J. Raptor Res. 42(2):99–109

THE INFLUENCE OF SALINITY ON THE DIET OF NESTING BALD EAGLES

A. CATHERINE MARKHAM[1] AND BRYAN D. WATTS
Center for Conservation Biology, College of William and Mary, P.O. Box 8795, Williamsburg, VA 23187 U.S.A.

ABSTRACT.—Although the breeding density of Bald Eagles (*Haliaeetus leucocephalus*) in the lower Chesapeake Bay is known to vary with salinity, the ecological factors that contribute to this distribution have not been explored. In an effort to examine whether variation in prey use is associated with nest density patterns, we investigated the influence of salinity (tidal-fresh vs. mesohaline zones) on Bald Eagle diet composition by using video-monitoring to observe food delivered to nests during the 2002–2003 breeding seasons. Delivered prey items were identified to the lowest taxonomic level possible and sizes were estimated relative to eagle bill length. We used species-specific length-weight relationships for prey to estimate biomass delivery. Overall, the diet included at least 12 species of fishes, three species of birds, four species of mammals, and four species of reptiles. Salinity had no significant influence on diet composition; Ictaluridae and Clupeidae species were the most frequent prey items in both salinity zones. We suggest that pairs nesting in both tidal-fresh and mesohaline zones have access to similar fish species. However, the length and biomass of fish prey varied with salinity such that larger prey on average were delivered to nests in the mesohaline reaches compared to tidal-fresh zones. Thus, we suggest that foraging eagles may be exploiting more energetically-favorable conditions in higher salinity waters. Temporally, diet composition varied between study years, potentially reflecting annual changes in the availability of prey species. We consider differences in weather patterns between study years as the most likely factor contributing to this interannual variation in diet.

KEY WORDS: *Bald Eagle*; Haliaeetus leucocephalus; *anadromous*; *Chesapeake Bay*; *diet*; *salinity.*

INFLUENCIA DE LA SALINIDAD SOBRE LA DIETA DE *HALIAEETUS LEUCOCEPHALUS* DURANTE LA ANIDACIÓN

RESUMEN.—Aunque se sabe que la densidad de aves reproductivas de la especie *Haliaeetus leucocephalus* en la parte baja de la bahía de Chesapeake varía con la salinidad, los factores ecológicos que contribuyen a esta distribución no han sido explorados. En un esfuerzo para examinar si la variación en el uso de presas está asociada con los patrones de densidad de nidos, investigamos la influencia de la salinidad (zona mareal-dulce vs. zona mesohalina) sobre la composición de la dieta de *H. leucocephalus.* Para ello utilizamos cámaras de video para monitorear el alimento llevado a los nidos durante las épocas reproductivas de 2002 y 2003. Los ítems de presas llevados fueron identificados al menor nivel taxonómico posible y sus tamaños fueron estimados con relación a la longitud del pico de las águilas. Utilizamos relaciones de longitud-peso específicas para las especies de presa para estimar la biomasa de alimentos entregada. En general, la dieta incluyó al menos 12 especies de peces, tres de aves, cuatro de mamíferos y cuatro de reptiles. La salinidad no tuvo una influencia significativa sobre la composición de la dieta; las especies de Ictaluridae y Clupeidae fueron los ítems más frecuentes entre las presas en ambas zonas de salinidad. Sugerimos que las parejas que anidan tanto en las zonas mareales-dulces como en la mesohalinas tienen acceso a especies de peces similares. Sin embargo, la longitud y la biomasa de peces presa varió con la salinidad de modo que, en promedio, se entregaron presas más grandes en los nidos de las áreas mesohalinas que en los de las áreas mareales-dulces. Por lo tanto, sugerimos que las águilas podrían estar explotando condiciones energéticas más favorables al buscar alimento en aguas con mayor salinidad. Temporalmente, la composición de la dieta varió entre los años de estudio, lo que potencialmente refleja cambios anuales en la disponibilidad de especies de presas. Consideramos que las diferencias en los patrones climáticos entre los años de estudio son el factor que más probablemente contribuye a la variación interanual en la dieta.

[Traducción del equipo editorial]

---

[1] Present address: Department of Ecology and Evolutionary Biology, Princeton University, Guyot Hall, Washington Rd., Princeton, NJ 08544 U.S.A.; Email address: amarkham@princeton.edu

Prey availability is a key determinant in the distribution (Dzus and Gerrard 1993), density (Gerrard et al. 1983), and success (Hansen 1987, Dykstra et al. 1998, Gill and Elliot 2003) of breeding Bald Eagles (*Haliaeetus leucocephalus*). However, directly assessing prey availability in natural systems is difficult due to the broad geographic range and flexible foraging habits of Bald Eagles (Gende et al. 1997). As a result, few investigations have examined variation in prey use within a breeding population and little has been reported about how diet varies along environmental gradients that determine prey distribution (but see Watson et al. 1991, Dzus and Gerrard 1993, Jackman et al. 2007).

In a recent investigation of population parameters for Bald Eagles in the lower Chesapeake Bay, Watts et al. (2006) found that shoreline areas surrounding low saline waters support higher breeding densities, have higher reproductive rates, collectively produce a greater number of young, and have experienced faster rates of population recovery compared to shoreline areas surrounding higher saline waters. This implies tidal-fresh reaches represent core breeding areas for Bald Eagles, yet the ecological advantages of these regions are unknown. One possible explanation for the observed pattern is that the influence of salinity on eagle breeding density is mediated through prey availability (Watts et al. 2006). In the Chesapeake Bay, Bald Eagles forage primarily on fish during their breeding season (Wallin 1982, Mersmann 1989). Fish communities are not uniform throughout the estuarine ecosystem and salinity is one of the key factors known to influence the abundance and distribution of fish species in Chesapeake Bay waters (Murdy et al. 1997, Jung 2002). This, along with data indicating that Bald Eagle breeding pairs typically forage within home ranges close to their nest site (<3 km; Buehler et al. 1991), suggests that eagles nesting in different salinity zones encounter different suites of prey species or experience different food resource levels.

