THE INFLUENCE OF SALINITY ON DIET COMPOSITION, PROVISIONING PATTERNS, AND NESTLING GROWTH IN BALD EAGLES IN THE LOWER CHESAPEAKE BAY

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To my family and friends, with all the love I have for them

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ABSTRACT

Breeding density for Bald Eagles (*Haliaeetus leucocephalus*) in the lower Chesapeake Bay has been shown to vary with salinity. Shoreline areas surrounding low saline waters currently support higher breeding densities and have experienced faster rates of population recovery compared to areas surrounding higher saline waters. This finding has broad implications for eagle management throughout the region. However, the ecological factors that contribute to this distribution have not been investigated.

We examined the influence of salinity (tidal fresh vs. mesohaline) on Bald Eagle diet composition, chick provisioning, and chick growth during the 2002-04 breeding seasons. We investigated diet and chick provisioning patterns by installing video-monitoring systems above nests along tidal-fresh and mesohaline reaches and recording nest activity 4 d/wk during the period of maximum chick growth. Videotapes were reviewed to quantify prey use and delivery rates. Prey were identified to the lowest taxonomic level possible and sizes were estimated relative to eagle bill length. We used species-specific, length-weight relationships and energy density values for prey to produce rates of biomass and energy delivery. We quantified chick growth by taking chick weights during two visits during the expected phase of exponential growth and fitting this data to a growth model to produce estimates of maximum growth rate, asymptotic weight, and time required to grow from t_{10} to t_{90}.

We found that patterns of chick provisioning and growth were influenced by salinity but that the composition of diet was not. In general, provisioning rates were higher in mesohaline compared to tidal-fresh salinity zones and nestlings along mesohaline reaches grew at faster rates and achieved greater asymptotic weight compared to nestlings in tidal-fresh zones. These findings suggest that Bald Eagles nesting along mesohaline reaches are more successful at meeting the energetic demands of brood-rearing compared to pairs nesting along tidal-fresh reaches. This finding is consistent with a recent investigation that has documented higher reproductive rates and proportion of three-chick broods along mesohaline reaches compared to tidal-fresh reaches.

THE INFLUENCE OF SALINITY ON DIET COMPOSITION, PROVISIONING PATTERNS, AND NESTLING GROWTH IN BALD EAGLES IN THE LOWER CHESAPEAKE BAY

GENERAL INTRODUCTION

Most studies concerning habitat use by breeding Bald Eagles (*Haliaeetus leucocephalus*) focus on microhabitat variables that are often measured at small scales specific to individual nest sites (e.g., Andrew and Mosher 1982, Chandler *et al.* 1995). However, multiscale studies indicate that species-habitat associations vary with spatial resolution (Thompson and McGarigal 2002). This suggests that a landscape perspective is required to accurately evaluate habitat suitability for nesting pairs. Further, given the profound influence of habitat quality on the distribution and fitness of raptors (Newton 1979), examining resource availability in the context of spatial variation may help elucidate landscape-level patterns of nesting density and nesting success. Yet how breeding Bald Eagles respond to the distribution of resources on a broad spatial level is rarely investigated (*but see* Dzus and Gerrard 1993).

A habitat requirement of particular importance to breeding Bald Eagles is adequate food supplies (e.g., Retfalvi 1970, Ofelt 1975, Dugoni *et al.* 1986, Knight *et al.* 1990). For pairs nesting in areas not significantly influenced by human disturbance, it has been suggested that prey availability is a key determinant of nest distribution (Dzus and Gerrard 1993), density (Gerrard *et al.* 1983), and success (Hansen 1987, Dykstra 1995). However, directly assessing prey availability in natural systems is difficult due to the broad geographic range and opportunistic feeding habits of Bald Eagles (Gende *et al.* 1997).

Recently, research has focused on understanding the pattern of Bald Eagle nest distribution in the lower Chesapeake Bay. The Chesapeake Bay is a typical coastal plain estuary (Day *et al.* 1989) and considered one of the largest and most productive ecosystems in North America. Its prolific aquatic resources have supported important commercial and recreational fisheries since the early 17th century, though populations of many traditionally exploited species have collapsed in recent decades (Rothschild *et al.* 1981). Principal factors contributing to this decline include over-harvesting, habitat degradation, and habitat alteration. Despite declines of commercially and recreationally important fish populations, monitoring by the Atlantic States Marine Fisheries Commission and state agencies report abundances of numerous species have stabilized or increased in recent years due to active management and stocking efforts.

Unlike the open ocean where salinity remains constant over vast expanses, estuaries are transitional environments where salinity varies between freshwater and saltwater, often over relatively short distances. Much of the spatial and temporal distribution of estuarine organisms, as well as overall species richness and rates of species turnover, can be understood in terms of this salinity gradient (Boesh 1977).

Along the salinity gradient in the lower Chesapeake Bay, the distribution of breeding Bald Eagles is not uniform. The area within a 3 km shoreline buffer of the tidal-fresh salinity reaches supports a significantly higher density of nesting pairs and greater overall young production than areas surrounding high salinity waters (Watts *et al. in press*). This implies tidal-fresh reaches represent core breeding areas for Bald Eagles, yet the ecological significance of these regions is unknown.

Watts *et al.* (*in press*) suggest that the influence of salinity on breeding density is mediated through prey availability. In the Chesapeake Bay, Bald Eagles prey primarily on fish during their breeding season (Wallin 1982, Mersmann 1989), yet fish communities are not uniform throughout the ecosystem. Salinity is one of the key factors known to influence the abundance and distribution of fish species in Bay waters (Murdy *et al.* 1997, Jung 2002). Variation in salinity tolerances between fish species has lead to species-specific distribution patterns and to the formation of predictable species assemblages that are salinity based. These patterns, 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 and/or experience different levels of food resources. However, how breeding eagles respond to potential differences in prey communities and prey availability between salinity zones has not been studied.

The goal of this thesis was to investigate the influence of salinity on diet composition, provisioning rates, and nestling growth in Bald Eagles. We used a two-fold approach to accomplish these objectives. First, we assessed the influence of salinity on diet composition in two salinity zones of the lower Chesapeake Bay to compare variation in prey use. Second, we investigated the potential influence of salinity on chick provisioning and growth rate as a means of assessing relative habitat quality. Together, these objectives explore the potential influence of salinity on Bald Eagle breeding ecology in ways that may help explain observed patterns of nest distribution. Figure 0.1 depicts the location of nests used in analyses within the study area of this investigation.

In Chapter 1, we describe the diet of breeding Bald Eagles and its spatial and temporal variability. In particular, diet composition and variation in the use of dominant fish groups are presented and analyzed. We consider processes that may influence prey selection and affect variation in prey use between study years.

In Chapter 2, we describe and analyze spatial and temporal patterns in provisioning rates and nestling growth. In addition, provisioning and growth rates are considered relative to values reported in other Bald Eagle nesting populations to provide an index of the overall habitat suitability of the Chesapeake Bay ecosystem compared to other breeding habitats.

In the next two chapters, we describe observations of infanticide and cannibalism at one of the nest sites used in this study. In Chapter 3, we document the event itself and discuss factors likely contributing to the nest failure, namely the loss of the adult male. Chapter 4 examines the consequences of mate loss on nestling care in more detail. We compare incubation and brooding patterns at two reference nests where the breeding pair remained intact through chick fledging to the occurrences at one nest where the male disappeared shortly after the hatching of the first chick.

Finally, in Chapter 5, we present an analysis of feeding patterns in nestling Bald Eagles. Specifically, we examine the distribution of inter-bite intervals to develop criteria for the delineation of feeding bouts. Application of these results will for the first time allow for the collection of feeding information that could be used to analyze the influence of behavioral and ecological factors that might contribute to the temporal structure of chick provisioning in Bald Eagles.

Conservation Implications. As Bald Eagle population numbers in the lower Chesapeake Bay continue to rise, issues regarding management practices and long-term sustainability of the species are becoming increasingly important. Preservation of habitat is fundamental in both regards and remains the only goal of the 1990 Chesapeake Bay Bald Eagle Recovery Plan that has not been met (Byrd *et al.* 1990). At present, this issue is particularly critical as the species faces both de-listing and unprecedented rates of habitat loss associated with human development (Therres *et al.* 1993, Watts *et al.* 1993).

It is our hope that this research will increase current knowledge of Bald Eagle prey use and availability in the lower Chesapeake Bay, therein providing information essential to determining core breeding areas and understanding the ecological processes that define them.

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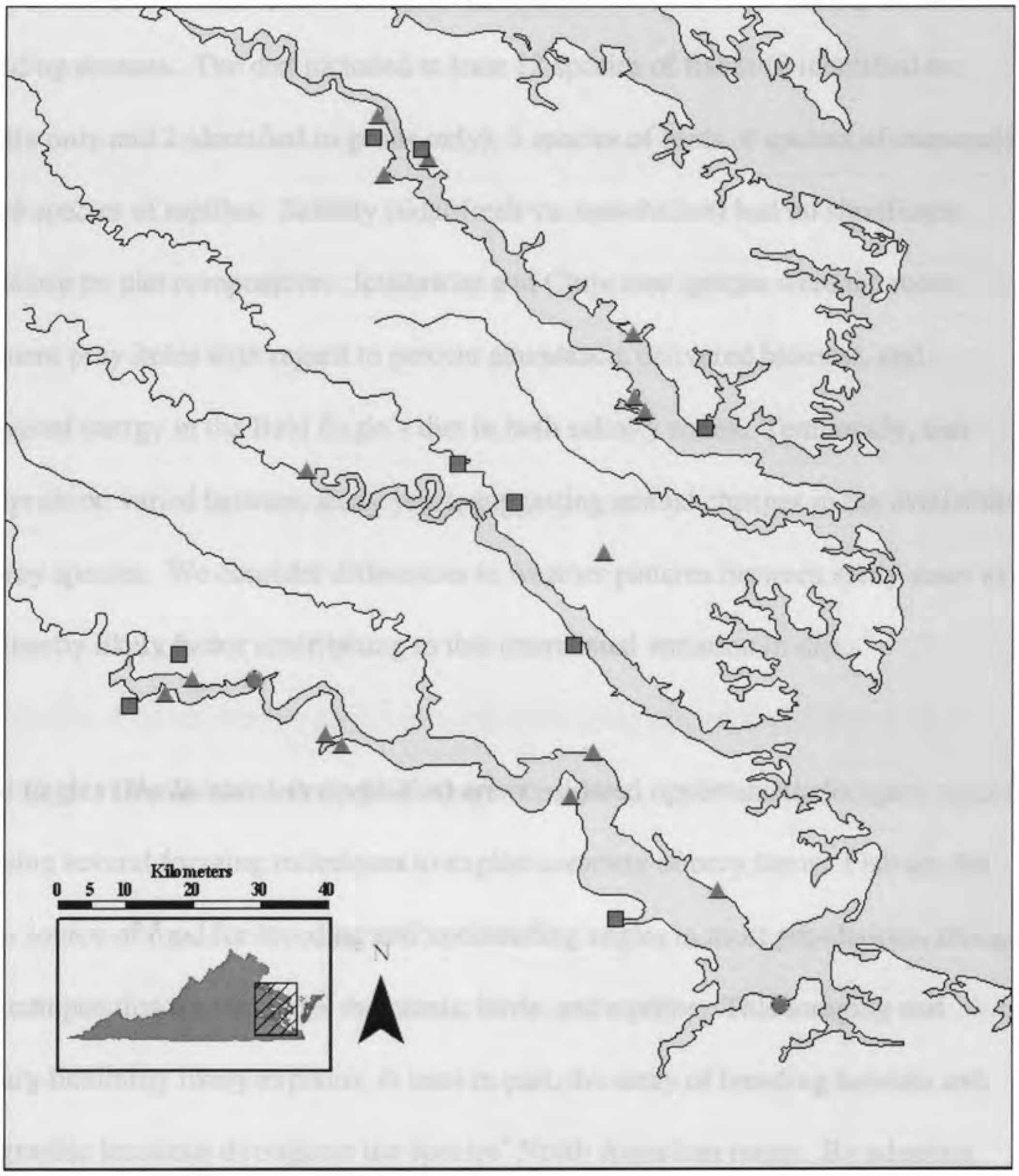
Figure 0.1. Locations of nests used (2002-04) in the lower Chesapeake Bay study area. Nests are distinguished between those used for video-monitoring (●), growth measurements (■), or both video-monitoring and growth measurements (▲).



CHAPTER 1

THE INFLUENCE OF SALINITY ON THE DIET COMPOSITION OF BREEDING BALD EAGLES IN THE LOWER CHESAPEAKE BAY

Abstract. We investigated the diet of Bald Eagles (*Haliaeetus leucocephalus*) in the lower Chesapeake Bay by video-recording food delivered to nests during the 2002-03 breeding seasons. The diet included at least 12 species of fishes (2 identified to family only and 2 identified to genus only), 3 species of birds, 4 species of mammals, and 4 species of reptiles. Salinity (tidal-fresh vs. mesohaline) had no significant influence on diet composition. Ictaluridae and Clupeidae species were the most frequent prey items with regard to percent abundance, delivered biomass, and delivered energy in the Bald Eagle's diet in both salinity zones. Temporally, diet composition varied between study years, suggesting annual changes in the availability of prey species. We consider differences in weather patterns between study years as the mostly likely factor contributing to this interannual variation in diet.

Bald Eagles (*Haliaeetus leucocephalus*) are considered opportunistic foragers capable of using several foraging techniques to exploit a variety of prey items. Fish are the main source of food for breeding and nonbreeding eagles in most populations, though diet composition also includes mammals, birds, and reptiles. This foraging and dietary flexibility likely explains, at least in part, the array of breeding habitats and geographic locations throughout the species' North American range. By adapting feeding strategies and preferences to locally available prey items, nesting eagles are successful at meeting the high energetic demands associated with chick rearing in a variety of ecosystems.

Despite considerable research emphasis placed on describing diet composition in different nesting localities (e.g., Retfalvi 1970, Ofelt 1975, Dugoni *et al.* 1986, Knight *et al.* 1990), few investigations have examined variation in prey use within a breeding population (*but see* Dzus and Gerrard 1993). As a result, little is known about how diet varies in continuous systems along the environmental gradients that determine prey distribution. This failing exists despite the recognition that regional influences are important in shaping local community structure; *i.e.* local communities are not governed solely by local processes (Ricklefs 1987, Ricklefs and Schluter 1993).

Bald Eagles in the Chesapeake Bay rely primarily upon fish during the breeding season (Wallin 1982, Mersmann 1989), yet the density and distribution of fish species throughout the Bay waters is not uniform. Salinity is a significant factor influencing the composition of fish communities in the estuarine ecosystem of the Chesapeake Bay (Murdy *et al.* 1997, Jung 2002). Predictable changes in the distribution, diversity, and abundance of resident fish species occur along the gradient from freshwater to seawater. In addition, salinity is integral to temporal changes that enhance this spatial variability in fish assemblages through the spawning migration of anadromous fish. Anadromous fish arriving from the open Bay or ocean waters migrate annually up the major tributaries to spawn in the freshwater portions of creeks and rivers. Though the interaction between anadromous fish and Bald Eagles is well researched in Pacific and inland eagle populations (e.g., Gerrard *et al.* 1975, Fitzner and Hanson 1979, Spencer *et al.* 1991, Hunt *et al.* 1992, McClelland *et al.* 1994, Restani *et al.* 2000), no published works have investigated the impact that this energy resource has on eagles nesting along the Atlantic coast waterways.

Here we investigate the potential influence of salinity on the diet composition of Bald Eagles in the lower Chesapeake Bay. Specifically, we evaluate the extent to which salinity contributes to spatial variation in various dimensions of diet. We also examine potential temporal 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 (refer to General Introduction for map of study area). 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) (DAWG 1997). This study limited nest selection to tidal-fresh and mesohaline reaches to (1) document extremes in salinity effects in river systems and (2) because Watts *et al.* (*in press*) documented significant differences in breeding density between salinity zones. Within these areas, we chose nests where the placement of video-recording equipment was possible. Nests that had a history of reliable production and regularly experienced human interaction were preferred. This selection procedure resulted in 9 nests in both the tidal-fresh and mesohaline reaches. One nest was included in both years of this study. Because nests were considered individual samples in all analyses, sample sizes presented here reflect unique pairing of nest and year.

Data collection at each nest was determined by nestling age estimated during aerial surveys and later confirmed by visual inspection of chicks. We divided the nesting cycle into 3 phases relative to the expected period of maximum growth in developing eaglets (Bortolotti 1984): before (0 – 14 d), during (15 – 45 d), and after (day 46 – until fledging) anticipated maximum growth. 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 2 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 nestling ages for data analysis.

Video-monitoring. We used a video-monitoring approach to study the diet of breeding Bald Eagles during the chick-rearing phase of the nesting cycle. The video system consisted of a waterproof, bullet security camera wired to a VHS videocassette recorder. 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 video recorder and a deep cycle, 12-volt marine battery. The video recorder and battery were placed in waterproof containers and positioned at a remote location approximately 250 m from nest to reduce disturbance and improve access for maintenance activities. Recording of nest activity was focused on the morning hours (beginning 1 h after sunrise) to include the expected peak period of chick provisioning (Jaffe 1980, Wallin 1982, Mersmann 1989) and thus document a maximum number of deliveries within the recording block. Recording bouts typically lasted 8 h, 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 zones in each study year. We changed the videotape daily and on every fourth visit replaced the battery.

