

## **A Classification-Tree Analysis of Nesting Habitat in an Island Population of Northern Harriers**

Authors: Massey, Blake, Bowen, Rhys, Griffin, Curtice, and McGarigal, Kevin

Source: *The Condor*, 110(1) : 177-183

Published By: American Ornithological Society

URL: <https://doi.org/10.1525/cond.2008.110.1.177>

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*The Condor* 110(1):177–183  
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## A CLASSIFICATION-TREE ANALYSIS OF NESTING HABITAT IN AN ISLAND POPULATION OF NORTHERN HARRIERS

BLAKE MASSEY<sup>1,3</sup>, RHYS BOWEN<sup>2</sup>, CURTICE GRIFFIN<sup>1</sup>, AND KEVIN MCGARIGAL<sup>1</sup>

<sup>1</sup>University of Massachusetts—Amherst, 160 Holdsworth Way, Amherst, MA 01003

<sup>2</sup>24 Beach St, Foxboro, MA 02035

**Abstract.** Nantucket Island, Massachusetts, hosts the largest population of breeding Northern Harriers (*Circus cyaneus*) in the northeastern United States. We analyzed 128

nest sites to determine landscape features influential to habitat selection. We performed a vegetation community use-availability study, and we used 70 GIS-derived landscape metrics to conduct a classification tree analysis. We used the classification tree results to quantify, predict, and map the preferred nesting habitat of harriers islandwide. The vegetation community use-availability study showed that harriers had a preference for herbaceous

Manuscript received 31 January 2007; accepted 4 January 2008.

<sup>3</sup>E-mail: [blakemassey@gmail.com](mailto:blakemassey@gmail.com)

*The Condor*, Vol. 110, Issue 1, pages 177–183. ISSN 0010-5422, electronic ISSN 1938-5422. © 2008 by The Cooper Ornithological Society. All rights reserved. Please direct all requests for permission to photocopy or reproduce article content through the University of California Press's Rights and Permissions website, <http://www.ucpressjournals.com/reprintInfo.asp>. DOI: 10.1525/cond.2008.110.1.177.

marsh and shrublands and that they used low vegetation and forested habitats less than expected by availability. Preferred nesting habitat had two classification nodes. The first node represents habitat distant from developed land and roads, out of forests, and in or immediately adjacent to wetlands. The second node represents habitat identical to the first node with respect to distance from high densities of development and forests, but is upland and contains only minimal developed land. We applied the classification tree's criteria to GIS data for the entire island to create an islandwide map of preferred nesting habitat. Although most of the island's preferred nesting habitat is currently preserved (86%), we suggest conserving the remaining unprotected areas to maintain important nesting habitats.

**Key words:** *Circus cyaneus*, classification tree, Nantucket, nesting habitat, Northern Harrier.

#### Un Análisis del Hábitat de Nidificación de una Población Isleña de *Circus cyaneus* Basado en Árboles de Clasificación

**Resumen.** La isla de Nantucket, Massachusetts, alberga la población más grande de *Circus cyaneus* del noreste de los Estados Unidos. Analizamos 128 sitios de nidificación para determinar las características del paisaje que influyen la selección de hábitat. Realizamos un estudio del uso y la disponibilidad de comunidades de vegetación, y utilizamos 70 mediciones del paisaje derivadas a partir de un SIG para realizar un análisis de árboles de clasificación. Utilizamos los resultados de este análisis para cuantificar, predecir y mapear el hábitat de nidificación preferido de esta especie a nivel de toda la isla. El estudio del uso y de la disponibilidad de comunidades de vegetación mostró que las aves prefieren los pantanos con vegetación herbácea y los matorrales, y que éstas utilizan los ambientes de vegetación baja y de bosques en un grado menor al esperado de acuerdo a su disponibilidad. El hábitat de nidificación preferido presentó dos nodos de clasificación. El primer nodo representa ambientes distantes de áreas desarrolladas y carreteras, por fuera de los bosques y dentro de, o inmediatamente adyacentes a, humedales. El segundo nodo representa ambientes idénticos a los del primer nodo con respecto a la distancia a lugares con alta densidad de áreas desarrolladas y bosques, pero corresponde a lugares de tierras altas y contiene sólo tierras con un nivel de desarrollo mínimo. Aplicamos los criterios del árbol de clasificación a los datos de SIG de toda la isla para crear un mapa del hábitat de nidificación preferido a nivel de la isla entera. Aunque la mayor parte del hábitat de nidificación preferido está actualmente preservado en la isla (86%), sugerimos conservar las áreas no protegidas restantes para mantener ambientes de nidificación importantes.