Here, we investigate the influence of salinity on the diet composition of Bald Eagles in the lower Chesapeake Bay to examine how breeding pairs respond to potential differences in prey communities and availability between salinity zones. Specifically, we (1) describe the diet of breeding Bald Eagles in the Chesapeake Bay region, (2) evaluate the extent to which salinity contributes to spatial variation in diet, and (3) investigate patterns of variation in diet between the two years of this study.

METHODS

We monitored 18 Bald Eagle nests in the lower Chesapeake Bay ≤3 km inland from the shorelines of the James, York, and Rappahannock rivers during the 2002 ($N = 8$) and 2003 ($N = 10$) breeding seasons (Fig. 1). Three areas were recognized along the estuarine salinity gradients of these tributaries: tidal-fresh (0.0–0.5 ppt salinity), oligohaline (0.5–5.0 ppt), and mesohaline (5.0–18.0 ppt; Chesapeake Bay Program Monitoring Subcommittee Data Analysis Work Group unpubl. data). We limited nest selection to tidal-fresh and mesohaline reaches to (1) examine extremes in salinity effects within river systems and (2) because Watts et al. (2006) documented significant differences in breeding density between these salinity zones.

To place video-recording equipment, we selected nests that had a history of reliable production and regularly experienced human interaction (with the reasoning that breeding pairs habituated to human presence were less likely to be disrupted by researcher activity). Using these criteria, we selected nine nests in each salinity zone. One nest in the mesohaline reach was used in both years of this study; because nests were considered individual samples in all analyses, samples sizes presented reflect the unique pairing of nest location and year.

Data collection at each nest was determined by nestling age, as estimated during aerial surveys and later confirmed by visual inspection of chicks. We divided the nesting cycle into three phases relative to the expected period of maximum growth in developing eaglets: before (0–14 d), during (15–45 d), and after (46 d–fledging) anticipated maximum growth (Bortolotti 1984). Recording effort at all nests was focused primarily on the maximum growth phase. By this age, eaglets are endothermic (14.7 d; Bortolotti 1984) and nest trees can be climbed for camera installation with minimal risk associated with exposing chicks to ambient temperatures. Further, nestlings in this phase experience the fastest rate of growth (Ricklefs 1967) and, accordingly, provisioning rates have the greatest impact on overall growth patterns (Bortolotti 1989). Monitoring for two nests began at hatching, and thus, also included the pre-maximum growth phase (cameras were installed prior to egg-laying); monitoring of 10 nests continued through fledging and therefore included the post-maximum phase. For nests with multiple young, we used the hatch date of the oldest nestling when assigning brood ages for data analysis. Hatch date was either (1) determined

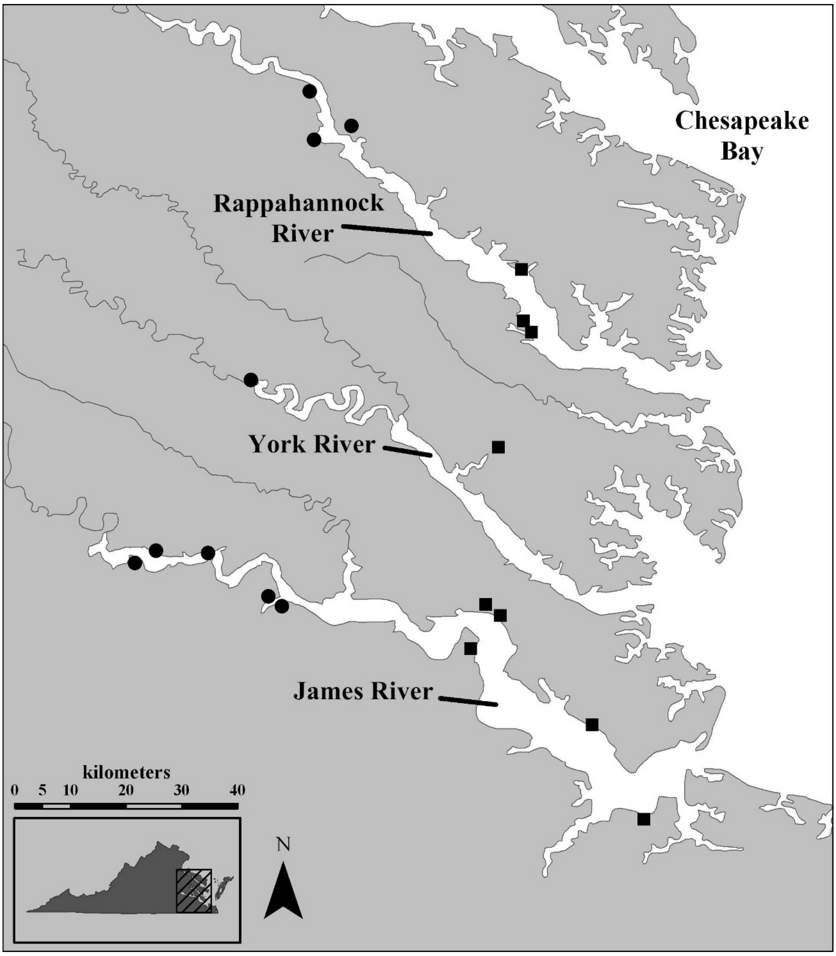

Figure 1. Locations of nests used (2002–2003) in the lower Chesapeake Bay study area. Nests are distinguished between those in tidal-fresh (●) and mesohaline (■) salinity zones.

from video-monitoring or (2) estimated based upon visual inspection of nestlings when they were between 15–20 d. Nests in both salinity reaches (tidal-fresh and mesohaline) included broods ranging in size from 1–3 chicks. Brood size did not vary with salinity for nests included in this study.

Video-monitoring. The video system consisted of a waterproof, bullet security camera wired to a VHS videocassette recorder. We used both color and black-and-white cameras. Video cameras were mounted to the nest tree approximately 1 m above the nest so that the entire nest surface was in view. Cameras were wired to a videorecorder and a deep cycle, 12-volt marine battery. The videorecorder and battery were placed in waterproof containers and positioned at a remote location approximately 250 m from the nest to reduce disturbance during maintenance activities. Recording of nest activity was focused on the morning hours (beginning 1 hr after sunrise) to include the expected peak period of chick provisioning (Jaffe 1980, Wallin 1982, Mersmann 1989). Recording bouts typically lasted 8 hr, the duration of standard T-160 VHS videotapes. Each nest was monitored in this fashion approximately 4 d/wk with effort taken to maintain equal sampling between salinity zones within each study year.

