

217
18

Movements and Bioenergetics of Canvasbacks Wintering in the Upper Chesapeake Bay

by

David W. Howerter

Thesis submitted to the Faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of
Master of Science
in
Fisheries and Wildlife Sciences

APPROVED:



Dr. Roy L. Kirkpatrick, Chairman



Dr. Michael R. Vaughan



Dr. James D. Fraser

October 1990

Blacksburg, Virginia

LD

5655

V855

1990

H696

C.2

Movements and Bioenergetics of Canvasbacks Wintering in the upper Chesapeake Bay

by

David W. Howerter

Dr. Roy L. Kirkpatrick, Chairman

Fisheries and Wildlife Sciences

(ABSTRACT)

The movement patterns, range areas and energetics of canvasbacks (*Aythya valisineria*) wintering in the upper Chesapeake Bay, Maryland, were investigated. Eighty-seven juvenile female canvasbacks were radio-tracked between 30 December 1988 and 25 March 1989. Diurnal time and energy budgets were constructed for a time of day-season matrix for canvasbacks using riverine and main bay habitats. Canvasbacks were very active at night, making regular and often lengthy crepuscular movements ($\bar{x} = 11.7$ km) from near shore habitats during the day to off shore habitats at night. Movement patterns were similar for birds using habitats on the eastern and western shores of the Bay. Canvasbacks had extensive home ranges averaging 14,286 ha, and used an average of 1.97 core areas. Sleeping was the predominant diurnal behavior. Telemetry indicated that canvasbacks actively fed at night. Canvasbacks spent more time in active behaviors (e.g. swimming, alert) on the eastern shore than on the western shore. Similarly, canvasbacks were more active during daytime hours at locations where artificial feeding occurred. Behavioral patterns were only weakly correlated with weather patterns. Canvasbacks appeared to reduce energy expenditure in mid-winter by reducing distances moved, reducing feeding activities and increasing the amount of time spent sleeping. This pattern was observed even though 1988-89 mid-winter weather conditions were very mild.

Acknowledgements

Many people and organizations were instrumental in the successful completion of this study. Funding was provided by the US Fish and Wildlife Service's Patuxent Wildlife Research Center and the Department of Fisheries and Wildlife Sciences at VPI & SU. I'd like to thank G. Michael Haramis and Dennis G. Jorde, biologists from Patuxent, for allowing me to cooperate with their study and track their radioed birds, and for arranging housing on Patuxent center grounds during my second field season. I'd like to thank Walter Rhodes, a fellow graduate student working on this project, for holding down the eastern half of the world while I was struggling with the western half. A special thanks needs to be extended to the innumerable landowners and agencies all up and down the Bay for allowing us to go stumbling around in their back yards at all hours of the day and night. I'd like to thank Joe Kesser, our pilot, for safely flying us around over the Bay at low altitudes at night.

I want to thank my graduate committee, Dr. Michael Vaughan, who was co-investigator on this project and who provided much logistical support and guidance when things were getting a little crazy; Dr. James Fraser for his knowledge of the Chesapeake Bay and for always being ready with a new idea when one was needed; and finally, my major adviser, Dr. Roy Kirkpatrick. Roy truly has a knack for knowing when to offer guidance and when to let you run

a little wild; when to let you stumble off your own cliffs and when to push you off those same cliffs; and probably most important when to ask the tough question and when to feign ignorance himself. I thank him for these qualities and for the patience and friendship he's shown me throughout my stay here.

I want to thank my fellow graduate students for maintaining a stimulating and productive atmosphere. And finally, I want to thank my parents, Bill and Doris Howerter, for their love and support.

Table of Contents

Introduction	1
Literature Cited.	2
Study Area	3
CHAPTER 1	5
Time-activity budgets of canvasbacks wintering on the upper Chesapeake Bay.	6
Introduction	7
Methods	9
Analysis	10
Results	12
Relationship Among Behaviors	12
Effect of Time, Season and Habitat	12
Effect of Artificial Feeding	14
Eastern vs. Western Shores	14
Influence of Weather	15
Table of Contents	v

Time Budget Estimation	16
Energy Budget Estimation	16
Disturbance	18
Discussion	19
LITERATURE CITED	24
Tables	28
CHAPTER 2	44
Movements and home ranges of canvasbacks wintering on the upper Chesapeake Bay. .	45
Introduction	46
Methods	48
Data processing	50
Results	51
Movements	51
Home Ranges	54
Discussion	56
LITERATURE CITED	61
Tables	64
Conclusions and Management Recommendations	75
LITERATURE CITED	78
Vita	80

List of Illustrations

Figure 1. Map of Chesapeake Bay illustrating study area. 4

List of Tables

Table 1.	Partial Spearman correlation coefficients between behaviors for canvasbacks wintering on the upper Chesapeake Bay.	29
Table 2.	MANOVA model of behavior proportions distributed over time, season, and habitat with all interactions.	30
Table 3.	Least squares estimates of diurnal time budgets, by time of day, for canvasbacks wintering on the upper Chesapeake Bay.	31
Table 4.	Least squares estimates of diurnal time budgets, by season, for canvasbacks wintering on the upper Chesapeake Bay.	32
Table 5.	Least squares estimates of diurnal time budgets, by habitat, for canvasbacks wintering on the upper Chesapeake Bay.	33
Table 6.	MANOVA model of behavior proportions distributed over artificial feeding conditions and habitats.	34
Table 7.	Least squares estimates of diurnal time budgets, by feeding regime, for canvasbacks wintering on the upper Chesapeake Bay.	35
Table 8.	Least squares estimates of diurnal time budgets, by habitat, for canvasbacks wintering on the upper Chesapeake Bay.	36
Table 9.	MANOVA model of behavior proportions distributed over eastern vs. western shores of the Chesapeake Bay and habitat types.	37
Table 10.	Least squares estimates of diurnal time budgets, by shore, for canvasbacks wintering on the upper Chesapeake Bay.	38
Table 11.	Least squares estimates of diurnal time budgets, by habitat, for canvasbacks wintering on the upper Chesapeake Bay.	39
Table 12.	Spearman correlation coefficients of selected variables with canvasback behaviors and energy expenditure.	40
Table 13.	Least squares estimates of overall diurnal time budgets, by habitat, for canvasbacks wintering on the upper Chesapeake Bay.	41
Table 14.	Weighted estimate of diurnal energy expenditure (kcal/bird/hr) for canvasbacks wintering on the upper Chesapeake Bay.	42

Table 15. Nocturnal feeding, by season, for juvenile female canvasbacks wintering on the upper Chesapeake Bay.	43
Table 16. Mean movement estimates for juvenile canvasbacks wintering on the upper Chesapeake Bay.	65
Table 17. Mean movement estimates by season, hunting season and shore for juvenile female canvasbacks wintering on the Chesapeake Bay	68
Table 18. Convex polygon and harmonic mean estimates of range and core area sizes for juvenile female canvasbacks.	69
Table 19. Weighted convex polygon and harmonic mean estimates of diurnal and nocturnal ranges and core area sizes.	71
Table 20. Comparison of diurnal and nocturnal ranges with weighted home ranges of juvenile female canvasbacks on the Chesapeake Bay.	73
Table 21. Comparison of range areas for juvenile female canvasbacks wintering on the eastern and western shores of the Chesapeake Bay	74

Introduction

Many North American waterfowl populations have been declining over the last 50 years. These declines have persisted even though habitats are apparently being under utilized (Trauger and Stout 1978). Fretwell (1972) has indicated that populations of bird species are often regulated during the nonbreeding season. This has led to much recent interest in factors affecting waterfowl populations on the wintering grounds.

Continent-wide, canvasback populations have been relatively stable; however, current populations are well below the target established by the North American Waterfowl Management Plan. To meet this target, canvasback populations will need to increase by approximately 40% over the next 10 years. Perry et al. (1981) showed that populations of canvasbacks wintering in the Chesapeake Bay have been declining sharply.

In 1987, my Advisory Committee approved a proposal to investigate certain aspects of the ecology of canvasbacks wintering on the upper Chesapeake Bay, Maryland. This study was accomplished concurrent to a study initiated by the Patuxent Wildlife Research Center (U. S. Fish and Wildlife Service) designed to quantify mortality and nutrition of wintering juvenile

female canvasbacks. Walter Rhodes also investigated specific habitat use of juvenile female canvasbacks in the Bay. The specific objectives of my portion of the study were the following:

- 1) To quantify daily time and energy budgets of canvasbacks wintering on the study area.
- 2) To quantify movement patterns of juvenile female canvasbacks on the study area.
- 3) To determine the minimum ranges needed by juvenile female canvasbacks to overwinter successfully on the Chesapeake Bay.

Literature Cited.

Fretwell, S. D. 1972. Populations in a seasonal environment. Princeton Univ. Press, Princeton, NJ. 217pp.

Perry, M. C., R. E. Munro and G. M. Haramis. 1981. Twenty-five year trends in diving duck populations in Chesapeake Bay. Trans. North Am. Wildl. Nat. Resour. Conf. 46:299-310.

Trauger, D. L. and J. H. Stout. 1974. Looking out for the canvasback, Part II: canvasbacks of the aspen parklands. Ducks Unlimited 38.

Study Area

The study area encompassed the portion of the upper Chesapeake Bay in Maryland from a northern boundary at the Hart-Miller Island complex on the western shore and the town of Tolchester on the eastern shore south to Cove Point just north of the mouth of the Patuxent River on the western shore and to the south shore of the Choptank River on the eastern shore (Fig. 1). All or portions of the Back, Patapsco, Magothy, Severn, South, Rhode and West Rivers on the western shore and the Chester River, Eastern Bay and the Choptank River on the eastern shore were included in the study area.

The western and eastern shores of the Bay present an interesting contrast in habitat considerations. The western shore is characterized by a generally urban setting. Ducks receive little hunting pressure, and the feeding of corn to ducks by private residents is common. The eastern shore, on the other hand, is largely rural, and waterfowl hunting is widespread and, in certain places, intense.

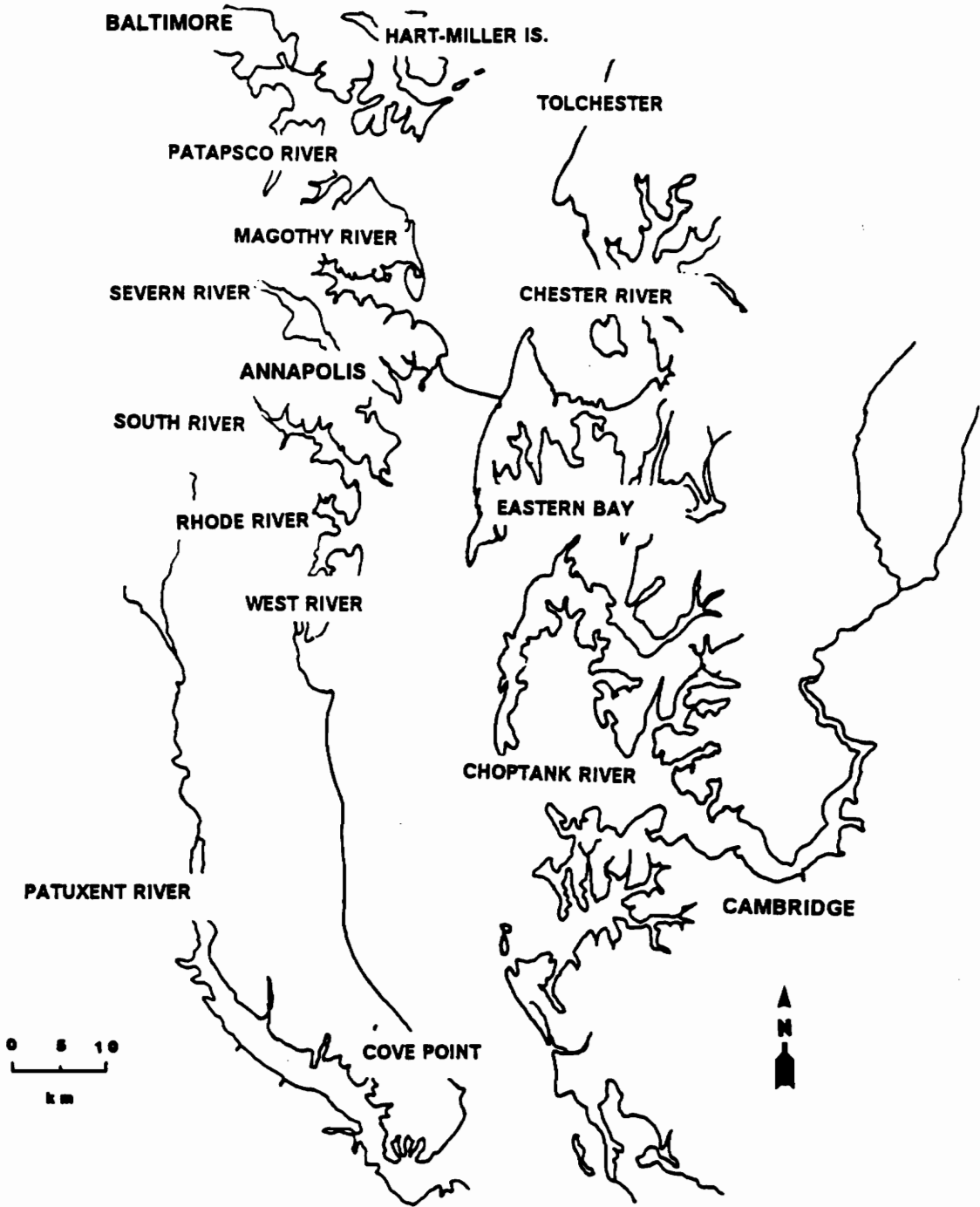


Figure 1. Map of upper Chesapeake Bay study area.