For Northern Harriers (*Circus cyaneus*) in the northeastern United States, much nesting habitat has been lost to vegetation succession, habitat degradation, and housing development (Serrentino and England 1989, Christiansen and Reinert 1990, Serrentino 1992), resulting in dramatic declines in their breeding numbers over the past few decades (Serrentino 1992). Breeding harriers have been nearly extirpated from mainland Connecticut, Massachusetts, and Rhode Island (Christiansen and Reinert 1990), and in coastal New England as a whole, they are now principally restricted to Cape Cod and offshore islands, including Martha's Vineyard and Nantucket (Christiansen and Reinert 1990, Serrentino 1992). Recent surveys of harrier nests on Nantucket indicate that this island population probably represents the last stronghold for breeding harriers in Massachusetts.

In most of the North American literature, harriers are associated with grassland or wetland habitats (Bildstein and MacWhirter 1996), where they nest on the ground, typically in clumps of taller, denser vegetation in grasslands or on vegetation mats in wetlands (Toland 1985, Grant et al. 1991, Serrentino 1992). On Nantucket, harriers were found nesting across the island in all major community types (herbaceous marsh, low vegetation, and shrubland) with the exception of forest (Bowen 2004). The extensive use of tall, dense shrubland habitats for nesting conflicts with most accounts of harrier nesting habitat, including the characterization of harriers as "obligate grassland species" (Vickery et al. 1999), and suggests that Nantucket's unique ecology may result in alternative nesting strategies.

The goal of this study was to identify the vegetation communities and landscape variables important to nesting harriers on Nantucket. We analyzed harrier selection of nesting habitats with two approaches. First, we performed a vegetation cover use-availability analysis to determine if nesting harriers selected vegetation cover types in proportion to their availability. Second, we calculated landscape metrics quantifying anthropogenic and vegetation features for both harrier nests and random points in the landscape. These landscape metrics were analyzed using a classification tree analysis (Breiman 1984), and the results were used to classify, predict, and map preferred harrier nesting habitat on Nantucket.

#### STUDY SITE

All fieldwork was conducted on Nantucket Island (70.1°N, 40.3°W), located approximately 40 km south of Cape Cod, Massachusetts. The island is nearly 12 500 ha in total area and is covered by a mosaic of habitats including grasslands, heathlands, shrublands, pine-dominated forests, and anthropogenic environments.

Shrublands and low vegetation (grasslands, heathlands, and intergrades between the two) make up the majority of the island's natural vegetation. Sandplain grasslands on Nantucket are dominated by little bluestem (*Schizachyrium scoparium*) and Pennsylvania sedge (*Carex pennsylvanica*; Dunwiddie 2001). Nantucket's coastal heathlands resemble grasslands but have a smaller component of forbs and grasses and a greater percentage of dwarf shrubs, especially members of the Ericaceae (heath; Dunwiddie 2001). However, on Nantucket, heathland and grassland communities are often intermixed and not easily distinguished in the field (Dunwiddie et al. 1996). Scrub oak (*Quercus ilicifolia*) shrublands are dominated by dense thickets of scrub oak that can reach canopy covers of 80%–100% and heights of 2–4 m and often replace grasslands and heathlands not subject to periodic disturbance such as fire, mowing, or grazing (Sorrie and Dunwiddie 1996). Pitch pine (*Pinus rigida*) forests are a successional stage of sandplain communities characterized by sparse to dense stands of pitch pine, and on Nantucket, replace grasslands, heathlands, and scrub oak. Forested areas occur along roads and in more developed areas of the island. A small portion of the island is wetland habitat dominated by herbaceous marsh. Houses and development are located across the island but concentrated around its north-central section centered on the town of Nantucket.

Nantucket may be particularly attractive to ground-nesting harriers because it is the only large offshore island in Massachusetts without any native carnivorous mammals capable of depredating raptor nests (e.g., red fox [*Vulpes vulpes*], coyote [*Canis latrans*], raccoon [*Procyon lotor*], striped skunk [*Mephitis*

*mephitis*], and Virginia opossum [*Didelphis virginiana*]); (Cardoza et al. 1999). Hence, it provides a favorable breeding habitat for the ground-nesting harrier.