During video review, we identified prey items to the lowest taxonomic level possible and recorded date, delivery time, and prey size. We grouped prey into four taxonomic classes (fish, birds, mammals, and reptiles) and developed methods for determining size and estimating biomass that reflected the morphological characteristics of each taxa. Similar methods were used to assess size and biomass of unidentified prey items. For all deliveries that were not whole, we estimated the intact proportion in 10% intervals.

We estimated the size of fish by visual comparison to adult bill length in half-bill-length increments. We then converted observations to mm using an estimate of mean bill length for eagles from the Chesapeake Bay population. The estimate (63.6 ± 3.40 mm; mean ± SD) used was derived from 26 adult and subadult specimens (11 females, 12 males, and three unsexed) housed in the bird collections of the Smithsonian National Museum of Natural History and Virginia Tech (B. Watts and A. Markham unpubl. data). Fish lengths were then converted to biomass using species-specific length-mass relationships (Appendix). We used values from closely related species if no length-mass conversions were available. For taxa with species members that were indistinguishable on videotape (e.g., Ictaluridae, Clupeidae, *Lepomis* spp., and *Pomoxis* spp.), biomass conversions were based on representative species. Biomass calculations for unidentified fish were estimated from a weighted average of all identified fish.

Birds were identified and assigned species-specific masses from Dunning (1992). Mammals were classified as either juvenile or adult depending on size (small or large) and assigned masses specific to regional specimens and appropriate for correct age/size category (Nowak and Paradiso 1983). We also estimated turtle size (carapace length) in relation to adult bill length. Whole weights for biomass conversions were estimated using species-specific allometric relationships between carapace length and mass derived from regional datasets (J. Mitchell unpubl. data). To be conservative in our calculations, we estimated the biomass of all unidentified prey items in relation to the approximate size (and associated mass) of adult mammals.

Statistical Analyses. We summarized all prey deliveries by presenting descriptive statistics on overall diet composition and prey size for all taxa to provide an overview of eagle diet within the study area during the brood-rearing period. We evaluated the possible influence of year and salinity on the use of broad taxonomic classes using a chi-square where the expected distribution of prey between the classes was derived from 2002 for comparisons between years and tidal-fresh for comparisons between salinity zones. We used a one-way analysis of variance (ANOVA) with year (two classes: 2002 and 2003) as a factor and individual nests as samples to evaluate the influence of year on overall species diversity. Only provisioning data collected during the period of maximum growth was used in further salinity zone comparisons.

We evaluated the influence of salinity and year on diet using two-way ANOVAs with salinity (two classes: tidal-fresh and mesohaline) and year (2002 and 2003) as factors and individual nests as samples. We tested a series of response variables including diet breadth and equitability, mean fish length and biomass, the importance of Ictaluridae and Clupeidae fish, and the importance of other fish species (not Ictaluridae and Clupeidae) collectively. At each nest, we computed species diversity (Simpson's D: Simpson 1949) to estimate diet breadth and equitability to estimate evenness. Equitability J was calculated as $J = H \log (S)$ where H is Shannon-Wiener index and S is the number of species in the diet (Pielou 1966). For fish species and groups, we used biomass delivery rate (g/h) and percentage of total fish biomass delivered as estimates of importance relative to the overall eagle diet. Because recording effort varied between nests, we used a Michaelis-Menton function to determine if diet breadth had reached an asymptote within the recordings for each nest (Miller and Wiegert 1989). Two nests that did not have adequate recording effort for diet to reach an asymptote were not included in salinity comparisons. All statistical computations were performed using the software package STATISTICA v.5 (StatSoft, Inc. 1995) with an alpha value for statistical significance set to 0.05.

RESULTS

Brood Size. Brood size for all nests observed for prey deliveries varied between one and three young with a mean of 1.8 ± 0.73 (SD). Brood size was higher in nests associated with tidal-fresh reaches compared to nests associated with mesohaline reaches (2.0 ± 0.71 and 1.6 ± 0.74, respectively) but this difference was not statistically distinguishable ($F_{1,16} = 1.13$, $P = 0.30$).

Overall Diet. Of the 765 prey deliveries recorded on 4098 hr (18 nests) of videotape, we identified 730 (95.4%) prey items representing at least 12 species of fishes, three species of birds, four species of mammals, and four species of reptiles (Table 1). Some fish species were indistinguishable on videotape and only family or genus level identification

Table 1. Diet of Bald Eagles nesting in the lower Chesapeake Bay based on video-observations of prey delivered to nests during the 2002–2003 breeding seasons.

	INDIVIDUALS (*N*)		BIOMASS (kg)	
SPECIES	TOTAL	%	TOTAL	%
Fish (Osteichthyes)				
American eel (*Anguilla rostrata*)	17	2.2	11.75	3.8
Atlantic croaker (*Micropogonias undulatus*)	45	5.9	20.55	6.6
Black crappie and white crappie (*Pomoxis* spp.)	10	1.3	2.43	0.8
Bluefish (*Pomatomus saltatrix*)	1	0.1	0.11	0.0
Clupeidae	284	27.1	111.05	26.4
Ictaluridae	234	30.6	95.30	30.7
Largemouth bass (*Micropterus salmoides*)	10	1.3	7.45	2.4
Lepomis spp.	10	1.3	2.45	0.8
Spot (*Leiostomus xanthurus*)	2	0.3	0.89	0.3
Striped bass (*Morone saxatilis*)	5	0.7	6.63	2.1
Summer flounder (*Paralichthys dentatus*)	1	0.1	0.46	0.1
Yellow perch (*Perca flavescens*)	1	0.1	0.34	0.1
Unidentified	75	9.8	19.14	6.2
Fish Subtotal	695	90.8	278.56	89.8
Birds (Aves)[a]	7	0.9	4.38	1.4
Mammals (Mammalia)[b]	20	2.6	12.65	4.1
Reptiles (Reptilia)[c]	8	1	2.42	0.8
Unidentified Prey	35	4.6	12.17	3.9
GRAND TOTAL	765	100.0	310.18	100.0

[a] Identified bird species: Double-crested Cormorant (*Phalacrocorax auritus*), Mallard (*Anas platyrhynchos*), and Rock Pigeon (*Columba livia*).

