bears, the predatory preference (eq. [3]; difference in mean length between senescent and bear-killed salmon) was plotted against the natural log of salmon density (fig. 3). The positive correlation between the predatory preference and density (least squares regression, $R^2 = 0.41$, $P < .01$) indicated that the tendency of bears to kill larger-than-average salmon was especially marked in years with low salmon abundance (fig. 3; table 1). This relationship was similar to that described for the interaction between SSD and in-stream density (fig. 2; table 1), although less pronounced.

Discussion

Our investigation into the magnitude and direction of selection by brown bears on sockeye salmon strongly indicated a correlation with prey density (fig. 2). The significant increase in the standardized selection differential, representing the observed shift in the sockeye length distribution resulting from predatory selection, with greater salmon density revealed greater directional selection (favoring smaller salmon) in years when salmon density was low. Conversely, when sockeye salmon densities were high, there was little or no directional selection from bear predation. Phenotypic selection by predation in this case varied in magnitude but not direction, with selection either favoring smaller size in salmon ($-SSD$ value) or not being statistically significant, across years and salmon densities.

These findings contrast with many previous examples of density-dependent selection within the literature in three distinct ways. First, the observed interaction between bears and sockeye salmon represents one of few examples of density-dependent selective predation (see Bartell 1982 for another). The vast majority of documented examples of density-dependent selection arise from sexual selection (Zeh 1987; Conner 1989; Tomkins and Brown 2004), competition (Joshi and Mueller 1996; Sinervo et al. 2000; Bolnick 2001), or nonpredatory mortality (Moorcroft et al. 1996). Second, the intensity of selection was greatest at low population densities. This directly contrasts with findings by Moorcroft et al. (1996) indicating stronger selection across phenotypes and sexes in years of high density, findings by Bolnick (2001) indicating more rapid adaptation to toxic environments as a result of stronger selection in high-density treatments, and observations by Zeh (1987) and Tomkins and Brown (2004) detailing stronger selection for secondary sexual characteristics under high-abundance (competitive) conditions. However, Conner (1989) found more intense selection under the low-density condition. Third, rather than the direction of selection responding to observed fluctuations in density (see Moorcroft et al. 1996), the intensity of selection varied in response to density (fig. 2).

The consistent direction of selection over time in this population contrasts with the observation that the direction of selection for components of fitness related to survival often varies among years (Siepielski et al. 2011) and speculation by Kingsolver and Diamond (2011) that changes in the direction of selection may be a key process maintaining phenotypic variation. In the case of salmon and bears, one might ask what processes allow large salmon to persist despite consistently negative selection differentials. First, the magnitude of directional selection was correlated with salmon density, which varied by more than an order of magnitude over this time series ($\text{density}_{\min} =$

