Research

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Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore

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Energy maximization, time minimization, and linear programming models subject to various constraints have dominated foraging ecology ideas and methods for decades. However, animals must use very complex physiological processes and foraging decisions to ensure fitness that in many cases may not be adequately described by these approaches. An example of this problem occurs when brown bears, *Ursus arctos,* have access to both abundant salmon and fruit. Salmon are one of the most energy and nutrient dense foods available to bears. Fruits are often high in soluble carbohydrates, low to deficient in many required nutrients, and more difficult to efficiently exploit. Therefore, wild brown bears that fatten primarily on fruits without access to salmon are 50% smaller than salmon-feeding bears. Thus, we predicted based on a linear, energy-maximizing model without dietary interaction effects that wild brown bears with access to both abundant salmon and fruit would feed almost exclusively on salmon. However, wild adult females with or without accompanying offspring foraged three times longer per day on fruit than on salmon. Similarly, the relative dry matter intake of ad libitum apples and salmon by captive, adult brown bears averaged 76±5% fruit and 24±5% salmon. Captive brown bears consuming mixed diets with intermediate dietary protein levels had 60% lower maintenance energy costs, 37% to 139% higher efficiencies of mass gain, and 72% to 520% higher maximum rates of gain than when they consumed either salmon or fruit alone. These relationships were nonlinear functions of dietary protein content in which salmon and fruit provided complementary nutritional resources. Both wild and captive bears attempted to regulate total protein, energy, and carbohydrate intake within a multidimensional intake target that both maximized energy intake and mass gain.

Most optimal foraging studies have used linear models to evaluate whether animals are energy maximizers or time minimizers (Stephens and Krebs 1986). Other complexities, such as consuming foods with required nutrients not met simultaneously to energy intake, avoiding predation, or avoiding plant secondary metabolite toxicity, can be included in such models (Pulliam 1975, Belovsky 1981, 1990, Stephens and Krebs 1986, Belovsky and Schmitz 1991, Ben-David et al. 2004, Moore et al. 2005, Marsh et al. 2006). However, many of the early models have been criticized as being nutritionally simplistic and biologically unrealistic (Hobbs 1990, Raubenheimer and Simpson 1997, Bergman et al. 2001, Simpson et al. 2004).

Increasingly, investigators have recognized that animals live in elementally, nutritionally imbalanced worlds and must utilize very complex physiological processes and foraging decisions to ensure fitness by responding to both nutritive and non-nutritive food components (Raubenheimer and Simpson 1997, Felicetti et al. 2003, Simpson et al. 2004, Frost et al. 2005, Marsh et al. 2006). Whereas many of the insights into these more complex physiological and foraging processes have occurred with insects and birds (Raubenheimer and

Simpson 1997, McWilliams et al. 2002, Simpson et al. 2004), we encountered similar complexities in understanding brown bear foraging ecology.

Beginning in early August concurrent to the appearance of many salmon runs and fruit crops, brown bears become hyperphagic as energy intake, growth, and fat accretion are maximized far beyond what occurs at other times (Hilderbrand et al. 1999a). Fat is the essential currency of successful hibernation and cub production (Farley and Robbins 1995, Barboza et al. 1998). Larger, fatter adult females produce faster growing cubs that survive better than do cubs produced by smaller, leaner females (Ramsay and Stirling 1988, Atkinson and Ramsay 1995). Similarly, dominance in males necessary to win breeding opportunities and defend estrus females is, in part, size-based. Brown bears are sexually dimorphic with adult males being 80% larger than adult females (Hilderbrand et al. 1999b). Thus, efficient foraging and growth by all age and sex classes during fall food abundances should be highly selected fitness characteristics.