[b] Identified mammal species: common muskrat (*Ondatra zibethicus*), eastern cottontail (*Sylvilagus floridanus*), eastern gray squirrel (*Sciurus carolinensis*), and woodchuck (*Marmota monax*).

[c] Identified reptile species: common musk turtle (*Sternotherus odoratus*), eastern mud turtle (*Kinosternon subrubrum*), eastern painted turtle (*Chrysemys picta picta*), and snapping turtle (*Chelydra serpentina*).

was possible. Specifically, we were not able to discriminate between species within two families (Ictaluridae and Clupeidae). Probable species represented were: channel catfish (*Ictalurus punctatus*), blue catfish (*I. furcatus*), and white catfish (*Ameiurus catus*) in the Ictaluridae family; and alewife (*Alosa pseudoharengus*), American shad (*A. sapidissima*), blueback herring (*A. aestivalis*), hickory shad (*A. mediocris*), and gizzard shad (*Dorosoma cepedianum*) in the Clupeidae. In addition, we were unable to discriminate between species within two genera (*Lepomis* spp. and *Pomoxis* spp). Probable species represented were: bluegill (*Lepomis macrochirus*), pumpkinseed (*L. gibbosus*), and redbreast sunfish (*L. auritus*) in the *Lepomis* genus; and black crappie (*Pomoxis nigromaculatus*) and white crappie (*P. annularis*) in *Pomoxis.*

By frequency of occurrence, fish constituted 96.0% of the identified prey, birds 0.5%, mammals 2.3%, and reptiles 1.2%. By delivered biomass, fish constituted 94.1% of the biomass delivered, birds 1.0%, mammals 4.1%, and reptiles 0.9%. Ictaluridae and Clupeidae were overwhelmingly the most common prey groups by frequency and biomass.

We were able to calculate biomass for 750 prey items (98.9% of observed deliveries). Including items of both partial and intact prey status, biomass of individual deliveries ranged from 1.3–2391.7 g with a mean of 414.5 g (SD = 291.5). Of the 620 identified fish, we were able to determine intact status and estimate total length for 473 items; biomass of intact fish ranged from 22.8–2391.7 g with a mean of 466.5 g (SD = 268.70).

Neither the importance of each taxonomic class (by percent biomass of all prey identified to class) in overall diet composition throughout the breeding season ($\chi^2_3 = 0.31$, $P = 0.96$) nor species diversity ($F_{1,14} = 0.03$, $P = 0.87$) varied significantly between the two years of this study. Ictaluridae and Clupeidae were dominant in the diet for both study years,

Figure 2. Influence of salinity and year on biomass delivery rate of Ictaluridae at Bald Eagle nests in the lower Chesapeake Bay during the 2002–2003 breeding seasons. Only deliveries made during the expected period of nestling maximum growth (15–45 d) were included in analysis.

with no significant between-year variation in combined use ($\chi^2_1 = 0.20$, $P = 0.65$).

Salinity and Yearly Comparisons. We observed 541 prey deliveries during 2176 hr of videorecording at the 16 nests with recording coverage adequate for statistical analysis. The proportion of diet represented by each taxonomic class (by percent biomass of all prey identified to class) did not vary significantly between salinity zones ($\chi^2_3 = 4.5$, $P = 0.21$) or years ($\chi^2_3 = 8.8$, $P = 0.07$). Fish dominated diet composition in both salinity zones and during both years.

The length ($F_{1,469} = 7.50$, $P = 0.006$) and biomass ($F_{1,469} = 7.56$, $P = 0.006$) of delivered fish were higher in the mesohaline compared to tidal-fresh reaches. Mean fish length was 40.0 (±7.48) cm and 42.4 (±10.39) cm in tidal-fresh and mesohaline zones, respectively. Fish mass was 434.9 (±235.64) g and 509.6 (±303.43) g for tidal-fresh and mesohaline zones, respectively. We observed no significant between year differences in length ($F_{1,469} = 0.18$, $P = 0.67$) or biomass ($F_{1,469} = 0.15$, $P = 0.70$).

Species diversity (Simpson's D) was higher in the mesohaline compared to tidal-fresh reaches ($F_{1,12} = 4.65$, $P = 0.052$). However, there was no significant difference between years in species diversity ($F_{1,12} = 0.22$, $P = 0.65$), though there was a trend toward higher diversity in 2002. Equitability was not different between salinity zones ($F_{1,12} = 3.07$, $P = 0.011$) or years ($F_{1,12} = 0.49$, $P > 0.50$).

The combined dietary proportion of Ictaluridae and Clupeidae expressed as percent biomass of delivered fish biomass did not vary between salinity zones ($F_{1,12} = 0.89$, $P = 0.36$) or years ($F_{1,12} = 4.58$, $P = 0.054$) and no interaction was detected ($F_{1,12} = 0.88$, $P = 0.37$). The proportion of Ictaluridae biomass in the diet was lower in 2002 compared to 2003 ($F_{1,12} = 4.59$, $P = 0.05$; Fig. 2); the proportion of Clupeidae biomass showed the reverse trend ($F_{1,12} = 6.04$, $P = 0.03$; Fig. 3). There was no significant effect of salinity on the dietary proportion of Ictaluridae ($F_{1,12} = 0.34$, $P = 0.57$) or Clupeidae biomass ($F_{1,12} = 0.61$, $P = 0.45$), although there was a trend toward a higher biomass proportion of each family in tidal-fresh reaches compared to mesohaline zones in 2002. No significant interaction was observed between salinity and year for either fish family ($F_{1,12} < 0.34$, $P = 0.57$). We also examined the prevalence of Ictaluridae and Clupeidae in the diet by considering the rates of biomass delivery for each family (Figs. 2 and 3). No statistically significant results were observed between salinity zones ($F_{1,12} < 0.36$, $P = 0.56$) or years ($F_{1,12} < 2.73$, $P = 0.12$) and no interaction was detected ($F_{1,12} < 0.28$, $P = 0.61$). Ictaluridae and Clupeidae showed reverse patterns between years with Ictaluridae delivery rates being higher in 2003 compared to 2002 and Clupeidae delivery rates having the opposite pattern. However, in 2002 both prey groups exhibited similar spatial patterns with deliv-