## METHODS

### DATA COLLECTION

We located a total of 140 harrier nests in the breeding seasons of 2000, 2002, and 2003. Twelve sites were within 10 m of a nest used in the previous study year and may have represented reuse by breeding pairs, so were excluded from the dataset. Thus, all 128 nests in our analyses represented unique nesting locations.

For comparison with the nest sites, we generated a set of 1000 random point locations in potential nesting habitat (all portions of the island except obviously unsuitable habitats such as pavement, dirt roads, houses, bare sand, mud, or open water) using Random Point Generator (Sawada 2002). We entered the nest sites and random points into a GIS database along with data layers of roads, buildings, hydrological features (streams, ponds, and wetlands), and vegetation cover types. We converted all GIS data to 5 m grid cells, the minimum mapping unit for our data.

### STATISTICAL ANALYSES

We compared vegetation cover use with availability using a chi-square goodness-of-fit analysis to test for nonrandom distribution of nests among vegetation cover types. Land cover preferences were quantified with the Manly-Chesson selectivity index (Manly et al. 1972, Chesson 1978). All statistical analyses were performed in SAS (SAS Institute 2001).

We used Spatial Analyst (ESRI 2002 a) and FRAGSTATS (McGarigal and Marks 1995) to calculate landscape metrics (Table 1) that measured both anthropogenic features and landscape vegetation patterns for every nest and random point. At each point, we calculated the size of the surrounding vegetation patch; the vegetation cover type; and distance to the nearest low vegetation, forest, and shrubland patch, hydrological feature, building, and unpaved, paved, and any-surface road. We also calculated the following neighborhood metrics around each

point: patch richness; percent cover of water, sand or mud, low vegetation, herbaceous marsh, shrubland, forest, and developed (including agricultural) land; total edge of low vegetation, shrubland, forest, and buildings; road density (both simple and distance-weighted, in which the values of closer features were weighted more heavily than those farther away), and number of buildings. For each point, we calculated these neighborhood metrics at a radius of 200 m, the approximate radius of harrier nesting territories on Nantucket (Bowen 2001), as well as radii of 50 m, 500 m, and 1 km to determine if harriers were responding to the landscape at multiple scales, as reported for other species of raptors (McGrath et al. 2003).

We built our classification tree model using program CART 4.0 (Steinberg and Colla 1997). We computed our model using gini splitting criteria, equal prior probabilities, 10-fold cross validation, and a 1:1 (nest: random point) misclassification cost ratio, and we selected the appropriate-sized tree using the 1 S.E. rule—all parameters designed to create a parsimonious classification tree with high predictive ability (Breiman 1984, De'ath and Fabricius 2000). This procedure selected habitats most frequently used for nest sites but may have excluded some outlier nesting habitat types.

In ArcView (ESRI 2002b), we applied the criteria from the classification model to a map of landscape metrics to obtain a prediction value (nesting or nonnesting habitat) for every grid cell on Nantucket. We mapped these predictions to create a map of preferred nesting habitat.

## RESULTS

Our vegetation cover use-availability analysis indicated that harriers on Nantucket do not nest randomly among cover types ( $\chi^2_3 = 33.4, P < 0.001$ ; Table 2). They showed a strong preference for herbaceous marsh and a preference for shrublands. Harriers used low vegetation less and forests far less than expected by availability.

The classification tree analysis showed high stability and generated five splits and six terminal nodes (Fig. 1), with terminal nodes 2 and 3 classified as nesting habitat. Terminal node 2 was defined by four criteria, namely:  $\leq 5\%$  developed land within

TABLE 1. Landscape metrics calculated for Northern Harrier nests from 2000, 2002, and 2003 and random points that were used in a classification tree analysis of nesting habitat on Nantucket Island, Massachusetts.

Landscape Metrics	
At each point	Within radii of 50 m, 200 m, 500 m, and 1 km <sup>b</sup> around point
Landscape cover type <sup>a</sup>	Density of roads (m area <sup>-1</sup> )
Patch size (ha)	Density of roads, distance-weighted (m area <sup>-1</sup> )
Distance (m) from nearest:	Number of buildings
Building	Patch richness (number of patches area <sup>-1</sup> )
Hydrological feature (stream, pond, wetland)	Percent land of cover types <sup>c</sup>
Patch of forest	Total edge of buildings (m area <sup>-1</sup> )
Patch of low vegetation	Total edge of forest, low vegetation, and shrubland (m area <sup>-1</sup> )
Patch of shrubland	
Paved road	
Unpaved road	
Road (any surface)	

<sup>a</sup>Nests and random points located on five cover types: herbaceous marsh, low vegetation, shrubland, forest, and developed land.