CHAPTER 1

Time-activity budgets of canvasbacks wintering on the upper Chesapeake Bay.

Introduction

The Chesapeake Bay traditionally has been very important as a wintering ground for canvasbacks (*Aythya valisineria*) wintering in the Atlantic Flyway. Munro and Perry (1981) reported that more than half of the Atlantic Flyway population of canvasbacks wintered on the upper Chesapeake Bay from 1956-1971. However, the proportion of Atlantic flyway canvasbacks wintering in the Bay has been declining steadily (Munro and Perry 1981, Perry et al. 1981, Perry 1982). Wintering populations of canvasbacks throughout the United States increased during the 1970's. The increase seen on a nationwide scale was not seen within the Chesapeake Bay. Estimated populations of canvasbacks wintering in the Bay have declined from a high of approximately 230,000 in the early 1950's to the current estimates of less than 40,000 (Perry et al. 1981). Perry et al. (1981) believed that habitat alteration on the wintering grounds, especially with regard to food resources, was responsible for this lack of response in Chesapeake Bay canvasback populations.

Canvasbacks are historically vegetarian (Bent 1923, Cottam 1939), with wildcelery (*Vallisneria americana*) being especially important as a food item. Recent studies have shown that wildcelery densities, and densities of submerged aquatic vegetation (SAV) in general, have declined severely within the Chesapeake Bay (Bayley et al. 1978, Munro and Perry 1981, Orth and Moore 1981, Orth et al. 1985). Increased turbidity through eutrophic processes and changes in salinity have been implicated as primary factors leading to this decline in SAV (Orth and Moore 1981).

Bayley et al. (1978) indicated that waterfowl use appeared to be related to abundance of SAV. Munro and Perry (1981) further investigated the relationship between the distribution and abundance of SAV and waterfowl distribution and abundance. They concluded that a biological relationship is implied, with waterfowl populations generally reflecting populations

of SAV, though few statistical relationships were found. Recent studies (Orth et al. 1985, Chesapeake Executive Council 1987) indicate that SAV may be increasing within the Bay.

Concurrent with this change in SAV abundance was a change in canvasback food habits. Prior to 1960, plant material accounted for more than 70% of the diet of canvasbacks wintering in the Chesapeake Bay; however, by the 1970's this percentage had declined to less than 10% (Munro and Perry 1981). Wildcelery made up more than 27% of the canvasback diet prior to 1960, but by the 1970's only trace amounts were found in the digestive tracts of birds examined (Perry 1982). The Baltic clam (*Macoma balthica*) currently is the predominant food item consumed by canvasbacks wintering in the Bay and accounts for approximately 84% of their diet; whereas corn (*Zea mays*) is the predominant plant food, accounting for approximately 4% of the canvasbacks' diet (Munro and Perry 1981). Lovvern (1987) speculated that clams may have been important as a food source during many winters due to restricted access to tubers because of icing conditions. He concluded, however, that tubers probably were very important during times of fattening (i.e. after arriving on and before departing from the wintering grounds) and present diets consisting only of clams may be inadequate during these times.

Serie et al. (1983) hypothesized that the distribution patterns of wintering canvasbacks "may result from the predictability of natural foods and the ability of canvasbacks to exploit these food resources." Given the dynamic nature of habitat availability, food habits and population numbers of canvasbacks wintering in the Chesapeake Bay, it becomes essential to identify the habitats actually being used and how canvasbacks are allocating their limited time and energy resources within these habitats.

Methods

Diurnal time-activity budgets were determined using scan sampling techniques. Rafts to be sampled were selected randomly from locations known to be used by ducks during the day. Rafts were sampled in the order in which they were selected, thereby accomplishing a random distribution by location over time. Flock sizes ranged from 30 to 15,500 with a mean of 1325 and a median of 400.

Flocks were sampled by placing a paper diaphragm with an approximately 1 mm hole punched in it over the eyepiece of a 15-60X spotting scope. This reduced the field-of-view substantially and, by using the zoom feature of the scope, allowed viewing of only one duck at a time. When scanning through the flock, only ducks that were centered in this reduced field of view were sampled. This eliminated the bias that can occur by sampling "interesting" individuals within the flock. Each flock was sampled for a maximum of 2 h, and an attempt was made to scan through all portions of the flock during the 2 h observation period.

Instantaneous scan samples are inappropriate for diving ducks because they underestimate active behaviors such as diving and flying (Altman 1974, Takekawa 1987). Therefore, behavioral observations were obtained in a manner similar to Takekawa (1987). Each duck was observed for 10 seconds. If the duck flew or dove during the 10 seconds, that behavior was recorded for the observation. If the bird neither dove nor flew, the behavior occurring at the end of the 10 second interval was recorded. Behaviors were tallied using a 10-key laboratory counter. Data were transferred to a field sheet after each scan. The number of ducks counted in each behavior was divided by the total number of observations for each scan. The resulting proportion was multiplied by 100 and this was assumed to be the percentage of time a duck could be expected to perform that behavior.

Behaviors were categorized as fly, feed, courtship, agonistic, swim, alert, comfort, rest and sleep. Flying included leaving the water surface and running along the surface of the water in preparation to take-off any time during the scan. Feeding included only actually diving below the water surface or occasional tipping up in shallow water. Courtship included all precopulatory behaviors as described by Hochbaum (1944). Agonism included both interspecific and intraspecific encounters. Behavior was categorized as swim if the bird was seen to be deliberately moving on the water surface from one point to another. Alert behavior included postures where the head was erect with neck extended. Comfort behaviors included preening, bathing and wing-flapping. Rest included sitting motionless with head exposed but withdrawn against the body. Sleep included postures with the bill tucked under a wing, and bird sitting motionless. In addition to behaviors, date, time, wind speed and direction, temperature, cloud cover, precipitation, ice cover, habitat type, flock size, flock composition and whether artificial feeding was evident were recorded for each scan.

If the flock was disturbed during an observation, the source and duration of the disturbance was recorded. Disturbances were categorized as either natural (e.g., gull or raptor) or man-made (e.g., pedestrian or boat). Scan sampling continued while the disturbance was present or until the flock flew away. These observations represented a sample of behavioral responses of canvasbacks to disturbance (Morton 1987).

Analysis

Multivariate analysis of variance (MANOVA) was used to assess the effect of time of day, season and habitat on behavioral patterns of canvasbacks. All behaviors were modeled as

mutually-inclusive dependent variables (Morton 1987). Additionally, 3-way analysis of variance (ANOVA) was used to investigate the effects of time of day, season and habitat on energy expenditure and each individual behavior. Behavioral proportions were arcsine-square root transformed to approach a Gaussian distribution prior to completing MANOVA or ANOVA procedures (Zar 1984).

For analysis, time of day was split into 3 time periods: <3.5 hours after sunrise (early), <3.5 hours before sunset (late), and the intervening time interval (mid-day). Season also was split into 3 periods: from postarrival in early December until 15 January (early), from 16 January to 15 February (mid), and from 16 February until the birds migrated in late March or early April(late). Habitat was categorized as main bay, which included rivers from their mouth upstream to a width of 0.5 km wide, and river, which included creeks and rivers <0.5 km wide. One impoundment was included in the river category.

Spearman rank correlations were used to assess the relationship of weather variables to energy expenditure and each behavior category. The effect of artificial feeding on overall time budget and each behavior was investigated using MANOVA and 2-way ANOVA procedures, with artificial feeding and habitat being included as the independent variables. A Wilcoxon 2-sample test was used to test the differences in behaviors between the eastern and western shores of the Bay.

Time budgets were calculated from least square means of behavioral proportions. Energy budgets were estimated from energy coefficients developed for waterfowl species and published in the literature (Wooley and Owen 1978, black duck; Takekawa 1987, canvasback). Significance for all statistical inferences was $p < 0.05$ unless otherwise indicated.

Results

Relationship Among Behaviors

Time-activity budgets for canvasbacks indicated that several behaviors were correlated. Canvasbacks spent much of the daylight hours sleeping. Sleeping was negatively correlated ($p < 0.001$) with all behaviors except agonism (Table 1). Agonistic encounters were extremely rare. In general, the slightly more active behaviors of rest, swim, comfort, courtship, and to a lesser extent, fly are all positively correlated with each other. This array of behaviors is fairly characteristic of the condition of the flock following a disturbance or the restlessness associated with the crepuscular movements of canvasbacks to and from their diurnal habitats. Feeding was positively correlated with swimming and negatively correlated with courtship activities, but correlations were weak.

Effect of Time, Season and Habitat

A MANOVA model indicated that time ($p < 0.0026$), season ($p < 0.0001$), and habitat ($p < 0.0001$) were significant in determining time-activity budgets for canvasbacks (Table 2). Analysis of variance was used to investigate which of the individual behaviors explained a significant portion of the variance within the MANOVA model. Means separation was accomplished by

performing pairwise comparisons of the least square means for each main effect. Only a few of the individual behaviors explained most of the within model variance for each main effect.

Swimming was the only behavior significantly ($p < 0.0002$) dependent on time (Table 3), with birds spending more time swimming during the early part of the day than during the mid or late periods ($p < 0.0005$). The behaviors significantly dependent on season were feed ($p < 0.0156$), sleep ($p < 0.0093$), swim ($p < 0.0012$), and courtship ($p < 0.0001$, Table 4).

Canvasbacks fed most early in the season and least during mid-winter. The difference in feeding frequency was significant between early and mid winter ($p < 0.006$). Feeding late in the season was intermediate to the other two seasons and not significantly different from either ($p > 0.13$). Birds slept less in late winter than either the early or mid portions of the winter ($p < 0.037$). The amount of time canvasbacks spent swimming increased throughout the winter, with differences between all three seasons being significant ($p < 0.05$). As was expected, courtship levels were significantly higher during the mid and late winter periods than during the early period ($p < 0.04$). Differences in courtship between mid and late winter were not significant ($p > 0.21$). Swim ($p < 0.0001$), comfort ($p < 0.0140$), and courtship ($p < 0.0255$) activities were significantly affected by habitat (Table 5). Birds spent more time swimming in main bay habitats than in riverine habitats ($p < 0.0001$); and conversely, spent more time in comfort ($p < 0.014$) and courtship ($p < 0.0255$) behaviors in riverine habitats than in the less protected habitats found in the main bay. Care must be taken when interpreting these results, as all interactions among time, season, and habitat also were significant. Significance levels may be misleading.

Effect of Artificial Feeding

Residents of the Chesapeake Bay commonly scatter corn into the water to enhance recreational viewing of waterfowl. Most of this artificial feeding occurs on the western shore of the Bay. With the absence of natural tubers, corn provides essentially the only vegetative foodstuff available to foraging canvasbacks and could, therefore, have a significant effect on the condition of wintering birds.