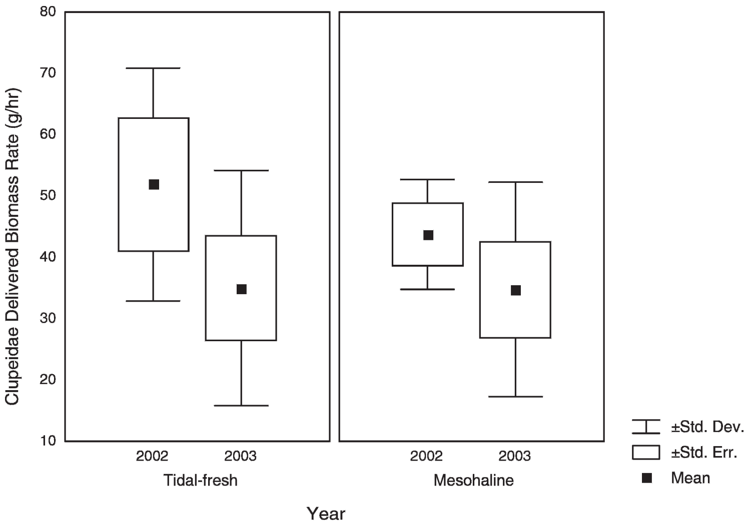

Figure 3. Influence of salinity and year on biomass delivery rate of Clupeidae at Bald Eagle nests in the lower Chesapeake Bay during the 2002–2003 breeding seasons. Only deliveries made during the expected period of nestling maximum growth (15–45 d) were included in analysis.

ery rates being higher in tidal-fresh compared to mesohaline reaches. Finally, no statistically significant results were observed in the rates of biomass delivery for other fish species (i.e., excluding Ictaluridae and Clupeidae) between salinity zones ($F_{1,12} = 0.26$, $P = 0.62$) or years ($F_{1,12} = 1.11$, $P = 0.31$) and no interaction was detected ($F_{1,12} = 0.49$, $P = 0.50$).

DISCUSSION

Overall Diet. Important prey identified in this investigation were similar to those noted in earlier studies of Bald Eagle diet in the Chesapeake Bay (e.g., Wallin 1982, Mersmann 1989); however, differences in the relative use of key species and prey taxa were apparent. We suggest that these discrepancies were largely the result of (1) variation in the foraging ecology of breeding versus nonbreeding eagles and (2) differences in the field techniques used to assess diet. For example, previous research focused on diet composition during the breeding season was consistent with our results that fish constitute the overwhelming majority of items delivered to nests (>98%; Wallin 1982). Outside the breeding season, eagles in the Chesapeake Bay ecosystem relied more heavily on other prey taxa such as birds and mammals (Mersmann 1989). This change in diet has been correlated with seasonal shifts in prey abundance and the eagle's ability to forage opportunistically on temporally abundant food resources (e.g., Watson et al. 1991, Ewins and Andress 1995). In addition, our findings indicated a greater proportion of small and soft-bodied fish relative to results from previous research in which diet was assessed by analyzing prey remains in or under nests (Cline and Clark 1981, Haines 1986). This is likely due to the eagle's ability to digest the fine bones associated with small mammals and many fish species (Imler and Kalmbach 1955, Duke et al. 1975). Thus, the differences between past and current findings likely reflect the improved accuracy of diet assessment using a video-sampling approach (Mersmann et al. 1992).

Ictaluridae and Clupeidae prey dominated the diet composition of breeding pairs in this study. The importance of catfish in the diet of Bald Eagles has been reported in numerous other foraging studies throughout the species' range (e.g., McEwan and Hirth 1980, Cash et al. 1985, Dugoni et al. 1986, Mabie et al. 1995). Bald Eagle predation on both nonmigratory (e.g., Mersmann 1989, Mabie et al. 1995) and migratory (e.g., Fitzner and Hanson 1979, Spencer et al. 1991, Hunt et al. 1992, McClelland et al. 1994) Clupeidae has also been previously documented. In the areas where research on Bald Eagles and anadromous fish interactions has been conducted, spawning runs do not coincide with the eagle breeding season. Two notable exceptions were described by Gerrard et al. (1975) and Gende et al. (1997), who documented higher productivity in eagle pairs nesting close to spawning grounds compared with pairs nesting farther away. Thus, a finding of particular interest here is the novelty of breeding eagles utilizing anadromous species within the Chesapeake Bay ecosystem.

Salinity and Yearly Comparisons. Previous research indicated that Bald Eagles seemed to alter prey size selection based upon energetic requirements. Jenkins and Jackman (1994) concluded that differences observed between breeding and nonbreeding eagles with regard to mean prey size supported optimal foraging models. In our study, adults on average delivered significantly larger fish (with regard to fish length and biomass) to nests in the mesohaline compared to tidal-fresh salinity zones. This suggested more energetically favorable conditions for foraging parents in higher salinity waters if adults in both salinity zones expended similar amounts of effort per capture. Further evaluation of this assumption is needed to determine the extent to which available prey sizes may influence patterns in nesting density and reproductive rates with salinity. In particular, an investigation of the energetic consequences of prey size variation during the breeding season (e.g., increased rates of nestling provisioning and growth) may add additional insight into understanding nest density patterns.

Our results showed that the diet composition of breeding Bald Eagles did not vary spatially along the salinity gradient of the lower Chesapeake Bay tributaries. In both tidal-fresh and mesohaline salinity zones, the diet was dominated by Ictaluridae and Clupeidae species. Additional fish species observed tended to occur in such small numbers that spatial differences in distribution were not detectable. This suggested that changes in salinity between tidal-fresh and mesohaline zones did not impose a significant constraint on diet composition as originally hypothesized.