<sup>b</sup>Each metric calculated at each scale independently; therefore, four metrics for each category of radius.

<sup>c</sup>Assessed for all seven cover types: water, sand or mud, herbaceous marsh, low vegetation, shrubland, forest, and developed land.

TABLE 2. The distribution of Northern Harrier nest sites from 2000, 2002, and 2003 among vegetation cover types on Nantucket Island, Massachusetts. According to the Manly-Chesson index (Manly et al. 1972, Chesson 1978), the distribution of nests, which was nonrandom among cover types, reflected a strong preference for herbaceous marsh and a preference for shrubland by harriers; low vegetation and forests were used less and far less, respectively, than expected by availability.

Cover type	Land cover		Nest locations			Manly-Chesson selectivity index <sup>c</sup>	Manly-Chesson selectivity index <sup>d</sup>
	Ha	%	No. <sup>a</sup>	%	Ex. <sup>b</sup>		
Herbaceous marsh	443	5	17	13	5	2.84	0.58
Shrubland	5141	54	87	68	54	1.25	0.26
Low vegetation	2304	24	23	18	24	0.74	0.15
Forest	1572	17	1	1	17	0.05	0.01
Total	9460	100	127	100	100	4.87	1.00

<sup>a</sup>Number of nests observed in habitat.

<sup>b</sup>Expected percent, if nests were randomly distributed among habitats ( $\chi^2_3 = 33.4$ ,  $P < 0.001$ ).

<sup>c</sup>Percent of nest locations per percent available cover.

<sup>d</sup>Selectivity indices standardized to sum to 1 (selectivity index divided by sum of selectivity indices).

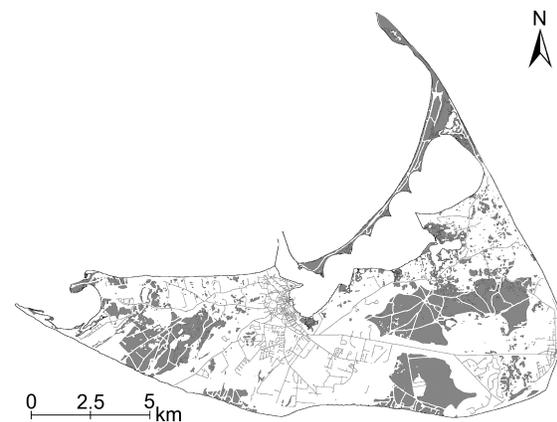
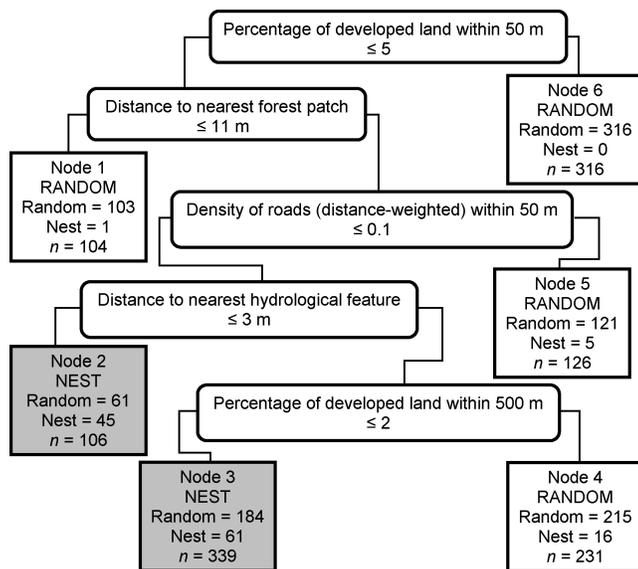


FIGURE 2. Map of Nantucket Island, Massachusetts showing the distribution of preferred nesting habitat (gray shading) for Northern Harriers from the 2000, 2002, and 2003 breeding seasons based on a classification tree analysis of nest-landscape relationships. Paved roads are shown for reference.