However, both subadult and adult, male and female Alaskan brown bears at two study sites (Glacier Creek, Kenai Peninsula and Douglas River, Alaska Peninsula) with abundant silver salmon, *Onchorhynchus kisutch,* or sockeye salmon, *O. nerka,* fed extensively on wild fruits, including crowberry, *Empetrum nigrum*, lowbush cranberry, *Vaccinium vitis idaea*, and bog blueberry, *Vaccinium uliginosum* (Rode et al. 2006a, 2006b, 2007, Fortin et al. 2007) (Fig. 1). Fruits accounted for 87.0 ± 15.2% of the residues in brown bear feces collected along salmon streams (Fortin et al. 2007). Because major fruit-producing shrub patches were well-defined and often distant from salmon streams (i.e. higher elevation sites), bears moved between these two food resources and did not feed on fruits solely during random encounters. Fruit-feeding at Douglas River ranged from 10 h day^{-1} for a subadult female to 6 h day^{-1} for a large adult male. Even though salmon were available only during the twice daily low tides (~9 h day^{-1}) at Douglas River, adult females at that site invested the same relative amount of time feeding on fruits as adult females at Glacier Creek where salmon were available 24 h day^{-1} (Fig. 1).

If bears are energy maximizers in the simplest sense, extensive fruit-feeding seems illogical because energy intake at all time scales (instantaneous, daily, and seasonal) and subsequent growth rates are at least three to four times lower when feeding on ad libitum fruit than when feeding on salmon (Welch et al. 1997, Hilderbrand et al. 1999a, 1999b). Even though as many as 13 500 fruits can be consumed per hour (Welch et al. 1997) as compared to the average capture rate of 2.8 ± 0.2 silver salmon h^{-1} at Douglas River (Rode et al. 2006a), silver salmon provided at least seven times more digestible energy per hour than fruit.

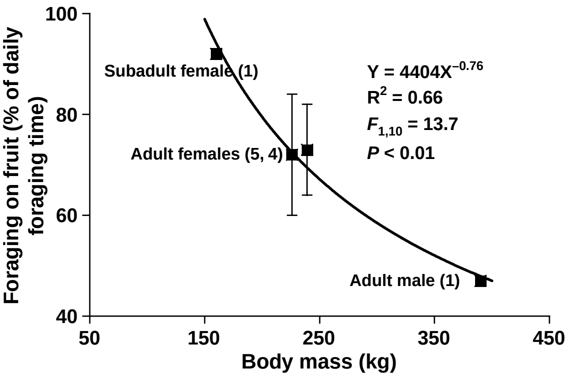

Fig. 1. The relative proportion (mean ± 1SD) of the day that 11 Alaskan brown bears in two populations spent feeding on fruit as compared to salmon during a time of both abundant salmon and fruit. Numbers in parentheses are sample sizes for each age and sex class wearing GPS collars. Regression statistics are for the individual animal data. Adult females were the primary focus of the studies because of their importance to population productivity and because 1) their home ranges are smaller than adult males and 2) they retain GPS collars better than adult males because of a larger ratio of head to neck circumferences. One study (Glacier Creek) collared five adult females only while the other study (Douglas River) collared four adult females, an adult male and subadult female (Rode et al. 2006b, Fortin et al. 2007, Rode et al. 2007).

Sockeye salmon spawning by the thousands in shallow, narrow, clear streams like Glacier Creek can be caught by bears in as little as 2.5 min with from 60 to 93% of all capture attempts being successful (Gende and Quinn 2004, Tollefson et al. 2005). The limit to salmon intake in such situations is not capture rate but the physiological capacity to digest and metabolize ingested nutrients (Hilderbrand et al. 1999a). Thus, linear foraging models that are not constrained by salmon capture rates and do not include interaction effects between different foods (i.e. perfectly substitutable resources; Whelan et al. 1998) always predict 100% salmon consumption for bears pursuing an energy-maximizing strategy (Fig. 2).

The decision to ingest both salmon and fruit occurred in all bears and was not caused by 1) bears fleeing salmon streams due to human encroachment, 2) the social exclusion of subordinate bears or females with accompanying offspring by dominant bears, or 3) inadequate time for catching salmon (Ben-David et al. 2004, Gende and Quinn 2004, 2006, Nevin and Gilbert 2005, Rode et al. 2006a). Human access was limited, adult males were uncommon, there was no choke-point (e.g. waterfalls or rapids) where a few males or barren females could restrict access to salmon, and daily fishing time did not limit salmon intake (Fig. 2) (Hilderbrand et al. 1999a, Rode et al. 2006a).

