

NUMERICAL AND FUNCTIONAL RESPONSES OF MIGRANT BALD EAGLES EXPLOITING A SEASONALLY CONCENTRATED FOOD SOURCE¹

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Abstract. We determined the numerical and functional responses of migrant Bald Eagles (*Haliaeetus leucocephalus*) feeding on spawning kokanee salmon (*Oncorhynchus nerka*) at Hauser Reservoir, Montana from 1991–1995. Number of Bald Eagles was positively correlated with the fluctuating number of salmon carcasses during four of five years. Immigration and emigration rates were similar across years and were facilitated by several behavioral and physical characteristics of eagles: group foraging, communal roosting, and keen eyesight. Number of subadult eagles showed closer synchrony with density of salmon carcasses than did adult eagles. Eagles scavenging for salmon exhibited a Type II functional response. Handling times of scavenging eagles remained constant across the range of salmon carcass densities, whereas daily attack rates increased. Functional responses of scavenging eagles differed between age groups; adults exhibited a Type I response, whereas that of subadults could not be characterized. Handling times of scavenging adults were constant, but those of subadults increased with salmon density. Attack rates of scavenging adults increased with salmon carcass density. Consumption rates differed between age groups and among eagles using foraging modes of scavenging, stooping, and pirating, which suggests that eagles viewed live and dead salmon as alternative prey types. Bald Eagle scavenging of kokanee salmon was inversely density dependent.

Key words: *Bald Eagle, functional response, Haliaeetus leucocephalus, kokanee salmon, migration, numerical response, Oncorhynchus nerka.*

INTRODUCTION

Predators often exhibit numerical and functional responses to fluctuating prey densities (Solomon 1949). Predators can respond numerically by changing birth and death rates, immigration and emigration rates, or both (Murdoch and Oaten 1975, Hassell 1978, Taylor 1984). As prey densities increase, consumption rates of predators may increase linearly (Type I functional response), at a decelerating rate (Type II), sigmoidally (Type III), or first increase and then decrease (Type IV) (Holling 1959b, 1961). Although it may be practical to measure numerical responses in field settings, functional responses are usually determined in laboratory experi-

ments. Quantifying components that determine the functional response (handling time, search rate) in the field is difficult because predation events are rarely observed. However, more field testing is necessary because some predators show variable functional responses as the spatial distribution of prey changes, as age composition of feeding groups varies, or as alternative prey become available (Hassell 1978, Murdoch and Sih 1978, Real 1979). Understanding how predators respond to variable ecological conditions also is a prerequisite to interpreting the consequences of predator-prey interactions on prey population size and community dynamics.

Field investigations of avian numerical and functional responses often concern the behavior of raptors during the breeding season (Adamcik et al. 1979, Korpimäki and Norrdahl 1991, Redpath and Thirgood 1999). Raptor studies are popular because assessing relative density of raptors and their prey is easily accomplished using well-established techniques, and because

¹ Received 19 November 1999. Accepted 12 April 2000.

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raptor diets can be determined by enumerating the undigested prey remains in the pellets raptors regurgitate after digestion. Although functional responses are inferred from pellet content, the mechanisms responsible for changes in feeding rates remain unknown because handling times and search rates are not measured (Holling 1959a). The ease of estimating diet from pellet analyses also has resulted in an overrepresentation of studies on raptors that exploit small mammals.

Bald Eagles (*Haliaeetus leucocephalus*) often forage in large groups when food resources are concentrated (McClelland et al. 1982, Stalmaster and Gessaman 1984), which allows direct observation of many predation events. For example, during autumn migration Bald Eagles congregate by the hundreds along the upper Missouri River to feed on spawning kokanee salmon (*Oncorhynchus nerka*). Examination of numerical and functional responses at this field site is tractable and of scientific interest for several reasons. First, the predator-prey system is simple, being composed primarily of two species which occur at high density. Other birds (Laridae, Corvidae) and mammals (Canidae, Mustelidae) inhabit the area but only occasionally feed on salmon carcasses. These circumstances simplify interpretation of eagle behavior because the complexity associated with competing predators and alternative prey is absent. Second, the number of spawning salmon fluctuates annually (Montana Department of Fish, Wildlife, and Parks [MDFWP] 1989), which makes across-year comparisons of eagle numerical and functional responses possible. Third, eagles forage for salmon by stooping, scavenging, and pirating. Each foraging technique has different costs and benefits (Stalmaster and Gessaman 1984, Knight and Skagen 1988, Bennetts and McClelland 1997), and although this type of behavioral plasticity can theoretically cause variable functional responses (Abrams 1982), it has received little empirical study.