The broad-scale use of Ictaluridae and Clupeidae may be interpreted through taxa-specific distribution patterns and life history characteristics. Although catfish belonging to the family Ictaluridae generally prefer low-saline waters, they are capable of utilizing a broad salinity range (Lippson et al. 1979, Dames et al. 1989, Jenkins and Burkhead 1994). Therefore, catfish seem to be available to eagles nesting in both tidal-fresh and mesohaline salinity zones. However, trawl surveys conducted by the Virginia Institute of Marine Science (VIMS) in the lower 35 km of the James, York, and Rappahannock rivers reported greatest overall catfish abundance occurring at upriver sampling stations where river salinities are highly diluted (VIMS unpubl. data). This finding was consistent with the trend we observed of higher catfish delivery rates and higher dietary proportion of catfish in lower salinity zones.

Fishes in the Clupeidae family are predominantly anadromous species that migrate from open bay or ocean waters to spawn in the freshwater portions of creeks and rivers. Within the Chesapeake Bay system, spawning runs are triggered by favorable water temperatures and typically extend from February through June (alewife, Munroe 2000; hickory shad, J. David, J. Miller, and W. Wilson unpubl. data). This time window is temporally synchronous with the nesting season of Bald Eagles, particularly coinciding with the period in which most nestlings in Virginia experience maximum growth, and thus, have the greatest energetic demands (April–mid-May). As in other predator species (Willson and Halupka 1995), Bald Eagles may have responded to the predictable and concentrated influx of energy-rich food resources associated with these annual spawning runs.

Unlike the anadromous Clupeidae, gizzard shad are year-round residents of the Chesapeake Bay ecosystem (Murdy et al. 1997). Gizzard shad are widely distributed through the bay waters with high abundances in the freshwater portions of the tributaries up to salinities as high as 22 ppt (Murdy et al. 1997). Because we were unable to distinguish different Clupeidae species, the relative importance of gizzard shad compared to anadromous *Alosa* spp. remains uncertain.

Record wet conditions and lower than average temperature were observed in 2003 throughout the southeast United States, including Virginia (Gleason et al. 2004). We consider these differences in rainfall and temperature between study years as the most likely factor influencing the observed annual variation in diet composition. Increased rainfall results in a rise in freshwater input, which consequently affects water flow, temperature, and turbidity in the tributary systems. These factors, in turn, negatively affect migration runs of anadromous species (Jung 2002) and could be responsible for the decreased relative importance of Clupeidae in the diet in 2003 compared to 2002. In addition, increased freshwater input influences salinity boundaries, effectively extending the freshwater portions of the tributaries. Reduced salinities may have expanded the foraging range of Ictaluridae species (Sauls et al. 1998), and thus, also explain the increased relative importance of catfish use in the mesohaline reaches in 2003. However, this alone does not explain the increased use of catfish in the tidal-fresh reaches in 2003.

ACKNOWLEDGMENTS

We owe special thanks to the numerous volunteers and landowners whose time and generosity made this study possible. We also thank Drs. H. Austin, M. Byrd, P. Heideman, and three anonymous reviewers for their valuable comments on earlier drafts of this manuscript. B. Paxton offered expertise in the field and created the study map. J. Mitchell shared morphometric data on turtle specimens essential in length-weight regression calculations. The Smithsonian Museum of Natural History and Virginia Tech allowed access to the Bald Eagle skins in their bird collections. This study was financially supported by the Center for Conservation Biology and grants from the College of William and Mary, the Mary and Daniel Loughran Foundation, the Northern Neck Audubon Society, the Virginia Society of Ornithology, and the Williamsburg Bird Club.

LITERATURE CITED

BORTOLOTTI, G.R. 1984. Physical development of nestling Bald Eagles with emphasis on the timing of growth events. *Wilson Bull.* 96:524–532.

———. 1989. Factors influencing the growth of Bald Eagles in north central Saskatchewan. *Can. J. Zool.* 67:606–611.

BUEHLER, D.A., T.J. MERSMANN, J.D. FRASER, AND J.K.D. SEEGAR. 1991. Differences in distribution of breeding, nonbreeding, and migrant Bald Eagles on the northern Chesapeake Bay. *Condor* 93:399–408.

CASH, R.J., P.J. AUSTIN-SMITH, D. BANKS, D. HARRIS, AND P.C. SMITH. 1985. Food remains from Bald Eagle nest sites on Cape Breton Island, Nova Scotia. *J. Wildl. Manage.* 49:223–225.

CLINE, K.W. AND W.S. CLARK. 1981. Chesapeake Bay Bald Eagle banding project: 1981 report and five-year summary. Raptor Information Center, Natl. Wildl. Fed., Washington, DC U.S.A.

DAMES, H., T. COON, AND J. ROBINSON. 1989. Movements of channel and flathead catfish between the Missouri River and a tributary, Perch Creek. *Trans. Am. Fish. Soc.* 188:670–679.

DAWSON, C.E. 1965. Length-weight relationships of some Gulf of Mexico fishes. *Trans. Am. Fish. Soc.* 94:279–280.

DUGONI, J.A., P.J. ZWANK, AND G.C. FURMAN. 1986. Foods of nesting Bald Eagles in Louisiana. *Raptor Res.* 20:124–127.

DUKE, G.E., A.A. JEGERS, G. LOFF, AND O.A. EVANSON. 1975. Gastric digestion in some raptors. *Comp. Biochem. Physiol.* 50A:646–656.

DUNNING, J.B. 1992. Handbook of avian body weights. C.R.C. Press, Orlando, FL U.S.A.

DYKSTRA, C.R., M.W. MEYER, D.K. WARNKE, W.H. KARASOV, D.E. ANDERSEN, W.W. BOWERMAN, IV, AND J.P. GIESY. 1998. Low reproductive rates of Lake Superior Bald Eagles: low food delivery rates or environmental contaminants? *J. Gt Lakes Res.* 24:32–44.