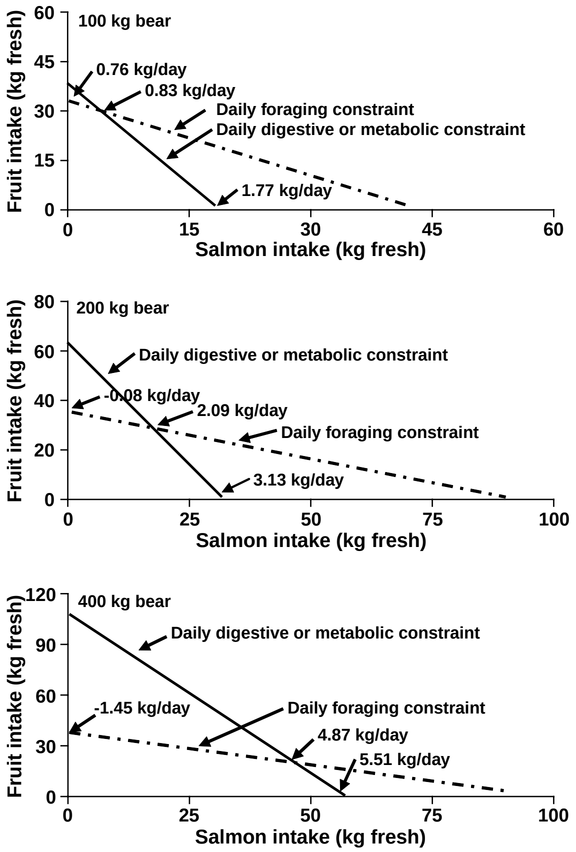

Fig. 2. Linear, energy-maximizing relationships and predicted mass gains for 100 to 400 kg bears having access to both abundant salmon and fruit. Daily intake was constrained either by physical digestive capacity and harvest rate (fruit) or maximum metabolic capacity (salmon) (Welch et al. 1997, Hilderbrand et al. 1999a, Rode et al. 2006a, Rode et al. 2006b). Maximum salmon intake was based on capture rates of 1.3 salmon h^{-1} and 4 h fishing day^{-1} for subadults (i.e. 100 kg bear) and 2.8 salmon h^{-1} and 9 h fishing day^{-1} for larger bears. The regressions between intake and growth in Felicetti et al. (2003) for fruit and Hilderbrand et al. (1999a) for salmon were used to predict growth of bears consuming 100% fruit, 100% salmon, and mixtures of the two foods at the intersection of the constraints posed by maximum foraging effort and maximum metabolic capacity. The prediction of growth rates when bears consumed mixtures of salmon and fruit assumed no dietary interaction effects and are, therefore, the weighted average that would occur based on intake of the two foods (Hilderbrand et al. 1999a, Felicetti et al. 2003, Rode et al. 2006a, 2006b).

Similarly, consuming fruit to meet a limiting mineral or vitamin in fresh salmon was unlikely. Whole, live-caught salmon are rich sources of required minerals, vitamins, essential fatty acids, and amino acids (Geraci 1986). In contrast, many fruits are rich in carbohydrates, low to deficient in protein, and deficient to adequate in required minerals and vitamins (Welch et al. 1997, Rode and Robbins 2000, Felicetti et al. 2003).

Thus, we hypothesized that feeding on both salmon and fruit was driven by the desire to regulate total protein, energy, and carbohydrate intake within a multidimensional intake target that increased the efficiency of gain beyond what could be accomplished with either food alone (Simpson et al. 2004, Simpson and Raubenheimer 2005). The combined value of the two foods to increase body mass would not be the weighted, arithmetic mean of each food's independent value, but greater than their sum and only partially dependent on their energy value (i.e. complementary resources; Whelan et al. 1998).

In earlier studies that made extensive use of pelleted diets, we determined that the maintenance energy cost and the net efficiency of gain above maintenance in brown bears varied 2.5 to 3 fold with dietary protein content (Rode and Robbins 2000, Felicetti et al. 2003). Either too little protein or too much increased the maintenance cost and decreased the efficiency of gain. Thus, we hypothesized that dietary mixing of high protein salmon and high carbohydrate fruit would 1) provide the necessary protein for maintenance and lean mass growth that is not supplied by fruit and 2) dilute the protein of salmon to a level that would minimize the maintenance energy cost and maximize the efficiency of growth by decreasing the costs of deaminating and excreting excess nitrogen. These additional costs do not occur in converting soluble carbohydrates to fat or in directly depositing absorbed dietary fat. However, salmon, like other animal tissues, contain insignificant amounts of carbohydrates (Robbins 1993). While parts of salmon do contain more fat than others and therefore could be an impetus for selective feeding, these tissues also carry a significant protein burden (e.g. fat-laden eggs with 66.4 ± 1.3% protein on a dry matter basis).