We predicted that Bald Eagles congregating at Hauser Reservoir would show a numerical response, without time lags, to fluctuating salmon numbers because other migrating raptors have displayed rapid numerical responses as they wandered in search of widely distributed prey (Phelan and Robertson 1978, Baker and Brooks 1981, McClelland et al. 1982). In addition, we predicted that number of adult eagles would

show greater synchrony with fluctuating salmon numbers than subadults because older birds are more proficient foragers and better at assessing habitat quality (Wunderle 1991). Predicting the functional response was difficult. In predator-prey systems composed of only two species, nearly all predators exhibited Type II functional responses (Murdoch and Oaten 1975), which meant that handling time and search rate remained constant as prey density changed (Holling 1959a). However, given the high degree of interference competition (i.e., piracy) observed among foraging eagles (Stalmaster and Gessaman 1984, Knight and Skagen 1988), it seemed more likely that handling time and search rate would vary with prey density. Therefore, we predicted that eagles would exhibit either a Type III or Type IV functional response.

METHODS

STUDY AREA

This study was conducted at Hauser Reservoir (23 river-km), the second of three impoundments along the upper Missouri River in west-central Montana (46°41'N, 111°49'W). Hundreds of eagles congregated at Hauser Reservoir during autumn migration to feed on spawning and dead salmon after an introduced kokanee salmon population proliferated during the 1980s (MDFWP 1989). The first 7 km of river below the upriver dam and adjacent public shoreline was closed from mid-October to mid-December to protect eagles from human disturbance.

NUMERICAL RESPONSE

To determine the numerical response, a four-person team conducted surveys by motorboat once a week from late September through December 1991–1995 to estimate the number of eagles congregating at Hauser Reservoir (Restani 2000). Observers independently counted eagles and classified each as adult (mostly white head and tail: eagles 3.5 years of age or older [McCollough 1989]), subadult (all other plumages), or unknown. The boat operator and one observer counted adults, while the other two observers counted subadults. Counts of adults and subadults were first averaged and then summed to produce the total survey estimate for each week.

We estimated relative prey abundance by counting the number of salmon carcasses on and within 2 m of two 0.8-km shoreline transects in

the primary spawning reach. We walked both shorelines and used a headlamp to count carcasses 1.5 hr before sunrise on the day of eagle surveys (1991–1995). The number of live salmon was not estimated. The ratio of live to dead salmon may have decreased as the spawning season of this semelparous species progressed, thus counts of carcasses may have misrepresented the total number of prey available (sum of live and dead salmon). The magnitude of this potential bias could not be determined because it depended on the difference in time between peak spawning activity and peak dying of salmon. We believe this difference was slight but chose to be conservative and therefore confined the most detailed analyses of functional responses to eagles that scavenged salmon because an unbiased estimate of the number of dead salmon was available.

FUNCTIONAL RESPONSE

To determine the functional response of scavenging eagles, we recorded the foraging behavior of Bald Eagles from a vehicle parked 20–150 m from the primary salmon spawning and eagle foraging sites. Observations were made at least three times per week from late October to mid-December 1992–1994 in each of two time periods: 0.5 hr before sunrise to noon and noon to 0.5 hr after sunset. We classified foraging eagles as adult or subadult, recorded the time of each foraging attempt, and estimated the fraction of salmon consumed (0, 1/3, 2/3, whole). We calculated the amount of salmon consumed per foraging attempt by multiplying the fraction consumed by mean mass of salmon (data in Restani 2000).