A MANOVA model indicated that artificial feeding ($p < 0.0001$) and habitat type ($p < 0.0091$) had a significant impact on overall time budgets for canvasbacks (Table 6). Habitat type was included in the model in an attempt to isolate the effects of the artificial feeding. Canvasbacks slept less ($p < 0.0001$) and rested ($p < 0.0001$), swam ($p < 0.0001$), preened ($p < 0.0190$), and courted ($p < 0.0001$) more in habitats where artificial feeding occurred (Table 7, 8).

Surprisingly, the proportion of time canvasbacks spent engaged in feeding activities was unaffected by artificial feeding. The MANOVA model indicated that there was a significant interaction between feeding and habitat effects.

Eastern vs. Western Shores

Habitats on the eastern shore of the Bay provide an interesting contrast to those on the western shore. The eastern shore is largely rural and residents of the eastern shore have a strong tradition of waterfowl hunting. Conversely, the western shore is largely urbanized with relatively little hunting pressure placed on waterfowl populations.

A MANOVA model was used to investigate differences in time budgets of canvasbacks wintering on the eastern shore of the Bay as opposed to those wintering on the western shore (Table 9). Again habitat type was included in the model in an attempt to isolate the effect of differences attributable to the east vs. west contrast independent of habitat differences. The MANOVA model indicated that there was a significant ($p < 0.0003$) difference in the time budgets of eastern shore birds when compared to those of western shore birds. Canvasbacks wintering on the eastern shore generally were more active than those wintering on the western shore (Table 10). Canvasbacks spent more time swimming ($p < 0.0002$) and in alert behaviors ($p < 0.0016$) on the eastern shore. The differences for flying ($p < 0.0770$) and comfort ($p < 0.0582$) behaviors were nearly significant, with both being higher for birds on the eastern shore. Birds on the western shore slept more ($p < 0.0003$) than birds on the eastern shore. The effect of different habitat types was not significant ($p < 0.0844$, Table 11). The shore*habitat interaction also was not significant ($p < 0.1963$).

Influence of Weather

Spearman rank correlations were used to assess the relationship of temperature, wind speed and cloud cover to behavioral patterns and energy expenditure of canvasbacks (Table 12). Percent of time spent feeding and percent of time spent sleeping were negatively correlated with temperature. Alert behavior was positively correlated with temperature. Energy expenditure was negatively correlated with temperature, as was expected. Courtship was negatively correlated with wind speed. Alert behavior was positively correlated with cloud cover. Sleeping and energy expenditure were negatively correlated with cloud cover. All correlations, except that for energy expenditure and temperature, were low ($r < 0.25$).

Time Budget Estimation

Time, season and habitat were important factors affecting behavioral patterns of canvasbacks wintering in the upper Chesapeake Bay. Due to the logistical difficulties of a large study area in an urban setting compounded by a highly mobile species, random sampling *by habitat* was impossible. Therefore, scan data were distributed *a posteriori* by time and season (Morton 1987). Means and standard errors were calculated using least square means. To derive these estimates, 2-way tables for time and season (3*3) were constructed for each habitat. Using least square means compensates for unbalanced sample sizes per cell, as well as accounting for any among cell covariations in calculating the standard error. A diurnal time budget was calculated from the least squares estimates of each behavior (Table 13).

Overall, canvasbacks spent most of the daylight hours loafing (Table 13). Sleeping and resting accounted for approximately 70% of the observed activities. Feeding during the diurnal hours was rare (4%), with most diurnal feeding activity associated with occurrences of artificial feeding. Both flying and agonistic behaviors also were extremely rare. The data presented here, however, represent an underestimation of overall time spent flying because, essentially as soon as birds took flight, it became impossible to sample them.

Energy Budget Estimation

Time budget estimates can be converted to energy budgets by weighting each behavioral estimate by the appropriate multiple of resting metabolic rate (RMR). Resting metabolic rate

is the rate of heat production of a fasted animal within its thermal neutral zone measured at rest and in the dark during the active phase of its daily cycle. This is in contrast to basal metabolic rate (BMR) which is measured much the same way, but during the rest phase of its daily cycle (Weathers et al. 1990). Multiples of RMR for waterfowl are available in the literature (Wooley and Owen 1978, Takekawa 1987). Most multiples for energy coefficients are from Wooley and Owen (1978) as developed for black ducks. The only behaviors that are likely to be significantly different in energy expenditure for diving ducks (canvasbacks) than for dabbling ducks (black ducks) are feeding and, less obviously, resting because canvasbacks rest on water while black ducks rest on land. Coefficients for feeding and resting were taken from Takekawa (1987), and were divided by 1.24 (King 1974) to convert from BMR to RMR so they would be comparable. Resting metabolic rate was calculated to be 5.103 kcal/bird/hour (King 1974). Costs of thermoregulation contribute significantly to overall energy expenditure. Takekawa (1987) developed an equation to predict increasing energy costs with decreasing water temperature. It was impractical, however to take water temperatures at the exact location the raft of birds was using, and given the change in water temperature associated with water depth, I was unwilling to make any assumptions about microhabitat by measuring water temperature at an adjacent site. Instead, costs of thermoregulation were developed from air temperature as described by Wooley (1976) and 1.4, 2.0 and 3.4 kcal/bird/hour were added to hourly energy expenditure for temperatures ranging from 5 - 10 C, 0 - 4 C, and -10 - 0 C, respectively. Temperatures ≥ 10 C were considered to be in the thermal neutral zone.

Energy expenditure (kcal/bird/hour) of canvasbacks at 5 C was calculated for both riverine and main bay habitats (Table 14). Hourly energy expenditure = [(multiple)(RMR) + cost of thermoregulation] x proportion of time spent in a given behavior. Total hourly expenditure was then summed to determine energy costs of all behaviors for a given habitat. Telemetry data indicated that canvasbacks spent approximately 53% of the diurnal hours in main bay habitats and 47% of the diurnal hours in riverine habitats throughout the winter. Total hourly energy expenditure was then weighted by these percentages. The resulting weighted value

(10.11 kcal) represented the hourly rate of energy expenditure at 5 C by an average canvasback wintering on the upper Chesapeake Bay.

The same approach was used to estimate energy expenditure for each scan and its corresponding temperature. Energy expenditure was negatively correlated with temperature and cloud cover and positively correlated with wind speed (Table 12). Wintering canvasbacks commonly are found in large flocks, often in association with large numbers of lesser scaup (*Aythya affinis*) and buffleheads (*Oxyura jamaicensis*). Energy expenditure tended to decrease with increased flock size, but was positively correlated with the percent of the flock made up by canvasbacks (Table 12).

Disturbance

Of the 67 flocks sampled during this study, 38 (57%) were disturbed at least once during the observation period (maximum 2 hours). A total of 57 separate disturbance events was recorded for the 38 disturbed flocks. Forty of the 57 recorded disturbance events (70%) were human-induced or human related. These included disturbances by recreational and work boats (12), pedestrians (10), people engaged in feeding ducks (10; note that these might or might not be construed as beneficial disturbances), dogs (3), vehicular traffic (2), chainsaws (2), and industrial noise (1). Eleven natural disturbances (19%) occurred. Included in this category were disturbances by gulls (8; *Larus marinus* and *L. argentatus*), other canvasbacks flying in to join the raft (2) and an osprey (1; *Pandion haliaetus*). Six disturbance sources (11%) were unidentified.

It should be noted here that quantifying disturbance in this way provides a very conservative estimate of overall disturbance levels. In many instances the disturbance source caused the birds to flush, swim out of range or viewing area of the scope, or otherwise disrupted scanning, thereby limiting the number of disturbance scans obtainable. Only 79 disturbance scans were recorded from the 57 individual disturbance events.

Canvasbacks react differently to human-induced as opposed to natural disturbances. Sixteen disturbances resulted in the raft of birds flushing. Of these, 13 were human-induced (32%) and 2 were natural (18%). One unknown disturbance caused birds to flush. Canvasbacks are especially sensitive to disturbances by boat traffic. Ten of the 12 recorded disturbances caused by boats resulted in the flock flushing from the area. Both of the natural disturbances resulting in birds taking flight were caused by gulls harassing the flock.

Discussion

The time-activity budget method for quantifying behaviors of wintering waterfowl has received much attention lately. Time budgets are useful in studies of wintering waterfowl because they effectively tie together many of the facets of waterfowl ecology of interest to managers of waterfowl populations. Time budgets are created on the premise that an organism optimally allocates its time and energy resources among different behaviors (Verner 1965). Fredrickson and Drobney (1979) proposed a schematic showing how time and energy budget data can assist in relating habitat selection, feeding ecology and nutrition, physiology and condition,

competition, behavior, and environmental factors for postbreeding waterfowl. Time activity budgets also are useful for identifying research needs for any of these topics (Paulus 1988).

Time budgets in this study were constructed using the technique suggested by Morton (1987). Least squares were used to estimate standard errors associated with each behavior. Additionally, overall energy expenditure as it relates to habitat use was calculated by weighting proportion estimates by the percent of time a bird could be expected to be found in that habitat, as determined from telemetry data.

In any time/energy budget study, it is important for the reader to recognize the limitations of the techniques. Weathers et al. (1984) found large errors in time budget estimates of energy expenditure when compared to estimates derived using doubly labeled water. Williams and Nagy (1984) found time budgets to perform much better in estimating energy expenditure than did Weathers et al. (1984). Lack of independence is a common problem with behavioral data. The distinction between statistical and biological independence often is not clear. In this study autocorrelation (tested with the Durban-Watson statistic) was significant in 4 of 19 flocks with a large enough number of scans to test (> 20). These flocks also are the ones that would be expected to show autocorrelative tendencies because they represent flocks with the smallest number of birds per scan, and thus the shortest time interval between scans. Furthermore, individual scans were used as the sampling unit because two-hour observation periods often bridged 2 different time periods. It is reasonable to expect some correlation of behaviors between scans. It is also reasonable to expect some correlation between hours, days, weeks, months, flocks using the same habitat, flocks using the same river system and flocks using the Bay in general. I believe that the influence of the slight dependence in the data presented here is small and conclude that estimates of time-energy budgets for canvasbacks on the Chesapeake Bay are accurate.

Observations of canvasbacks on the Chesapeake Bay indicated that sleeping was the most frequent behavior during the diurnal hours. This is a condition commonly seen in wintering waterfowl (Pedroli 1982, Miller 1985, Paulus 1988, Perry et al. 1989, Bergan et al. 1989).

Canvasbacks showed little variation in activity levels throughout the day. Swimming frequencies were highest early in the day. Wintering lesser scaup (*Aythya affinis*) and ring-necked ducks (*Aythya collaris*) also showed high levels of locomotion during the early period of the day (Bergan et al. 1989), but they also showed an increased occurrence of locomotion late in the day that was not seen in canvasbacks.

Canvasbacks displayed seasonal differences in the allotment of time for different behaviors. Canvasbacks slept more in early and mid winter than late in the winter. Perry et al. (1989) also showed an increase in the level of inactivity during the mid winter months for captive canvasbacks (Perry's mid winter category encompassed the early and mid winter categories used in this study). Perry theorized that this decreased activity during the coldest months was probably related to energy conservation.

Canvasbacks fed most during the early winter and least during mid winter. This pattern has been seen for pintails (*Anas acuta*, Miller 1985) and other waterfowl (Paulus 1988). Perry et al. (1989) also showed decreased feeding activity in mid winter for captive canvasbacks and believed that this was probably another energy conservation mechanism. This pattern of decreased feeding in mid winter was demonstrated in captive canvasbacks regardless of whether birds were fed *ad libitum* or food stressed (Perry et al. 1986). Decreased feeding in mid winter also occurred during our study even though weather conditions were mild during the winter of 1988-89. This persistence in behavioral patterns indicates that some endogenous rhythm may be acting on canvasbacks to reduce metabolic costs during the traditionally coldest months. Gadwalls (*Anas strepera*) (Paulus 1984), and ring-necked ducks and lesser scaup (Hohman 1984, Bergan et al. 1989) have shown an alternate feeding strategy whereby levels of feeding increase throughout the winter.

Swimming and courtship behaviors were higher in mid and late winter than in early winter. These behaviors are highly correlated and increases in swimming behavior probably resulted from increases in courtship. Although these increases in active behaviors may seem to contradict the idea of energy conservation in mid winter, it may actually reflect a flexibility in behavior whereby birds may be able to respond to mild temperatures by engaging in more productive behaviors. Similarly, birds spent more time swimming, resting, preening and courting in habitats where artificial feeding occurred. Again, this may represent a situation where increased food availability allowed birds to engage in more productive activities even though no differences were detected in actual feeding frequencies.