Other potential explanations for fruit-feeding in the presence of abundant salmon could include: 1) bears became satiated and bored when feeding on salmon as daily energy and nutrient requirements can be met quickly and time minimization has little meaning for the top predator, 2) bears desired a sweet treat or a food of a different texture, 3) bears continued sampling the nutritional environment to evaluate changing food resources (i.e. contrafreeloading), 4) bears needed gastrointestinal bulk for fecal formation, 5) bears merely continued to forage while traveling on a daily basis throughout their home range for non-nutritional purposes, or 6) bears experienced the same side-effects, such as ketosis, diarrhea, calciuria, and headaches, that humans can when consuming high meat-low carbohydrate diets (Steffen and Nettleton 2006). Whereas any of these ideas may be true, they either can not explain the extent of fruit-feeding or would be very difficult to test. Therefore, this study focused on determining if a combination of nutritional and foraging constraints can explain bear foraging behavior.

Methods

The extent and value of dietary mixing of Chinook salmon, *Oncorhynchus tshawytscha,* and fruit (apples, *Malus pumila*) were studied in captive brown bears at the Washington State Univ. Bear Research, Education and Conservation Center. Although captive and wild bears have different foraging constraints, captive bears provide the opportunity to determine if there is an underlying physiological basis for this process. By examining free-choice dietary mixing and the relationships between intake and growth when bears consumed diets of salmon only, fruit only, or mixtures of salmon and fruit during September and October, we could determine if bears voluntarily chose a mixed diet in the absence of foraging costs, social interactions, or predation risks and if those choices were related to an altered efficiency of growth at a given level of energy intake.

Diet selection study

Four bears, two adult females that were 16 years old and averaged 185 kg, and two adult males that were 17 years old and averaged 305 kg, were used in the diet selection study. These older bears had consumed salmon, apples and various mixtures of these foods over many years and, therefore, presumably had some degree of nutritional wisdom. However, none of the bears had been given ad libitum access to both salmon and apples at the same time.

They were confined individually in 3 × 10 m concrete-floored pens and offered food in two distinct piles, one of which was ad libitum apples (3% protein in the dry matter) supplemented with all required minerals and vitamins (Felicetti et al. 2003). Mineral-vitamin supplementation of the fruit was necessary to eliminate potential choices driven by nutrients other than protein, carbohydrates, and energy. We previously used apples as a surrogate for wild fruits as they are readily available, can be economically fed ad libitum to large brown bears, and are very similar in dry matter, protein, carbohydrate, and digestible energy content to many wild fruits (Welch et al. 1997, Rode and Robbins 2000, Felicetti et al. 2003). The other pile was ad libitum, mature, Chinook salmon (70% protein) provided by Dworshak National Fish Hatchery, Orofino, ID.

To ensure that excess apples and salmon were always available, each bear was fed four times day^{-1}. All foods offered and rejected were weighed daily. The trials continued for 15 days at which time each bear had a relatively stable intake and selection of the two foods for at least five continuous days. Bears were weighed to the nearest 0.1 kg on an electronic platform scale at the beginning and end of each trial. Body fat content of the bears was determined at the start of each trial by bioelectrical impedance analysis (Farley and Robbins 1994).

Bears were fed at restricted levels for several months prior to each trial because intake varies with the condition of each bear and length of time on ad libitum intake. Body fat content of the four bears averaged 29 ± 5%, which is intermediate to that occurring in wild, salmon-feeding bears prior to having access to salmon (~20%) and after three months of feeding on salmon (~35%) (Hilderbrand et al. 1999a). Maximum daily food intake was calculated as the highest consecutive five-day average during each trial. Intake characteristics of these bears were compared to earlier studies in which bears consumed only salmon (Hilderbrand et al. 1999a) or only fruit (Welch et al. 1997). We compared maximum energy intakes across studies as this presumably represented the upper physiological limit to either gastrointestinal capacity or nutrient metabolism and Hilderbrand et al. (1999a) and Welch et al. (1997) had previously reported such values.