Observations of individual foraging bouts began when eagles secured a salmon and ended when the salmon was consumed, dropped, or lost to a pirating conspecific. We attempted to record all foraging attempts. Foraging attempts were categorized as: (1) stooping, any flight during which an eagle circled low over the water and dropped its legs, regardless of whether a salmon was struck or captured, (2) scavenging, an eagle landed on the ground and approached a salmon carcass washed ashore, (3) pirating, any approach, whether on the ground or in flight, where an attacking eagle came within 1 m of an eagle with a salmon.

We estimated daily consumption rate of eagles (using all three foraging modes) by dividing

total salmon consumed (g) by the maximum daily count of eagles recorded at 1-hr intervals during foraging observations (see Stalmaster and Gessaman 1984). Handling time was the number of minutes it took an individual eagle to consume a whole salmon once seized. Overall daily attack rate was calculated as the total number of foraging attempts (by stooping, scavenging, and pirating) divided by total number of eagles. We also calculated daily consumption rates, handling times, and attack rates for eagles using each of the three foraging modes. Analyses of functional responses (all eagles and by the two age groups) were confined to scavenging eagles because an unbiased estimate of salmon carcass density was available. Scavenging consumption rates, attack rates, and handling times also were calculated for both subadult and adult eagles.

STATISTICAL ANALYSES

We used parametric tests and, if necessary, transformed data prior to analyses to ensure normality (Kolmogorov-Smirnov test) and homogeneity of variances (Levene's test) (SAS Institute 1990). We used ANOVA (Tukey's post-hoc tests) and *t*-tests to compare means among or between groups, respectively. Simple linear regression was used to determine the numerical response. To describe the functional response of scavenging eagles, we first averaged consumption rates ($n = 54$ days of observation) by salmon carcass density and then fitted those points ($n = 13$ – 15) to simple linear and non-linear (disc equation [Holling 1959a], log, and quadratic) regression models; the best fit is reported. We similarly determined how handling time and attack rates of scavenging eagles varied with density of salmon carcasses. We also tested numerical and functional response data for differences between subadults and adults. Frequency data were analyzed with chi-square tests. Untransformed means \pm SE are reported in text, tables, and figures to facilitate interpretation.

RESULTS

NUMERICAL RESPONSE

Each autumn migrating Bald Eagles arrived at Hauser Reservoir in early October and yearly counts of eagles and kokanee salmon peaked over a 3.5-week period from mid-November to early December (Fig. 1). A strong positive relationship between eagle and salmon carcass numbers occurred each year except in 1995, the

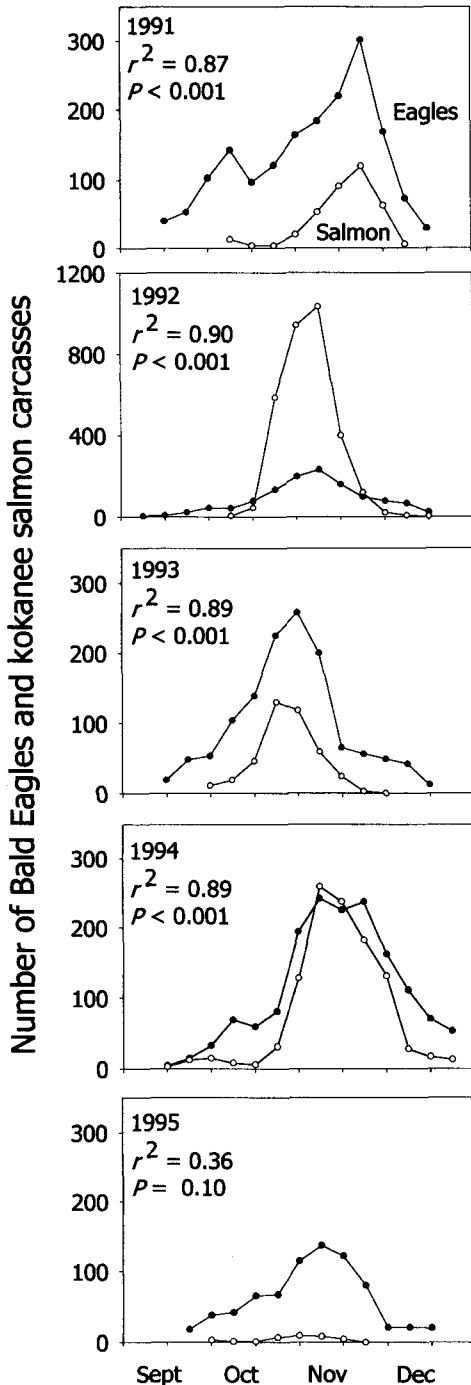


FIGURE 1. Simple linear regression of the numerical response of Bald Eagles feeding on kokanee salmon at Hauser Reservoir, Montana, 1991–1995. Points represent weekly counts and each panel is drawn on the same scale except 1992. Salmon estimates represent carcasses.