Canvasbacks spent more time swimming in main bay habitats and more time in comfort and courtship behaviors in riverine habitats. These behavioral differences may reflect differences in microhabitat (Jorde et al. 1984). Birds using habitats in the eastern shore of the Bay were more active than birds on the western shore. Eastern shore birds slept less and spent more time in swimming, alert, flying and courtship behaviors. These differences can most likely be attributed to higher levels of boat traffic (work boats) and increased disturbance by pedestrians at one location (Cambridge, MD).

Weather variables were related to behavior and energy expenditure for canvasbacks. As temperatures decreased, time spent sleeping and feeding increased. This pattern is rather common in waterfowl. Hepp (1985) found that gadwall, pintail and green-winged teal all increased time spent feeding and rates of feeding as temperatures decreased. Similarly, Nilsson (1970) found increased feeding rates for goldeneye (*Bucephala clangola*) and tufted ducks (*Aythya fuligula*) as temperatures decreased. Goudie and Ankney (1986) believed that two alternate strategies might be used by ducks of different body sizes. They provided evidence that small ducks increased feeding with decreasing temperatures, but large ducks (i.e. eiders and scoters) fed less as temperatures decreased, and suggested that the larger

ducks had more energy reserves and, therefore, were able to "wait out" periods of severe weather.

Canvasbacks were very active at night. Jorde and Owen (1988) point out the need to estimate nocturnal time and energy budgets. Because the canvasbacks in this study spent the nocturnal hours in deep water habitats far from shore, direct observation of nocturnal behavioral patterns was not possible. It was, however, possible to estimate feeding frequencies of radio-marked juvenile female canvasbacks (Chapter 2). Radio-implanted canvasbacks were located using a fixed-wing aircraft one night per week (11 flights; flight times were from 1800-2300 hrs.). If a bird was diving at the time it was being tracked, the radio signal would disappear very abruptly. In this way it was possible to estimate simple feeding frequencies for nocturnal canvasbacks. Birds were feeding in 156 (39.8%) of 392 nocturnal radio locations. As with diurnal time budgets, feeding frequencies were lowest in mid winter although this decline was not significant ($\chi^2 = 1.26$, $df = 2$, $p > 0.5$, Table 15).

Kendeigh (1970) provided an equation to estimate total energy needed for existence (EE) based on the weight of a bird at 0 C. Nilsson (1980, as cited by Korschgen et al. 1988) indicated that actual daily energy expenditure is approximately twice EE because existence energy does not take into account energy for molting, migration, growth or fat deposition. Using this relationship, canvasbacks wintering on the Chesapeake Bay (average weight 1200 g) would use approximately 370 kcal/bird/day. Calculations for weighted diurnal energy budgets in this study indicate that canvasbacks expend approximately 120 kcal/bird/12 h. Subtraction yields an estimate of 250 kcal/bird expended during the nocturnal hours. Using the estimate of 39.8% feeding and our calculations for hourly energy expenditure (HEE), energy expenditure for nocturnal feeding alone would amount to approximately 160 kcal. Assuming that the remaining 60.2% of the time canvasbacks are resting, they would use an additional 73 kcal for the nocturnal period. This leaves a balance of approximately 17 kcal.

Much of this energy would be used in the crepuscular flights to and from the feeding areas. This seems to be a reasonable estimate of nocturnal energy budgets.

LITERATURE CITED

- Altman, J. 1974. Observational study of behavior: sampling methods. *Behaviour*. 49:227-267.
- Bayley, S., V. D. Sotts, P.F. Springer and J. Steenis. 1978. Changes in submerged aquatic macrophyte populations at the head of Chesapeake Bay, 1958-1975. *Estuaries* 1:73-84.
- Bent, A. C. 1923. Life histories of North American wildfowl. Order: Anseres (Part 1). Bull. 126. U.S. Nat. Museum, Washington, D.C. 244pp.
- Bergan, J. F., L. M. Smith and J. J. Mayer. 1989. Time-activity budgets of diving ducks wintering in South Carolina. *J. Wildl. Manage.* 53:769-776.
- Chesapeake Executive Council. 1987. Second annual progress report. 33pp.
- Cottam, C. 1939. Food habits of North American diving ducks. U.S. Dept. Agr. Tech. Bull. 643. 139pp.
- Fredrickson L. H. and R. D. Drobney. 1979. Habitat utilization by postbreeding waterfowl. Pages 119-131 in T. A. Bookout, ed. *Waterfowl and wetlands - an integrated review*. Proc. 1977 Symp., Madison, WI, N. Cent. Sect., The Wildlife Society.
- Goudie, R. J. and C. D. Ankney. 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. *Ecology* 67:1475-1482.
- Hepp, G. R. 1984. Effects of environmental parameters on the foraging behavior of three species of wintering dabbling ducks (Anatini). *Can J. Zool.* 63:289-294.

- Hochbaum, H. A. 1944. The canvasback on a prairie marsh. Univ. Nebraska Press, Lincoln. 207pp.
- Hohman, W. L. 1984. Diurnal time-activity budgets for ring-necked ducks wintering in central Florida. Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies. 38:158-164.
- Jorde, D. G., G. L. Krapu, R. D. Crawford and M. A. Hay. 1984. Effects of weather on habitat selection and behavior of mallards wintering in Nebraska. Condor 86:258-265.
- _____ and R. B. Owen, Jr. 1988. The need for nocturnal activity and energy budgets of waterfowl. Pages 169-180 in M. W. Weller, ed. Waterfowl in winter. Univ. Minnesota Press, Minneapolis. 624pp.
- King, J. R. 1974. Consequences of body size for avian energetics. Pages 4-85 in R. A. Paynter, Jr., ed. Avian energetics. Publ. Nuttall Ornithol. Club 15, Cambridge, Mass.
- Korshgen, C. E., L. S. George and W. L. Green. 1988. Feeding ecology of canvasbacks staging in Pool 7 of the upper Mississippi River. Pages 237-249 in M. W. Weller, ed. Waterfowl in winter. Univ. Minnesota Press, Minneapolis. 624pp.
- Lovvern, J. R. 1987. Behavior, energetics, and habitat relations of canvasback ducks during winter and early spring migration. Unpubl. PhD. Diss., Univ. of Wisconsin, Madison, WI. 173pp.
- Miller, M. R. 1985. Time budgets of northern pintails wintering in the Sacramento Valley, California. Wildfowl 36:53-64.
- Morton, J. M. 1987. Habitat use and energetics of American black ducks wintering at Chincoteague, Virginia. Unpublished M.S. thesis. VPI&SU, Blacksburg, VA. 147pp.
- Munro, R. E. and M. C. Perry. 1981. Distribution and abundance of waterfowl and submerged aquatic vegetation in Chesapeake Bay. Final Report to FWS/OBS-78/D-X0391. 180pp.
- Nilsson, L. 1970. Food-seeking activity of south Swedish diving ducks in the non-breeding season. Oikos 21:145-154.
- Orth, R. J. and K. A. Moore. 1981. Submerged aquatic vegetation of the Chesapeake Bay: past, present and future. Trans. North Am. Wildl. Nat. Resour. Conf. 46:271-283.

- _____, J. Simons, V. Carter, L. Hindman, S. Hodges, K. Moore and N. Rybicki. 1985. Distribution of submerged aquatic vegetation in the Chesapeake Bay - 1985. Virginia Inst. Marine Sci., Unpb. Rep. 296pp.
- Paulus, S. L. 1984. Activity budgets of nonbreeding gadwalls in Louisiana. *J. Wildl. Manage.* 48:371-380.
- _____. 1988. Time-activity budgets of nonbreeding Anatidae: a review. Pages 135-152 in M. W. Weller, ed. *Waterfowl in winter*. Univ. Minnesota Press, Minneapolis. 624pp.
- Pedroli, J. 1982. Activity and time budget of tufted ducks on Swiss lakes during winter. *Wildfowl* 105-112.
- Perry, M. C. 1982. Distribution and food habits of canvasbacks in the northeast. *Trans. N.E. Sect. Wildl. Soc.* 39:56-67.
- _____, W. J. Kuenzel, B. K. Williams and J. A. Serafin. 1986. Influence of nutrients on feed intake and condition of captive canvasbacks in winter. *J. Wildl. Manage.* 50:427-434.
- _____, R. E. Munro and G. M. Haramis. 1981. Twenty-five year trends in diving duck populations in Chesapeake Bay. *Trans. North Am. Wildl. Nat. Resour. Conf.* 46:299-310.
- _____, B. K. Williams and H. H. Obrecht III. 1989. Behaviour of captive canvasbacks *Aythya valisineria* fed different diets during winter. *Wildfowl* 40:80-87.
- Serie, J. R., D. L. Trauger and D. E. Sharp. 1983. Migration and winter distributions of canvasbacks staging on the upper Mississippi River. *J. Wildl. Manage.* 47:741-753.
- Takekawa, J. Y. 1987. Energetics of canvasbacks staging on an Upper Mississippi River pool during fall migration. PhD. Diss. Iowa State University, Ames. 189pp.
- Verner, J. 1965. Time budget of the male long-billed marsh wren during the breeding season. *Condor* 67:125-139.
- Weathers, W. W., W. A. Buttemer, A. M. Hayworth and K. A. Nagy. 1984. An evaluation of time-budget estimates of daily energy expenditure in birds. *Auk* 101:459-472.
- _____, W. D. Koenig and M. T. Stanback. 1990. Breeding energetics and thermal ecology of the acorn woodpecker in central coastal California. *Condor* 92:341-359.

- Williams, J. B. and K. A. Nagy. 1984. Daily energy expenditure of savannah sparrows: comparison of time-energy budget and doubly-labeled water estimates. *Auk* 101:221-229.
- Wooley, J. B. and R. B. Owen, Jr. 1978. Energy costs of activity and daily energy expenditure in the black duck. *J. Wildl. Manage.* 42:739-745.
- Zar, J. H. 1974. *Biostatistical analysis*. Prentice-Hall Inc., Englewood Cliffs, NJ. 620pp.

Tables

Table 1. Partial Spearman correlation coefficients between behaviors for canvasbacks wintering on the upper Chesapeake Bay.

BEHAVIOR	Feed	Rest	Sleep	Swim	Fly	Comfort	Alert	Court	Agonistic
Rest	-0.002								
Sleep	-0.234 ***	-0.476 ***							
Swim	0.117 **	0.235 ***	-0.559 ***						
Fly	-0.008	-0.018	-0.164 ***	0.113 **					
Comfort	0.021	0.190 ***	-0.526 ***	0.136 ***	-0.037				
Alert	0.012	0.108 **	-0.391 ***	0.103 **	0.208 ***	0.027			
Courtship	-0.116 **	0.194 ***	-0.380 ***	0.241 ***	0.003	0.144 ***	0.089 *		
Agonistic	0.027	-0.031	-0.006	0.019	0.048	-0.014	0.036	-0.058	
Energy	0.464 ***	0.153 ***	-0.731 ***	0.413 ***	0.228 ***	0.328 ***	0.259 ***	0.238 ***	0.017

* $p \leq 0.05$
 ** $p \leq 0.01$
 *** $p \leq 0.001$

Table 2. Mean squares, Wilks' criterion (λ), and approximate F-statistics from MANOVA model of behavior proportions distributed over time, season, and habitat with all interactions.