Growth study

The efficiency of gain by bears consuming a diet composed of 23% salmon: 77% apples on a fresh weight basis was determined during 15-day feeding trials. This ratio of salmon to apples provided a dietary protein content of 25%, which should meet all maintenance and growth requirements for bears of all ages without being excessive (Felicetti et al. 2003). Six bears, three males and three females, ranging in age and mass from eight months, 50 kg to 20 years, 282 kg were fed individually in 3 × 10 m concrete-floored pens. Bears were randomly assigned at the start of each trial to feeding levels that ranged from weight stasis to significant growth. Because of the need for bears to eat the two foods in the ratio offered, the highest levels of intake were below ad libitum. Bears were weighed and body fat content determined by bioelectrical impedance analysis at the beginning and end of each feeding trial. Body fat content averaged 19 ± 6% at the start of the trials and 25 ± 4% at the end.

Nutritional and statistical analyses

Small samples of each food were collected daily, frozen, freeze-dried, and ground. Crude protein and gross energy content were determined using a carbon-nitrogen analyzer and bomb calorimeter. Digestible energy coefficients for both salmon (93.0 ± 0.8%) and apples (65.7 ± 3.2%) were determined previously (Hilderbrand et al. 1999a, Rode and Robbins 2000). All analyses were in duplicate and corrected to a 100% dry matter basis by determining the dry matter content of subsamples dried at 100°C.

Linear and curvilinear least squares regressions (PROC REG; Anonymous 1998) were used to model the relationships between intake, dietary protein content, and body mass. Differences in slopes of regressions were tested using small sample t-tests (Kleinbaum and Kupper 1978). ANOVA was used to test for differences between means (Anonymous 1998). Means are reported ± 1 SD.

Results

Diet selection study

The relative dry matter intake of ad libitum apples and salmon by captive, adult bears averaged 76 ± 5% fruit and 24 ± 5% salmon. The preference for fruit was even greater on a fresh weight basis (84 ± 5%) because apples contained less dry matter (17.4%) than salmon (28.5%). The protein content of the selected diet averaged 19 ± 3% (dry matter basis). Maximum daily intake of the mixture of salmon and apples averaged 30 ± 9% of body mass. Maximum digestible energy intake of the mixture (855 ± 122 kcal kg$^{-0.75}$ day^{-1}) did not differ ($t = -0.49$, $p = 0.64$) from that of salmon alone (826 ± 33), but was higher ($t = 5.37$, $p = 0.003$) than the maximum intake of fruit alone (552 ± 47).

Growth study

The regression between intake and growth of bears eating a mixed diet fell outside the bounds created by the individual salmon and apple regressions and was not equal to the weighted average of the regressions developed by feeding bears only salmon and only apples (Fig. 3). Digestible energy intake at weight stasis when consuming the mixed diet (102 kcal kg$^{-0.75}$ day^{-1}) was approximately 60% lower than when bears consumed only salmon (231) or only apples (271). This result was a highly predictable function of dietary protein content and occurred across a variety of diet types (Fig. 4a).

The efficiencies of growth above weight stasis (i.e. the slopes of the regressions, Fig. 3) were significantly lower when consuming apples only as compared to salmon only ($t = 4.12$, $p < 0.01$) or the mixed diet ($t = 3.71$, $p < 0.01$). Mass gain above maintenance required 18.9 kcal of digestible energy g^{-1} gain when consuming only apples, 10.8 kcal when consuming only salmon, and 7.9 ± 1.1 kcal on all other pelleted and mixed diets containing from 12 to 35% dietary protein (Fig. 4b). Thus, there was a positive interaction effect on both the maintenance cost and the efficiency of gain above maintenance when dietary mixing produced intermediate dietary protein levels.