year of lowest prey availability. Eagles responded to the fluctuating number of salmon carcasses without time lags in 1991, 1992, and 1994. Mean weekly number of eagles was similar among years ($F_{4,61} = 1.5$, $P = 0.21$), despite differences in mean weekly counts of salmon ($F_{4,46} = 3.5$, $P < 0.02$). A linear relationship did not exist between peak counts of eagles and salmon across years ($r^2 = 0.01$, $P = 0.85$, $n = 5$).

Each year approximately twice as many subadult as adult eagles (57–71% versus 29–43%) were counted during weekly surveys ($n = 12$ –14 counts per year). Number of subadults was more strongly correlated than adults with the number of salmon carcasses in 1992 ($r^2 = 0.92$ versus 0.77, $P < 0.001$) and 1994 ($r^2 = 0.89$ versus 0.68, $P < 0.001$), the years when salmon were abundant. No strong differences existed between age groups in 1991 ($r^2 = 0.85$ versus 0.87, $P < 0.001$), 1993 ($r^2 = 0.81$ versus 0.91, $P < 0.001$), and 1995 ($r^2 = 0.34$ versus 0.34, $P < 0.02$). The number of subadults and adults peaked the same week from 1991–1993, whereas subadults peaked earlier than adults in 1994 and 1995 by one and two weeks, respectively.

FUNCTIONAL RESPONSE

Consumption rates of Bald Eagles feeding on kokanee salmon at Hauser Reservoir were estimated from a sample of 3,907 foraging attempts over 54 days of observation (1992–1994). Although significant populations of waterfowl and fish species other than kokanee salmon inhabited Hauser Reservoir, eagles rarely attacked (2 of 3,907 foraging attempts) these alternative prey. Eagles foraged for salmon by stooping ($n = 1,246$), scavenging ($n = 680$), and pirating ($n = 1,981$). Eagles scavenged more and stooped less during 1992 ($n = 1,262$) and 1994 ($n = 1,806$) than in 1993 ($n = 839$), the year salmon were least common ($\chi^2_4 = 51.7$, $P < 0.001$).

We combined all yearly data for analyses of scavenging functional responses because mass of kokanee salmon and consumption rates (g eagle⁻¹ day⁻¹) were similar among years (Table 1). Significant differences in consumption rates, attack rates, and handling times existed among foraging modes (Table 2). Scavenging eagles exhibited a Type II functional response (Fig. 2). Handling times of scavenging eagles remained constant across the range of salmon densities ($r^2 = 0.17$, $P = 0.15$, $n = 14$), whereas attack rates increased ($r^2 = 0.31$, $P < 0.04$, $n = 15$) (Fig.

TABLE 1. Mean ± SE mass (g) of kokanee salmon carcasses and mean ± SE attack (attempts eagle⁻¹ day⁻¹) and consumption (g eagle⁻¹ day⁻¹) rates of Bald Eagles feeding on salmon at Hauser Reservoir, Montana, 1992–1994. All *P* > 0.5.

Year	Salmon mass (<i>n</i>)	Attack rate (<i>n</i>)	Consumption rate (<i>n</i>)
1992	831.1 ± 38.3 (40)	3.1 ± 0.2 (21)	656.5 ± 45.0 (21)
1993	882.5 ± 35.4 (40)	3.2 ± 0.3 (14)	611.3 ± 52.2 (14)
1994	859.5 ± 34.7 (40)	3.2 ± 0.2 (19)	642.5 ± 45.9 (19)
Mean	857.4 ± 20.8 (120)	3.2 ± 0.1 (54)	639.8 ± 27.0 (54)
<i>F</i> (df)	0.5 (2, 117)	<0.1 (2, 51)	0.1 (2, 51)

3). Piracy attempts directed against scavenging eagles increased with salmon density ($r^2 = 0.33$, $P < 0.04$, $n = 14$). Proportion of all salmon carcasses available that were consumed by scavenging eagles was inversely density dependent (Fig. 4).