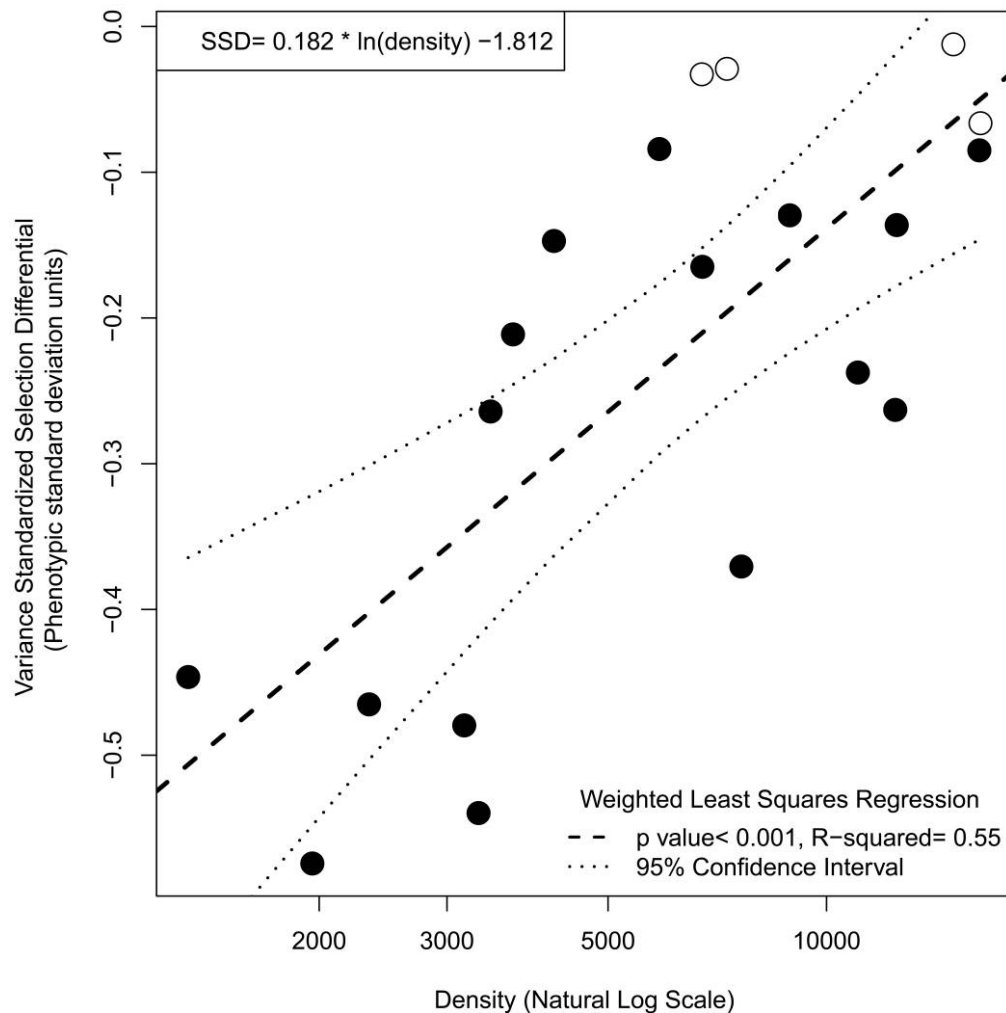


Figure 2: Variance-standardized selection differentials (SSDs) calculated for each year plotted against the natural log of in-stream salmon density. The dashed line represents the weighted least squares regression, and the dotted lines represent the 95% confidence interval around that regression. Open circles designate years in which SSDs were not significantly different from 0 (t -test, $P > .05$).

1,320, $\text{density}_{\max} = 16,296$, $\sigma_{\text{density}} = 4,869$), and this variation in the magnitude of selection over time should facilitate the persistence of large fish in years of high salmon density. Additionally, the presence of large phenotypes could be maintained by environmental variability or positive correlations observed between female fecundity and size (Quinn et al. 1995) and male reproductive success and length (Carlson et al. 2009). Regardless of what factors may limit the evolutionary effect of directional selection, predatory selection consistently favored small size, and the magnitude of this selection was correlated with salmon density.

SSDs are commonly used for describing the shift in a phenotypic distribution in response to a selective event (Endler 1986; Kingsolver et al. 2001; Kendall and Quinn

2009), and it is important to understand that such a shift (and similar calculated SSD values) may arise under two separate scenarios. First, the selective agent (in this case, the predator) may be highly selective with respect to a specific trait but remove only a small proportion of the population (e.g., if bear predation was highly selective with respect to length but bears killed only a small fraction of the available fish). However, a similar selection differential could result if the mortality agent was only slightly selective with respect to phenotype but exerted a high mortality rate, resulting in a similar shift in the mean of the trait under selection (e.g., if bears showed only weak selection but killed most of the fish). These selection regimes differ mechanistically, though they have the same result from the evolutionary perspective of the prey. Too few studies make

Table 1: Annual data and derived selection metrics

Year	In-stream density	Variance-standardized selection differential	Predatory preference	No. measured fish	Observed bear mortalities	Observed natural mortalities
1990	6,733	-.033	-4.57	773	<i>148</i>	625
1991	16,296	-.066	-13.99	1,128	<i>165</i>	963
1992	7,292	-.029	-7.02	943	<i>119</i>	835
1993	4,212	-.147	-12.38	576	<i>196</i>	380
1997	5,884	-.084	-4.24	3,094	4,176	1,017
1998	12,436	-.263	-14.85	7,772	5,878	5,169
1999	16,239	-.085	-10.52	2,426	2,834	9,578
2000	3,169	-.479	-18.75	1,886	2,591	302
2001	1,957	-.574	-19.25	1,368	1,617	77
2002	7,633	-.370	-20.53	2,477	4,470	2,105
2003	8,899	-.129	-5.92	2,173	4,506	3,058
2004	2,343	-.465	-18.83	1,402	1,555	497
2005	3,445	-.264	-26.25	2,078	1,123	1,261
2006	14,952	-.012	-1.64	2,514	2,517	11,877
2007	6,744	-.165	-8.19	3,413	3,182	2,756
2008	3,699	-.211	-12.51	2,806	1,707	1,820
2009	1,320	-.446	-21.89	422	993	218
2010	12,494	-.136	-5.01	1,708	6,689	2,897
2011	11,046	-.237	-8.26	1,606	7,693	255
2012	3,316	-.540	-19.39	675	2,739	188