DZUS, E.H. AND J.M. GERRARD. 1993. Factors influencing Bald Eagle densities in northcentral Saskatchewan. *J. Wildl. Manage.* 57:771–778.

EWINS, P.J. AND R.A. ANDRESS. 1995. The diet of Bald Eagles, *Haliaeetus leucocephalus*, wintering in the lower Great Lakes basin. *Can. Field-Nat.* 109:418–425.

FESSLER, F.R. 1949. A survey of fish populations in small ponds by two methods of analysis. M.S. thesis, Iowa State College, Ames, IA U.S.A.

FITZNER, R.E. AND W.C. HANSON. 1979. A congregation of wintering Bald Eagles. *Condor* 81:311–313.

FORTIN, R. AND E. MAGNIN. 1972. Croissance en longueur et en poids des perchaudes *Perca flavescens* de la Grande Anse de l'ile Perrot au lac Saint-Louis. *J. Fish. Res. Board Can.* 29:517–523.

GENDE, S.M., M.F. WILLSON, AND M. JACOBSEN. 1997. Reproductive success of Bald Eagles (*Haliaeetus leucocephalus*) and its association with habitat or landscape features and weather in southeast Alaska. *Can. J. Zool.* 75:1595–1604.

GERRARD, J.M., P.N. GERRARD, G.R. BORTOLOTTI, AND D.W.A. WHITFIELD. 1983. A 14-year study of Bald Eagle reproduction on Besnard Lake, Saskatchewan. Pages 47–58 *in* D.M. Bird [ED.], Biology and management of Bald Eagles and Ospreys. Harpell Press, Ste. Anne de Bellevue, Quebec, Canada.

———, ———, W.J. MAHER, AND D.W.A. WHITFIELD. 1975. Factors influencing nest site selection of Bald Eagles in northern Saskatchewan and Manitoba. *Blue Jay* 33:169–176.

GILL, C.E. AND J.E. ELLIOTT. 2003. Influence of food supply and chlorinated hydrocarbon contaminants on breeding success of Bald Eagles. *Ecotoxicology* 12:95–111.

GLEASON, K.L., A.M. WAPLE, T. EICHLER, AND G.D. BELL. 2004. Regional climate, North America, United States of America. Pages S32–S33 *in* D.H. Levinson and A.M. Waple [EDS.], State of the climate in 2003. *Bull. Am. Meteorol. Soc.* 85(6).

HAIMOVICI, M. AND G. VELASCO. 2000. Length-weight relationships of marine fishes from southern Brazil. *Naga ICLARM Quarterly* 23:19–23.

HAINES, S.L. 1986. The feeding, roosting, and perching behavior of the Bald Eagle (*Haliaeetus leucocephalus*) of Mason Neck, Virginia, with special reference to the development of Mason Neck State Park. M.S. thesis, George Mason Univ., Fairfax, VA U.S.A.

HANSEN, A.J. 1987. Regulation of Bald Eagle reproductive rates in southeast Alaska. *Ecology* 68:1387–1392.

HANSEN, R.A. AND A.G. EVERSOLE. 1984. Age, growth and sex ratio of American eels in brackish-water portions of a South Carolina river. *Trans. Am. Fish. Soc.* 113:744–749.

HENDERSON, E.M. 1979. Summer flounder (*Paralichthys dentatus*) in the northwest Atlantic. National Marine Fisheries Service, Northeast Fisheries Center, Woods Hole Laboratory Reference Number 79–31.

HUNT, W.G., B.S. JOHNSON, AND R.E. JACKMAN. 1992. Carrying capacity for Bald Eagles wintering along a northwestern river. *J. Raptor Res.* 26:49–60.

IMLER, R.H. AND E.R. KALMBACH. 1955. The Bald Eagle and its economic status. U.S. Fish and Wildl. Service Circular No. 30.

JACKMAN, R.E., W.G. HUNT, AND N.L. HUTCHINS. 2007. Bald Eagle foraging and reservoir management in northern California. *J. Raptor Res.* 41:202–211.

JAFFE, N.B. 1980. Nest site selection and foraging behavior of the Bald Eagle (*Haliaeetus leucocephalus*) in Virginia. M.A. thesis, College of William and Mary, Williamsburg, VA U.S.A.

JENKINS, J.M. AND R.E. JACKMAN. 1994. Field experiments in prey selection by resident Bald Eagles in the breeding and nonbreeding season. *J. Field Ornithol.* 65:441–446.

JENKINS, R.E. AND N.M. BURKHEAD. 1994. Freshwater fishes of Virginia. American Fisheries Society, Bethesda, MD U.S.A.

JUNG, S. 2002. Fish community structure and the spatial and temporal variability in recruitment and biomass production in Chesapeake Bay. Ph.D. dissertation, Univ. of Maryland, College Park, MD U.S.A.

LIPPSON, A.J., M.S. HAIRE, A.F. HOLLAND, F. JACOBS, J. JENSEN, R.L. MORAN-JOHNSON, T.T. POLGAR, AND W.A. RICHKUS. 1979. Environmental atlas of the Potomac estuary. Martin Marietta Corporation for MD Dept. Natural Resources, Baltimore, MD U.S.A.

MABIE, D.W., M.T. MERENDINO, AND D.H. REID. 1995. Prey of nesting Bald Eagles in Texas. *J. Raptor Res.* 29:10–14.

MANSUETI, R. 1961. Age, growth and movements of the striped bass, *Roccus saxatilis*, taken in size selective gear. *Chesapeake Sci.* 2:9–36.

MCCLELLAND, B.R., L.S. YOUNG, P.T. MCCLELLAND, J.G. CRENSHAW, H.L. ALLEN, AND D.S. SHEA. 1994. Migration ecology of Bald Eagles from autumn concentrations in Glacier National Park, Montana. *Wildl. Monogr.* 125:1–61.

MCEWAN, L.C. AND D.H. HIRTH. 1980. Food habits of the Bald Eagle in north-central Florida. *Condor* 82:229–231.

MERSMANN, T.J. 1989. Foraging ecology of Bald Eagles on the northern Chesapeake Bay with an examination of techniques used in the study of Bald Eagle food habits. M.S. thesis, Virginia Polytechnic Institute and State Univ., Blacksburg, VA U.S.A.