Subadult and adult eagles had similar mean consumption rates and handling times when scavenging salmon, but subadults had higher attack rates (Table 3). The functional response of scavenging subadults could not be characterized (all $P > 0.6$, linear and non-linear regression), whereas adults exhibited a Type I response ($y = 113.4 + 0.2x$; $r^2 = 0.28$, $P < 0.05$, $n = 15$). Handling times of scavenging subadults tended to increase with salmon number ($r^2 = 0.27$, $P = 0.07$, $n = 13$), whereas handling times of adults remained constant ($r^2 = 0.04$, $P = 0.50$, $n = 13$). Subadults did not increase scavenging attack rates with salmon number ($r^2 = 0.05$, $P = 0.42$, $n = 15$), but adults did ($r^2 = 0.58$, $P < 0.01$, $n = 15$). As salmon density rose, both age groups, particularly subadults, increased piracy attempts against scavenging eagles (subadults: $r^2 = 0.47$, $P < 0.01$, $n = 14$; adults: $r^2 = 0.28$, $P = 0.06$, $n = 14$). Mean number of pirates attempting to steal salmon from scavenging subadult (1.1 ± 1.0 , $n = 476$) and adult (1.2 ± 1.2 ,

$n = 227$) eagles was similar ($t_{701} = 0.70$, $P = 0.48$).

DISCUSSION

NUMERICAL RESPONSE

As predicted, Bald Eagles showed a strong numerical response to the number of kokanee salmon carcasses. Moreover, eagles tracked a prey base that shifted in peak availability from early December to mid-November 1991–1995, which established that prey availability rather than environmental conditions or the timing of autumn migration controlled the numerical response. This synchrony occurred at an autumn migratory stopover and was manifest in rates of immigration and emigration. Despite significant differences in prey abundance from 1991–1995, two lines of evidence indicated that immigration and emigration rates were similar each year: (1) mean weekly number of eagles was similar each year (this study), and (2) mean residence time of radio-tagged eagles was similar (Restani 2000).

Although Bald Eagles are generalist predators, their ability to track salmon without time lags when foraging as specialists supports the hypothesis that diet breadth delimits the numer-

TABLE 2. Mean ± SE foraging parameters of Bald Eagles feeding on kokanee salmon at Hauser Reservoir, Montana, 1992–1994.

	Foraging mode			<i>F</i> (df)	<i>P</i>
	Scavenging (<i>n</i>)	Stooping (<i>n</i>)	Pirating (<i>n</i>)		
Consumption rate (g eagle ⁻¹ day ⁻¹) ^a	168.6 ± 15.0 (54)	260.8 ± 17.6 (54)	210.6 ± 15.5 (54)	4.4 (2, 159)	<0.02
Attack rate (attempts eagle ⁻¹ day ⁻¹) ^b	0.5 ± 0.1 (54)	1.1 ± 0.1 (54)	1.5 ± 0.1 (54)	67.1 (2, 159)	<0.001
Handling time (min salmon ⁻¹) ^c	10.5 ± 0.5 (103)	13.4 ± 0.4 (229)	11.2 ± 1.0 (32)	12.8 (2, 361)	<0.001

^a Scavenging < stooping and pirating.
^b Scavenging < stooping < pirating.
^c Scavenging and pirating < stooping.