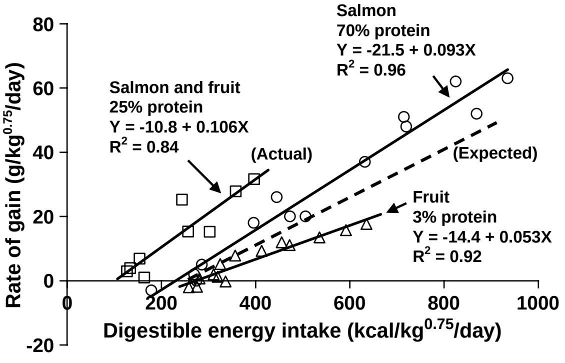

Fig. 3. The relationship between digestible energy intake and growth when captive brown bears consumed diets of either salmon only (Hilderbrand et al. 1999a; $F_{1,13} = 328.3$, $p < 0.001$), apples only (Welch et al. 1997, Rode and Robbins 2000, Felicetti et al. 2003; $F_{1,13} = 131.1$, $p < 0.001$), or a mixture of 77% apples and 23% salmon (current study; $F_{1,8} = 35.9$, $p < 0.001$). The dashed line is where the mixed diet data and regression should be if there were no interaction effects between apples and salmon and, therefore, the nutritional value of the mixed diet was the weighted, arithmetic mean of each food's independent value.

The combination of these two effects produced maximum rates of gain per unit of energy intake that peaked near the dietary protein content chosen by the captive adults (i.e. 19 ± 3%) (Fig. 5). Predicted growth rates using the intercepts and slopes of Fig. 4a and 4b at the maximum intakes observed when captive bears were offered food ad libitum ranged from 93 ± 15 g kg$^{-0.75}$ day^{-1} when consuming a mixture of salmon and fruit with 19% protein to 54 ± 3 g kg$^{-0.75}$ day^{-1} when consuming only salmon to 15 ± 3 g kg$^{-0.75}$ day^{-1} when consuming only fruit. Thus, while captive bears fed either ad libitum salmon or ad libitum salmon and apples consumed the same number of digestible calories, those consuming the mixed diet at the most efficient dietary protein level would gain 72% faster than those consuming salmon alone (Fig. 3–5).

Discussion

Brown bears that forage on abundant salmon can benefit by leaving spawning streams to consume abundant fruit, even though fruit consumption does not conform to a simplistic energy maximization foraging strategy (Fig. 2). Consuming inadequate or

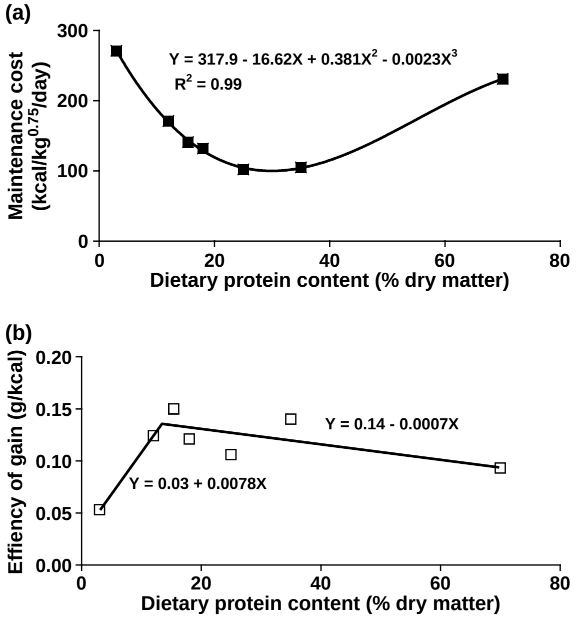

Fig. 4. (a) digestible energy intake at weight stasis (i.e. x-intercepts of Fig. 3; for the regression: $F_{3,6} = 856.5$, $p < 0.0001$, all coefficients significant at $p < 0.002$) and (b) the efficiency of gain above maintenance (i.e. slopes of regressions, Fig. 3) as a function of dietary protein content for a variety of diets fed to captive brown bears. For example, the x-intercept value plotted for the fruit diet from Fig. 3 is $14.4 \div 0.053 = 271$ kcal $kg^{-0.75}$ day^{-1} (Fig. 4a), and the slope is 0.053 g^{-1} gain $kcal^{-1}$ of digestible energy intake (Fig. 4b). Diets included fresh and dried apples, pelleted diets having from 3 to 35% protein, salmon, and the current fruit and salmon mixture (Welch et al. 1997, Hilderbrand et al. 1999a, Rode and Robbins 2000, Felicetti et al. 2003, and current study). Regression statistics are not provided for the equations of part (b) because of the limited and overlapping data used to create each of the two linear regressions. Choice of regressions was based on 1) knowledge of the interactions between dietary protein content and energy intake, dietary induced thermogenesis, and energy content and composition of mass gain (Raubenheimer and Simpson 1997, Felicetti et al. 2003, Simpson and Raubenheimer 2005) and 2) identification of the model (cubic, linear, quadratic, or exponential-linear) that provided the highest F-statistic and lowest p-value.