We identified prey items to the lowest taxonomic level possible and recorded the date, delivery time, and prey size. We grouped prey into 4 taxonomic classes (fish, birds, mammals, and reptiles) and developed methods for prey size determination and biomass/energy estimation to reflect the morphological characteristics of each taxa. Similar methods were used to assess size, biomass, and energy of unidentified prey items. For all deliveries that were not whole, we estimated the intact proportion in 10% intervals.

Fish – We estimated the size of fish by visual comparison to adult bill length in ½ bill length increments. We then converted observations to mm using an estimate of average bill length for eagles from the Chesapeake Bay population. The estimate (mean ± standard deviation = 63.6 ± 3.40 mm) used was derived from 26 adult and subadult specimens (11 females, 12 males, and 3 unsexed) housed in the bird collections of the Smithsonian National Museum of Natural History and Virginia Tech. Fish lengths were then converted to biomass using length-weight relationships; biomass values, in turn, were converted to energy estimates using energy density (caloric content) values. Whenever possible, we used species-specific equations from the literature for both biomass (Appendix 1) and energy density (Appendix 2) conversions. Otherwise, we used values from closely related species. For taxa with species members that were indistinguishable on videotape (e.g., Ictaluridae, Clupeidae, *Lepomis* spp. and *Pomoxis* spp.), biomass and energy conversions were based on representative species. Biomass and energy calculations for unidentified fish were estimated by using a weighted average of all identified fish.

Birds and Mammals – Birds that could be identified were assigned masses from Dunning (1992) and energy content was assumed to be 8.2 kJ/g wet mass (Stalmaster and Gessaman 1982). 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. Mammalian energy content was assumed to be 5.2 kJ/g wet mass (Kirkley and Gessaman 1990).

Reptiles (*Turtles*) – We estimated turtle size (carapace length) in relation to adult bill length in ½ bill length increments. Whole weights for energy density conversions were estimated using species-specific, allometric relationships between carapace length and mass derived from large, regional data sets (J. C. Mitchell unpubl. data).

In the absence of reptile-specific energy density values, we used the mammalian value of 5.2 kJ/g wet mass (Kirkley and Gessaman 1990) for calculations.

Unidentified Items – We estimated the biomass of unidentified prey items in relation to the approximate size (and associated weight) of adult mammals. Energy conversions were based on mammalian values (5.2 kJ/g wet mass) to calculate the most conservative energy delivered.

Statistical Analysis. We summarized diet information in two different ways for presentation and analysis. All prey items delivered to nests were summarized to represent an overview of eagle diet within the study area during the brood-rearing period. Descriptive statistics on overall diet composition and prey size are presented for all taxa. We evaluate possible differences between years in terms of the relative contribution of broad taxonomic classes using frequency statistics. Because the focus of recording effort was within the maximum growth period of development and recording effort outside of this period was uneven with respect to years, salinity, and nests, diet information was summarized within this period only for the more rigorous comparisons between salinity zones.

We evaluated the influence of salinity and year on diet using two-way ANOVAs with salinity (2 ranks including tidal-fresh and mesohaline) and year (2 ranks including 2002 and 2003) as factors and individual nests as samples. We tested a series of dependent variables that represent different dimensions of the diet including diet breadth and equitability, average delivered fish length and biomass, the importance of Ictaluridae and Clupeidae fish, and the importance of other prey. At east nest, we computed species diversity (Simpson's D: Simpson 1949) to estimate diet breadth and equitability to estimate evenness. We evaluated the influence of salinity and year on the importance of Ictaluridae, Clupeidae, and other prey to the overall diet by investigation (1) percent biomass of total delivered fish biomass and percent energy of total delivered fish energy and (2) biomass delivery rate (g/h) and energy delivery rates (kJ/h). 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). Nests that did not have adequate recording effort for diet to reach an asymptote were not included in salinity comparisons.

RESULTS

Overall Diet Description. Of the 765 deliveries recorded on 4,098 h (18 nests) of videotape, we identified 730 (95.4%) prey items representing at least 12 species of fishes, 3 species of bird, 4 species of mammal, and 4 species of reptiles (Table 1.1). Among the identified prey items, we were unable to discriminate between closely related species within 4 of the observed fish taxa. Two taxa were identified to family group and probably were represented by the following species that were indistinguishable on videotape: Ictaluridae – channel catfish (*Ictalurus punctatus*), blue catfish (*I. furctatus*), and white catfish (*Ameiurus catus*); and Clupeidae – Alewife (*A. pseudoharengus*), American shad (*A. sapidissima*), blueback herring (*Alosa aestivalis*), hickory shad (*A. mediocris*); and *Dorosoma* – gizzard shad (*D.*

cepedianum). In addition, we were unable to discriminate between species in the *Lepomis* and *Pomoxis* genera. Probable species represented within these genera were: *Lepomis* spp. – bluegill (*L. macrochirus*), pumpkinseed (*L. gibbosus*), and redbreast sunfish (*L. auritus*); and *Pomoxis* spp. – black crappie (*P. nigromaculatus*) and white crappie (*P. annularis*).

By frequency of occurrence, fish constituted 96.0% of the total identified prey, birds 0.5%, mammals 2.3%, and reptiles 1.2%. By delivered biomass, fish constituted 94.1% of the total biomass delivered, birds 1.0%, mammals 4.1% and reptiles 0.9%. By delivered energy, fish constituted 94.3% of the total energy delivered, birds 1.5%, mammals 3.4% and reptiles 0.7%. Ictaluridae and Clupeidae were overwhelmingly the most common prey groups by % abundance, % biomass, and % energy. Atlantic croaker (*Micropogonias undulatus*), American eel (*Anguilla rostrata*), *Lepomis* spp., largemouth bass (*Micropterus salmoides*), and *Pomoxis* spp. followed next in percent abundance (in decreasing order). We observed relatively few prey deliveries ($n \leq 5$) from the remaining fish species recorded in the diet: bluefish (*Pomatomus saltatrix*), spot (*Leiostomus xanthurus*), striped bass (*Morone saxatilis*), summer flounder (*Paralichthys dentatus*), and yellow perch (*Perca flavescens*).

We were able to calculate biomass for 750 prey items (98.9% total deliveries observed). Including items of both partial and intact prey status, biomass ranged from 1.3 – 2391.7 g with a mean ± standard deviation of 414.5 ± 291.51 g. Of the 620 identified fish, we were able to determine intact status and estimate total length for 473 items (76.3%). Species-specific information on average length delivered is presented in Table 2. Average biomass of intact fish ranged from 22.8 – 2391.7 g with a mean ± standard deviation of 466.5 ± 268.70 g. Length and biomass distributions for intact fish are illustrated in Figure 1.1 and Figure 1.2, respectively.

The importance of each taxonomic class in overall diet composition throughout the breeding season (by percent biomass of all prey identified to class) did not vary significantly between the two years of this study ($\chi^2 = 0.31$, df = 3, $P > 0.05$). Species diversity did not vary significantly between the years of this study (one-way ANOVA, $F_{(1, 14)} = 0.03$, $P > 0.05$). Ictaluridae and Clupeidae were dominants in the diet for both study years, with no significant between-year variation in combined use expressed as percent biomass relative to other identified fish ($\chi^2 = 0.20$, df = 1, $P > 0.05$).

Salinity and Yearly Comparisons. At 16 nests with adequate recording coverage for statistical analysis, we observed 541 prey deliveries made during 2,176 h of videorecording the maximum growth phase. Within this time period, 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 ($\chi^2 = 4.5$, df = 3, $P > 0.05$) or years ($\chi^2 = 8.8$, df = 3, $P > 0.05$). Fish dominated diet composition in both salinity zones and both years.

The length (two-way ANOVA, $F_{(1, 469)} = 7.50$, $P = 0.006$) and biomass (two-way ANOVA, $F_{(1, 469)} = 7.56$, $P = 0.006$) of delivered fish varied significantly between salinity zones, but we observed no significant between year differences in length (two-way ANOVA, $F_{(1, 469)} = 0.18$, $P > 0.05$) or biomass (two-way ANOVA, $F_{(1, 469)} =$

0.15, $P > 0.05$). Both indices of fish size were lower in the tidal-fresh compared to mesohaline salinity zones. Mean ± standard deviation for fish length was 40.0 ± 7.48 cm in the tidal-fresh compared to 42.4 ± 10.39 cm in the mesohaline salinity zone. Mean ± standard deviation for fish weight was 434.9 ± 235. 64 g in the tidal-fresh zone compared to 509.6 ± 303.43 g at nests in the mesohaline portions.

Species diversity was nearly significantly higher in the mesohaline compared to tidal-fresh reaches (two-way ANOVA, $F_{(1, 12)} = 4.65$, $P = 0.052$). However, there was no significant difference between years in species diversity (two-way ANOVA, $F_{(1, 12)} = 0.22$, $P > 0.05$), though there was a trend toward higher diversity in 2002. Equitability did not show significant variation between salinity zones (two-way ANOVA, $F_{(1, 12)} = 3.07$, $P > 0.05$) or years (two-way ANOVA, $F_{(1, 12)} = 0.49$, $P > 0.05$).

The dietary proportion of Ictaluridae and Clupeidae expressed as percent biomass and percent energy of total delivered fish biomass and energy, respectively, did not vary significantly between salinity zones (all two-way ANOVAs, $F_{(1, 12)} < 0.89$, $P > 0.05$). Between year differences for percent energy of Ictaluridae were significant (two-way ANOVA, $F_{(1, 12)} = 4.91$, $P = 0.047$); all other measures approached significance between years (all two-way ANOVAs, $F_{(1, 12)} < 4.58$, $P > 0.5$). For all proportions, no significant interaction was observed between salinity and year (all two-way ANOVAs, $F_{(1, 12)} < 0.32$, $P > 0.05$). Overall, the proportion of Ictaluridae biomass and energy in the diet was significantly higher in 2002 compared to 2003; the proportion of Clupeidae biomass and energy showed the reverse trend.

We also examined the prevalence of Ictaluridae and Clupeidae in the diet by considering the rates of biomass and energy delivery for each species-group.

Interesting trends are apparent, though no statistically significant results were observed between salinity zones (all two-way ANOVAs, $F_{(1, 12)} < 0.36$, $P > 0.05$) or years (all two-way ANOVAs, $F_{(1, 12)} < 2.73$, $P > 0.05$) and no interaction was detected (all two-way ANOVAs, $F_{(1, 12)} < 0.28$, $P > 0.05$). Delivery rates of biomass (Figure 1.3) and energy (Figure 1.4) for Ictaluridae were higher in tidal-fresh compared to mesohaline salinity zones and higher in 2002 compared to 2003. Biomass (Figure 1.5) and energy (Figure 1.6) delivery rates for Clupeidae showed the reverse trends: rates were lower in tidal-fresh and 2002 compared to mesohaline salinity zone and 2003, respectively.

DISCUSSION

Overall Diet.

Diet Composition in Comparison to Previous Bay-area Studies – Important prey identified in this investigation were similar to those noted in previous diet studies of Bald Eagles in the Chesapeake Bay. However, differences in the relative use of prey taxa and key species are apparent. Most notably, we observed a greater dietary proportion of Clupeidae species, a family either un-detected or noted as having a minor contribution to diet composition in earlier Bay-area studies. Further, our results vary in that birds, mammals, and reptiles comprised relatively insignificant proportion of overall diet compared to fish. We consider these discrepancies to be largely the result of (1) variation in the foraging ecology of breeding versus nonbreeding eagles, (2) differences in the field techniques used to assess diet, and/or

(3) changes in the geographic distribution of prey resources between study site locations.

Bald Eagle diet composition varies seasonally with changes in relative prey abundance and availability (Stalmaster 1987). Previous research in the Chesapeake Bay focused on diet composition during the breeding season is consistent with our result that fish constitute the overwhelming majority of items delivered to nests (> 98%: Wallin 1982). However, outside the breeding season, eagles in the Bay ecosystem rely more heavily on other prey taxa such as birds (primarily waterfowl) and mammals (Mersmann 1989). This prey switching behavior 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). Specific to the Bay region, two eagle studies suggest temporal variation in prey availability. Buehler *et al.* (1991) alluded to the fact that live fish are relatively scarce or unavailable in deep water during winter months in the upper Chesapeake Bay. DeLong *et al.* (1989) assessed prey availability with gillnet sampling and found that fish numbers in the upper Bay declined seasonally November through March while waterfowl abundances peaked in winter months until April.

A variety of field techniques have been used to determine Bald Eagle diet composition in the Chesapeake Bay: direct observation, video-monitoring, pellet analysis, and collection of prey remains. Direct observations and video-monitoring are considered the most reliable measures; analysis of pellet and prey remains may bias the perceived relative use of food types characterized by persistent remains, *i.e.*

large skulls, feathers, and shells (Mersmann *et al.* 1992). This is likely due to the eagle's ability to digest the fine bones associated with small mammals and most fish species (Imler and Kalmbach 1955, Duke *et al.* 1975). The discrepancy between known consumption and detection in pellet and/or prey remains of various fish species has been reported in numerous studies (e.g., LaBonde 1981, Dugoni *et al.* 1986).

Similar inconsistencies are apparent between our results and previous Bay area studies that have quantified diet by the analysis of pellets and prey remains. Both Cline and Clark (1981) and Haines (1986) reported larger percentages of bony fish, mammals, birds, and reptiles compared to the findings of this investigation. In addition, small and soft-bodied fish were generally listed with relative proportions well below those observed in our analyses. Tyrell (1936) reported a larger number of bird species compared to fish species in the diet of nesting eagles, though overall contribution to diet was thought to be small.

In contrast, other studies that have assessed diet in the Chesapeake Bay through either direct observation or video-monitoring report fish use patterns comparable to our observations (Wallin 1982, Mersmann 1989). However, the prominent fish species reported varies with study location. Mersmann (1989) documented the importance of gizzard shad, channel catfish, Atlantic menhaden (*Brevoortia tyrannus*), and white perch (*Morone americana*) at roost sites in the upper Chesapeake Bay. In the lower Chesapeake Bay, Wallin (1982) observed that Atlantic menhaden and American eel were the most common prey species.

Diet Composition in Comparison to Other Breeding Locations – 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., Florida: McEwan and Hirth 1980, Nova Scotia: Cash *et al.* 1985, Louisiana: Dugoni *et al.* 1986, Texas: Mabie *et al.* 1995). Clupeidae predation has been documented, though species identified were non-anadromous residents (Mersmann 1989, Mabie 1995). An interesting ecological relationship present in the Bay ecosystem is that most of the Clupeidae species observed here are highly migratory. The importance of anadromous fish runs has been documented in numerous eagle populations, though where the most comprehensive work has been conducted these runs do not coincide with the breeding season (e.g., Fitzner and Hanson 1979, Spencer *et al.* 1991, Hunt *et al.* 1992, McClelland *et al.* 1994). Two notable exceptions are results from Gerrard *et al.* (1975) and Gende *et al.* (1997), which document eagle pairs nesting close to spawning grounds have higher nest productivity compared with pairs nesting farther away.

Prey Size – Ultimately, the size of prey delivered to nestlings is limited by the weight adults can carry. Palmer (1988) suggests that the maximum load capacity for raptors is approximately 33% adult body mass. Considering mean weights for adult female eagles in the Chesapeake Bay area, this suggests a prey load capacity of 1,374.0 ± 293.81 g ($n = 66$: National Wildlife Health Center's Madison Lab, Wisconsin, unpubl. data). Data on male weights were excluded to provide a more conservative prey load estimate.

The mean prey biomass reported in this study was well below approximated load capacity, indicating that adults are capable of delivering much larger items than the average size observed (approximately 30%). However, in 7 instances the biomass of delivered prey items exceeded the upper limits of this range, revealing some flexibility in load capacity.

The size of prey delivered to nestlings by their parents can also reveal several aspects of adult foraging ecology. For fish, the average biomass was generally well below the maximum carrying capacity of eagles. Our observed distribution of fish length was comparable to both Haywood and Ohmart (1986) and Grubb (1995).

Spatial and Temporal Comparisons.

Prey Size – Previous research indicates that Bald Eagles may 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 selection supported optimal foraging models. As central place foragers, nesting adults benefit energetically from selecting larger prey items (Orians and Pearson 1979, Schoener 1979). In our study, adults delivered significantly larger fish, on average, to nests in the mesohaline compared to tidal-fresh salinity zones. This suggests more energetically favorable conditions for foraging parents in higher salinity waters, assuming adults in both salinity zones utilized comparable foraging areas.

Influence of Salinity on Diet Composition – Our results show 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, diet was dominated by Ictaluridae and Clupeidae species-groups. Additional fish species observed tended to occur in such small numbers that geographic differences in distribution were not detectable. This suggests that changes in salinity between mesohaline and tidal-fresh zones may not impose as significant a barrier to the distribution of prey species as originally hypothesized. The broad-scale use of Ictaluridae and Clupeidae may be interpreted through taxa-specific distribution patterns and life history characteristics that indicate potential reasons for their susceptibility to predation.