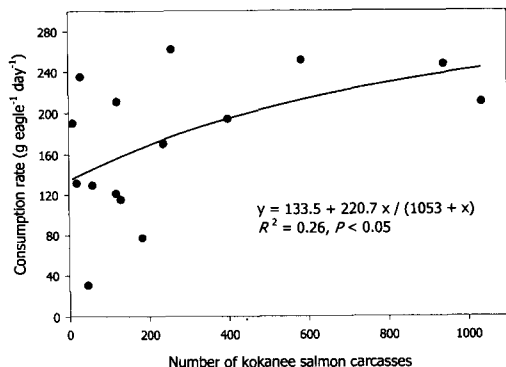


FIGURE 2. Type II functional response of Bald Eagles scavenging kokanee salmon at Hauser Reservoir, Montana, 1992–1994. Each point represents mean consumption rate.

ical response (Andersson and Erlinge 1977). This hypothesis stems almost exclusively from studies of solitary raptors exploiting microtine prey. Nomadic food specialists exhibit the greatest synchrony with prey, whereas resident generalists follow prey increases with time lags. When behaviorally flexible eagles are freed from territorial constraints imposed by breeding, they also can respond to changes in prey number quickly (McClelland et al. 1982, Knight and Knight 1983).

Sociality appears to play an important role in shaping the numerical response of Bald Eagles during the nonbreeding season. If eagles can see each other from 40–65 km (McClelland et al. 1982), then eagles migrating through an 80–130 km wide corridor around Hauser Reservoir could be attracted to the abundant prey base by noting the presence of other eagles, which often soar in large groups after morning foraging periods. Bald Eagles that depart communal roosts used in autumn and winter also follow each other to foraging sites (Knight and Knight 1983). How eagles assess declining number of salmon remains unknown because departure from Hauser Reservoir occurs before consumption rates decrease (Restani 2000).

Bald Eagles congregating at Glacier National Park, Montana during autumn migration exhibited a linear numerical response to kokanee salmon from 1979–1989 (McClelland et al. 1982, Spencer et al. 1991). In contrast, we found that peak numbers of eagles and salmon were unrelated despite a ten-fold increase in prey abundance from 1991–1995. Lack of foraging

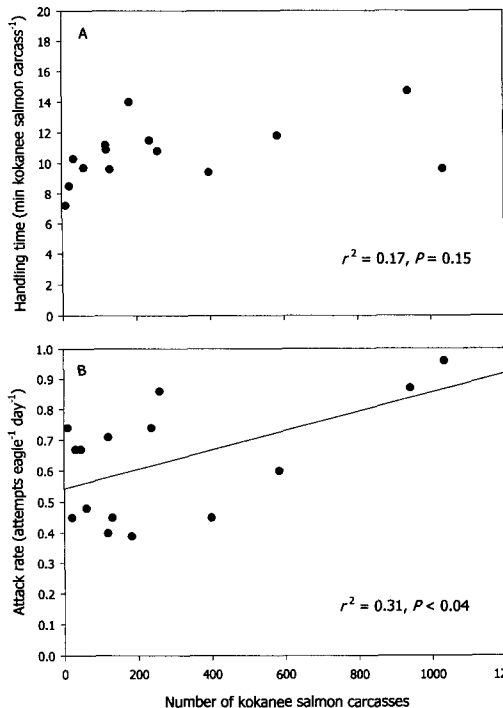


FIGURE 3. Simple linear regression of mean handling times (top panel) and mean attack rates (bottom panel) of Bald Eagles scavenging kokanee salmon at Hauser Reservoir, Montana, 1992–1994.

habitat at Hauser Reservoir probably moderated the numerical response. Most of the shoreline along the reservoir was unforested, which reduced foraging opportunities for this sit-and-wait predator. The reservoir also lacked small islands and exposed gravel bars, habitats suit-

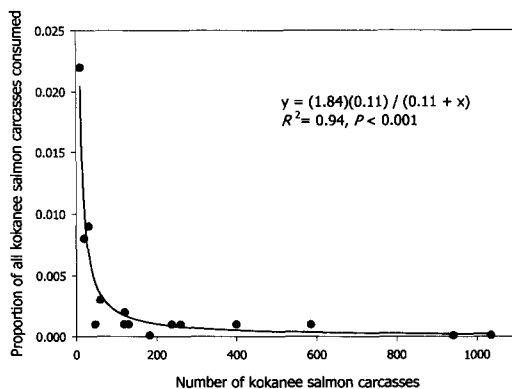


FIGURE 4. Proportion of kokanee salmon carcasses consumed by Bald Eagles at Hauser Reservoir, Montana, 1992–1994.