	Feed	Rest	Sleep	Swim	Fly	Comfort	Alert	Court	Agonistic
TIME (2) ¹	0.046 ²	0.002	0.272	0.387	0.001	0.142	0.020	0.005	0.000
$\lambda = 0.937^3$ F = 2.13 df = 20, 1276 p < 0.0026	.1311 ⁴	.9587	.1872	.0002	.7165	.0650	.6700	.8488	.6917
SEASON (2)	0.096	0.074	0.762	0.305	0.001	0.006	0.047	0.359	0.001
$\lambda = 0.837$ F = 5.92 df = 20, 1276 p < 0.0001	.0156	.1941	.0093	.0012	.7060	.8990	.3960	.0001	.2292
TIME*SEASON (4)	0.080	0.064	0.180	0.203	0.002	0.098	0.068	0.022	0.002
$\lambda = 0.888$ F = 1.93 df = 40, 2421 p < 0.0005	.0078	.2237	.3493	.0013	.6927	.1083	.2555	.5902	.0816
HABITAT (1)	0.048	0.010	0.292	1.031	0.003	0.313	0.003	0.155	0.001
$\lambda = 0.920$ F = 5.53 df = 10, 638 p < 0.0001	.1484	.6412	.1794	.0001	.3489	.0140	.8116	.0255	.3692
TIME*HABITAT (2)	0.218	0.165	1.842	0.723	0.004	0.105	0.023	0.077	0.001
$\lambda = 0.879$ F = 4.26 df = 20, 1276 p < 0.0001	.0001	.0264	.0001	.0001	.2883	.1306	.6406	.0845	.2649
SEASON*HABITAT (2)	0.381	0.012	1.314	0.264	0.001	0.170	0.003	0.043	0.002
$\lambda = 0.856$ F = 5.17 df = 20, 1276 p < 0.0001	.0001	.7718	.0003	.0029	.6967	.0374	.9369	.2473	.1440
TIME*SEASON*HABITAT (4)	0.040	0.170	0.428	0.262	0.000	0.031	0.049	0.078	0.001
$\lambda = 0.860$ F = 2.45 df = 40, 2421 p < 0.0001	.1372	.0505	.0328	.0001	.9796	.6599	.4212	.0398	.2067
MS ERROR (647)	0.023	0.045	0.162	0.045	0.003	0.052	0.051	0.031	0.001

¹Number in parenthesis denotes degrees of freedom for ANOVA model of each behavior.

²Mean squares for each behavior from ANOVA models. Based on 665 scan observations of 67 flocks; proportions were arcsine-square root transformed (Zar 1984).

³Wilks' criterion for MANOVA.

⁴Probability that F (critical) > F (calculated).

Table 3. Least squares estimates¹ of diurnal time budgets, by time of day, for canvasbacks wintering in the upper Chesapeake Bay, December-April 1987 and 1988.

TIME OF DAY ²		Feed	Rest	Sleep	Swim	Fly	Comfort	Alert	Court	Agonistic
EARLY	proportion	.056	.059	.574	.181	.002	.076	.030	.021	.000
	SE	.016	.022	.057	.023	.004	.023	.027	.017	.002
MID	proportion	.029	.059	.660	.063	.002	.106	.048	.031	.001
	SE	.006	.008	.022	.009	.002	.010	.010	.007	.001
LATE	proportion	.034	.057	.671	.043	.003	.127	.033	.031	.001
	SE	.007	.010	.026	.010	.002	.011	.012	.008	.001

¹Mean proportions and standard errors calculated from least square means of two-way tables for season*habitat (3x2) interactions, by time of day, for each behavior. Based on 665 scan observations of 67 flocks.

²EARLY = <3.5 hours after sunrise; LATE = <3.5 hours before sunset; MID = the intervening time period.

Table 4. Least squares estimates¹ of diurnal time budgets, by season, for canvasbacks wintering in the upper Chesapeake Bay, December-April 1987 and 1988.

SEASON ²		Feed	Rest	Sleep	Swim	Fly	Comfort	Alert	Court	Agonistic
EARLY	proportion	.052	.049	.722	.045	.001	.106	.021	.002	.001
	SE	.009	.013	.033	.013	.002	.015	.015	.010	.001
MID	proportion	.026	.074	.640	.075	.001	.097	.039	.048	.000
	SE	.007	.009	.025	.010	.002	.011	.012	.007	.001
LATE	proportion	.040	.052	.523	.168	.005	.107	.051	.033	.001
	SE	.015	.020	.051	.020	.004	.023	.024	.015	.002

¹Mean proportions and standard errors calculated from least square means of two-way tables for time*habitat (3x2) interactions, by season, for each behavior. Based on 665 scan observations of 67 flocks.

² EARLY = post arrival to 15 January; MID = 16 January to 15 February; LATE = 16 February to departure.

Table 5. Least squares estimates¹ of diurnal time budgets, by habitat, for canvasbacks wintering in the upper Chesapeake Bay, December-April 1987 and 1988.

		Feed	Rest	Sleep	Swim	Fly	Comfort	Alert	Court	Agonistic
MAINBAY	proportion	.047	.053	.613	.148	.001	.084	.036	.016	.001
	SE	.014	.015	.040	.017	.001	.018	.019	.009	.001
RIVER	proportion	.032	.064	.656	.044	.003	.123	.037	.040	.001
	SE	.004	.008	.021	.008	.002	.009	.010	.007	.001

¹Mean proportions and standard errors calculated from least square means of two-way tables for time*season (3x3) interactions, by habitat, for each behavior. Based on 665 scan observations of 67 flocks.

Table 6. Mean squares, Wilks' criterion (λ), and approximate F-statistics from MANOVA model of behavior proportions distributed over artificial feeding conditions and habitats.

	Feed	Rest	Sleep	Swim	Fly	Comfort	Alert	Court	Agonistic
FEEDING (1) ¹	0.004 ²	0.805	5.269	0.704	0.000	0.291	0.196	0.664	0.000
$\lambda = 0.878^3$ F = 9.07 df = 10, 652 p < 0.0001	.6795 ⁴	.0001	.0001	.0001	.7971	.0190	.0512	.0001	.5001
HABITAT (1)	0.002	0.073	0.864	0.003	0.001	0.340	0.013	0.498	0.000
$\lambda = 0.965$ F = 2.38 df = 10, 652 p < 0.0091	.7788	.2089	.0250	.8039	.6686	.0113	.6161	.0001	.7970
FEEDING*HABITAT (1)	0.307	0.249	3.930	0.599	0.004	0.701	0.169	0.014	0.000
$\lambda = 0.928$ F = 5.02 df = 10, 652 p < 0.0001	.0004	.0205	.0001	.0004	.2437	.0003	.0697	.5114	.9570
MS ERROR (661)	0.025	0.046	0.168	0.048	0.003	0.053	0.051	0.033	0.001

¹Number in parenthesis denotes degrees of freedom for ANOVA model of each behavior.

²Mean squares for each behavior from ANOVA models. Based on 665 scan observations of 67 flocks; proportions were arcsine-square root transformed (Zar 1984).

³Wilks' criterion for MANOVA.

⁴Probability that F (critical) > F (calculated).

Table 7. Least squares estimates¹ of diurnal time budgets, by occurrence of artificial feeding, for canvasbacks wintering in the upper Chesapeake Bay, December-April 1987 and 1988.

		Feed	Rest	Sleep	Swim	Fly	Comfort	Alert	Court	Agonistic
FEEDING	proportion	.023	.071	.618	.069	.003	.117	.050	.048	.001
	SE	.004	.005	.014	.005	.001	.006	.006	.004	.000
NO FEEDING	proportion	.024	.036	.771	.032	.002	.088	.033	.014	.000
	SE	.007	.010	.025	.010	.002	.011	.011	.007	.001

¹Mean proportions and standard errors calculated from least square means of habitat, by occurrence of artificial feeding, for each behavior. Based on 665 scan observations of 67 flocks.

Table 8. Least squares estimates¹ of diurnal time budgets, by habitat, for canvasbacks wintering in the upper Chesapeake Bay, December-April 1987 and 1988.

		Feed	Rest	Sleep	Swim	Fly	Comfort	Alert	Court	Agonistic
MAINBAY	proportion	.022	.048	.726	.055	.002	.090	.040	.017	.001
	SE	.007	.009	.023	.009	.002	.010	.011	.007	.001
RIVER	proportion	.025	.059	.663	.047	.003	.115	.043	.045	.001
	SE	.005	.006	.017	.007	.001	.008	.008	.005	.001

¹Mean proportions and standard errors calculated from least square means of artificial feeding, by habitat, for each behavior. Based on 665 scan observations of 67 flocks.

Table 9. Mean squares, Wilks' criterion (λ), and approximate F-statistics from MANOVA model of behavior proportions distributed over eastern vs. western shores of the Chesapeake Bay and habitat types.

	Feed	Rest	Sleep	Swim	Fly	Comfort	Alert	Court	Agonistic
SHORE (1) ¹	0.033 ²	0.038	2.311	0.650	0.009	0.191	0.511	0.001	0.001
$\lambda = 0.951^3$ F = 3.30 df = 10, 652 p < 0.0003	.2502 ⁴	.3675	.0003	.0002	.0770	.0582	.0016	.8734	.3510
HABITAT (1)	0.076	0.038	0.067	0.108	0.016	0.003	0.032	0.033	0.000
$\lambda = 0.975$ F = 1.67 df = 10, 652 p < 0.0844	.0833	.3671	.5305	.1311	.0191	.8244	.4300	.3218	.8290
SHORE*HABITAT (1)	0.014	0.062	3.206	0.037	0.010	0.070	0.033	0.112	0.000
$\lambda = 0.980$ F = 1.36 df = 10, 652 p < 0.1963	.4528	.2523	.2728	.3798	.0686	.2492	.4188	.0687	.8290
MS ERROR (661)	0.025	0.047	0.171	0.047	0.003	0.053	0.051	0.034	0.001

¹Number in parenthesis denotes degrees of freedom for ANOVA model of each behavior.

²Mean squares for each behavior from ANOVA models. Based on 665 scan observations of 67 flocks; proportions were arcsine-square root transformed (Zar 1984).

³Wilks' criterion for MANOVA.

⁴Probability that F (critical) > F (calculated).

Table 10. Least squares estimates¹ of diurnal time budgets, by shore, for canvasbacks wintering in the upper Chesapeake Bay, December-April 1987 and 1988.

		Feed	Rest	Sleep	Swim	Fly	Comfort	Alert	Court	Agonistic
EAST	proportion	.012	.076	.504	.120	.006	.146	.104	.032	.000
	SE	.013	.016	.043	.017	.003	.019	.020	.013	.001
WEST	proportion	.026	.061	.677	.052	.002	.103	.039	.038	.001
	SE	.004	.005	.013	.005	.001	.006	.006	.004	.000

¹Mean proportions and standard errors calculated from least square means of habitat, by shore, for each behavior. Based on 665 scan observations of 67 flocks.

Table 11. Least squares estimates¹ of diurnal time budgets, by habitat, for canvasbacks wintering in the upper Chesapeake Bay, December-April 1987 and 1988.

		Feed	Rest	Sleep	Swim	Fly	Comfort	Alert	Court	Agonistic
MAINBAY	proportion	.029	.071	.579	.096	.001	.127	.064	.030	.001
	SE	.006	.008	.021	.008	.001	.009	.010	.006	.001
RIVER	proportion	.009	.065	.602	.076	.007	.123	.078	.039	.000
	SE	.012	.015	.040	.016	.003	.017	.018	.012	.001

¹Mean proportions and standard errors calculated from least square means of shore, by habitat, for each behavior. Based on 665 scan observations of 67 flocks.

Table 12. Spearman correlation coefficients of selected variables with canvasback behaviors (proportion of time) and energy expenditure (kcal/bird/hr) in the upper Chesapeake Bay, Maryland December-April 1987 and 1988.

Variable ¹	Feed	Rest	Sleep	Swim	Fly	Comfort	Alert	Court	Agonistic	Energy
Temperature	-.116 ²		-.098			.152				-.418
Wind speed								-.123		.203
Cloud cover			-.097			.086				-.150
Flock size	-.208		.130	.096		.084		.113		-.119
# Canvasbacks in flock	-.197		.132	.096				.119		-.102
% Canvasbacks in flock			-.109		-.093			.102		.188
Scan size			.256			-.086		-.104	.118	-.185

¹Temperature in °C, wind speed in mph, cloud cover in 10% increments, flock size is total number of birds in flock (mixed species), scan size is number of observations in scan.

²Only those coefficients significantly ($p \leq .05$) greater than zero are shown. Based on 665 scans of 67 flocks.

Table 13. Least squares estimates¹ of diurnal time budgets, by habitat, for canvasbacks wintering in the upper Chesapeake Bay, December-April 1987 and 1988.

		Feed	Rest	Sleep	Swim	Fly	Comfort	Alert	Court	Agonistic
MAINBAY	proportion	.047	.053	.613	.148	.001	.084	.036	.016	.001
	SE	.014	.015	.040	.017	.001	.018	.019	.009	.001
RIVER	proportion	.032	.064	.656	.044	.003	.123	.037	.040	.001
	SE	.004	.008	.021	.008	.002	.009	.010	.007	.001
OVERALL ²		.040	.058	.633	.099	.001	.102	.036	.027	.001

¹Mean proportions and standard errors calculated from least square means of two-way tables for time*season (3x3) interactions, by habitat, for each behavior. Based on 665 scan observations of 67 flocks.