FIGURE 1. Classification tree of preferred nesting habitat of Northern Harriers from the 2000, 2002, and 2003 breeding seasons on Nantucket Island, Massachusetts—calculated using 70 landscape metrics and a 1:1 misclassification cost ratio for nests to random points—showing splits, terminal nodes, and frequency data. Terminal nodes (1 through 6) are labeled from left to right and classified as NEST (grey) or RANDOM (white). All data points (128 nests and 1000 random points) start at the top node and follow the tree down, going left at decision nodes if they met the criterion and right if they did not, until reaching a terminal node.

50 m, > 11 m from forest,  $\leq 0.1$  m road (distance-weighted) within 50 m, and  $\leq 3$  m from a hydrological feature. Terminal node 3 datapoints shared the first three criteria but were > 3 m from hydrological features and had  $\leq 2\%$  developed land within 500 m. In descriptive terms, terminal node 2 represents habitat distant from high densities of developed land and roads, out of forests, and in or immediately adjacent to wetlands. Terminal node 3 represents habitat identical to that of node 2 with respect to distance from high densities of development (developed land and roads) and forests, but the habitat is upland (i.e., not in or immediately

adjacent to a wetland) and contains only a minimal percent of developed land within 500 m. This tree's correct cross-validation classification rate for nests was 83% (106 of 128 nests).

We applied the criteria from the classification tree to island-wide grid maps in ArcView (ESRI 2002b) to produce a map of preferred nesting habitat (Fig. 2). Preferred nesting habitat occupied 2649 ha and consisted of terminal nodes 2 (wetlands: 684 ha) and 3 (uplands: 1965 ha; Table 3).

## DISCUSSION

Our finding from the use-availability analysis, that harriers on Nantucket strongly preferred the herbaceous marsh cover type for nesting habitat, agrees with many previous studies that report harriers using wetlands (Simmons and Smith 1985, Grant et al. 1991, Redpath et al. 1998). Although harriers are known to commonly nest in clumps of taller, denser vegetation in grasslands (Toland 1985, Grant et al. 1991), their extensive use of tall, dense shrubland has rarely been documented in previous studies, with the notable exception of coastal Massachusetts shrublands

TABLE 3. Characteristics of preferred nesting habitat of Northern Harriers on Nantucket Island, Massachusetts, based on a classification tree analysis of nests from 2000, 2002, and 2003 and showing total area, area protected, percent protected, and total number of nests in wetland, upland, and all habitat.

Characteristic	Habitat		
	Wetland	Upland	All
Total area (ha)	684	1965	2649
Area protected <sup>a</sup> (ha)	456	1811	2267
Area protected (%)	67	92	86
Nests in habitat <sup>b</sup>	45	61	106

<sup>a</sup>Owned by nonprofit conservation organizations, and local, state, and federal agencies (Nantucket Conservation Foundation 2004).

<sup>b</sup>Out of 128 total nests found islandwide.

reported by Christiansen and Reinert (1990). This may indicate relatively unusual use of this habitat on Nantucket, Martha's Vineyard, and, to a lesser degree, Cape Cod (RB, unpubl. data). In contrast to other studies, harriers on Nantucket nested in low vegetation less frequently than expected by its availability, which may result from their increased use of shrublands. Otherwise, harriers on Nantucket avoided nesting in mature forested habitats, concordant with many previous studies (Watson 1977, Petty and Anderson 1986, Etheridge et al. 1997).

Our preferred nesting habitat classification and map defines consistently selected nesting habitat. Both nest nodes of the tree (nodes 2 and 3) indicate that harriers avoid nearby development (developed land and roads) and forested habitats, but differentiate between the harriers' criteria in wetland and upland habitats. In wetlands, harriers preferred being in or immediately adjacent to wetlands without any additional criteria, but in upland areas, harriers avoided development within 500 m.

Wetlands were particularly preferred, as 45 of the 128 nests were placed in them (including in shrubby as well as herbaceous marshes) despite their relative scarcity. When nesting in this habitat, harriers seemed more willing to tolerate development between 50 and 500 m, and a few nest sites showed particular evidence of this pattern. This implies that upland nesting habitat may be more negatively affected by nearby development than are wetland areas. In New Brunswick, harriers preferred nesting in wetter habitats and may have selected these areas because of lower predation rates (Simmons and Smith 1985).