Note: Numbers of observed mortalities in italics come from years in which tagging data were used to assess selective predation.

this distinction, and we encourage those using this metric to report which of these processes was responsible for the patterns of selection differentials observed. Otherwise, it is impossible to determine whether variation in selection differential values resulted from variability in selection or simply variability in exploitation rate. Our finding, that predatory preference (eq. [3]) also correlated with prey density (fig. 3), indicated that shifts in salmon length distributions were not driven merely by density-dependent variation in predation rate (Quinn et al. 2003) but also by changes in predatory behavior.

In the search for a biologically relevant explanation for the mechanism driving the observed density dependence in predatory selection, we confronted our results with the literature on optimal foraging theory. Theory predicts that an optimally efficient predator will modify its behavior to maximize energetic intake per unit time, by either reducing the time spent in pursuit of prey or selectively feeding on items (or individuals) that provide the greatest energetic reward per unit of energy invested in search or capture (Emlen 1966; MacArthur and Pianka 1966). With respect to variation in food abundance or density of prey over time, optimal foraging theory would predict that the predator should become more selective when prey abundance or density is greater (Emlen 1966; MacArthur and Pianka 1966). Emlen (1966, p. 617) further concluded that predatory selectivity is directly related to predatory satiation and that animals should necessarily be “more indiscrim-

inate when starved or when food is scarce.” This prediction contrasts with the observed pattern of less selective feeding by bears when salmon density was higher (fig. 2). However, MacArthur and Pianka (1966) postulated that efficiency of capture may also affect predatory diet diversity, speculating that increased specialization may be linked to greater difficulty in pursuit. This idea is consistent with our findings that when prey density was low, the predator practiced more specialized (selective) consumption, under the assumption that at low density, prey are more difficult to catch (requiring greater energetic expenditure per successful capture).

The observed nonstationarity and density dependence in predatory selection described here are important from the perspective of salmon ecology because they indicate that reproductive success of phenotypes depends on salmon density on the spawning grounds. Fleming and Gross (1994) also found that sexual selection on body size varied with density of coho salmon, but in that case smaller males achieved greater mating success in years of higher density. The success of these small males resulted from increased efficacy of their alternative reproductive tactic (sneak fertilization) rather than changes in predation. The importance of evaluating how the direction and magnitude of selection change with density was noted by Einum et al. (2008), as a clear understanding of these processes may provide a more complete understanding of the selection mechanisms shaping an observed phenotypic landscape.