Catfish belonging to the family Ictaluridae are considered predominately freshwater, resident species common in the tributaries of the lower Chesapeake Bay. Though catfish generally prefer low-saline water, they are capable of utilizing a broad salinity range (Lippson *et al.* 1979, Dames *et al.* 1989, Jenkins and Burkhead 1994) and therefore are 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 is consistent with the observed trend towards higher catfish delivery rates and higher dietary proportion of catfish in low salinity zones.

Several hypotheses have been proposed to explain the prevalence of catfish, a benthic-feeding fish, in the diet of Bald Eagles. We believe that catfish were a targeted food source primarily because of their susceptibility to predation due to increased vulnerability to aerial attacks given their (1) downward orientation (Todd *et al.* 1982) and (2) preferred foraging in shallows and riffles (Haywood and Ohmart 1986). In addition, abundance of moribund catfish present a potentially easily accessible food source. In research in the northern Chesapeake Bay, DeLong (1990) concluded that dead channel catfish, the most frequently encountered floating moribund fish, are likely more available to Bald Eagles than live channel catfish during the spring and summer. When status at capture was possible to assess, Mersmann (1989) noted that all catfish taken by eagles in the northern Bay were dead fish. In our study, only 12.7% of all observed intact catfish (n = 181) were positively determined to be live on delivery to the nest. Interpretation of this value is limited, however, because we are unable to make assumptions about the relative condition of remaining catfish deliveries (e.g., fairly fresh, recently decomposing, rancid).

In contrast to resident Ictaluridae, most species likely comprising the Clupeidae family are anadromous fish that migrate from open Bay or ocean waters to spawn in the freshwater portions of creeks and rivers. Triggered by favorable water temperatures, the spawning runs of most anadromous clupeids in this region begin as early as February and extends as late early June (alewife: Monroe 2000, hickory shad: Davis *et al.* 1970). These annual spawning migrations provide predictable, energy-rich food resources for terrestrial predators (Wilson and Halipka 1995). In the Chesapeake Bay, anadromous spawning runs temporally coincide with the nesting season of Bald Eagles. Specifically, the spawning time period coincides with the period in which most nestlings in Virginia experience maximum growth and thus have the greatest energetic demands (April – mid-May: B.D. Watts, unpubl. data), suggesting a selective advantage for breeding during the period of spawning runs.

There is circumstantial evidence suggesting that an ecological interaction between breeding Bald Eagles and anadromous fish may exist in other populations along the Atlantic coast as well. Breeding habitat for both eagles and *Alosa* spp. extend from Florida northward to Maine. Latitudinal variation in the eagle breeding cycles (Buehler 2000) and timing of fish runs (American shad: Limburg *et al.* 2003) co-vary such that populations of both predator and prey breed earlier further south. However, no work to date has examined the apparent synchrony in these patterns on a broad geographic scale.

Several factors likely contribute to the susceptibility of anadromous fish to predation. First, visibility and accessibility are enhanced by the behavioral characteristics of *Alosa* spp. *Alosa* spp. are schooling fish and typically swim in congregated numbers in the upper portion of the water column (Monroe 2000). Second, anadromous shad/herring require time for physiological adjustment to changes in salinity. Leggett (1976) observed the American shad required 2 – 3 d to adapt to freshwater, and high stress and mortality were evident in the actual 2.5 h transfer period between fresh and salt water (Leggett and O'Boyle 1976). This suggests spawning alosids may congregate in low-saline portions of the river as they adapt to the physiological stress of the system, therein presenting a concentrated food resource for foraging eagles. Third, post-spawning mortality, as with moribund catfish, presents an easily accessible forage base. However, there is little conclusive data available on post-spawning mortality in the Bay region, though some indication is provided by the percentage of repeat spawners. Joseph and Davis (1965) documented as many as 60% of spawning alewives and 44 – 65% blueback herring in Virginia were repeat spawners. Leggett and Carscadden (1974) report lower percentages of repeat spawners in American shad: 27% and 24% in the James and York Rivers, respectively. This suggests that a sizeable proportion of spawning clupeids may not survive migratory runs.

In contrast to anadromous Clupeidae, gizzard shad are year-round, predominantly freshwater residents in the Chesapeake Bay ecosystem (Murdy *et al.* 1997). For much of the year, gizzard shad are widely distributed throughout the Bay water with high abundances in the freshwater portions of the tributaries up to salinities as high as 22 ppt (Murdy *et al.* 1997). However, as in anadromous species, adult gizzard shad congregate in the tidal-fresh reaches to spawn in March – May. Yet, unlike anadromous Clupeidae which typically do not feed during spawning runs and show marked decreases in weight (Monroe 2000), gizzard shad forage year-round and, consequently, body condition does not deteriorate due to starvation during spawning. Thus, gizzard shad may provide a potentially higher quality food source compared to anadromous *Alosa* spp. Further, both adult and young gizzard shad remain in shallow portions of low saline waters throughout the summer months in contrast to individual anadromous shad and herring that typically leave the Bay system after 4 – 5 d (alewife: Kissil 1974, blueback herring: Kaluda *et al.* 1991).

Thus the duration of prey availability is longer than that supplied by anadromous species.

Our results indicate that Bald Eagles utilized Clupeidae prey throughout the length of the tributaries, regardless of salinity zone. One possible explanation for this is that anadromous fish could disperse into narrow channel widths beyond Bald Eagle foraging preference (< 200 m: Watts *et al.* 1994) in the tidal-fresh reaches to spawn, thus making them as transient and inaccessible to eagles in the low saline waters as the high saline waters. Second, different factors affecting susceptibility might affect shad in different salinity zones, such as exhaustion in tidal-fresh reaches and physiological adjustment in mesohaline zones. Finally, the Clupeidae species represented in the diet of breeding eagles may have included high percentages of gizzard shad. Given the prevalence of gizzard shad along the length of the tributaries, a more even distribution of food resources would have been presented to eagles in different salinity zones.

Influence of Year on Diet Composition – Weather anomalies regarding both precipitation and temperature were reported in 2003 with record wet conditions and lower than average temperature were observed 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 dietary variation.

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 impact migration runs of anadromous species (Jung 2002) and could be responsible for the decreased relative importance of shad/herring 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 expand 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. This alone, however, does not explain the increased use of catfish in the tidal-fresh reaches in 2003. A rise in Ictaluridae use here would not have been expected unless preferred prey were not available. Thus, it appears that eagles may select Clupeidae when available, despite previous research indicating that Bald Eagles preferentially select catfish over gizzard shad in experimental trials (DeLong *et al.* 1989). This compensatory use of Ictaluridae and Clupeidae is supported by the fact that no significant annual variation in patterns of prey use for other species was observed.

Sources of Error. In a short-term study such as this one, annual variation in abiotic (*i.e.* rainfall) and biotic (*i.e.* fish stocks) factors can have a significant impact on year-specific salinity distribution. However, the segmentation scheme used as reference to delineate salinity boundaries was based on long-term averages of several environmental characteristics. Thus, generalized boundaries may not necessarily be applicable when investigating yearly effects.

Another potential source of error arises from uncertainty in the foraging range of breeding eagles in the Chesapeake Bay. We limited nest selection in this study to locations that were ≤ 3 km from the tributary's shoreline. This distance was based on previous research indicating that breeding eagles in the Chesapeake Bay typically forage in an area < 3 km from their nest site (Buehler *et al.* 1991). By focusing on nests near the shoreline, we hoped to increase the probability that the breeding pair would primarily forage in the appropriate salinity zone. However, we could not control for pairs possibly foraging in different salinity zones associated with inland lakes, reservoirs, and freshwater creeks.

Species-specific demographics may also influence prey selection between years. Anadromous fish stocks vary in strength annually as cohorts reach sexual maturity (Murdy *et al.* 1997). For example, year-class strength of American shad probably is determined by numbers that survive embryonic and larval stages (Crecco and Savoy 1984), and survival during critical early life stages is correlated with environmental factors (Crecco *et al.* 1983, 1986; Crecco and Savoy 1984; Savoy and Crecco 1988).

Conclusions. The results of this study indicate that diet composition with regard to major species groups did not vary with river salinity. This finding suggests that nesting pairs in both tidal-fresh and mesohaline salinity zones have access to similar fish species. Thus, the documented differences in Bald Eagle breeding density between salinity zones does not appear to be driven by variation in prey assemblages.

However, this finding does not eliminate the possibility that the difference in eagle breeding density throughout the lower Bay ecosystem is correlated to variation in prey availability. Though we sought to quantify prey use by considering diet composition, no work was done to assess variation in prey densities. Future initiatives would benefit greatly from examining the effects of food limitation on such variables as nestling growth and survival to determine if habitat quality, as related to food resources, varies between salinity zones.

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Figure 1.1. Length distribution of fish delivered to nestling Bald Eagles during the 2002-03 breeding seasons in the lower Chesapeake Bay. Only deliveries of whole (intact) fish included.

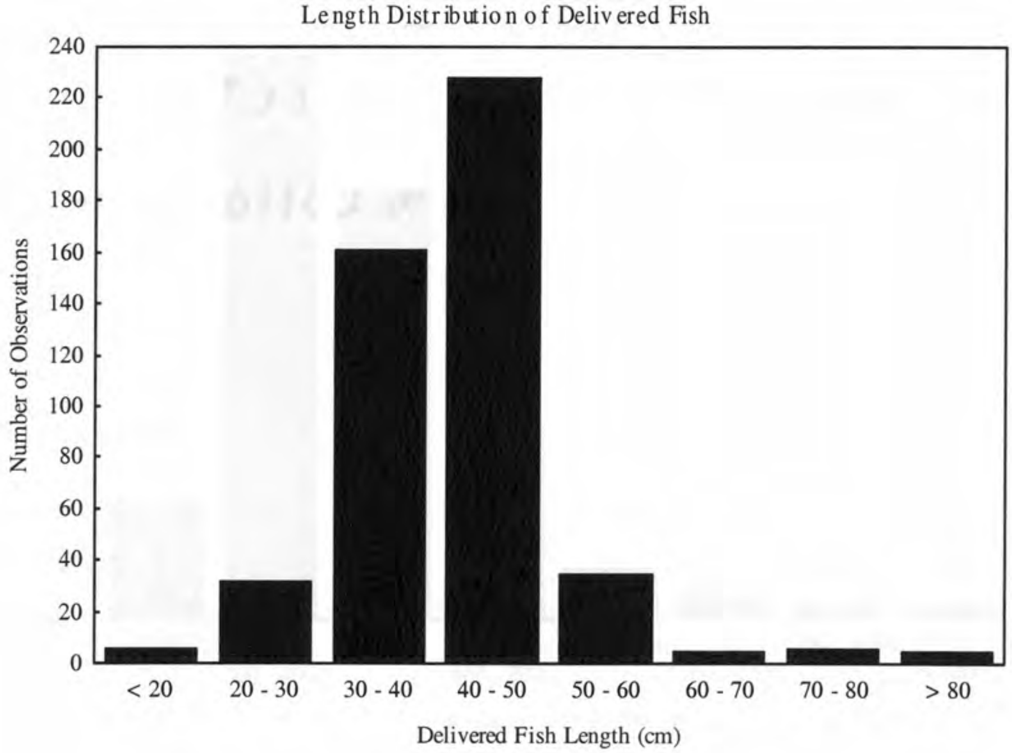

Figure 1.2. Biomass distribution of fish delivered to nestling Bald Eagles during the 2002-03 breeding seasons in the lower Chesapeake Bay. Only deliveries of whole (intact) fish included.

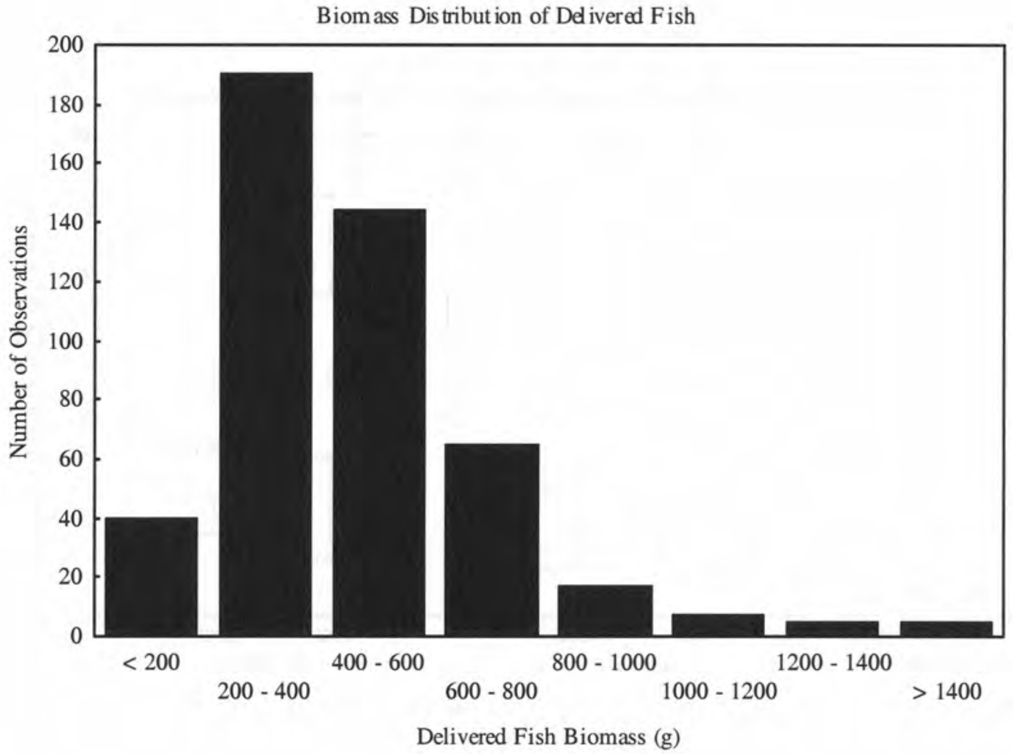

Figure 1.3. Influence of salinity and year on biomass delivery rate of Ictaluridae at Bald Eagle nests in the lower Chesapeake Bay during the 2002-03 breeding seasons. Only deliveries made during the expected period of nestling maximum growth (15 – 45 d) included in analysis.

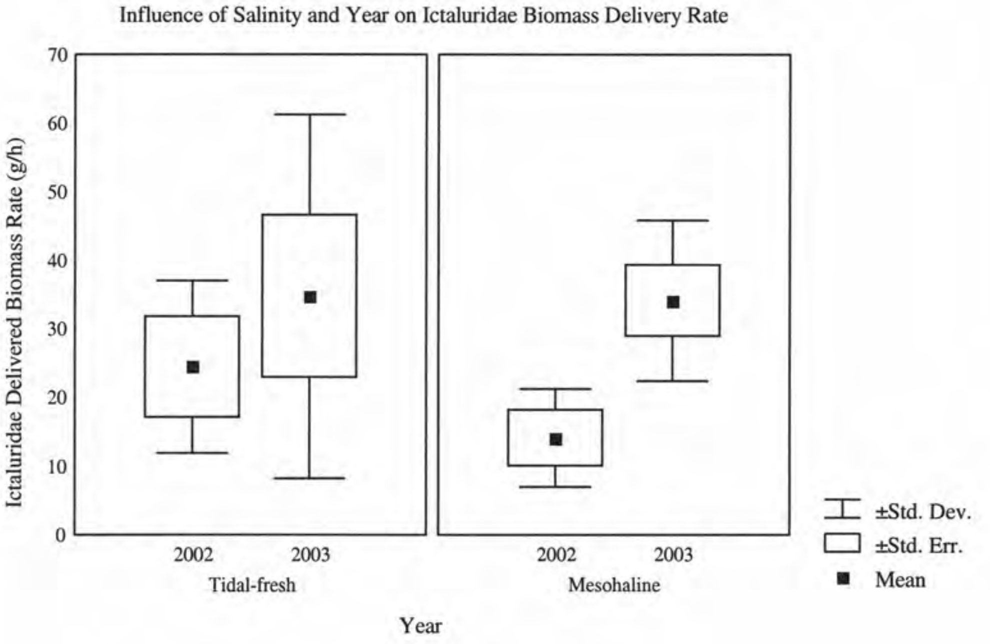

Figure 1.4. Influence of salinity and year on energy delivery rate of Ictaluridae at Bald Eagle nests in the lower Chesapeake Bay during the 2002-03 breeding seasons. Only deliveries made during the expected period of nestling maximum growth (15 – 45 d) included in analysis.