²Overall proportion = mean proportion after weighting each proportion by the amount of time spent in that habitat (based on telemetry data). Main bay and river were weighted .530 and .470, respectively.

Table 14. Weighted estimate of diurnal energy expenditure (kcal/bird/hr) at 5C for canvasbacks using riverine and main bay habitats in the upper Chesapeake Bay, December-April 1987 and 1988.

	Feed	Rest	Sleep	Swim	Fly	Comfort	Alert	Court	Agonistic	Total	Weighted
	6.2 ¹	1.6	1.2	2.2	12.5	2.1	2.2	2.4	2.4		Total
MAINBAY	proportion	.047	.613	.148	.001	.084	.036	.016	.001	1.00	
	HEE ²	1.55	0.51	4.61	0.07	1.02	0.45	0.22	0.01	10.31	5.46 ³
RIVER	proportion	.032	.064	.044	.003	.123	.037	.040	.001	1.00	
	HEE	1.06	0.61	4.94	0.20	1.49	0.47	0.55	0.01	9.89	4.65
											10.11

¹Energetic cost of behavior expressed as multiple of resting metabolic rate (RMR). All coefficients are from Wolley and Owen (1978) except coefficients for feed and rest which are from Takekawa (1987) and divided by 1.24 to convert from BMR to RMR (King 1974).

²Hourly Energy Expenditure = [(multiple)(RMR) + cost of thermoregulation] x proportion of time spent in behavior. RMR = 5.103 kcal/bird/hour. Cost of thermoregulation at 5C = 1.4 kcal/bird/hour. Total = ΣHEE. (Albright et al. 1983, Morton 1987, Takekawa 1987).

³Weighted total = total energy expenditure (kcal/bird/hour) within habitat multiplied by the proportion of time spent in each habitat (based on telemetry data). Main bay and river were weighted .530 and .470, respectively.

Table 15. Nocturnal feeding, by season, for juvenile female canvasbacks wintering on the upper Chesapeake Bay, December 1988-March 1989

	EARLY	MID	LATE	TOTAL
NOT FEEDING	29 ¹ 29.5 .008 59.2	104 98.7 .281 63.4	103 107.8 .211 57.5	236
FEEDING	20 19.5 .013 40.8	60 65.3 .425 36.6	76 71.2 .319 42.5	156
TOTAL	49	179	164	392

¹Numbers (in order) are observed count, expected count, cell χ^2 , and column percent. Overall $\chi^2 = 1.25$, $df = 2$, $p = 0.534$.

CHAPTER 2

**Movements and home ranges of canvasbacks
wintering on the upper Chesapeake Bay.**

Introduction

Populations of canvasbacks wintering in the Chesapeake Bay have declined sharply over the last three decades. Habitat degradation often has been implicated in this decline. In the early 1970's the major tuber-producing plant foods for canvasbacks in the Chesapeake also underwent a severe decline (Bayley et al. 1978, Munro and Perry 1981, Orth and Moore 1981, Orth et al. 1985). Lovvern (1989) reported an apparent population shift for wintering canvasbacks from the upper Chesapeake Bay to more southern wintering grounds in Virginia and North Carolina that corresponds well with this period of declining aquatic vegetation. Perry and Uhler (1988) believed that this change in canvasback distributions and the decline of plant foods may be interrelated.

When contemplating the implications of a major habitat loss to a wildlife population, such as the loss of foraging habitat to canvasbacks, one factor that must be considered is the juxtapositioning of remaining or alternate habitat components. In the case of canvasbacks, the loss of foraging habitat could potentially result in an increase in the distances canvasbacks must travel to meet both their nutritional and security requirements. Any increase in travel distance could manifest itself as costly to canvasback populations in several ways: 1) Flight is an energetically costly behavior--increases in flight distances or times, therefore, increase daily energy expenditure; 2) Increased time spent in travel may reduce the time available for birds to engage in more productive activities such as feeding or courtship, and; 3) Increased flight time results in increased exposure to predation and hunting pressure (canvasbacks are still subject to hunting harassment and mortality, even though canvasback hunting seasons are closed in the Atlantic Flyway; Haramis pers. comm.). Clearly, the understanding of distribution and movement patterns is essential in understanding how canvasbacks are responding to a changing environment.

Disparities in sex ratios of canvasbacks have been well documented in the literature (e.g., DeGraff et al. 1961, Trauger 1974, Alexander 1983), with males composing a significantly higher proportion of the population than females (1988 trapping data on the Chesapeake Bay revealed sex ratios of 3.53 males/female for adults and 1.57 males/female for juvenile birds, Haramis pers. comm.). These divergent sex ratios may be indicative of low production and differential mortality between sexes and are thus of high interest to biologists. Haramis et al. (1985) stated that the magnitude and direction of sex ratios indicate the degree of reproductive success of that population. Olson (1965) conducted a study of the differential vulnerability of male and female canvasbacks to hunting and found that females were more susceptible to hunting mortality than were males. Other studies also indicate that annual survival is higher for males than for females (Longwell and Stotts 1958, DeGraff et al. 1961, Geis and Crissey 1969, Welling and Sladen 1979, Haramis et al. 1985). Identifying the factors that may lead to this reduced survival in female canvasbacks is vital to fully understanding the complexities associated with the life cycle of the canvasback.

Nichols and Haramis (1980a), while also finding differential sex ratios in canvasback populations, pointed out the need to consider geographical variation when comparing populations. Another study by Nichols and Haramis (1980b) found sex-specific differences in winter distributions of canvasbacks. Males generally wintered farther to the north. Possible explanations for these distribution patterns presented by the authors included 1) possible reproductive benefits by northern-wintering males reaching the breeding grounds first; 2) dimorphic body sizes between sexes rendering the smaller females more susceptible to inclement weather and food shortages; 3) intraspecific interactions whereby males may restrict access of females to food supplies when food is scarce. These observations generally are supported by the findings of Alexander (1983). Given the low survival rates and apparent competitive disadvantages faced by juvenile female canvasbacks in the Chesapeake Bay, it becomes obvious that these young female birds are the critical cohort to consider when investigating causes for population declines.

Methods

During the first year of the study, 78 juvenile female canvasbacks were captured, banded, and radio-tagged by Patuxent Wildlife Research Center personnel from 14-23 December 1987.

Eighty seven juvenile females were radio marked during the second year of the study.

Trapping during the second year took place from 13-21 December 1988. Corral traps baited with corn were used to capture birds (Haramis et al. 1987). Captured birds were aged by plumage characteristics and cloacal examination.

Following capture, juvenile female canvasbacks were transported to the veterinary hospital located at PWRC. Radio transmitters were surgically implanted abdominally by staff veterinarians (Olsen et al. 1990). Transmitters were manufactured by Telonics Telemetry and Electronics Consultants, Mesa, AZ. Radios weighed approximately 20 g, operated at 164-165 megahertz and had a coiled internal transmitting antenna. Thermally operated mortality switches were included in the radio package. Prior to surgery, mass (nearest 10 g) and wing length (nearest 1 mm) were recorded for each bird. Crops were palpated to determine the presence or absence of corn to correct mass. Following surgery, ducks were injected subcutaneously with 50 cc of a glucose-electrolyte mixture to prevent dehydration and anemia and were allowed to recover overnight. Birds were released at the original trap site the following morning.

Radio locations were plotted on 1:24,000 U.S. Geological Survey topographic maps. Date, time, habitat type, total flock size (mixed species), number of canvasbacks present in the flock, and whether or not the radioed bird was feeding also were recorded. A vehicle mounted null-peak antenna system was used for tracking from the ground.

During the first year of the study, we systematically attempted to locate as many radioed birds as possible on the study area, every three hours. Our first round of tracking began 1-2 hours before sunrise (0500 hours), and tracking continued throughout the day. Our last round of tracking for the day was completed 1-2 hours after sunset (2000 hours). This schedule was repeated for two consecutive days per week and allowed us to monitor four consecutive crepuscular movements. To quantify nighttime movements we radio-tracked birds one night per week, on the night following our 2-day tracking period. Two tracking schedules were followed, and these alternated weekly; one week we began tracking at 1700 hours (before sunset) and ended at 0200 hours, the following week we began tracking at 2300 hours and ended at 0800 hours (after sunrise). As with the daytime tracking, we attempted to locate birds every 3 hours.

Unfortunately, due to the limited range of the radios from the ground, coupled with the high mobility of the ducks, which move offshore at night, night-time locations were difficult to obtain. With birds often being at the very extremes of radio range, we concluded that reliability of many of our night-time locations was less than acceptable. Data from the first year of the study were excluded from analysis and are not presented here. For the second year of the study we adopted an alternative tracking strategy. Data from the first year was sufficient to indicate that canvasbacks are rather sedentary throughout the day, as well as throughout the night. Major movements generally occurred only during the hours surrounding dawn and dusk. In view of this information, we altered our tracking regimes accordingly. During the second field season, on the first day of our weekly tracking period, we attempted to get only one location per bird per day for as many birds as possible within the study area. Birds located during the day were then relocated that night using a fixed-wing aircraft (Cessna 172). On the day following this night flight, birds were again located once from the ground, thereby, obtaining one complete 24-hour movement cycle. In addition, on one day per week we continued to intensively monitor birds (every 3 hours) from the ground during the daytime hours. The strategy adopted for the second year of the study yielded far more reliable results.

Tests indicated that locations obtained from the aircraft were accurate to within 250 m. Daytime locations for both years were essentially always visual and accurate to within the size of the raft.

Data processing

Radio locations were converted to UTM coordinates by placing a 1:24,000 overlay gridded in 100 m blocks on 1:24,000 National Wetland Inventory (NWI) maps. Distances between locations were calculated using the MATRIX procedure on SAS (1985). Kruskal-Wallis tests were used to determine how mean daily distances moved changed throughout the winter. For analysis, season was split into 3 periods: from post-trapping in December until 15 January (early), from 16 January to 15 February (mid), and from 16 February until the birds migrated in late March or early April (late). A Wilcoxon 2-sample test was used to test for differences during and after the waterfowl hunting season on the Bay.

Linear relationships between weather (wind speed, temperature and cloud cover) and movement patterns were investigated using Spearman Rank correlations. National Weather Service data collected at the Baltimore-Washington International Airport for the three hour interval corresponding to the crepuscular periods were used for this analysis. Spearman correlations also were used to determine the relationship between the mass of bird at the time of trapping and movement patterns of radioed birds throughout the winter. A Kruskal-Wallis test was used to compare movement patterns among ducks that only used habitats on the eastern shore of the Bay with those only using habitats on the western shore and with those that used habitats on both shores.

The harmonic means procedure of Program Home Range (Samuel et al. 1983) was used to estimate sizes of areas used regularly by juvenile female canvasbacks. The convex polygon procedure was used to estimate the entire area needed by juvenile ducks in order to overwinter successfully in the upper Chesapeake Bay. Wilcoxon tests were used to test differences in home ranges between birds using either the east or west shore of the Bay.

Results

Movements

Radio-implanted canvasbacks were located on the study area with a vehicle-mounted receiving system on two consecutive days and with a fixed-wing aircraft during the intervening night. This tracking regime provided estimates of morning and evening crepuscular movements and estimates of a complete 24-hour movement cycle. Birds that were located during at least 2 consecutive tracking periods (Day 1 - Night or Night - Day2) were included in the analysis for crepuscular movements, but only birds located during all 3 consecutive tracking periods (Day 1 - Night - Day 2) were included for analysis of 24-hour movement patterns (Table 16).

Crepuscular movements did not differ among seasons for either evening movements (Kruskal-Wallis test, $p = 0.42$, Table 17) or morning movements ($p = 0.54$). When the entire

24-hour cycle was considered, however, distances moved among seasons was marginally significant (Kruskal-Wallis, $p = 0.058$) with birds tending to move less in mid winter than either early winter (Wilcoxon 2-sample tests, $p=0.074$) or late winter ($p = 0.037$). Distances moved did not differ between early and late winter ($p = 0.777$).