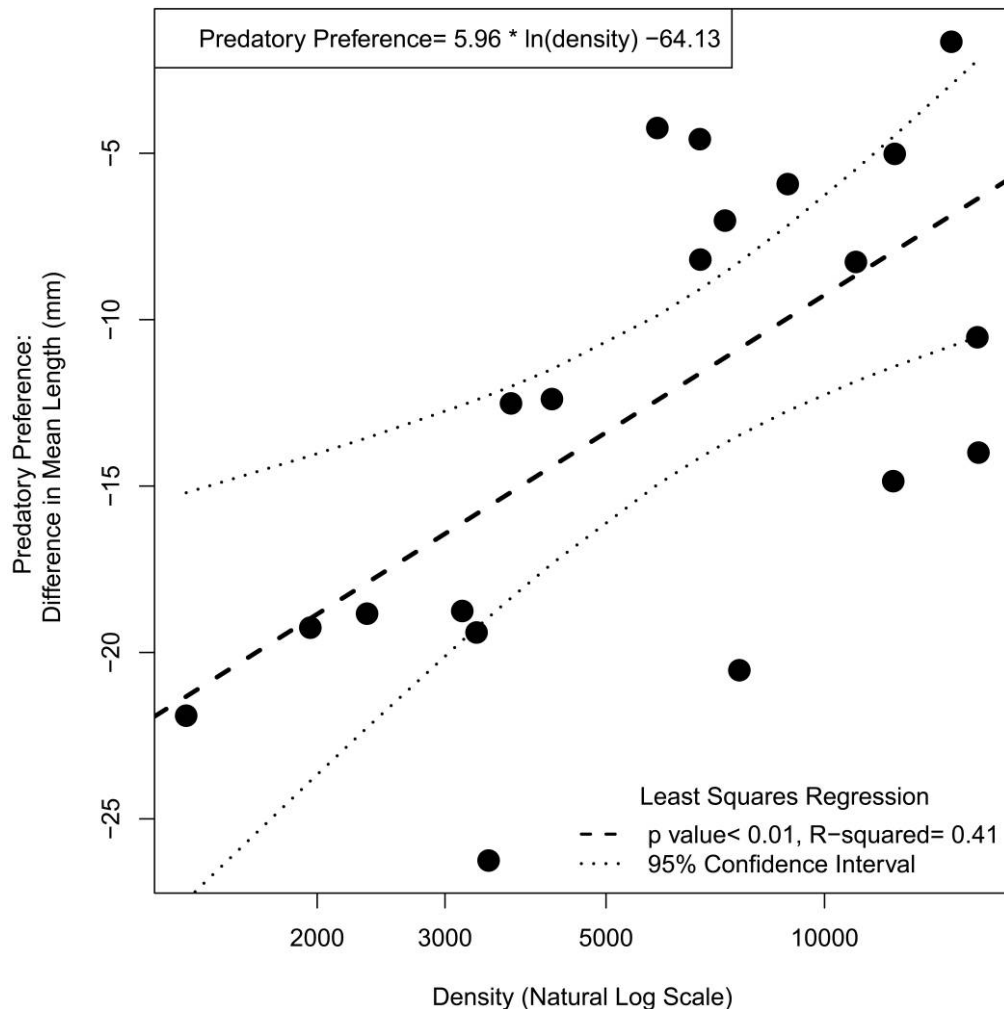


Figure 3: Relationship between predatory preference (difference in mean length of natural [senescent] and bear-killed salmon; eq. [3]) and total in-stream salmon density across years (1990–1993, 1997–2012). Dashed line indicates least squares fit of linear model to these data, and dotted lines indicate associated 95% confidence interval.

Einum et al. (2008) further concluded that salmonids may be ideal subjects for such evaluations of density-dependent selection, given the large body of empirical work on their evolutionary ecology. However, Einum et al. (2008) speculated that variation in predation rate might be the critical driver of density-dependent variation in predatory selection, while our results indicate that this variation is also driven by changes in predatory preference (behavior) with respect to salmon size as a function of density.

Our results strongly suggest that the abundance of the prey population must be considered when evaluating the evolutionary influence of predatory selection. For example, the commercial gill net fishery that operates in Bristol Bay, Alaska, may impose both direct and indirect selection on body size of sockeye salmon. The fishery is managed to

allow the estimated carrying capacity of the system for sockeye salmon to be reached each year, with the remaining salmon available for capture (Minard and Meacham 1987). This policy has the effect of reducing the average and variation in density on the breeding grounds. Sockeye salmon returning to Hansen Creek are subject to annual harvest rates between 19% and 86% (mean, 54%; Kendall et al. 2009). In addition to this exploitation rate, the gill net fishery is selective for body size (Kendall and Quinn 2009). Given the relationship between salmon density and predatory selection demonstrated here (fig. 2), the commercial fishery imposes two distinct forms of selection for smaller body size on the salmon population. In the absence of a large-scale commercial fishery (prior to 1893), returning adult sockeye salmon would have been free from

fishing that now tends to catch larger fish at a higher rate than smaller fish. In addition, the breeding ground densities would have been ~54% higher on average than are now observed. Higher in-stream densities would result in less directional selection, favoring smaller size, resulting from density-dependent predatory selection. Thus, the commercial fishery has resulted in both direct selection for smaller size due to the gear employed and indirect selection from the reduction in salmon density and associated increased selectivity by bears. In the face of future environmental uncertainty and resultant variability in salmon abundance (Hilborn et al. 2003), a clear understanding of the biological interactions driving evolutionary change within these species is of great importance.