TABLE 3. Mean \pm SE age-specific foraging parameters of Bald Eagles scavenging kokanee salmon at Hauser Reservoir, Montana, 1992–1994.

	Subadult	Adult	<i>t</i>	<i>P</i>	<i>n</i>
Consumption rate (g eagle ⁻¹ day ⁻¹)	198.5 \pm 19.3	161.7 \pm 19.1	1.3	0.18	108
Attack rate (attempts eagle ⁻¹ day ⁻¹)	0.7 \pm 0.1	0.5 \pm 0.1	2.0	<0.05	108
Handling time (min salmon ⁻¹)	10.5 \pm 0.6	10.6 \pm 0.9	<0.1	0.95	103

able for scavenging. Housing developments along an additional 2–3 km shoreline further diminished the amount of foraging habitat. None of these limiting factors existed in Glacier National Park.

FUNCTIONAL RESPONSE

Contrary to predictions, Bald Eagles scavenging kokanee salmon carcasses at Hauser Reservoir exhibited a Type II functional response, consumption rates characterized by constant handling time and search rate (Holling 1959a). Eagles maintained constant handling times over the range of salmon densities despite interference competition (i.e., piracy) increasing with number of carcasses. Handling time was composed of time devoted to feeding and time devoted to vigilance, two mutually exclusive components. Vigilance level of Bald Eagles increased with frequency of piracy (Knight and Knight 1986), so eagles must have increased feeding rates (bites min⁻¹) to maintain constant handling time. Attack rate, the product of search rate (area time⁻¹) and prey density (number area⁻¹) (Holling 1959a), increased with number of salmon carcasses. Increases in prey density most likely accounted for changes in attack rate because if search rate had increased with prey density, a Type III functional response would have been produced.

Adult eagles scavenging kokanee salmon exhibited a Type I functional response, whereas the response of subadults could not be categorized. Previous studies reporting age-specific functional responses identified size and dominance as the mechanisms producing age-dependent behavior (Hassell et al. 1976, Murdoch and Sih 1978, Sih 1981). However, Bald Eagles of different ages were of similar size (Restani 2000), and dominance was independent of age in other studies (Knight and Skagen 1988, Garcelon 1990). Differences in allocation of foraging effort between stooping and scavenging, constrained by age-dependent foraging proficiency (Bennetts and

McClelland 1997), produced variable functional responses to prey increases. Adults switched from live to dead salmon when carcasses became abundant, but subadults did not adjust scavenging attack rates.

Interference competition, mediated through food piracy, also affected the functional response of eagles scavenging in groups. When density of salmon carcasses increased, subadult scavengers incurred a foraging cost (i.e., increased handling time) because piracy attempts rose. Our inability to characterize the functional response of subadults suggests that pirating eagles prevent an increase in consumption rates with prey density (see also Stalmaster and Gesaman 1984). In contrast, adults were able to maintain constant handling times despite this competition, which was reflected in an increasing (Type I) functional response.

Finally, significant differences exist in consumption rates, handling times, and attack rates among Bald Eagles using foraging modes of stooping, scavenging, and pirating. Further study is needed to evaluate the possibility that interactions among the different foraging modes influence functional responses. Estimates of the number of live salmon and determination of stooping and pirating functional responses are necessary to test the hypothesis that live and dead salmon represent distinct prey “types,” and that eagles respond to densities of each. Piracy behavior probably plays an important role in group foraging dynamics of eagles because it is so common and increases with the number of salmon carcasses.

ACKNOWLEDGMENTS

We thank K. Sullivan, M. Ritchie, B. Gilbert, J. Gesaman, and E. Evans for valuable discussions and guidance throughout this project. They, N. Clum, J. Roper, and two anonymous reviewers commented on earlier drafts of this manuscript. The following kindly assisted with data collection: A. Bath, G. Beauvais, N. Carlson, G. Doney, R. Hogan, M. McFadzen, P. Martin, C. Pucie, S. Toussaint, M. Vekasy, and C. Wight-

man. Funding and equipment for this project were provided by the U.S. Bureau of Land Management, U.S. Bureau of Reclamation, Montana Power Company, Montana Department of Fish, Wildlife, and Parks, U.S. Forest Service, and U.S. Fish and Wildlife Service.

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