Waterfowl hunting season on the Chesapeake Bay results in a relatively high level of disturbance on the shoreline and also increased boat traffic. In 1989 the waterfowl hunting season opened before the beginning of our field season and closed on 21 January. Differences in movement patterns during and after the hunting season were investigated (Table 17). Distances moved in the morning, evening and 24-hours tended to be higher during the hunting season than after the season was closed. However, none of these differences were significant (Wilcoxon 2-sample tests, $p = 0.340$, $p = 0.194$ and $p = 0.205$, respectively). It should be noted that the hunting season corresponded with the "early winter" category in the previous analysis.

No significant differences were detected in movement patterns during the morning ($p = 0.118$), evening ($p = 0.362$), or 24-hour cycle ($p = 0.198$) among portions of the canvasback population using exclusively habitats on the eastern shore of the Bay, or those birds using exclusively the western shore of the Bay or birds that used both shores of the Bay throughout the winter (Table 16). Distances moved in the morning were not significantly different from distances moved in the evening (Wilcoxon 2-sample test, $z=0.133$, $p=0.89$).

The relationships between crepuscular movements and weather variables were investigated using Spearman correlation procedures. Morning crepuscular movements were not correlated with temperature ($r = -0.019$, $p = 0.74$), cloud cover ($r = -0.050$, $p = 0.37$), or wind speed ($r = 0.059$, $p = 0.30$). Evening movements also were not correlated with temperature ($r = -0.072$, $p = 0.19$) or cloud cover ($r = -0.019$, $p = 0.73$). Evening movements were, however, negatively correlated with wind speed ($r = -0.125$, $p = 0.02$). Mean daily distances

moved throughout the winter were not correlated with mass of birds at time of capture ($r = 0.166$, $p = 0.19$).

Canvasbacks were relatively sedentary during the daytime hours. Diurnal movements were calculated from locations obtained three times per day at three hour intervals, one day per week. These distances represent minimum distances because in many cases if a bird moved during the day, it left the area of intensive tracking. Overall, 62.3% of the birds located at least once on intensive tracking days did not move at all during the day. Approximately 32.4% moved once during the daylight hours; 4.9% moved twice and one bird (0.5%) moved 4 times in one day. Average diurnal distance moved for all birds (including birds that did not move at all) was 287.0 m ($n=41$, $SE=88.12$, range 0-2388 m). These distances did not vary with season (Kruskal-Wallis, $p=0.22$), but birds tended to move more during hunting season (Wilcoxon, $z=-1.68$, $p=0.09$) than after hunting season. Those birds that did move, moved an average of 2598.3 m ($n=18$, $SE=707.8$) to a new location.

When testing for differences in populations, it is important to consider location differences (generally the mean of a population) *and* dispersion differences (some measure of variation). Because variation is large in the data presented above, the possibility that variances might be masking actual differences in movement patterns was a concern. To investigate this, the Lewontin variance ratio test for heterogeneity in coefficients of variation (Zar 1984) was used. No significant differences were found for movement patterns (morning, evening or 24 hour) for different seasons, hunting conditions or shores of the Bay. Therefore, the inferences made above are believed appropriate.

Home Ranges

The harmonic means (Dixon and Chapman 1980) and minimum convex polygon (Hayne 1949) procedures of Program Home Range (Samuel et al. 1985b) were used to estimate ranges of canvasbacks wintering on the upper Chesapeake Bay. Harmonic means procedures were used to calculate 95% and 50% use contours. In addition, the harmonic means procedure uses a one sided Kolmogorov goodness-of-fit procedure to compare the utilization distribution of known bird locations with an expected uniform use model to identify areas of concentrated use, or core areas, within the home range (Samuel et al. 1985). Minimum convex polygons included 100% of locations.

Only birds with ≥ 20 locations, at least 5 of which were nocturnal, were used in home range analysis. A plot of home range size versus sample size indicated that home range size reached a plateau between sample sizes of 18-20. Spearman rank correlations indicated home range size and sample size were not related for 95% contours ($r=0.13$, $n=32$, $p>0.47$), 50% contours ($r=-0.06$, $n=32$, $p>0.73$), core areas ($r=-0.04$, $n=29$, $p>0.82$) or convex polygons ($r=-0.19$, $n=32$, $p>0.29$) when birds with fewer than 20 locations were excluded.

Canvasbacks on the Chesapeake Bay showed strong crepuscular movements from near shore habitats during the daylight hours to off shore habitats at night (Rhodes 1990). Sampling procedures used during this study resulted in approximately twice as many diurnal locations as nocturnal locations. This unequal sampling could bias home range estimates toward areas used diurnally. Samuel and Garton (1987) suggested weighting home range data to reflect the amount of time an animal spends in each habitat and also as a method for incorporating "bursts" of relocation data into home range analyses. Harmonic means home ranges were calculated for canvasbacks in two ways: (1) using unweighted data, and (2) using the same data with nocturnal locations weighted twice as heavily as locations obtained during the day.

Both estimates are presented in Table 17. A paired t-test suggested no differences between weighted vs. unweighted range estimates for the 95% contour ($t = 0.35$, $p > 0.72$), 50% contours ($t = 0.91$, $p > 0.36$), or core areas ($t = -0.55$, $p > 0.50$). Therefore, home range estimates using weighted data were used in the following analysis. Convex polygon estimates were not weighted.

Adams and Davis (1967) originally pointed out the need to describe the "internal anatomy" of an animal's home range. The identification of core areas is one way to explain use patterns within the home range. On average, canvasbacks wintering on the Chesapeake Bay used 1.97 ($n = 31$, $SE = 0.22$) core areas. These core areas accounted for 25.1% ($n = 31$, $SE = 1.06$) of the home range area and 61.5% ($n = 31$, $SE = 1.20$) of the use (Table 18). The crepuscular movements of canvasbacks provide another way to investigate use patterns within the home range. The movements at dawn and dusk for canvasbacks actually result in a highly predictable condition of two relatively discrete range areas (one near shore, the other farther off shore) for each bird, with a transitional zone in which birds were essentially never found. To better understand this phenomenon, separate range areas were estimated for diurnal and nocturnal use. (Tables 19). Diurnal home ranges, when combined with nocturnal ranges (transition zones excluded) compose only 75-83% of the entire estimated home ranges. Transitional areas between the two account for the remainder. Nocturnal and diurnal core areas when summed are nearly identical to the core areas of the entire weighted home ranges (Table 20).

Home ranges were calculated for 22 birds that used only habitats on the western shore of the Bay and 10 birds that used habitats only on the eastern shore of the Bay. Only one bird (4790) that met the ≥ 20 minimum observation requirement used habitats on both shores of the Bay. This bird was excluded from analysis but range areas are presented in Tables 18 and 19. Range areas were similar for birds on both shores of the Bay, with the only significant differences being that birds in the western shore had significantly larger diurnal ranges at the

50% contour and significantly larger nocturnal convex polygons than birds on the eastern shore (Table 21).

Discussion

An underlying assumption of any telemetry study is that the sample of animals radioed accurately reflect the true population for the parameters of interest. Several recent manuscripts have addressed the effects of radio transmitters on the behavior and energy balance of avian species. Caccamise and Hedin (1985) provide a method for selecting transmitter size based on aerodynamic principles of avian flight. The transmitter used for the canvasbacks in this study weighed approximately 20 g. The mean mass of the birds used to calculate movement patterns and range areas was 1202 g (range 920-1415 g). The 20 g transmitter represents from 1.4-2.2% of the birds body mass. This is considerably below the "5% rule" often applied to telemetry studies.

Traditional back-mounted radio harnesses affect avian flight by increasing the weight a bird must carry and by increasing body drag during flight (Pennycuick and Fuller 1987) In this study radios were implanted abdominally, so only the the weight component was increased with drag coefficients remaining unchanged. Gessaman and Nagy (1988) found that increased drag was the most significant cause for increases in flight times and metabolism during flights of 90 and 320 km for homing pigeons (*Columba livia*) harnessed with dummy radio transmitters. Obrecht et al. (1988) tested the effect of the increased drag associated with different styles of back pack transmitters and found that radios can reduce flight ranges for

snow geese (*Chen caerulescens*) from 2.5-16.2%. Pennycuik and Fuller (1987) state that increases in weight are most important during low speed maneuvers such as taking off and landing. Sedinger et al. (1990) found no increases in energy expenditure of Pacific black brant (*Branta bernicla nigricans*) wearing back-mounted radios, but they did not address the costs of locomotion.

Abdominally implanted radios appear to be a good option for telemetry applications involving diving ducks. In addition to not increasing costs of flight associated with drag, having the radio implanted provides a thermally stable environment and reduces the likelihood of the radio acting as a "heat sink" (Korschgen 1984, Fuller 1987). Having the radio package implanted also makes it less likely to alter the bird's center of gravity.

It is a reasonable assumption that radioed canvasbacks in this study are representative of juvenile female canvasbacks wintering in the upper Chesapeake Bay and, to a large extent, all canvasbacks wintering on the Bay. Birds appeared to recover quickly from surgery, and when released, all immediately rejoined the raft of birds positioned just off shore. Radios apparently did not hamper flying abilities because radioed canvasbacks averaged movements of over 11 km during a 24 hour period (\bar{x} = 11.7 km, n = 64, SE = 1.2) with one recorded movement of over 82 km during one 24 hour cycle. Additionally, one bird during the winter of 1988-89 moved south to the Pamlico River in North Carolina. Also, 4 birds that had been radioed in 1987 were recaptured on the study area in 1988 and 8 birds radioed in 1988 were recaptured in 1989 (third year of PWRC's mortality study). Canvasbacks are highly gregarious in winter. At no time during the 1988-89 field season were radioed canvasbacks seen alone -- indicating that habitat selection and movement patterns were not different from nonradioed birds. I conclude from this evidence that canvasbacks used in this study are representative of juvenile female canvasbacks throughout the upper Chesapeake Bay and that radios did not significantly alter movements or activity patterns.

The concept of a "home range" is difficult to apply to wintering waterfowl in general, and canvasbacks, specifically. Canvasbacks are highly mobile and sufficiently plastic in their behavior to be capable of leaving an entire region in the face of adverse weather conditions. The winter of 1988-89 was rather mild (January temperatures averaged 2.9 C warmer than normal, National Weather Service Data for Baltimore-Washington International airport), and only one bird left the state of Maryland. Several others, however, dispersed from the study area (mainly to the Patuxent and Potomac river systems). In addition to being highly mobile, canvasbacks are rather unusual in the way they use diurnal habitats, relative to other wildlife species. Although the Chesapeake Bay seemingly provides a wide range of potential habitats, canvasbacks tend to repeatedly and predictably use the same discrete locations. For this reason, it was not uncommon for all the diurnal radio locations for any one bird to be in only a few separate areas for the entire winter. Superficially, this may seem to reflect observer bias because only a finite number of locations were visited during tracking. Obviously, it is only possible to find birds where you look for them. However, it is important to remember that PWRC personnel were conducting weekly (minimum) telemetry flights, and any time birds were located at a "new" location, that location was added to our route. We were successful in locating the birds used in home range analysis approximately 70% of the time.

Program HOME RANGE (Samuel et al. 1985) identifies statistical outliers in home range data using a "binomial test of observation density" and a "weighted bivariate normal test". The authors of the program recommend the exclusion of these points to avoid overestimating the size of home ranges. Outliers were not excluded from this analysis because, due to the specific and sometimes widely spatially separated diurnal habitats canvasbacks use, statistical outliers were not always indicative of biological outliers. In most instances points identified as outliers represented areas that the ducks used for a relatively short time immediately after arriving on Bay in late Fall or just prior to leaving the Bay in Spring. And, while very temporary, I considered these to be essential portions of the bird's home range.

The 95% contour and convex polygon estimates of home range are the ones that have the highest potential to be influenced by the presence of outliers in the data.

Given the degraded state of the Bay, the most interesting question is not really to estimate overall home ranges of canvasbacks, but to estimate the mean minimum ranges needed by canvasbacks to overwinter successfully. It is reasonable to hypothesize that the minimum ranges for canvasbacks using the Bay at present may be different from the ranges of birds in historical (or future?) times. The lack of SAV and increased shoreline development may be causing canvasbacks to use larger ranges to meet the minimum nutritive and refuging requirements. Alternatively, restricted resources may be restricting the birds to a tighter set of habitat options than in historical times. More than 61% of radio locations fell within designated core areas. Harmonic contours may be more useful as relative measures of dispersion, with mean crepuscular movements between roosting and foraging sites being the most "biologically valid datum for describing minimum home range size" (Morton 1987).