The avoidance of development by harriers for nesting habitat may threaten their future on Nantucket. The island's human population and number of housing units have increased tremendously over the past 30 years, and with an estimated population growth rate of 13% (from 9520 to 10 724) between 2000 and 2003, Nantucket was Massachusetts's fastest growing county (U. S. Census Bureau, Population Division 2004). Christensen and Reinert (1990) also reported that harriers avoid human development and activity, especially in coastal habitats. Thus, minimizing the impacts of Nantucket's increasing human population may be critical to protecting the island's harriers. Similarly, the unsuitability of forested habitats as preferred nesting habitat may also threaten harriers on Nantucket. Forested habitats are increasing on the island and will expand further if they are not logged or otherwise undergo disturbance (Tiffany and Eveleigh 1985).

From a landscape metric perspective, the dominant explanatory features for predicting preferred nesting habitat occurred

within 50 m of the nest. The notable exception was in uplands, where harriers located their nests >500 m from developed areas. Otherwise, we did not find any strong effects of landscape metrics at the 200 m, 500 m, or 1 km scales, suggesting that harrier nest site selection is based on habitat features within a relatively small area around the nest.

Interestingly, there were no splits in our classification tree model based on a preference for shrublands or herbaceous marsh. However, since our vegetation cover map could not distinguish small (2–3 m wide) patches of taller, shrubby vegetation within grasslands and heathlands where harriers typically nested, the selection of shrublands in the models may have been underestimated. For herbaceous marsh, the split based on distance to wetlands may have had a slightly stronger effect, masking any splits based on herbaceous marsh.

Raptors may select nest sites based on distance to foraging areas (Janes 1985) or total availability of suitable foraging habitat near the nests (Simmons and Smith 1985). However, we found no evidence that harriers on Nantucket prefer nesting habitats within some threshold distance of shrubland, low vegetation, or herbaceous marsh, or with a minimum percentage of a certain vegetation cover type around the nest. Harriers' ability to fly >100 km per day (Simmons 2000) may offset any relation between nest sites and foraging areas, especially on a relatively small island such as Nantucket.

Of the 2649 ha of preferred nesting habitat, 2266 ha (86%) are owned by nonprofit conservation organizations and local, state, and federal agencies (Nantucket Conservation Foundation 2004). Their acquiring the last portion of preferred nesting habitat would help secure the remaining unprotected areas that are important harrier nesting habitats.

The preference of harriers for nesting in herbaceous marsh and shrubland indicates that these habitats should be a priority for harrier habitat conservation, but management actions that increase the extent of scrub oak could have adverse effects on other species on the island that require grasslands and heathlands. The sandplain grassland and heathland communities of Nantucket are globally endangered and host a variety of rare plants, birds, and invertebrates (Dunwiddie et al. 1997). These communities are threatened by housing development and vegetation succession by woody species, such as pitch pine and scrub oak (Dunwiddie 1989), and conservation of these communities requires frequent disturbance regimes. It is important that these imperiled communities be maintained and not replaced by scrub oak despite its value for nesting harriers. If these habitats are managed for nesting harriers, disturbance regimes will have to be rotational and timed to minimize disturbance to the birds. Duebbert and Lokemon (1977) reported that harriers nested only in areas not mowed, burned, or grazed for 2–5 years. Serrentino (1992) recommended that no mowing, burning, or grazing occur near harrier nests during the courtship and nesting season, which is April to mid-August on Nantucket (Bowen 2001, 2003).

In the future, the conservation of harriers and other threatened taxa on Nantucket will depend on the availability of a combination of shrublands, grasslands, and heathlands. Conservation organizations on Nantucket can help by reducing or preventing the expansion of pine forests, efficiently managing heathlands and grasslands, and protecting preferred nesting habitats that are not currently included in the conservation network.

We would like to thank the Partnership for Harrier Habitat Preservation for funding this study, and the Nantucket Conservation Foundation, Massachusetts Audubon Society, and Nantucket

Land Bank for providing study sites. We would also like to recognize Karen Combs-Beattie, Ernie Steinauer, and Scott Melvin for their guidance and hard work in making this project possible. Additionally, we appreciate the efforts of two wonderful field assistants, Leah Menyo and Jillian Drury. Finally, we are very grateful for the helpful suggestions on the manuscript by the reviewers and editors at *The Condor*.