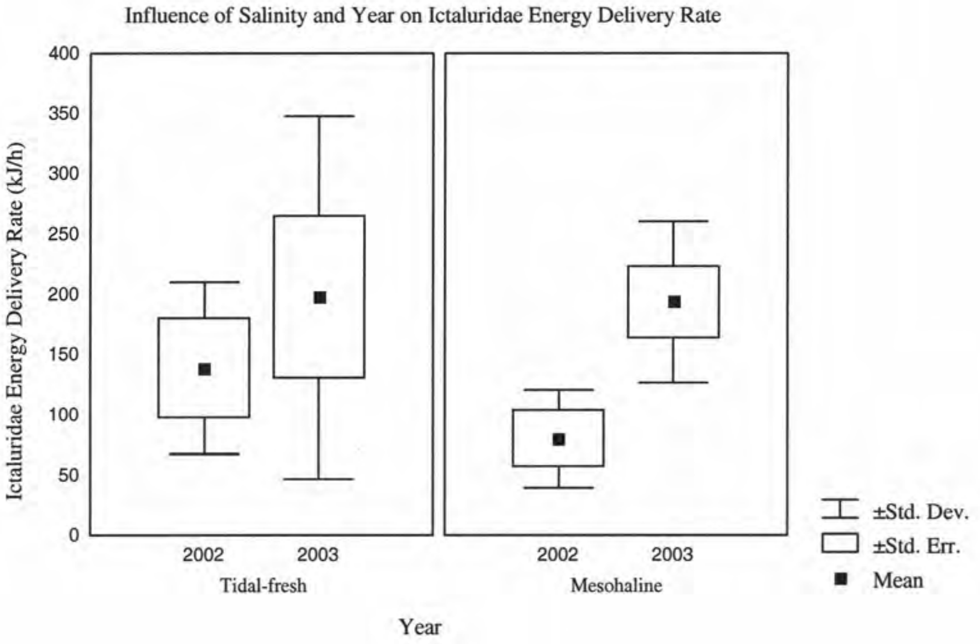

Figure 1.5. Influence of salinity and year on biomass delivery rate of Clupeidae at Bald Eagle nests in the lower Chesapeake Bay during the 2002-03 breeding seasons. Only deliveries made during the expected period of nestling maximum growth (15 – 45 d) included in analysis.

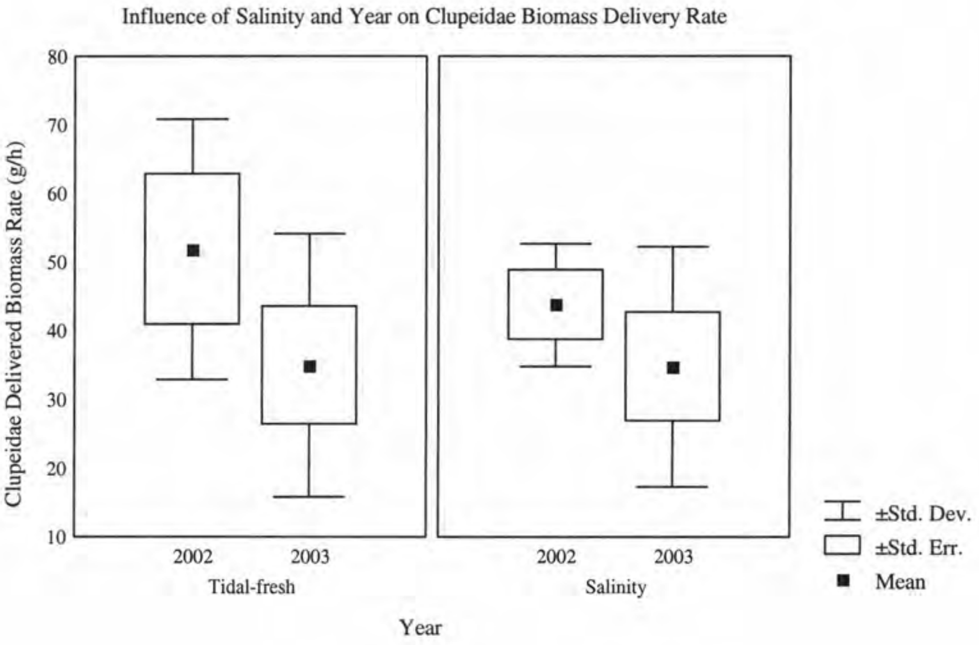

Figure 1.6. Influence of salinity and year on energy delivery rate of Clupeidae at Bald Eagle nests in the lower Chesapeake Bay during the 2002-03 breeding seasons. Only deliveries made during the expected period of nestling maximum growth (15 – 45 d) included in analysis.

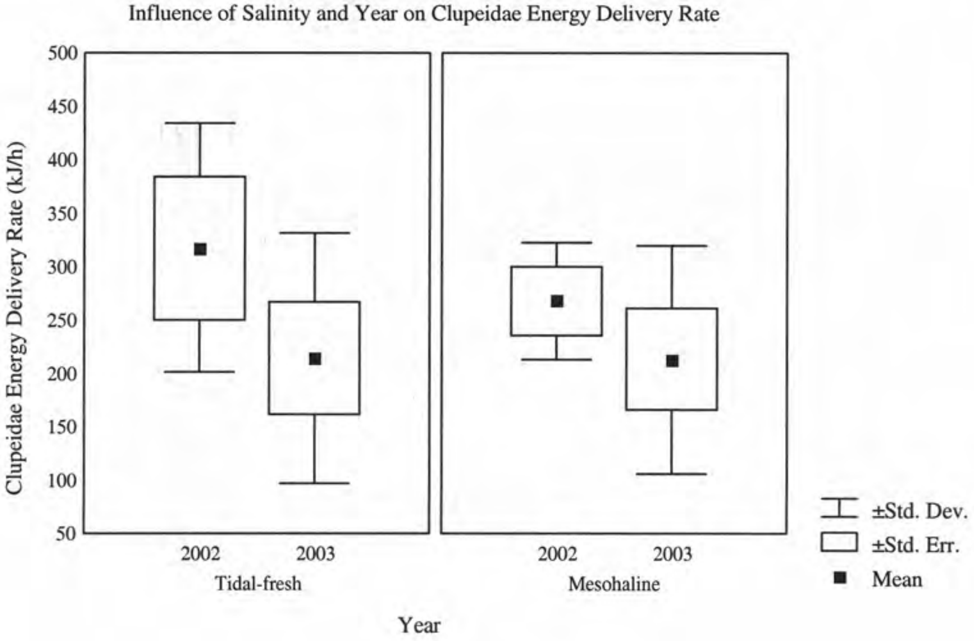

Table 1.1. Diet of Bald Eagles nesting in the lower Chesapeake Bay based on video-observations of prey delivered to nests during the 2002-03 breeding seasons.

Species	Individuals (*n*)		Biomass (g)		Energy (kJ)	
	Total	%	Total	%	Total	%
Fish (Osteichthyes)						
American eel (*Anguilla rostrata*)	17	2.2	11,752.9	3.8	148,997.8	8.1
Atlantic croaker (*Micropogonias undulatus*)	45	5.9	20,554.1	6.6	135,978.5	7.4
Black crappie and white crappie (*Pomoxis* spp.)	10	1.3	2,433.7	0.8	10,708.1	0.6
Bluefish (*Pomatomus saltatrix*)	1	0.1	109.4	0.0	524.9	0.0
Clupeidae	284	27.1	111,054.0	26.4	544,664.7	22.8
Ictaluridae	234	30.6	95,302.5	30.7	540,365.0	29.3
Largemouth bass (*Micropterus salmoides*)	10	1.3	7,446.8	2.4	31,276.4	1.7
Lepomis spp.	10	1.3	2,447.2	0.8	10,767.5	0.6
Spot (*Leiostomus xanthurus*)	2	0.3	889.1	0.3	6,223.9	0.3
Striped bass (*Morone saxatilis*)	5	0.7	6,628.6	2.1	150,168.5	8.2
Summer flounder (*Paralichthys dentatus*)	1	0.1	462.9	0.1	2,304.7	0.1
Yellow perch (*Perca flavescens*)	1	0.1	336.4	0.1	1,412.9	0.1
Unidentified	75	9.8	19,143.1	6.2	80,094.7	4.3
Fish Subtotal	695	90.8	278,560.5	89.8	1,663,487.4	90.3
Birds (Aves)						
Double-crested Cormorant (*Phalacrocorax auritus*)	1	0.1	1,674.0	0.5	13,726.8	0.7
Mallard (*Anas platyrhynchos*)	1	0.1	649.2	0.2	8,872.4	0.5
Rock Pigeon (*Columba livia*)	1	0.1	354.5	0.1	2,906.9	0.2
Unidentified	4	0.5	1,698.5	0.5	13,927.7	0.8
Bird Subtotal	7	0.9	4,376.2	1.4	39,433.8	2.1

Table 1.1. Continued.

Species	Individuals (*n*)		Biomass (g)		Energy (kJ)	
	Total	%	Total	%	Total	%
Mammals (Mammalia)						
Common muskrat (*Ondatra zibethicus*)	4	0.5	3,000.0	1.0	15,300.0	0.8
Eastern cottontail (*Sylvilagus floridanus*)	4	0.5	3,800.0	1.2	19,380.0	1.1
Eastern gray squirrel (*Sciurus carolinensis*)	4	0.5	1,482.0	0.5	7,558.2	0.4
Unidentified rodent (Rodentia)	1	0.1	1,000.0	0.3	5,100.0	0.3
Woodchuck (*Marmota monax*)	2	0.3	2,000.0	0.6	10,200.0	0.6
Unidentified	5	0.7	1,370.5	0.4	6,989.6	0.4
Mammal Subtotal	20	2.6	12,652.5	4.1	64,527.8	3.5
Reptiles (Reptilia)						
Common musk turtle (*Sternotherus odoratus*)	5	0.7	806.5	0.3	4,113.3	0.2
Eastern mud turtle (*Kinosternon subrubrum*)	1	0.1	550.7	0.2	2,808.3	0.2
Eastern painted turtle (*Chrysemys picta picta*)	1	0.1	119.7	0.0	610.5	0.0
Snapping turtle (*Chelydra serpentina*)	1	0.1	939.8	0.3	4,793.1	0.3
Reptile Subtotal	8	1.0	2,416.7	0.8	12,325.3	0.7
Unidentifieds	35	4.6	12,171.5	3.9	62,074.7	3.4
GRAND TOTAL	765	100.0	310,177.4	100.0	1,841,848.9	100.0

Table 1.2. Average length of fish delivered to Bald Eagle nests during the 2002-03 breeding seasons. Values presented as mean ± SD.

Species	***n***	**Length (cm)**
American eel (*Anguilla rostrata*)	17	61.0 ± 5.34
Atlantic croaker (*Micropogonias undulatus*)	33	39.6 ± 0.93
Black crappie and white crappie (*Pomoxis* spp.)	7	25.9 ± 1.76
Bluefish (*Pomatomus saltatrix*)	1	22.3
Clupeidae	218	41.9 ± 0.43
Ictaluridae	186	40.3 ± 0.54
Largemouth bass (*Micropterus salmoides*)	8	39.8 ± 2.75
Lepomis spp.	10	23.9 ± 2.38
Spot (*Leiostomus xanthurus*)	2	33.4 ± 1.59
Striped bass (*Morone saxatilis*)	4	46.9 ± 3.53
Summer flounder (*Paralichthys dentatus*)	1	38.2
Yellow perch (*Perca flavescens*)	1	31.8

Appendix 1.1. Biomass conversions used for fish and turtle species identified in the diet of Bald Eagles nesting in the lower Chesapeake Bay during 2002-03 breeding seasons. In conversion equations, mass (M) in grams and length (L) in centimeters.

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

Appendix 1.2. Energy conversions used for fish species identified in the diet of Bald Eagles nesting in the lower Chesapeake Bay during 2002-03 breeding seasons. In conversion equations, energy (E) is in kJ and mass (M) in grams.

Species	**Energy Conversion**	**Reference**
American eel (*Anguilla rostrata*)	E = 12.68*M	McLean 1986
Atlantic croaker (*Micropogonias undulatus*)	E = 6.276*M	McLean 1986
Bluefish (*Pomatomus saltatrix*)	E = 4.8*M	Steimle and Terranova 1985
Clupeidae (used mean for *Alosa sapidissima, A. aestivalis, A. mediocris,* and *A. pseudoharengus*)	E = 6.125*M	Steimle and Terranova 1985
Ictaluridae (used channel catfish, *Ictalurus punctatus*)	E = 5.67*M	Brugger 1993
Lepomis spp. (used bluegill, *L. macrochirus*)	E = 4.4*M	Minton and McLean 1982
Spot (*Leiostomus xanthurus*)	E = 7.0*M	Steimle and Terranova 1985
Summer flounder (*Paralichthys dentatus*)	E = 4.97896*M	McLean 1986
Yellow perch (*Perca flavescens*)	E = 4.2*M	Dykstra 1995

CHAPTER 2

THE INFLUENCE OF SALINITY ON PROVISIONING RATES AND NESTLING GROWTH IN BALD EAGLES IN THE LOWER CHESAPEAKE BAY

Abstract. We measured provisioning and growth patterns in Bald Eagle (*Haliaeetus leucocephalus*) chicks from nests in two salinity zones of the lower Chesapeake Bay during the 2002-04 breeding seasons. Rates of provisioning were assessed 3 ways: delivered prey, delivered consumable biomass, and delivered consumable energy. In general, provisioning rates were higher in mesohaline compared to tidal-fresh salinity zones and higher in 2003 compared to 2002. Four measures of growth were calculated for each chick: asymptotic weight, instantaneous growth rate, time required to reach 90% asymptotic weight (t_{90}), and time interval between 10 – 90% of growth ($t_{10\text{-}90}$). Female nestlings achieved greater asymptotic weights, experienced faster growth rates, and required longer time intervals to reach t_{90} for the duration of $t_{10\text{-}90}$ compared to male nestlings. Nestlings in mesohaline reaches grew at faster rates and achieved greater asymptotic weight than nestlings in tidal-fresh zones. Growth measures were depressed in 2003 compared to other study years. Measures of provisioning and growth rates were significantly correlated, a finding consistent with a general hypothesis that growth of chicks reflects prey provisioning. Compared to previous investigations in other Bald Eagle breeding populations, indices of energy delivery and growth rates were higher in our study. This may reflect high habitat quality in the lower Chesapeake Bay and suggests that nesting eagles in this area are successful at meeting the energetic demands of brood rearing.

Parental ability to provision offspring is influenced by a suite of both intrinsic (*i.e.* parent experience, quality, and physiological constraints) and extrinsic (*i.e.* food availability, weather, and habitat quality) factors (Ricklefs 1983). The quality of breeding habitat is one ecological aspect that incorporates several of these factors, potentially influencing foraging rate, provisioning rate, chick growth, survival, and fitness in birds of prey. Accordingly, habitat selection theory suggests that resource availability is a critical factor in influencing where an individual preferentially distributes itself in a heterogeneous environment. Thus, areas supporting the greatest density of pairs are often considered habitats of highest suitability (Orians and Wittenberger 1991).

For Bald Eagles (*Haliaeetus leucocephalus*) nesting in the lower Chesapeake Bay, the areas surrounding the tidal-fresh salinity reaches of the Bay currently support a greater nesting density and have experienced faster rates of population increase than areas surrounding higher saline waters (Watts *et al. in press*). This finding implies that habitat quality varies spatially along the salinity gradient in the Bay, though the specific habitat attributes that drive these patterns are not clear. Watts *et al.* (*in press*) suggest that variation in prey availability, mediated through changes in the salinity of Bay waters, may be one factor responsible for these observed patterns.

A recent investigation has examined the influence of salinity on diet composition in Bald Eagles in the lower Chesapeake Bay (Chapter 1). Results indicate that dominant prey taxa do not vary significantly between tidal-fresh and mesohaline salinity zones. This suggests that pairs nesting in close proximity to these zones have similar prey utilization patterns, despite the documented influence of salinity on fish distribution in the Bay waters (Murdy *et al.* 1997, Jung 2002). However, while diet studies elucidate patterns of prey use, they potentially mask spatial variation in prey abundance and availability.

In birds, provisioning rates decline with decreasing prey availability (Newton 1979) and offspring experience slower growth rates under poorer food conditions (Ricklefs *et al.* 1998, Schew and Ricklefs 1998). Among raptors, the amount of prey available to foraging adults can affect both the rate at which parents provision dependent young and the rate of nestling growth (Moss 1979, Gebhardt-Henrich 1990, Steidl and Griffin 1991, Keller and Van Noordwijk 1994). Specifically for Bald Eagles, Bortolotti (1989) concluded that (1) nestlings raised in areas of high prey availability grew faster than chicks in areas of lower productivity and (2) growth rate was significantly correlated with the total prey biomass delivered to nestlings. Intraspecific variation in the rate of food delivery (Collopy 1984) and the growth trajectories of young (Quinney *et al.* 1986) in different areas can thus be an indicator of the spatial distribution of prey resources.

This paper examines variation in provisioning and growth rates in nestling Bald Eagles between two salinity zones in the lower Chesapeake Bay to investigate the potential influence of salinity on Bald Eagles. We expect variations in provisioning rates and growth to be positively correlated and indicate possible differences in habitat quality, potentially determined by differences in prey availability between salinity zones and years.

STUDY AREA AND METHODS

We monitored Bald Eagle nests in the lower Chesapeake Bay ≤ 3 km inland from the shorelines of the James, York, and Rappahannock Rivers during the 2002-04 breeding seasons (refer to General Introduction for map of study area). Three salinity zones 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) (DAWG 1997). This study limited nest selection to tidal-fresh and mesohaline reaches (1) to document extremes in salinity effects along tributaries and (2) because Watts *et al.* (*in press*) documented significant differences in Bald Eagle breeding density between these salinity zones. Within these areas, nest selection was based on accessibility and whether the placement of video-recording equipment was possible. In addition, nests with a documented history of reliable chick production and a moderate level of interaction with humans were preferred. We quantified both chick provisioning and growth for 10 nests and 8 nests along tidal-fresh and mesohaline reaches, respectively. We also measured chick growth at an additional 6 nests in the tidal-fresh reaches and 4 nests in the mesohaline reaches. One nest was included in all 3 years of this study and 1 nest was used for 2 years. Because nests were considered individual samples in all analyses, sample sizes presented here reflect unique pairing of nest location with year.