Summary

The direction and magnitude of predatory selection by brown bears on Pacific salmon depended on the in-stream density of those salmon. A multiyear analysis of a population of sockeye salmon in Alaska indicated that (1) predators tended to kill large salmon and, thus, selection favored small size in both sexes; (2) there was greater selection intensity (more negative SSD values) during years when salmon were less abundant; and (3) variation in calculated selection differentials with prey density may result from variation in predation rate (numerical) or predatory preference (behavioral). In the case of bears preying on salmon, low density increased both the proportion of salmon killed and the tendency of bears to kill larger-than-average fish.

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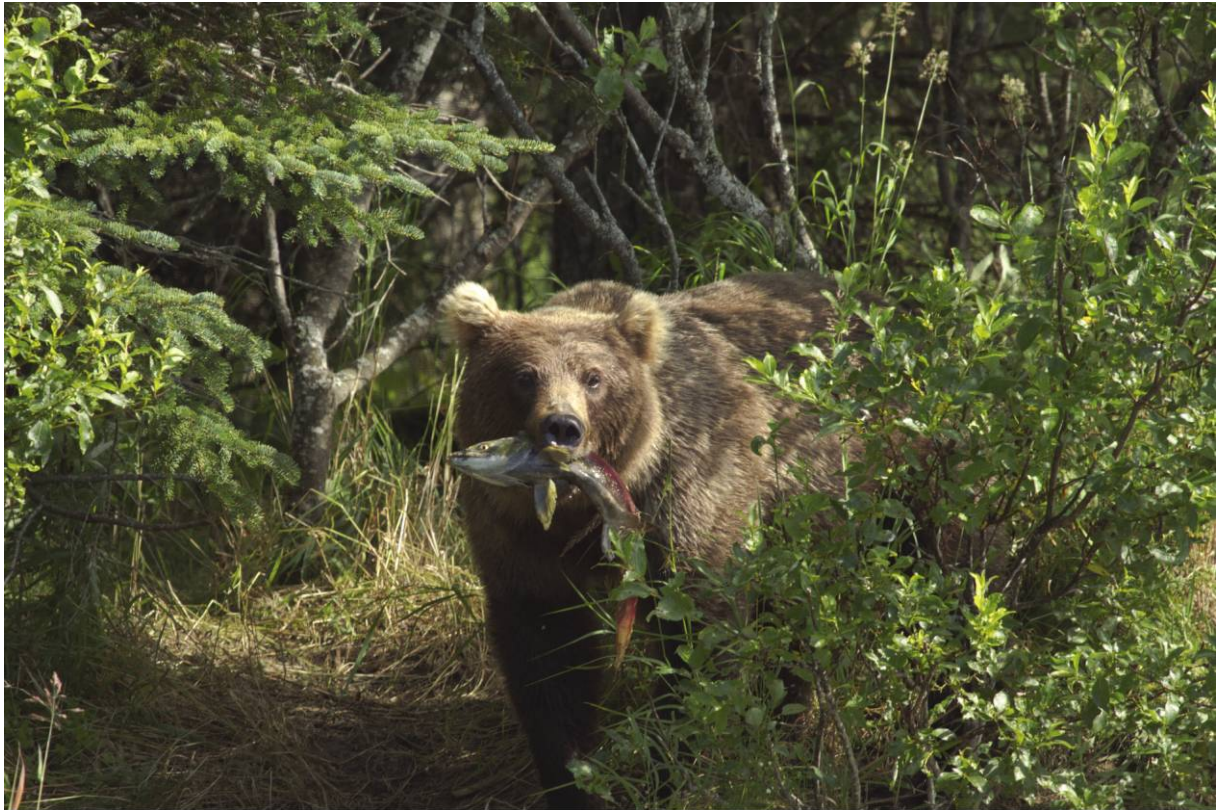
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Top, bear holding female sockeye salmon, removed from a Bristol Bay, Alaska, stream during spawning (credit: Jason Ching, SAFS, University of Washington). Bottom left, male sockeye salmon in shallow water near the mouth of Hansen Creek, Alaska (credit: Curry J. Cunningham). Bottom right, measurement of a male sockeye salmon from Hansen Creek, Alaska, during a stream survey. The conspicuous removal of brain and muscle tissue indicates that this was the result of predation by a brown bear (credit: Curry J. Cunningham).