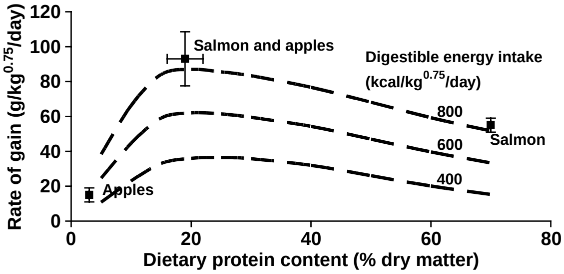

Fig. 5. Illustration of the effect of nutritionally optimizing protein intake on growth rates when brown bears consume various levels of energy. The curves depicting growth at 400, 600, and 800 kcal $kg^{-0.75}$ day^{-1} were produced by using the equations of Fig. 4a and 4b to provide the regression constants for predicting growth rates at six dietary protein levels between 3 to 70% protein. Those values were plotted and fitted with smooth curves for each level of energy intake. For comparison, estimated growth rates are shown at the maximum intakes that occurred when captive brown bears consumed apples only (552 ± 47 kcal $kg^{-0.75}$ day^{-1}) (Welch et al. 1997), salmon only (826 ± 33) (Hilderbrand et al. 1999a), and the salmon–apple mixture (855 ± 122) containing 19 ± 3% protein (current study). These latter points illustrate 1) the importance of nutritionally optimizing dietary protein content while energy maximizing and 2) the apparent nutritional wisdom of the four adult, captive bears that mixed salmon and apples to create a dietary protein level that maximized mass gain.

excess protein, even when part of a high energy diet, occurs at a cost that both captive and wild bears apparently sense and avoid when possible. When foraging constraints and the nonlinear benefits of consuming complementary foods were included in the model, the optimal dietary mix of salmon and fruit that maximized growth shifted towards higher relative intake of fruit as bear size decreased (Fig. 6), which was the pattern observed in the wild (Fig. 1). Similarly, the relative growth benefit of dietary mixing increased as bear size decreased (Fig. 6). For example, predicted growth rates due to dietary mixing increased 82% in a 100 kg bear relative to consuming only salmon, but increased only 21% in a 400 kg bear.

These patterns occur because smaller bears are less constrained by fruit harvesting rates relative to their total daily energy requirement than are larger bears (Welch et al. 1997). Therefore, small bears can more fully offset the reduced energy intake associated with decreased salmon consumption by increasing fruit consumption to optimize protein, energy and carbohydrate intake. Thus, while all bears energy maximize and attempt to nutritionally optimize, only the smaller bears are able to both energy maximize and nutritionally optimize fully when consuming small, dispersed, wild berries. However, this pattern of small bears benefiting by feeding more on fruit and large bears benefiting by feeding more on salmon also conforms to the previous explanation of this phenomena, which is that 1) salmon are the preferred food for all age and sex classes (i.e. Fig. 2), 2) subordinate bears must avoid the high density of large, dominant, aggressive, and potentially dangerous adult bears, particularly males, that many salmon streams attract, and, therefore, 3) small bears are relegated to feeding on less nutritious, less preferred fruit (Ben-David et al. 2004, Gende and Quinn 2006, Rode et al. 2006a).