The timing of data collection at each nest was determined by nestling age as estimated during aerial surveys and later confirmed by visual inspection of chicks. Data collection was focused on the expected period of maximum growth ($t_{10\text{-}90}$) for two main reasons. First, nestlings in this phase experience the fastest rate of growth

(Ricklefs 1998) and, accordingly, prey delivery rates have the greatest impact on overall growth patterns (Bortolotti 1989). Second, energetic requirements are influenced by chick age (Cairns 1987) and thus standardizing data collection relative to hatching date is essential for removing the confounding influence of brood age on provisioning rates. For nests with multiple young, we used the hatch date of the oldest nestling when assigning nestling ages for data analysis.

Bortolotti (1984) calculated t_{10} and t_{90} for Bald Eagles in Saskatchewan at 10 and 55 d, respectively. Given the smaller body mass of adult birds in the Chesapeake Bay population (Palmer 1988), we assumed chicks in our study area would achieve both measures at an earlier age. Additionally, in order to minimize impacts to broods, we only considered working with chicks in the time window after the development of endothermic capabilities (14.7 d: Bortolotti 1984a) and prior to the age at which nestlings will prematurely jump from the nest upon the approach of researchers (60 d: K. W. Cline pers. comm.) With these considerations, we recorded first measurements between 15 – 20 d and second measurements between 40 – 45 d. Video-recording was concentrated on the time interval between measurements with a subsample (n = 7) of nests recording activities until chick fledging.

Video-monitoring. We used a video-monitoring approach to quantify provisioning rates for selected broods. A waterproof, bullet security camera was mounted to each nest tree approximately 1 m above the nest so that the entire nest surface was in view. The video camera was wired to a standard videocassette recorder and a deep-cycle, 12-volt marine battery. The videocassette recorder and battery were placed in waterproof containers and positioned at a remote location approximately 250 m from nest to reduce disturbance and improve access for maintenance activities.

We focused recording time on the morning hours (beginning 1 h after sunrise) to include the expected peak period of chick provisioning (Jaffe 1980, Wallin 1982, Mersmann 1989) and thus maximize the number of deliveries within the recording block. Each recording bout typically lasted 8 h, the duration of standard T-160 videocassette tape length. All nests were monitored in this fashion approximately 4 d/wk with efforts made to maintain equal recording effort between salinity zones in each study year. We changed the videotape daily and on every fourth visit replaced the battery. A sub-sample of full day coverage (sunrise to sunset) was recorded at select nests for analysis of day-long variation in provisioning rates.

We identified prey items to the lowest taxonomic level possible and recorded date, delivery time, and prey size (estimated as a multiple of adult's bill length to the nearest ½ bill length). We used published mass-length regressions and energy density conversions to calculate delivered biomass and energy as described in Chapter 1. In this study, we performed additional calculations to derive consumable biomass and energy values from previously determined values of delivered biomass and energy as described below.

In estimating consumable portions, we considered major prey taxa separately and referred to both video-footage and previous studies of Bald Eagle feeding behaviors. For fish, generally all species and size classes were assumed to be totally edible based upon video review, though large catfish (Ictaluridae) were a notable exception. For this family, we used the size limit applied by Dykstra (1995) of 305 mm as a distinction between totally and partially edible prey: catfish under 305 mm were assumed to be completely edible whereas catfish over 305 mm were estimated to be 90% edible. For birds and mammals, we used Stalmaster and Gessaman's (1982) estimation that prey items in these classes were 85% edible. For turtles, we considered shell weight to represent the only unusable biomass of intact prey items. We determined percent edible to be 24% from measurements of 18 turtle shells collected in and below nests during 2002 and 2003. We measured the carapace length with dial calipers (± 0.1 mm) and weighed each shell on an electronic balance (± 0.1 g). We then used carapace length to calculate expected total weight (as derived from length-weight equations of locally measured specimens: J. C. Mitchell unpubl. data). Next, shell weight was subtracted from expected total weight. Finally, this figure was divided by total weight, leaving a value indicative of the percent biomass available for consumption.

Provisioning Analysis. In order to examine whether provisioning patterns varied throughout the day, we analyzed delivery rates (deliveries/nest/h) on the subsample of days for which all daylight hours were recorded (*n* = 112). Daylight hours were divided into 2 approximately equal time periods (sunrise – 1400 and 1400 – sunset) and we compared delivery rates between time blocks. Prey delivery was 1.19 times more frequent in the morning than evening, but differences between time blocks were not statistically significant (one-way ANOVA, $F_{(1, 10)} = 1.15$, $P > .05$). This pattern was based on observations throughout the nestling period observed in this study (15 d – fledging) and showed that coverage focused on morning and early afternoon hours was sufficient to interpret chick food intake in this species. Further, we found morning delivery rates were predictive of full-day delivery rates (Regression, $R^2 = 0.62$, $F_{(1, 54)} = 92.43$, $P < 0.001$). Therefore, further provisioning analyses presented in this paper are focused exclusively on the time period of sunrise – 1400.

We summarized provisioning rates in several ways for presentation and analysis: delivery rate of prey (*n*/10 h), delivery rate of consumable biomass (g/h), and delivery rate of consumable energy (kJ/h). All 3 measures were considered in each separate analysis for the effect of chick age, brood size, salinity, and year on provisioning. To examine the effect of nestling age on provisioning patterns, we subdivided chick ages during expected maximum growth into 5-d blocks (between ages 20 and 40 d), took mean rates, and used one-way Repeated Measure ANOVAs to test for age effects using nests as samples. We used one-way Repeated Measure ANOVAs to examine the effect of brood size on nest provisioning rates. We also investigated the relationship between brood size and provisioning by considering per capita delivery rates (provisioning/nestling/d) and using one-way ANOVAs. We evaluated the influence of salinity and year on per capita provisioning using a two-way Repeated Measure ANOVAs with salinity (2 ranks including tidal-fresh and mesohaline) and year (2 ranks including 2002 and 2003) as factors and individual nests as samples. The influence of salinity and brood size on per capita brood provisioning was also examined using a two-way Repeated Measure ANOVA with salinity (2 ranks including tidal-fresh and mesohaline) and brood size (3 ranks including 1, 2, and 3 chick broods) as factors and individual nests as samples. All statistical tests were considered significant at the $\alpha = 0.05$ level.

Growth Measurements. Morphometric measurements were taken on each chick twice during the expected maximum growth period. Nestlings were lowered to researchers on the ground, banded with United States Geological Survey (USGS) aluminum bands, and weighed on an electronic balance (± 0.5 g). We estimated crop fullness by palpation and used a categorical scale to approximate crop mass as follows: full crop = 0.3 kg; more than half full crop = 0.2 kg; less than half full crop = 0.1 kg; empty crop = 0 kg (based on values for White-tailed Eagles (*Haliaeetus albicilla*): Helander 1981). The resulting weight (gross weight – crop weight) reflected the actual body mass of chicks and was the value used in growth analysis.

In addition to weight, we recorded a series of morphometric measures cited in previous research as useful indices for age and sex determination (Bortolotti 1984b): (1) wing length, length of unflattened wing chord (chord of arc) to tip of manus or to tip of longest primary, depending on age of the nestlings; (2) culmen length, the length of exposed culmen without cere; (3) bill depth, depth of closed bill measured at the leading edge of the cere; and (4) hallux claw length, length of the exposed hallux claw from the tip to the dorsal side where the edge of the skin begins. Wing length was measured with a metal ruler (± 1 mm) and culmen length, bill depth, and hallux claw length were measured with dial calipers (± 0.1 mm). All measurements were repeated three times to increase accuracy and, when applicable, taken consistently from the left side of the bird's body. Mean values from the three measurements taken were used in subsequent analyses.

Nestling sex was determined by DNA analysis of blood samples. At the time of second growth measurements at each nest, we pulled two contour feathers from the ventral tract of each chick and placed 1 – 2 drops of blood on sexing cards later submitted for laboratory analysis (Avian Biotech International©). For birds with inconclusive DNA results (*n* = 4), sex was determined by screening morphometric variables against birds of known sex for their predictive value. A combination of weight and culmen length with age provided a clear separation for known-sex birds and was used to classify sex of unknown birds.

Growth Analysis. Of the 51 chicks for which initial morphometric measurements were taken, we excluded 5 chicks from growth analyses. Two nests suffered a mortality of 1 chick each between measurement dates, and weight data for 1 nest with a 3-chick brood was not recorded. We derived individual growth curves for each nestling based on logistic models following methods outlined in Ricklefs (1983) and under the assumption that the growth of Bald Eagles was best approximated by the Gompertz equation (Bortolotti 1984a).

First approximation of asymptotic weight for eagles of the lower Chesapeake Bay was estimated from the mean weight of 134 adult-plumaged, Bay area birds: male: *n* = 68, weight = 3,149.2 ± 971.40 g; female: *n* = 66, weight = 4,225.0 ± 1,313.21 g (National Wildlife Health Center's Madison Lab, Wisconsin, unpubl. data). These values were calculated by limiting the Madison Lab's Bald Eagle necropsy dataset to include only (1) adult-plumaged carcasses found within the Chesapeake Bay drainage that were in good or excellent condition when weighed and (2) recoveries that occurred at dates when migrants are not common in the Bay area, *i.e.* when recoveries were most likely to be resident breeders (*see* Buehler *et al.*1991).

Five parameters were derived from each growth curve for analysis: asymptotic weight, instantaneous growth rate, average growth rate during maximum growth phase, the time required to reach 90% asymptotic weight (t_{90}), and the time required to grow from 10 – 90% asymptotic weight ($t_{10\text{-}90}$). Individual asymptotes were calculated using three data points: weight at hatching (85 g: Bortolotti 1984a), first weight measurement taken in this study, and second weight measurement taken in this study. Instantaneous growth grate was determined by calculating the slope of the line tangent to the inflection point on the growth curve. Mathematical representations of additional parameters are available in Ricklefs (1967).

We used one-way ANOVAs to examine the effect of gender on growth. One-way ANOVAs were also used to examine the effect of hatch order on growth. We evaluated the influence of salinity and year on growth using two-way ANOVAs with salinity (2 ranks including tidal-fresh and mesohaline) and year (2 ranks including 2002 and 2003) as factors and individual nests as samples. We used regressions to test for correlations in brood provisioning rates and total chick mass. All statistical tests were considered significant at the $\alpha = 0.05$ level.

RESULTS

Provisioning Rates. Provisioning rates did not vary significantly with chick age within this growth period both for consumable biomass (one-way Repeated Measures ANOVA, $F_{(5, 71)} = 0.14$, $P > 0.05$) and consumable energy (one-way Repeated Measures ANOVA, $F_{(5, 71)} = 0.31$, $P > 0.05$), suggesting that energetic demands of nestlings and/or parental ability to provide for young was consistent throughout this growth interval. Therefore, we summarized provisioning rates throughout this entire period to represent overall delivery patterns in further analyses.

Brood size had a significant influence on all 3 estimates of brood provisioning examined such that the rates of prey item delivery (one-way Repeated Measures ANOVA, $F_{(2, 74)} = 5.91$, $P = 0.004$), consumable biomass delivery (one-way Repeated Measures ANOVA, $F_{(2, 74)} = 8.07$, $P < 0.001$), and consumable energy delivery (one-way Repeated Measures ANOVA, $F_{(2, 74)} = 8.68$, $P < 0.001$) to entire broods increased with the number of chicks per nest (Table 1). In contrast, patterns of per capita provisioning showed the reverse trend with rates declining significantly as brood size increased (all one-way ANOVAs, $F_{(2, 15)} > 4.00$, $P < 0.05$). This suggests that although parents adjusted efforts to meet the increasing energetic demands of larger broods, individual nestlings of two or three chick broods were not provisioned at a rate comparable to what single chicks received. Post-hoc analysis (Tukey's Honestly Significant Test) showed that all comparisons of 1 and 2-chick broods were not significant ($P > 0.2$), but all comparisons of 3-chick broods with 1 and 2-chick broods were significant ($P < 0.05$). Therefore, we limited additional analyses (unless otherwise noted) to data from nests with 1 or 2 chicks ($n = 12$) to minimize the effect of brood size and isolate the influence of other factors on provisioning patterns.

Trends in per capita provisioning rates of prey items (Figure 2.1), consumable biomass (Figure 2.2), and consumable energy (Figure 2.3) varied between salinity zone and year. All rates were higher in mesohaline compared to tidal-fresh salinity zones, though only per capita rates for consumable biomass (two-way Repeated Measures ANOVA, $F_{(1, 35)} = 5.44$, $P = 0.026$) and consumable energy (two-way

Repeated Measures ANOVA, $F_{(1, 35)} = 9.63$, $P = 0.004$) delivery showed significant variation with salinity. All per capita rates of provisioning were higher in 2003 compared to 2002. Statistically significant differences, however, occurred only for prey number (two-way Repeated Measures ANOVA, $F_{(1, 35)} = 4.42$, $P = 0.043$) and consumable biomass (two-way Repeated Measures ANOVA, $F_{(1, 35)} = 4.95$, $P = 0.033$). There was no significant difference between year in per capita delivery rate for consumable energy but results were near-significant (two-way Repeated Measures ANOVA, $F_{(1, 35)} = 3.38$, $P = 0.074$). There was no significant interaction between salinity and year.

Parents at nests in mesohaline reaches were more successful at providing the additional resources required by larger broods compared to adults nesting in tidal-fresh zones with regard to provisioning rates of prey items (Figure 2.4), consumable biomass (Figure 2.5), and consumable energy (Figure 2.6) (all brood sizes considered). For all provisioning measures, statistically significant results were recorded (all two-way Repeated Measures ANOVAs, $F_{(1, 44)} > 4.00$, $P < 0.05$). Further, there was a significant interaction between brood size and salinity for rates of prey delivery (two-way Repeated Measures ANOVA, $F_{(2, 44)} = 4.54$, $P = 0.016$) and consumable energy (two-way Repeated Measures ANOVA, $F_{(2, 44)} = 6.23$, $P = 0.004$). The interaction for rate of consumable biomass delivery was nearly significant (two-way Repeated Measures ANOVA, $F_{(2, 44)} = 2.50$, $P = 0.094$).

Growth. Of the 46 nestlings used in growth analyses, 24 (52%) were male and 22 (48%) were female. Nestling sex had a significant effect on all of the growth parameters examined, supporting previous research citing gender differences in Bald Eagle growth and development (Bortolotti 1984b). Results obtained were consistent with theoretical patterns of growth that correlate greater asymptotic weight with (1) higher growth rate, (2) greater time required to reach t_{90}, and (3) longer interval required for t_{10-90} (Ricklefs 1968).

Asymptotic weight was greater in females (4,611.4 ± 356.20 g) compared to males (3,481.3 ± 191.57 g), a result consistent (though noticeably more pronounced) to reported sexual dimorphism in the species (Bortolotti 1984b). During the maximum growth phase, females grew at an average rate of 105.1 ± 46.12 g/d, compared to male growth rate of 82.0 ± 34.33 g/d. Time required for growth also varied between sexes. Females required significantly more time to reach t_{90} (one-way ANOVA, $F_{(1, 44)} = 10.98$, $P = 0.002$) and for the t_{10-90} interval (one-way ANOVA, $F_{(1, 44)} = 10.31$, $P = 0.002$) compared to males. Female nestlings reached t_{90} at an older age (42.4 ± 7.32 d) than males (36.2 ± 5.13 d), and the t_{10-90} time period was longer in female nestlings (30.4 ± 4.26 d) compared to male nestlings (35.3 ± 5.99 d).

To examine the influence of brood size on nestling growth, we compared instantaneous growth rate, the time required to reach t_{90}, and the time required for t_{10-90} for first, second, and third hatched chicks. Trends in mean values for each parameter indicate decreasing growth rate and increasing time required for growth in later hatched chicks (Table 2). Hatch order had a significant effect on instantaneous growth rate (one-way ANOVA, $F_{(2, 43)} = 3.28$, $P = 0.047$), but not on time required to reach t_{90} (one-way ANOVA, $F_{(2, 43)} = 0.28$, $P = 0.05$) or the time required for t_{10-90} (one-way ANOVA, $F_{(2, 43)} = 0.32$, $P > 0.05$).

Between salinity zones, patterns in the growth parameters examined were consistent and reflected that nestlings tended to grow faster and achieve greater asymptotic weights in mesohaline compared to tidal-fresh reaches (Table 3). However, significant differences were only observed for instantaneous growth rates (two-way ANOVA, $F_{(1, 31)} = 11.01$, $P = 0.002$). Growth measures did not vary significantly between years, though instantaneous growth rate was nearly significant (two-way ANOVA, $F_{(2, 31)} = 3.21$, $P = 0.054$). In general, 2003 was a poor growth year compared to 2002 and 2004 in that nestlings required more time to develop and reached lower asymptotic weights. No significant interaction between salinity and year were observed (all two-way ANOVAs, $F_{(2, 31)} < 0.10$, $P > 0.05$).