———, D.A. BUEHLER, J.D. FRASER, AND J.K.D. SEEGAR. 1992. Assessing bias in studies of Bald Eagle food habits. *J. Wildl. Manage.* 56:73–78.

MILLER, R.J. AND R.G. WIEGERT. 1989. Documenting completeness, species-area relationships, and the species-abundance distribution of a regional flora. *Ecology* 70:16–22.

MUNCY, R.J. 1959. Age and growth of channel catfish from the Des Moines River, Boone County, Iowa, 1955 and 1956. *Iowa J. Sci.* 34:127–137.

———. 1960. A study of the comparative efficiency between nylon and linen gillnets. *Chesapeake Sci.* 1:96–102.

MUNROE, T.A. 2000. An overview of the biology, ecology, and fisheries of the Clupeoid fishes occurring in the Gulf of Maine. Northeast Fisheries Science Center Ref. Doc. 00-02, Woods Hole, MA U.S.A.

MURDY, E.O., R.S. BIRDSONG, AND J.A. MUSICK. 1997. Fishes of the Chesapeake Bay. Smithsonian Institution Press, Washington, DC U.S.A.

NOWAK, R.M. AND J.L. PARADISO. 1983. Walker's mammals of the world, Fourth Ed. Johns Hopkins Univ. Press, Baltimore, MD U.S.A.

PIELOU, E.C. 1966. The measurement of diversity in different types of biological collections. *J. Theor. Biol.* 13:131–144.

RICKLEFS, R.E. 1967. A graphical model for fitting equations to growth curves. *Ecology* 48:978–983.

SAULS, B., D. DOWLING, J. ODENKIRK, AND E. COSBY. 1998. Catfish population in Chesapeake Bay. Chesapeake Bay Program, Environmental Protection Agency, Annapolis, MD U.S.A.

SHIELDS, J.T. 1955. Report of fisheries investigations during the second year of impoundment of Fort Randall Reservoir, South Dakota, 1954. Progress Report 55-4. South Dakota Dept. Game, Fish and Parks, Pierre, SD U.S.A.

SIMPSON, E.H. 1949. Measurement of diversity. *Nature* 163:688.

SPENCER, C.N., B.R. MCCLELLAND, AND J.A. STANFORD. 1991. Shrimp stocking, salmon collapse, and eagle displacement. *Bioscience* 41:14–21.

STATSOFT, INC. 1995. Statistica for Windows version 5.0. Tulsa, OK U.S.A.

WALLIN, D.O. 1982. The influence of environmental conditions on the breeding behavior of the Bald Eagle (*Haliaeetus leucocephalus*) in Virginia. M.A. thesis, College of William and Mary, Williamsburg, VA U.S.A.

WATSON, J.W., M.G. GARRETT, AND R.G. ANTHONY. 1991. Foraging ecology of Bald Eagles in the Columbia River estuary. *J. Wildl. Manage.* 55:492–499.

WATTS, B.D., A.C. MARKHAM, AND M.A. BYRD. 2006. Salinity and population parameters of Bald Eagles (*Haliaeetus leucocephalus*) in the lower Chesapeake Bay. *Auk* 123:393–404.

WILK, S.J., W.W. MORSE, AND D.E. RALPH. 1978. Length-weight relationships of fishes collected in the New York Bight. *Bull. NJ Acad. Sci.* 23:58–64.

WILLSON, M.F. AND K.C. HALUPKA. 1995. Anadromous fish as keystone species in vertebrate communities. *Conserv. Biol.* 9:489–497.

Received 1 November 2005; accepted 18 January 2008
Associate Editor: James C. Bednarz

Appendix. Biomass conversions used for fish and turtle species identified in the diet of Bald Eagles nesting in the lower Chesapeake Bay during 2002–2003 breeding seasons. In conversion equations, mass (M) in grams and length (L) in centimeters.

SPECIES	BIOMASS CONVERSION	REFERENCE
American eel (*Anguilla rostrata*)	$M = 0.00166 \times L^{3.07}$	Hansen and Eversole 1984
Atlantic croaker (*Micropogonias undulatus*)	$M = 0.0031 \times L^{3.25}$	Wilk et al. 1978
Bluefish (*Pomatomus saltatrix*)	$M = 0.01356415 \times L^{2.898996}$	Haimovici and Velasco 2000
Clupeidae (used American shad, *Alosa sapidissima*)	$M = 0.0065 \times L^{2.959}$	Muncy 1960
Ictaluridae (used channel catfish, *Ictalurus punctatus*)	$M = 0.00397 \times L^{3.133}$	Muncy 1959
Largemouth bass (*Micropterus salmoides*)	$M = 0.00728 \times L^{3.113}$	Fessler 1949
Lepomis spp. (used bluegill, *L. macrochirus*)	$M = 0.00698 \times L^{3.209}$	Fessler 1949
Pomoxis spp. (used black crappie, *P. nigromaculatus*)	$M = 0.0101 \times L^{3.074}$	Shields 1955
Spot (*Leiostomus xanthurus*)	$M = 0.00921 \times L^{3.072}$	Dawson 1965
Striped bass (*Morone saxatilis*)	$M = 0.00614 \times L^{3.153}$	Mansueti 1961
Summer flounder (*Paralichthys dentatus*)	$M = 0.00544 \times L^{3.117}$	Henderson 1979
Yellow perch (*Perca flavescens*)	$M = 0.00785 \times L^{3.083}$	Fortin and Magnin 1972
Common musk turtle (*Sternotherus odoratus*)	$M = 0.24400 \times L^{2.7819}$	J. Mitchell unpubl. data
Eastern mud turtle (*Kinosternon subrubrum*)	$M = 0.25300 \times L^{3.0220}$	J. Mitchell unpubl. data
Eastern painted turtle (*Chrysemys picta picta*)	$M = 0.30500 \times L^{2.6480}$	J. Mitchell unpubl. data
Snapping turtle (*Chelydra serpentina*)	$M = 0.22000 \times L^{3.0220}$	J. Mitchell unpubl. data