Thus, while both explanations produce the same result and may act synergistically when fishing opportunities

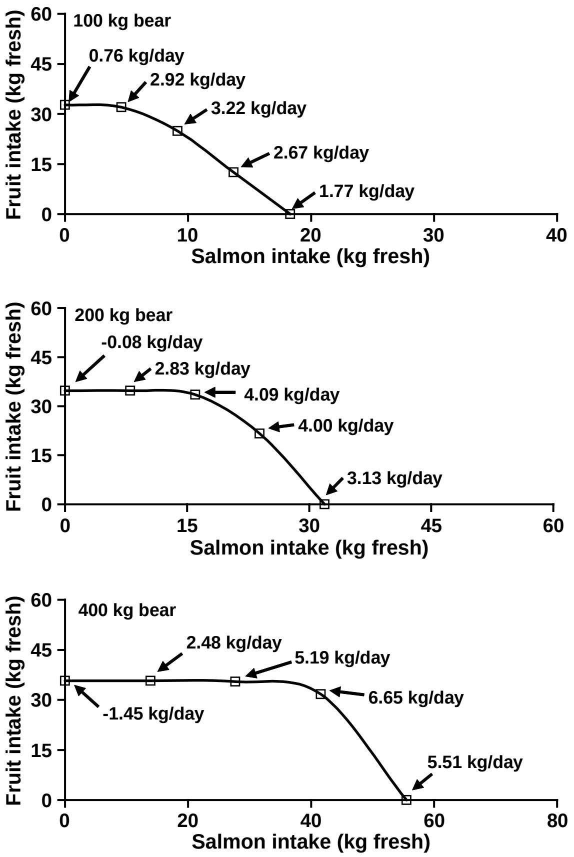

Fig. 6. Estimated growth rates at varying levels of fruit and salmon intake by free-ranging brown bears. Growth rates at a given fruit and salmon intake were predicted from the regression intercepts and slopes of Fig. 4a and 4b. The open squares on each graph represent 100%, 75%, 50%, 25% and 0% of the maximum daily salmon intake. The model assumed that all bears attempted to ingest fruit up to the daily digestive capacity to fully replace the deficit in digestible energy intake created by the reduced salmon intake. However, the model constrained foraging to a maximum of 15 h day^{-1}, with no more than 12 h day^{-1} available for fruit harvesting (Welch et al. 1997).

are limited, the stimulus differs in being negative in the predation avoidance hypothesis and positive in the increased growth rate hypothesis. The latter appears most important in the current study because large, captive bears preferred fruit over salmon, captive bears voluntarily chose the mixture of fruit and salmon that maximized growth per unit of energy intake in the absence of social interactions and foraging constraints (Fig. 5), the pattern of fruit and salmon consumption observed in wild bears (Fig. 1) conforms to the pattern predicted based solely on foraging constraints and the growth rate hypothesis (Fig. 6), and even the wild adult male and adult females without cubs (i.e. dominant bears) foraged extensively on fruit (Fig. 1). Thus, neither wild nor captive bears appeared to treat fruit as an inferior dietary choice when combined with salmon in a mixed diet. However, there may be additional reasons why smaller bears might purposefully decrease salmon foraging time and increase fruit foraging as long as minimally adequate salmon or other protein sources are consumed to maximize growth.

In summary, instantaneous intake of energy as measured by harvesting rates, daily digestible energy intake as constrained by gut capacity or available foraging time, and linear and nonlinear combinations of both failed to explain diet mixing in wild and captive brown bears, although these techniques have successfully predicted bite size, diet composition, and food patch selection in many herbivores, nectivores, and carnivores (Belovsky 1981, Wilmshurst et al. 1995, Shipley et al. 1999, Bergman et al. 2001, Simpson et al. 2004). While various nutrients and antinutrients have been identified in many models as minimum or maximum constraints on acquiring energy (Pulliam 1975, Belovsky 1981, 1990), this approach does not allow fitness or the value of the model currency to change gradually and curvilinearly with intake of a constraining nutrient (Simpson et al. 2004). The current study demonstrated that 1) protein cannot be treated as a minimum constraint (i.e. bears must ingest $\geq$15% dietary protein) on diet selection by brown bears and 2) foraging rates on small berries will prevent very large brown bears from consuming the most preferred and efficient diet that would maximize their growth rate. Instead, the efficiency of energy use and gain in body mass changes continuously with the relative and absolute amounts of energy and protein ingested, and small subordinate bears may be the only ones capable of mixing salmon and wild fruits in ways that maximize metabolic efficiency to create the most preferred diet. Thus, foraging models developed for some omnivores and herbivores that use single currencies measured over short time scales to explain diet selection by adults may not explain diet selection across the wider population.

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