The daily change in chick mass for all nestlings in a brood was significantly correlated with the provisioning rates for both consumable biomass (Regression, $R^2 = 0.43$, $F_{(1, 13)} = 9.90$, $P = 0.007$) and consumable energy (Regression, $R^2 = 0.47$, $F_{(1, 13)} = 11.42$, $P = 0.005$).

DISCUSSION

Overall Patterns of Provisioning and Growth. Our provisioning results expressed as the number of prey deliveries per day are within the range of findings in previous investigations (Table 4). However, the frequency of individual deliveries is not always directly related to its nutritional value due to variation in the size and energy density of prey items. Rates of consumable biomass and consumable energy delivery thus provide more biologically meaningful, but seldom calculated, provisioning indices.

Interestingly, the consumable biomass delivery rates (1,167.9 ± 955.24 g/d, mean ± standard deviation) and energy delivery rates (6,949.8 ± 6,288.64 kJ/d) observed in this study were considerably higher than those reported for chicks in Wisconsin, despite the fact that lower rates of prey delivery (2.9 ± 2.00 deliveries/d) were observed in our investigation (Dykstra 1995). This comparison has several important implications. First, it indicates that adults in the lower Chesapeake Bay utilized a foraging strategy to deliver fewer, higher quality prey (greater average biomass and energy density per item) compared to pairs nesting in Wisconsin. With regard to total daily energy delivered, this strategy effectively compensated for the lower feeding frequency (deliveries/d) in Bay area nests compared to sites monitored in Wisconsin. Second, it indicates that nestlings in the lower Chesapeake Bay received, on average, more energy per day than chicks in Wisconsin. Differences in energy delivery rate, the most critical measure of provisioning, suggest that the lower Chesapeake Bay study area provides a higher quality habitat with regard to food resources than territories monitored in Wisconsin. The extraordinary overall ecosystem productivity of the Chesapeake Bay estuary, particularly in contrast to the oligotrophic lakes dominating the Wisconsin study area, likely contributes to this finding.

That eagles observed in this study are utilizing high energy resources in the lower Chesapeake Bay is further supported by comparing the per capita rates of consumable energy delivery to the metabolic requirements of nestlings. The per capita delivery rates of consumable energy for eaglets in our study (4,109.8 ± 3,604.12 kJ/d/chick) is noticeably greater than the field metabolic rate of nestling

Bald Eagles in the wild (2,429 ± 100 kJ/d: Dykstra 2001) and held in captivity (2,148 kJ/d: Dykstra *et al.* 1997). This suggests that parents in the Bay region are successful at providing food resources to meet and likely exceed the estimated energetic requirements of growing chicks, a factor that may be manifest in increased rates of nestling growth.

Further indication of the high quality habitat in the Bay region is suggested by growth parameter comparisons between nestlings in different populations. Values for the growth rate constant *K* determined for eagles in this study were higher than those reported for chicks in Saskatchewan, indicating that nestlings are growing at a faster rate in the lower Chesapeake Bay region compared to Saskatchewan. We calculated *K* values for female nestlings as 0.1001 ± 0.01230 g/d (mean ± standard deviation) and male nestlings as 0.0883 ± 0.01421 g/d. In comparison, Bortolotti (1984) derived *K* for male and female Bald Eagles nestlings in Saskatchewan as 0.0683 ± 0.00330 g/d (mean ± standard deviation) and 0.0683 ± 0.00403 g/d, respectively. Additional indications of faster growth in the Bay region are evident in younger age at which 90% asymptotic weight is achieved and shorter time interval required between 10 – 90% of growth (Bortolotti 1984). These differences lend additional support to the conclusion that the productivity of the Chesapeake Bay ecosystem has a significant influence on resident Bald Eagles.

Spatial Patterns of Provisioning and Growth. Our results indicate that Bald Eagles nesting in proximity to higher saline water in the lower Chesapeake Bay tributaries are more successful at meeting the energetic demands of brood rearing than pairs nesting in lower salinity reaches. This interpretation is based on a comparison of rates of nestling growth and provisioning, as well as the ability of parents to provide for maximum brood sizes.

Rates of growth were positively correlated with rates of provisioning such that young in mesohaline zones experienced higher growth and provisioning than chicks in tidal-fresh zones. Intraspecific variation in growth is often attributed to differences in the rate and amount of food supplied to adults by nestlings, which in turn is likely associated with the availability of food (Harris 1969, Boersma 1978, Barrett *et al.* 1987, Monaghen *et al.* 1989). Thus, one possible explanation for differences in growth and provisioning rates is that the availability of prey differs between these salinity zones and parents in mesohaline reaches are better able to provide the food resources required by dependent offspring.

Previous research examining dietary differences between tidal-fresh and mesohaline reaches in the lower Chesapeake Bay indicated that Bald Eagles were utilizing similar prey species regardless of salinity zone (Chapter 1). This study suggests that although eagles in different salinity zones exploit similar food resources, spatial variation exists in the quantity and quality of delivered prey. This variation may be due to differences in prey availability and/or abundance. Similar conclusions were reached by Bortolotti (1989) who attributed relatively lower rates of growth and provisioning within a subpopulation of nesting Bald Eagles in Saskatchewan to decreased local prey availability, as assessed by lower gillnet capture rates (Bortolotti 1989).

Spatial comparison of delivery rates to nests of varying brood sizes indicates that pairs are better able to cope with the demands of 3-chick broods in the mesohaline compared to tidal-fresh reaches. This finding supports the significant variation in the production of 3-chick broods along the salinity gradient of the Bay ecosystem. A higher proportion of 3-chick broods were found at nests near higher salinity water compared to low saline zones based on productivity records from 1990 – 2000 (B. D. Watts and M. A. Byrd unpubl. data).

Influence of Year on Provisioning and Growth. We observed significant differences in provisioning and growth rates between the study years of this investigation. Though several factors may have contributed to this variation, we consider dramatic changes in the patterns of precipitation as the dominant source of these differences.

In 2003, record wet conditions and lower than average temperatures were observed throughout the southeast United States, including Virginia (Gleason *et al.* 2004). The influence of weather anomalies on provisioning and growth rates has been documented in several raptor species such that in poor weather conditions parents deliver less food to nestlings and experience lower breeding success than mild weather in (Ridpath and Brooker 1985, Mearns and Newton 1988, Pietiainen 1989, Steenhof *et al.* 1997, Dawson and Bortolotti 2000).

Specifically for Bald Eagles, severe weather conditions affect foraging and provisioning in several ways. First, cold, wet weather influences the daily time budget of adults particularly when nestlings are in the early stages of growth. Chicks younger than 14.7 d are not capable of thermoregulation (Bortolotti 1984a) and require brooding by parents to stay warm, though nestlings as old as 5 wks may be brooded in extreme weather (Warnke *et al.* 2002). Stalmaster (1984) observed that the energy metabolism of adult Bald Eagles increased with low temperatures and high rain, and we predict nestlings would have similar metabolic responses. Thus wet conditions may confine adults to the nest, reducing available time for foraging despite expected increases in food requirements associated with increased energy expenditure. Second, poor weather conditions may make food acquisition more difficult. The negative effect of rain on foraging success in raptor species has been attributed to decreased visibility (Grubb 1977) and alteration of prey behavior (Stinson 1980). Both of these factors may make it more difficult for adults to meet the energetic demands of the brood.

Patterns in overall productivity in the lower Chesapeake Bay lend further support to the idea that weather extremes in 2003 affected chick provisioning and growth. The breeding population experienced a higher than normal failure rate and a lower than average brood size during the 2003 season (Watts and Byrd 2003). Past anomalies in the long-term monitoring of nests in Virginia have also typically been correlated to seasons characterized by poor weather conditions, *i.e.* cold temperatures and high precipitation (B. D. Watts *pers. comm.*). In our study, brood reduction between the dates of our first and second climbs was documented twice in 2003 but not at all in 2002.

A pattern worthy of mention is that though significant year-to-year variation in provisioning and growth patterns were observed, rates for both provisioning and growth were consistently higher in the mesohaline compared to tidal-fresh reaches. Thus, even amidst annual variation, adults in these reaches are more successful at providing food resources to their offspring.

Sources of Error. Individual differences among adult pairs with respect to age, experience, and condition potentially affect the rates assessed in this study. Comparing nest provisioning rates and offspring growth among birds of unknown age has been criticized because older individuals in long-lived species often experience greater nesting success (De Steven 1978), foraging efficiency (Orians 1969), and nestling growth rates (LaQuette and Weimerskirsch 1990). Among Bald Eagles, Bennetts and McClelland (1997) observed that the ability of adults to obtain food increases with age, presumably as a reflection of experience. Though potentially important, addressing this concern was not feasible due to the inability to visually age birds over 4 years. However, all territories used in this study had been established for more than 5 years which provides some possible indication of parental experience.

Hatching order has been shown to significantly influence growth rates in some raptor species (Massemin *et al.* 2002). Size advantages associated with older siblings potentially influence nestling hierarchies such that larger chicks dominate smaller nestlings. In eagles, the effect of this is particularly manifest at mealtimes with larger nestlings receiving a disproportionate amount of food resources (Mayburg 1974, Gargett 1982, Collopy 1986). Bortolotti (1986) observed similar patterns in dominance and provisioning specifically among Bald Eagle nestlings. This potentially confounds measures of food limitation if not all nest mates are affected comparably, or at all. We restricted comparisons between salinity zones to 1 and 2 chick broods to reduce the influence of hatching order on results.

The distinction between growth and development is critical to address. We limited analyses strictly to measures of growth, defined as the ontogenic increase in body mass, and made no effort in this investigation to assess variation in maturation patterns (development). However, avian research reveals a high degree of developmental flexibility in some bird species (Schew and Ricklefs 1998) and work is currently in progress to review video-footage for indications of developmental plasticity in Bald Eagles. Tapes are being reviewed to determine whether variation in the timing of developmental landmarks (e.g., eruption of feathers and fledging date) is correlated to variation in growth rate and/or provisioning patterns.

Conclusions. Successful conservation should maintain or improve high quality sites rather than focusing on poor sites while allowing key areas to deteriorate (Dias 1996). However, determining core breeding areas may not be clear-cut. The results of this study in conjunction with other lines of evidence provide seemingly paradoxical findings as to where core habitat reaches lie for Bald Eagles in the lower Chesapeake Bay.

Several aspects of historical and current patterns of Bald Eagle distribution suggest that the tidal-fresh reaches represent the preferred portions of habitat in the lower Chesapeake Bay ecosystem. First, where individuals originally settle in a habitat is considered an indication of preferred breeding areas (Bernsteain *et al.* 1993). In the Chesapeake Bay, widespread use of DDT and associated low nest productivity caused the eagle population to plummet dramatically and reached an all-time population low in the 1970's (Watts and Byrd 2002). As the local population recovered from near extinction in the following decades, tidal-fresh reaches of the Bay ecosystem were the first areas to show recolonization attempts (Watts *et al. in press*). Second, the distribution of raptor species reflects variation in habitat quality: higher occupancy in high quality territories compared to low quality territories has been observed in several species (Korpimaki 1988, Newton and Marquiss 1991, Redpath 1995, and Kostrzewa 1996). In the lower Chesapeake Bay, the tidal-fresh portions of the tributaries support the greatest density of nesting Bald Eagles compared to other salinity zones (Watts *et al. in pres*s). Third, the destination of migrant eagles reflects habitat quality, particularly with regard to food resources (Dzus and Gerrard 1993). Nonbreeding eagles, freed from the constraint of foraging close to their nests, are motivated to move in response to local prey availability (Servheen and English 1979, Hunt *et al.* 1992, Dzus and Gerrard 1993). The fact that eagles migrating to the Bay watershed during the spring and summer months form concentrations in low salinity areas thus suggests that prey availability may be greater in the tidal-fresh zones.

In contrast to these considerations, however, the results of this study provide evidence that birds in mesohaline reaches are more successful at meeting the energetic demands of brood-rearing. This finding is further supported by the markedly higher per capita productivity in this salinity zone (Watts *et al. in press*). Given greater indices of individual fitness, why these areas fail to support higher density of breeding pairs remains uncertain.

The influence of social factors, namely competition, is one possible explanation as to why measures of fitness are lower in the tidal-fresh salinity zone compared to the mesohaline reaches. Bald Eagles are territorial birds, particularly during the breeding season (Buehler 2000), and the impact migrant eagles have on nesting pairs is not clear. The migrant influx may potentially increase competition for resources (prey and perch trees), raise energy expenditure in antagonistic encounters, and require greater investment in territory defense at the expense of foraging effort. Though high conspecific density has been associated with lower provisioning rates and nest productivity in other raptors (Virani and Harper 2004), further work is needed to clarify these interactions for Bald Eagles.

Though the results of this study indicate mesohaline reaches are more energetically profitable for nesting eagles, we suggest management and conservation efforts focus primarily on the tidal-fresh reaches. These are the most profitable areas in that they support the greatest number of breeding pairs and overall chicks produced, in addition to their value as a migration destination for other eagle populations. Further, we suggest efforts should be taken to incorporate the findings of this study with regard to patterns of prey use, biomass and energy requirements, and energetic pathways relied upon by nesting eagles to manage the ecosystem for Bald Eagles as a whole, integrating patterns of distribution for predator and prey.

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Figure 2.1. Influence of salinity and year on per capita rates of prey delivery at Bald Eagle nests in the lower Chesapeake Bay during the 2002-03 breeding seasons.

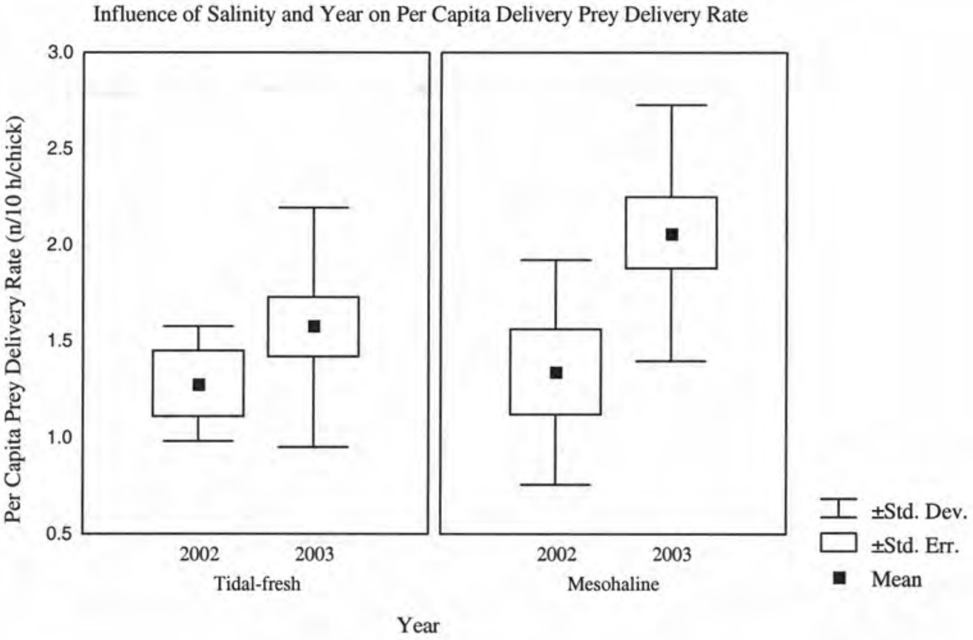

Figure 2.2. Influence of salinity and year on per capita rates of consumable biomass delivery at Bald Eagle nests in the lower Chesapeake Bay during the 2002-03 breeding seasons.

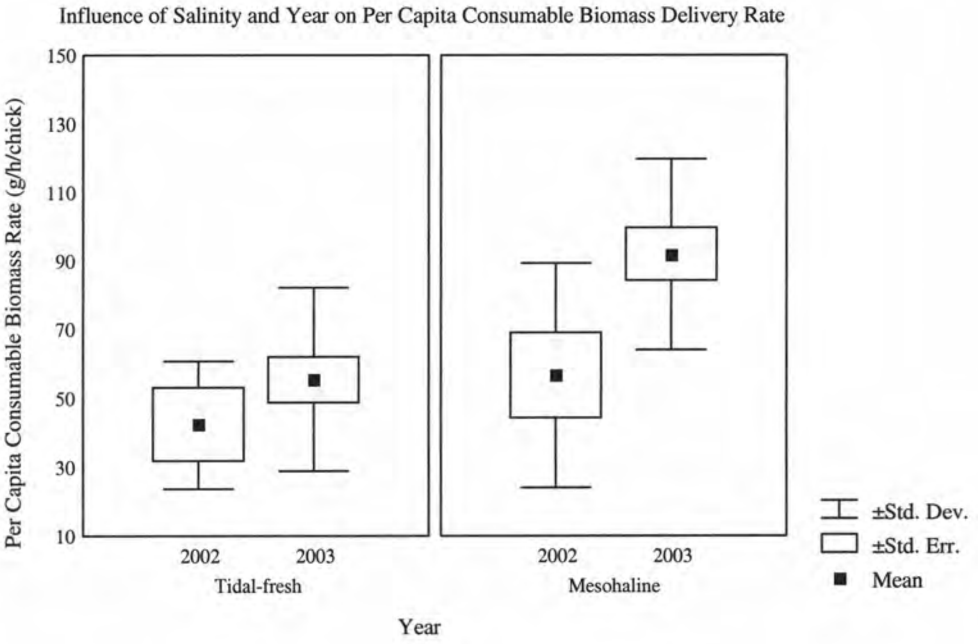

Figure 2.3. Influence of salinity and year on per capita rates of consumable energy delivery at Bald Eagle nests in the lower Chesapeake Bay during the 2002-03 breeding seasons.