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*The Condor* 110(1):183–187  
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## THE INFLUENCE OF SALINITY ON PROVISIONING RATES AND NESTLING GROWTH IN BALD EAGLES IN THE LOWER CHESAPEAKE BAY

A. CATHERINE MARKHAM<sup>1</sup> AND BRYAN D. WATTS

*Center for Conservation Biology, College of William and Mary, P.O. Box 8795, Williamsburg, VA 23187-8795*

**Abstract.** We measured provisioning and growth patterns in Bald Eagle (*Haliaeetus leucocephalus*) chicks from nests in two salinity zones in the lower Chesapeake Bay. Nestlings in mesohaline reaches experienced higher per capita consumable energy provisioning rates and had higher instantaneous growth rates compared to nestlings in tidal-fresh salinity zones. These results 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, a finding consistent with documented higher reproductive rates and proportion of three-chick broods along mesohaline reaches compared to tidal-fresh reaches. The results of this study have important conservation implications for Bald Eagles by addressing issues related to variation in habitat quality within a continuous ecosystem and the determination of core breeding zones.

**Key words:** *anadromous, Bald Eagle, Chesapeake Bay, growth, Haliaeetus leucocephalus, provisioning, salinity.*

La Influencia de la Salinidad sobre las Tasas de Aprovechamiento y Crecimiento de los Pichones de *Haliaeetus leucocephalus* en la Parte Baja de la Bahía Chesapeake

**Resumen.** Medimos los patrones de provechamiento y crecimiento de los pichones de *Haliaeetus leucocephalus* provenientes de nidos de dos zonas salinas de la parte baja de la Bahía Chesapeake. Los pichones de las zonas de salinidad intermedia experimentaron tasas de provechamiento de energía consumible per capita mayores y tuvieron tasas de crecimiento instantáneo mayores comparadas con las de los pichones de las zonas de agua dulce con influencia marina.

Estos resultados sugieren que las águilas que nidifican a lo largo de las zonas de salinidad intermedia fueron más exitosas en alcanzar las demandas energéticas de cría de los pichones, comparado con las parejas que nidifican a lo largo de las zonas de agua dulce con influencia marina. Esto concuerda con hallazgos que documentan tasas reproductivas mayores y proporciones de nidadas de tres pichones a lo largo de las zonas de salinidad intermedia en comparación con las zonas de agua dulce con influencia marina. Los resultados de este estudio tienen implicancias importantes para la conservación de *H. leucocephalus* porque analizan aspectos relacionados a la variación en la calidad del hábitat en un ecosistema continuo y a la determinación de zonas núcleo de nidificación.

For Bald Eagles (*Haliaeetus leucocephalus*) nesting in the lower Chesapeake Bay, shoreline areas surrounding tidally influenced freshwater reaches (i.e., tidal-fresh) currently support a greater nesting density and have experienced faster rates of population increase than areas surrounding higher salinity waters (Watts et al. 2006). These findings imply that habitat quality varies spatially along the salinity gradient of the bay, though the specific attributes that drive these patterns are not clear. Watts et al. (2006) proposed that variation in prey availability, mediated through changes in the salinity of the bay water, may be one factor responsible for the observed patterns.

A recent investigation examined the influence of salinity on diet composition in breeding Bald Eagles within this region and found that dominant prey taxa did not vary significantly between tidal-fresh and mesohaline salinity reaches (Markham 2004). This suggests that pairs nesting within each zone utilized similar prey resources despite the documented influence of salinity on fish distribution in the bay (Murdy et al. 1997, Jung 2002). However, this finding of a similarity in patterns of prey use does not preclude the possibility that nesting pairs experience 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

Manuscript received 21 September 2006; accepted 5 October 2007.

<sup>1</sup>Present address: Department of Ecology and Evolutionary Biology, Princeton University, Guyot Hall, Washington Rd., Princeton, NJ 08544-1003. E-mail: [amarkham@princeton.edu](mailto:amarkham@princeton.edu)

*The Condor*, Vol. 110, Issue 1, pages 183–187. ISSN 0010-5422, electronic ISSN 1938-5422. © 2008 by The Cooper Ornithological Society. All rights reserved. Please direct all requests for permission to photocopy or reproduce article content through the University of California Press's Rights and Permissions website, <http://www.ucpressjournals.com/reprintInfo.asp>. DOI: 10.1525/cond.2008.110.1.183.