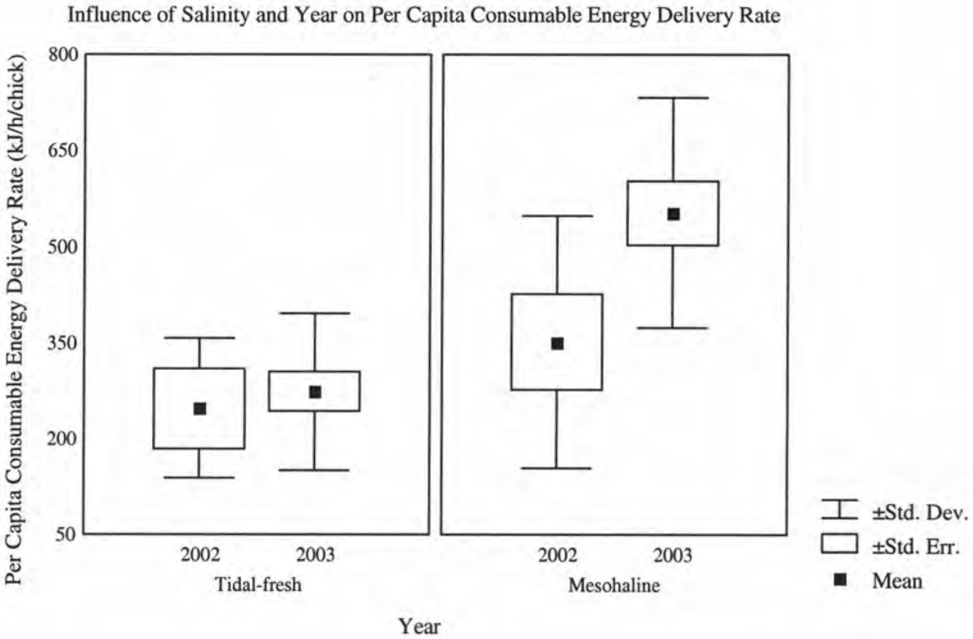

Figure 2.4. Influence of salinity and brood size on per capita rates of prey delivery at Bald Eagle nests in the lower Chesapeake Bay during the 2002-03 breeding seasons.

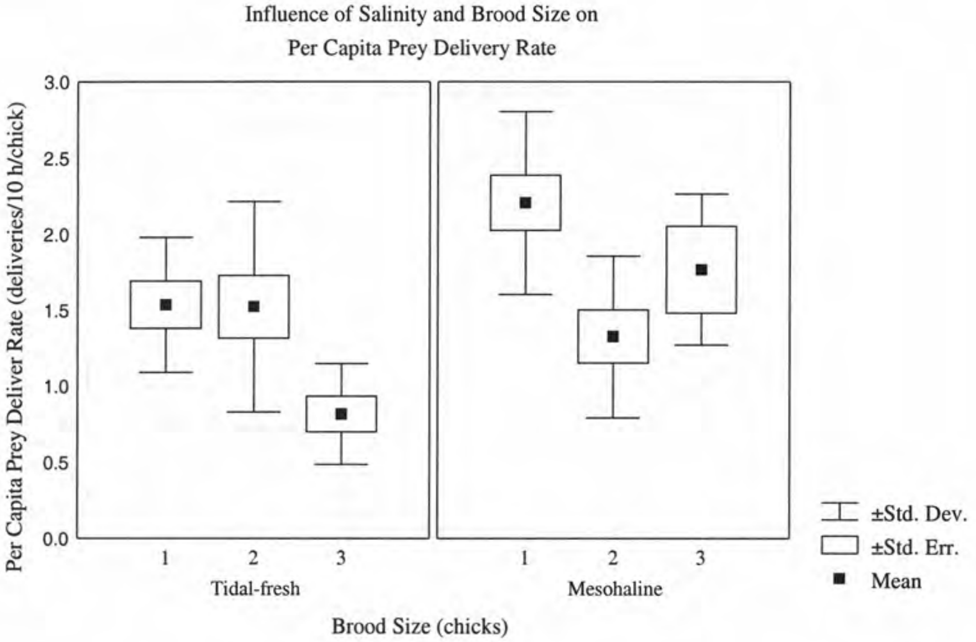

Figure 2.5. Influence of salinity and brood size on per capita rates of consumable biomass delivery at Bald Eagle nests in the lower Chesapeake Bay during the 2002-03 breeding seasons.

Figure 2.6. Influence of salinity and brood size on per capita rates of per capita consumable energy delivery at Bald Eagle nests in the lower Chesapeake Bay during the 2002-03 breeding seasons.

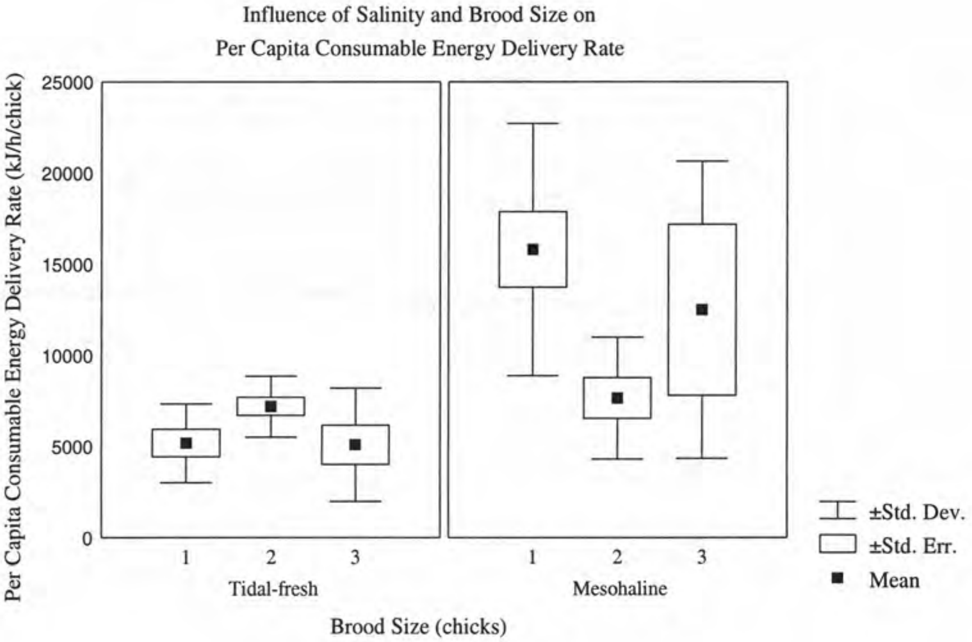

Table 2.1. The effect of brood size on 3 estimates of brood provisioning at Bald Eagle nests in the lower Chesapeake Bay during the 2002-03 breeding seasons: rates of prey item, consumable biomass, and consumable energy delivery to nests (mean ± standard deviation).

	1 chick	**2 chicks**	**3 chicks**
Prey Delivery Rate (deliveries/10 h)	1.9 ± 0.63	2.9 ± 1.24	3.2 ± 1.70
Consumable Biomass Delivery Rate (g/d)	82.0 ± 34.33	105.1 ± 46.12	137.2 ± 69.71
Consumable Energy Delivery Rate (kJ/d)	453.2 ± 227.00	614.7 ± 276.49	827.2 ± 435.15

Table 2.2. The effect of hatch order on 3 measures of growth for Bald Eagle nestlings in the lower Chesapeake Bay during the 2002-04 breeding seasons: instantaneous growth rate, the time required to reach 90% asymptotic weight (t_{90}), and the time interval between 10 – 90% of growth ($t_{10\text{-}90}$). Values presented as mean ± standard deviation.

	First Chick	**Second Chick**	**Third Chick**
Growth Rate (g/d)	146.9 ± 24.29	133.5 ± 12.46	123.4 ± 13.15
t_{90} (d)	38.7 ± 5.57	39.5 ± 8.95	42.0 ± 7.93
$t_{10\text{-}90}$ (d)	32.3 ± 4.59	33.1 ± 7.26	34.7 ± 6.60

Table 2.3. Spatial comparison between two salinity zones (tidal-fresh and mesohaline) of growth parameters (mean ± standard deviation) for Bald Eagle nestlings in the lower Chesapeake Bay during the 2002-04 breeding seasons.

	2002	**2003**	**2004**
Growth Rate (g/d)			
Tidal-fresh	140.5 ± 10.58	120.5 ± 18.05	138.4 ± 20.40
Mesohaline	161.1 ± 29.07	147.5 ± 17.09	159.5 ± 14.45
$t_{10\text{-}90}$ (d)			
Tidal-fresh	33.8 ± 6.20	35.4 ± 6.99	30.5 ± 6.72
Mesohaline	28.0 ± 2.57	33.4 ± 5.97	28.7 ± 1.85

Table 2.4. Comparison of prey delivery rates (number of deliveries/d) reported in previous studies of nesting Bald Eagles.

Location	**Rate (Prey deliveries/d)**	**Reference**
Alaska	2.3 – 3.6	Cain 1985
Arizona	2.2	Grubb 1995
Minnesota	4	Harper 1974
Ohio	2.5 – 4.0	Herrick 1924
Virginia	3.6[1]	Wallin 1982
Virginia	2.9 ± 2.03[2]	This study
Wisconsin	2.6, 3.4[3]	Kozie 1986
Wisconsin	5.41	Dykstra 1995
Wisconsin	5.2	Warnke *et al.* 2002
Saskatchewan	5.0 – 5.8	Bortolotti 1986

[1] Daily rate calculated for presentation here from reported number of deliveries/h standardized by number of daylight hours for nest locations during study period.

[2] Mean ± standard deviation.

[3] Mean values for 1 and 2 chick broods, respectively.

CHAPTER 3

DOCUMENTATION OF INFANTICIDE AND CANNIBALISM IN BALD EAGLES

Non-kin infanticide, the killing of dependent young by unrelated conspecifics, occurs in a wide array of taxonomic groups including mammals, insects, fish, and birds (Hrdy 1979, Hrdy and Hausfater 1984). Several hypotheses have been proposed to explain this behavior by focusing on the potential advantages accrued by the perpetrator. For example, infanticide may confer nutritional benefits, remove potential competitors, or permit access to limited resources including food, nest sites, or space (Hrdy 1979).

In many social contexts, the adaptive advantages of cannibalism are closely linked with infanticide (Mock 1984). For example, the consumption of conspecifics may provide nourishment, lower the reproductive success of competitors, and reduce intraspecific competition for resources by lowering population density (Stanback and Koenig 1992). Since the fitness benefits of infanticide and cannibalism are not mutually exclusive, Stanback and Koenig (1992) note that it is "difficult to distinguish between the following scenarios: (a) selection that favors cannibalism, for which infanticide is often a necessary prerequisite, and (b) selection that favors infanticide, for which cannibalism is a subsequent option."

Among birds, infanticide encompasses a variety of species and social contexts (Mock 1984). Several studies have reported infanticide by unmated males, which has been interpreted as a means of obtaining breeding opportunities under conditions of high competition for mates and nest sites (Vehrencamp 1977, Betram 1979, Trail *et* *al.* 1981, Crook and Shields 1985, Freed 1986). Some accounts document cannibalism following the killing of young by unrelated adults (e.g., Balda and Bateman 1976, Village 1983). Among raptors, however, reports of infanticide are scarce (*but see* Wiemeyer 1981, Bortolotti *et al.* 1991, Webster *et al.* 1999) and we found no direct observations of cannibalism linked with infanticide in the literature available to us.

Here we describe a case of infanticide and cannibalism in the Bald Eagle (*Haliaeetus leucocephalus*). We report on a nest where the resident male disappeared shortly after chick hatching and the female assumed all parental responsibilities unaided until nest failure. The first instance of cannibalism occurred when the youngest of three chicks died and was fed to its siblings by the female parent. Additional cannibalistic acts occurred following infanticide when an intruder male invaded the nest, killing and consuming both of the remaining chicks.

STUDY AREA AND METHODS

We video monitored a Bald Eagle nest on a tributary of the James River in Virginia in 2002 as part of a larger study on the diet and provisioning patterns of nesting Bald Eagles in the lower Chesapeake Bay. A small, bullet security camera was mounted directly above the nest and wired to power (a deep-cycle 12-v marine battery) and recording (a timelapse videocassette recorder) equipment positioned 250 m from the base of the nest tree. Details of the camera system components are provided in Chapter 1.

We installed the camera system in January, prior to egg laying, and monitored nest activities from 20 February 2002 – 11 April 2002. We recorded nest activity during the incubation phase (26 d) and nestling phase before (1 d) and after (13 d) mate loss. We positioned the camera so that the entire surface of the nest was in view and made no attempts at additional observations other than those recorded on videotape. Recording of nest activity typically included all daylight hours (sunrise – sunset).

Since the nest had multiple young, we used the date of first egg laying and first chick hatching when determining nesting phase and assigning nestling ages. During tape review, we identified individual adult birds by differences in body size consistent with reported sexual dimorphism in the species (Bortolotti 1984) and unique plumage characteristics. We also used relative body size to identify nestlings. Bald Eagle chicks hatch asynchronously (Gerrard and Bortolotti 1988); thus, nestlings shortly after hatch date are often easy to distinguish on the basis of size.

RESULTS

At the start of video-monitoring, we observed both breeding adults contributing to nest maintenance. Recordings on 20 February marked our initial observation of the first egg and the laying of the second egg. By 24 February, the three-egg clutch was complete. The first chick hatched on 26 March after a minimum 34 d incubation. The second and third chicks hatched 3 and 4 d later, respectively. Throughout this time period, we consistently observed both adults sharing in the incubation and brooding responsibilities.

Beginning 30 March (nestling age was 5 d), the resident adult male was not observed on the nest. We believe this mate died; an adult male was treated and released by the Virginia Game Department biologist within 1 km of the nest site earlier in the nesting season. The bird had suffered injuries after a fishing hook became imbedded in its wing. Though the damage was deemed "minor" and the bird was released immediately, concurrence of events with disappearance of the resident male suggests the injuries proved fatal.

On 3 April, the youngest of three chicks was observed to be lethargic and did not exhibit food begging behavior; the sibling chicks, by comparison, were active and readily begged for and received food. The youngest chick was brooded by the female overnight, but was motionless and presumed dead when first visible the following morning. The adult attempted to preferentially brood the dead chick on two occasions, leaving both older siblings exposed. On 4 April at 13:17, the adult picked up the dead chick's body and began feeding it to the other nestlings.

Two other incidences of cannibalism occurred in conjunction with infanticide over a two-day time period during which an intruder male was recorded repeatedly on the nest. Plumage patterns indicate that this male was four years old. On the first day, 9 April, the female was observed delivering prey items to the nest, brooding, and provisioning the chicks. At 15:52, following a feeding bout, the female left the nest and the intruder male arrived within 1 min. The male approached the chicks and grasped the larger (older) of the two in its talons, moved it to the nest edge, and pinned it down while eating it. At 16:10, the adult left the larger chick's carcass and repeated the same behavior of grasping and pinning the second chick. The adult female arrived on the nest at 16:11 and immediately flushed the intruder from view.

On the second day, 10 April, we witnessed a similar pattern. The male arrived twice on the nest when the female was absent from view. The female returned to the nest within 1 min on both occasions, immediately flushing the male. Intermittently, the female attempted to brood and feed the chick. At 12:24, after the absence of the female for over 90 min, the male landed on the nest and began picking at prey remains. After alternating between a prey item and the chick, the adult pinned the struggling chick down with its talons and began ripping the nestling apart with its beak.

The following day, 11 April, both adults were observed landing on the nest, though neither individual remained for longer than 1 min. It appeared as though antagonistic interaction continued with the female chasing the male off the nest surface on one occasion.

DISCUSSION

Given the loss of the original male and subsequent invasion by an intruder male, we consider the observed account of infanticide in the context of mate replacement. Mate replacement within (Kozie 1986, Grubb *et al.* 1988, Jenkins and Jackman 1993, Anthony *et al.* 1994, Kennedy and McTaggart-Cowan 1998) and between breeding seasons (Herrick 1932) has been previously documented in Bald Eagles. Though we know of no previous accounts of infanticide following replacement for Bald Eagles, the killing of young by unrelated adult males has been observed in several other avian species. This act has typically been interpreted as enabling the performer to secure mating opportunities sooner than would be possible if the female's offspring continued to be reared (Crook and Shields 1985, Moller 1988).

However, of the theoretical models described by Rohwer (1986) for mate replacement during a nesting season, the natural history characteristics of the Bald Eagle (*i.e.* unlikely renesting within the same season and increased breeding success with experience) suggest that adoption of existing clutches is more adaptive to replacements than infanticide. In a similar situation to our observation reported by Grubb *et al.* (1988), a replacement male was observed assisting the female in parental duties. In observations made by Jenkins and Jackman (1993), however, a replacement female remained indifferent to eggs present despite the attempt of the male parent to continue incubation. Fostering experiments reported by Postupalsky (1975) were successful in introducing 9 wk old nestlings at active eagle nests where both members of the breeding pair were intact, suggesting that Bald Eagles will accept and raise offspring other than their own.

Why different behavioral strategies were adopted in these situations is not clear. The case of indifference may be explained as a gender distinction in adaptive strategies since sexually selected replacement behavior has been shown to occur in other species (e.g., Crook and Shields 1985, Freed 1986, Robertson and Stutchbury 1988). Among the accounts involving male replacements, the variable responses may have been due to differences in the nest stage at the time of replacement. The observation by Grubb *et al.* (1988) occurred on the threshold of hatching, whereas the young in our observations were nearly two weeks old. The age of the replacement adult may also be a contributing factor. Anthony *et al.* (1994) report that nests where one member of the breeding pair had near-adult plumage, defined as having a partially white tail and horizontal line of dark feathers in the eye region, were rarely successful. Further, they conclude that nest failure in an observed instance of mate replacement was specifically attributed to the near-adult status of the replacement. Whether or not the age of the nestlings and/or replacement adult were a significant distinction in the conditional responses observed here is not clear.

Unfortunately, no conclusive evidence is available on whether or not the intruder male went on to form a pair bond with the resident female. The only observations made were that both adults returned to the nest to feed the following day. A breeding attempt was documented at the nest the following year during aerial survey flights (B. D. Watts pers. comm.), but adult identification was not possible since the unique plumage characteristics used to distinguish the birds in 2002 would have been lost with annual feather molt. Thus, some caution is needed in interpreting this account of infanticide in the context of territory takeover and mate replacement until additional information is available about the frequency and the conditions under which it occurs.

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CHAPTER 4

THE CONSEQUENCE OF MATE LOSS ON BROOD CARE IN BALD EAGLES

Biparental care of offspring (Stalmaster 1987) and territory defense (Mahaffy and Frenzel 1987) have been well documented in Bald Eagles (*Haliaeetus leucocephalus*). The extent to which the investment of both adults is necessary to raise any or all young to independence, however, has not been addressed. The results of most avian mate-removal studies to date suggest that males are beneficial but not necessarily essential for the rearing of at least some offspring (e.g., Lyon *et al.* 1987, Dunn and Hannon 1989, Wolf *et al.* 1990). However, the timing of mate loss may be critical; an unaided female may not be able to compensate for a male's absence if it occurs early in the growth phase of chicks, particularly before nestlings are functionally homeothermic (Sasavári 1986).

Here we report on observations of a Bald Eagle nest where the adult male is lost shortly after chick hatching. This nest failed to fledge any young: the youngest nestling died at 4 d and the second and third hatched nestlings were cannibalized by an intruding male Bald Eagle at ages 15 and 13 d, respectively. We quantified the time spent brooding nestlings after the disappearance of the male to evaluate the effect of mate loss. To place these observations in context, a comparison of both incubation and brooding patterns is made to two reference Bald Eagle nests where the mating pair remained intact throughout the breeding season.

STUDY AREA AND METHODS

We observed three Bald Eagle nests in the lower Chesapeake Bay region using small, security video cameras during the 2002 ($n = 1$) and 2003 ($n = 2$) breeding seasons. Video-monitoring was conducted as part of a larger study on diet and provisioning patterns of nesting Bald Eagles in Virginia.

Camera systems were installed in January prior to egg laying and nests were monitored approximately 4 d/wk from February-April through the incubation and early nestling phases. Cameras were positioned so that the entire surface of the nest was in view and no additional observations other than those recorded on videotape were attempted. Details of video system components are provided in Chapter 1. Standard T-160 VHS videotapes were used to record for 8 h/d beginning 1 h after sunrise. We also used timelapse videocassette recorders when available for full-day (dawn – dusk) coverage.

We recorded information on start and end times for incubation/brooding bouts as well as the identity of the parent providing care. Time intervals were measured using a stopwatch (± 1.0) while reviewing videotapes. Incubation was defined as an adult covering 100% of the eggs in a sitting posture. Brooding was defined as an adult covering 50% of at least one chick (Warnke *et al.* 2002). Bald Eagles exhibit reversed sexual size dimorphism (Bortolotti 1984b); thus, paired birds were not difficult to sex on the basis of size. Size differences were also used to identify nestlings in each brood. Bald Eagle chicks hatch asynchronously (Gerrard and Bortolotti 1988) and nestlings shortly after hatch date are not difficult to distinguish based on size differences associated with age. We used the date of hatch of the oldest chick when assigning nestling ages for data analysis and determining nesting phase (hatching of first chick marked the effective change from incubation to brooding).

Statistical Analyses. We constructed Chi-square contingency tables (Zar 1974) to test for significant differences in the time spent brooding between the nest with the unaided female ("Hoffler Creek") and the nests with paired adults ("reference" nests). Combining data from both reference nests was validated by first testing for significant differences between them for time spent brooding nestlings 5 – 14 d ($\chi^2 = 0.15$, df = 1, $P > 0.5$). Due to a small sample size for full day coverage, only morning hours (0600 – 1400) were used in incubation/brooding analyses. However, we did review all available video footage and considered activities directly surrounding the infanticide and cannibalism of the nestlings regardless of recording time. All statistical tests were considered significant at the $\alpha = 0.05$ level.

RESULTS

We recorded (473 h) of incubation activities (all 3 nests combined). Parental effort in this phase was comparable between nests. The percent of time that eggs were exposed (not brooded) at Hoffler Creek was 1.8% compared to percent exposure of 2.0% and 1.6% at the reference nests. At all nests, both adults contributed nearly equal effort to incubation responsibilities (Table 1) and daily incubation patterns typically consisted of several alternating male and female bouts. Average incubation bout duration was 98.7 ± 81.23 min ($n = 184$) for females and 71.38 ± 49.06 min ($n = 182$) for males.

During the brooding phase, 129 h (all 3 nests combined) were recorded when nestlings were between 5 – 14 d. Within this period, the time that nestlings were brooded was significantly lower at Hoffler Creek compared to the reference nests ($\chi^2 = 428.96$, df = 1, $P < 0.001$). Nestlings were left exposed for a greater percent of recorded time (36.3%) at Hoffler Creek compared to the combined exposure time at the other two nests (22.6%). At control nests, gender differences in brooding care were more pronounced than relative roles during incubation with females brooding chicks for a greater percent of the time compared to males (Table 2). Average brooding bout duration was 42.4 ± 25.01 min ($n = 49$) for the unaided female, 40.2 ± 30.22 min ($n = 154$) for references females and 30.0 ± 19.76 min ($n = 22$) for reference males. These results indicate that the unaided female was unable to provide brood care equivalent to that received at nests where the breeding pair remained intact.

DISCUSSION

Male and female Bald Eagles typically share in parental care of dependent offspring and, when mating pairs were intact, results of this study are consistent with previously observed patterns with regard to parental roles and time budgets (Cain 1985). Because of the substantial involvement of both sexes, loss of a breeding adult potentially has significant consequences for both the remaining parent and offspring. Following mate loss, time spent brooding was significantly lower at Hoffler Creek compared to sites where both adults contributed to offspring care. These differences may have important consequences for nestling survival by limiting the female's ability to thermoregulate, provisioning, and protect young.

Nestling Bald Eagles are not capable of maintaining their own body temperature until approximately 14.7 d (Bortolotti 1984a), though nest observations suggest that adults will brood chicks up to 5 wks (Warnke *et al.* 2002). The shorter brooding bout length and related increase in exposure time following mate loss undoubtedly placed physiological stress on all nestlings in the failed nest. The effects of these stressors were likely most severe for the youngest sibling given its smaller size and presumably greater need for parental care.

Several lines of evidence suggest that food delivered to the nest did not adequately meet the energetic demands of the nestlings. First, the youngest chick on several occasions was lethargic and unresponsive, compared to its siblings and chicks of comparable age in control nests. Dykstra (1995) found that nestlings suffering from stress were less active than in conditions where food was not limiting. Second, food limitation is a key proximate cause of brood reduction amongst broodmates through both direct (e.g., aggressive encounters) and indirect (e.g., competition for provisioning) means (Mock *et al.* 1987). Third, the fact that this chick was later cannibalized lends further support to severe food limitation at the nest. During periods of food scarcity, progeny are sometimes used as a resource to sustain relatives. The energy gained from cannibalism allows the parent to remain continually with the brood, thereby decreasing the chances of death among the remaining offspring from predation and exposure (Polis 1981).

Young nestlings, unable to defend themselves, are particularly susceptible to both intraspecific and interspecific predation and time spent away from the nests leaves territories open to intrusion and nestlings susceptible to predation. Direct accounts of predation are uncommon, though Warnke *et al.* (2002) observed adult nest attendance to be highest in the first 4 wks post hatch and suggested this was due to the vulnerability of young to both weather and predation.

Little conclusive information is available on intraspecific nestling predation in Bald Eagles (*but see* Broley 1947, Nash *et al.* 1980, Gerrard and Bortolotti 1988, Mabie *et al.* 1994, Doyle 1995). Even less has been documented about the threat of intraspecific predation in Bald Eagles. Several authors allude to competition for nesting territories during the breeding season, often when young are present in the nest (Kennedy and McTaggart-Cowan 1998), yet we found only one documented account of intraspecific infanticide in Bald Eagles. An adult eagle was observed attacking and killing a 5 wk old nestling shortly after researchers had placed the eaglet in the nest as part of a reintroduction program (R. B. Owen, Jr., pers. comm.: *in* Wiemeyer 1981). At the Hoffler Creek nest, the remaining two chicks were killed and cannibalized by an intruder male 6 d after the youngest sibling died (within 11 d following the disappearance of the male: *see* Chapter 3).

In conclusion, we judge the female's failure to adequately balance responsibilities alone on (*i.e.* brooding and provisioning) and away from (*i.e.* foraging and territory defense) the nest as being responsible for the death of all three nestlings and the ultimate failure of the breeding attempt. Specifically, we suggest that the death of the youngest sibling resulted from the combined effects of exposure and starvation, resulting indirectly from the loss of the adult male and directly from competition amongst nestlings. We consider the circumstances surrounding the predation of the remaining chicks to be a result of decreased nest vigilance by the female under the constraint of conflicting responsibilities to protect and provide for the brood, again factors indirectly associated with the loss of the adult male. These observations suggest that mate loss in Bald Eagles when incurred early in the season appears energetically challenging to the surviving parent and may make successful rearing of the brood nearly impossible.

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Table 4.1. Comparison gender effort in percent time spent incubating (relative to total time eggs were incubated) for Bald Eagles in the lower Chesapeake Bay. Breeding pairs remained intact at all nest sites during the incubation phase. The adult male later disappeared from Hoffler Creek when nestlings were 5 d. Breeding pairs remained intact through fledging at reference nests.

Nest	Female Effort	Male Effort
Reference A	56.3%	43.7%
Reference B	48.0%	52.0%
Hoffler Creek	69.1%	30.9%

Table 4.2. Comparison gender effort in percent time spent brooding (relative to total time chicks were brooded) for Bald Eagles in the lower Chesapeake Bay. Data limited to nestlings age 5 – 14 d. The male at Hoffler Creek disappeared when nestlings were 5 d. Breeding pairs remained intact through fledging at reference nests.

Nest	Female Effort	Male Effort
Reference A	88.3%	11.7%
Reference B	68.7%	31.3%
Hoffler Creek	100.0%	N/A

CHAPTER 5

DEFINING FEEDING BOUT LENGTH FOR NESTLING BALD EAGLES

The quality of parental care is a highly adapted trait with obvious ties to fitness in species with altricial young. In these species, survival to independence depends directly on a parent's ability to provide the energy and nutrients required by offspring for growth and development. For many raptors, provisioning of young includes not just the capture and delivery of prey, but also the tearing and feeding of prey items to chicks. Thus, the amount of food nestlings ingest depends not only on the delivered food resources, but also on the quantity directly provisioned by adults during feeding bouts. Duration of feeding bouts is influenced, in turn, by numerous factors such as chick age, brood size, and parental experience. A full investigation of these factors may provide insight into the constraints under which many species operate to raise young to independence.

For species that are not time-limited, the temporal pattern of feeding may be complex throughout the day. For this reason, a prerequisite for investigating the structure of provisioning is a clear definition of a feeding bout. Here we examine the distribution of inter-bite intervals to develop criteria for the delineation of feeding bouts in Bald Eagles (*Haliaeetus leucocephalus*).

METHODS

Data were collected from 16 Bald Eagle nests video-monitored from nestling age 15 d through fledging. We mounted small, bullet security cameras in nest trees to record feeding patterns at close range with minimal disturbance to breeding adults and chicks. Details of system components are provided in Chapter 1.

Videotapes were reviewed to quantify inter-bite intervals during chick provisioning. We recorded the amount of time (± 1.0 s) elapsed between bites either provisioned to offspring or consumed by the adult. Presumably, intervals between bites included both intervals within feeding bouts as well as intervals between bouts.

A criterion to delineate the end of a feeding bout was derived using the log-frequency method suggested by Sibly *et al.* (1990). Data were summarized to generate the frequency of inter-bite intervals in 5 s increment periods. We then plotted the logarithm of the survivorship function *l*(x).

RESULTS AND DISCUSSION

Out of 3,681 observed inter-bite intervals, inter-bite intervals ranged from 1.0 – 24,409.0 s with a mean ± standard deviation of 98.5 ± 1,098.37 s. In nearly all feeding instances observed, the taxon of the provisioning prey item was fish though some mammal prey items were documented.

The frequency distribution of inter-bite intervals approximates a negative exponential function. Inspection of the log frequency plot of the survivorship function reveals a sharp transition between relatively short intervals and relatively long intervals in the region of 40 s (Figure 5.1). We interpret the region of short intervals to reflect feeding bouts and the region of long intervals to reflect time periods between feeding bouts. We suggest that an inter-bite interval that exceeds 40 s may be used to identify the end of a feeding bout for Bald Eagles.

The definition of the bout criterion, *i.e.* knowing when a behavior pattern begins and ends, is a critical aspect of behavioral studies. The first step in provisioning pattern analysis is the estimation of appropriate feeding bout criterion. Application of a 40 s rule to delineate feeding bouts will for the first time allow for the collection of feeding information that could be used to analyze the influence of behavioral and ecological factors that might contribute to the temporal structure chick provisioning in Bald Eagles.

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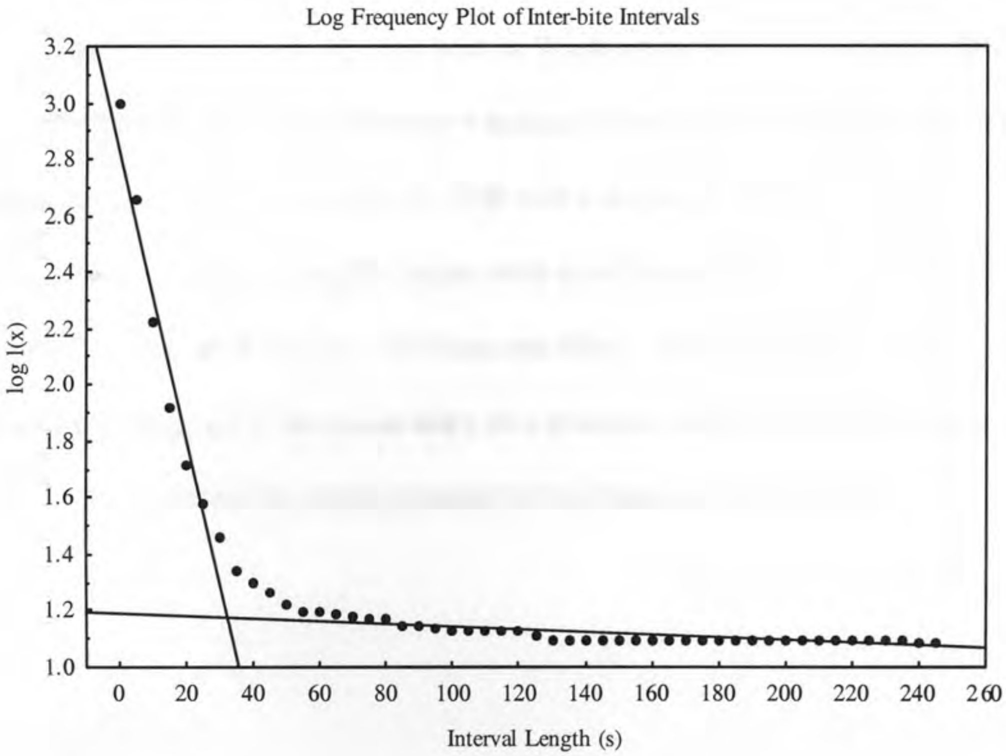
Figure 5.1. Log frequency plot of the distribution of inter-bite intervals. Only intervals interval lengths < 250 s are shown here for clarity.



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