As stated above, canvasbacks often will use the same diurnal and nocturnal locations repeatedly for up to several weeks at a time. The factors that cause any given bird or an entire raft to abandon a location it has been using in favor of a new location are largely unknown. Weather variables have been implicated in causing local distributional changes in mallards (*Anas platyrhynchos*) (Jorde et al. 1984). Relationships between movement patterns and weather variables were weak for canvasbacks. This is not surprising because weather conditions were mild during the winter of 1988-89. Nichols et al. (1983) indicated that mallard distributions gradually shifted south with decreasing temperatures on a regional scale. This trend was not seen on the much more localized scale within the Bay. Northing UTM's for radio locations were not correlated with average daily temperatures ($r=0.02$, $p=0.55$). Instead, it seems likely that distributions of canvasbacks within the Bay (and regionally) respond to a "threshold temperature" (i.e. when icing occurs). Evening crepuscular movements were negatively correlated with wind speed. This was the only significant relationship between

weather and movement patterns. Bennett and Bolen (1978) also determined that wind speed was the most important weather variable affecting wintering green-winged teal (*Anas crecca*), with increased wind resulting in increased stress and a lowered condition index.

The fact that evening movements were more closely correlated with weather variables than were morning movements may present weak evidence that evening movements were more important for determining range areas than morning movements. In effect, in the morning canvasbacks may just be returning to shoreline habitats. Range sizes did not differ for the eastern and western shores of the Bay. Similarly, crepuscular and 24 hour movement patterns did not differ for the different shores. This implies that land use patterns are not proximate factors affecting movements. Land use patterns may, however, be the ultimate factor insofar as they impact such habitat parameters as foraging areas through such factors as pollution and eutrophication.

Twenty-four hour movements tended to be shorter in mid winter than in either early or late winter. This is consistent with the theory that during times of low temperature, waterfowl attempt to reduce energetically expensive behaviors (Kendeigh 1969, Prince 1977). Because the winter of 1988-89 was mild, it might be expected that movement patterns would remain the same throughout the winter. Perry et al. (1986, 1989), however found that captive canvasbacks reduced food intake and activity even when food was presented *ad libitum*, and speculated that canvasbacks may have evolved an endogenous rhythm to reduce energy expenditure during the coldest months. The data presented here provide additional evidence that this may, in fact, be the case, and further provide evidence that this rhythm, if it does exist, is triggered by photoperiodism and not temperature. January temperatures were actually warmer than temperatures in either December or February during 1988-89.

LITERATURE CITED

- Adams, L. and S.D. Davis. 1967. The internal anatomy of home range. *J. Mammal.* 48:529-536.
- Alexander, W. C. 1983. Differential sex distributions of wintering diving ducks (Aythyini) in North America. *American Birds* 37:26-29.
- Bayley, S., V. D. Stotts, P. F. Springer and J. Steenis. 1978. Changes in submerged aquatic macrophyte populations at the head of Chesapeake Bay, 1958-1975. *Estuaries* 1:73-84.
- Bennett, J. W. and E. G. Bolen. 1978. Stress response in wintering green-winged teal. *J. Wildl. Manage.* 42:81-86.
- Caccamise, D. F. and R. S. Hedin. 1985. An aerodynamic basis for selecting transmitter loads in birds. *Wilson Bull.* 97:306-318.
- DeGraff, L. W., D. D. Foley and D. Benson. 1961. Distribution and mortality of canvasbacks banded in New York. *N.Y. Fish and Game J.* 8:69-87.
- Dixon, R. D. and J. A. Chapman. 1980. Harmonic means measure of animal activity areas. *Ecology* 61:1040-1044.
- Fredrickson L. H. and R. D. Drobney. 1979. Habitat utilization by postbreeding waterfowl. Pages 119-131 *in* T. A. Bookout, ed. *Waterfowl and wetlands - an integrated review.* Proc. 1977 Symp., Madison, WI, N. Cent. Sect., The Wildlife Society.
- Fuller, M. R. 1987. Applications and considerations for wildlife telemetry. *J. Raptor Res.* 21:126-128.
- Gessaman, J. A. 1988. Transmitter loads affect the flight speed and metabolism of homing pigeons. *Condor* 90:662-668.
- Haramis, G. M., J. R. Goldsberry, D. G. McAuley and E. L. Derleth. 1985. An aerial photographic census of Chesapeake Bay and North Carolina canvasbacks. *J. Wildl. Manage.* 49:449-454.
- Hayne, D. W. 1949. Calculation of size of home range. 1949. *J. Mammal.* 30:1-18.

- Jorde, D. G., G. L. Krapu, R. D. Crawford and M. A. Hay. 1984. Effects of weather on habitat selection and behavior of mallards wintering in Nebraska. *Condor* 86:258-265.
- Korshgen, C. E., S. J. Maxson and V. B. Kuechle. 1984. Evaluation of implanted radio transmitters in ducks. *J. Wildl. Manage.* 48:982-987.
- Longwell, J. R. and V. Stotts. 1958. Some observations on the recovery of diving ducks banded in the Maryland portion of the Chesapeake Bay. *Proc. S.E. Assoc. Game and Fish Commissioners Conf.* 12:285-291.
- Lovvern, J. R. 1989. Distributional responses of canvasback ducks to weather and habitat change. *J. App. Ecology* 26:113-130.
- Morton, J. M. 1987. Habitat use and energetics of American black ducks wintering at Chincoteague, Virginia. Unpublished M.S. thesis. VPI&SU, Blacksburg, VA. 147pp.
- Munro, R. E. and M. C. Perry. 1981. Distribution and abundance of waterfowl and submerged aquatic vegetation in Chesapeake Bay. Final Report to FWS/OBS-78/D-X0391. 180pp.
- Nichols, J. D. and G. M. Haramis. 1980(a). Inferences regarding survival and recovery rates of winter-banded canvasbacks. *J. Wildl. Manage.* 44:164-173.
- _____ and _____. 1980(b). Sex-specific differences in winter distribution patterns of canvasbacks. *Condor.* 82:406-416.
- _____, K. R. Reinecke and J. E. Hines. 1983. Factors affecting the distribution of mallards wintering in the Mississippi alluvial valley. *Auk* 932-946.
- Obrecht, H. H., C. J. Pennycuick and M. R. Fuller. 1988. Wind tunnel experiments to assess the effects of back-mounted radio transmitters on bird body drag. *J. Exp. Biol.* 135:265-273.
- Olsen, G. H., J. F. Dein, G. M. Haramis and D. G. Jorde. 1990. A surgical technique for implanting radio transmitters in wintering canvasbacks. Unpubl. manuscript.
- Olson, D. P. 1965. Differential vulnerability of male and female canvasbacks to hunting. *Trans. North Am. Wildl. Nat. Resour. Conf.* 30:121-135.
- Orth, R. J. and K. A. Moore. 1981. Submerged aquatic vegetation of the Chesapeake Bay: past, present and future. *Trans. North Am. Wildl. Nat. Resour. Conf.* 46:271-283.

- _____, J. Simons, V. Carter, L. Hindman, S. Hodges, K. Moore and N. Rybicki. 1985. Distribution of submerged aquatic vegetation in the Chesapeake Bay - 1985. Virginia Inst. Marine Sci., Unpb. Rep. 296pp.
- Pennycuik, C. J. and M. R. Fuller. 1987. Considerations of effects of radio-transmitters on bird flight. Pages 327-330 in H. P. Kimmich and M. R. Neuman, eds. Biotelemetry IX.
- Perry, M. C., W. J. Kuenzel, B. K. Williams and J. A. Serafin. 1986. Influence of nutrients on feed intake and condition of captive canvasbacks in winter. J. Wildl. Manage. 50:427-434.
- _____ and F. M. Uhler. 1988. Food habits and distribution of wintering canvasbacks, *Aythya valisineria* on Chesapeake Bay. Estuaries 11:57-67.
- _____, B. K. Williams and H. H. Obrecht III. 1989. Behaviour of captive canvasbacks *Aythya valisineria* fed different diets during winter. Wildfowl 40:80-87.
- Samuel, M. D. and E. O. Garton. 1987. Incorporating activity time in harmonic home range analysis. J. Wildl. Manage. 51:254-257.
- _____, D. J. Pierce and E. O. Garton. 1985. Identifying areas of concentrated use within the home range. J. Animal Ecol. 54:711-719.
- _____, _____, _____, L. J. Nelson and K. R. Dixon. 1983. User's manual for Program Home Range. Contribution #259, Forest, Wildlife and Range Experiment Station, U. of Idaho, Moscow. 64pp.
- Sedinger, J. S., R. G. White and W. E. Hauer. 1990. Effects of carrying radio transmitters on energy expenditures of Pacific black brant. J. Wildl. Manage. 54:42-45.
- Takekawa, J. Y. 1987. Energetics of canvasbacks staging on an Upper Mississippi River pool during fall migration. PhD. Diss. Iowa State University, Ames. 189pp.
- Trauger, D. L. 1974. Looking out for the canvasback, Part 1. Ducks Unlimited. 38:12-15.
- Welling, C. H. and W. J. L. Sladen. 1979. Canvasback sex ratios on Rhode and West Rivers, Chesapeake Bay, 1972-78. J. Wildl. Manage. 23:253-261.
- Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall Inc., Englewood Cliffs, NJ. 620pp.

Tables

Table 16. Mean movement estimates for juvenile female canvasbacks wintering on the upper Chesapeake Bay, Maryland, December 1988-March 1989.

FREQ	MOVEMENT ¹ (m)		
	PM (n)	AM (n)	24 HOUR (n)
<u>Western Shore</u>			
4051	8319 (1)	8319 (1)	16639 (1)
4102	2595 (8)	3838 (10)	6625 (9)
4161	1881 (8)	3977 (6)	3323 (6)
4171	4473 (6)	4473 (6)	8946 (6)
4241	3289 (8)	2336 (8)	6676 (8)
4301	8186 (3)	11150 (3)	15619 (3)
4311	2442 (8)	2011 (8)	4454 (8)
4332	2894 (10)	2770 (10)	5665 (10)
4391	2682 (8)	2656 (8)	5887 (8)
4432	4818 (7)	6101 (8)	8906 (7)
4462	5647 (6)	4492 (6)	10583 (6)
4471	10603 (6)	10244 (6)	17433 (6)
4491	11840 (5)	11901 (5)	21652 (5)
4591	2304 (8)	1668 (8)	4515 (8)
4632	6341 (1)	10473 (3)	26947 (1)
4651	6992 (2)	6992 (2)	13984 (2)
4721	4340 (7)	4829 (4)	11086 (4)
4820	4341 (4)	2572 (3)	5143 (3)
4830	8986 (5)	9985 (5)	20271 (4)
4842	5785 (5)	5639 (5)	12566 (5)
4881	3108 (7)	5335 (7)	8444 (7)
4891	3048 (4)	3091 (5)	6097 (4)
4921	3046 (4)	3046 (4)	6092 (4)
4931	5263 (1)	6577 (1)	9520 (1)
4950	2397 (3)	2253 (3)	4651 (3)
4981	7771 (7)	9070 (8)	18577 (7)
5000	10762 (2)	15871 (1)	31742 (1)

Table 16, Cont.

FREQ	MOVEMENT ¹ (m)		
	PM (n)	AM (n)	24 HOUR (n)
5022	1884 (2)	4662 (2)	8279 (2)
5201	2805 (9)	1996 (7)	5065 (7)
5220	7041 (1)	7041 (1)	14081 (1)
5271	4270 (3)	3718 (2)	7437 (2)
5401	3678 (4)	3068 (4)	6790 (4)
5411	1508 (8)	1429 (8)	2769 (8)
5570	8968 (7)	5009 (8)	14483 (7)
5610	4095 (5)	3577 (4)	7461 (4)
5722	6952 (8)	6122 (8)	13074 (8)
5831	1574 (6)	1590 (6)	10068 (5)
5842	17444 (2)	16457 (2)	62913 (1)
5911	26321 (3)	**	**
5941	2536 (7)	2667 (7)	5132 (7)
5960	5068 (7)	5090 (5)	10180 (5)
<u>Eastern Shore</u>			
4201	1679 (7)	2030 (6)	6625 (6)
4291	1937 (7)	1732 (8)	3680 (7)
4451	5273 (9)	5888 (8)	10506 (8)
4701	3368 (2)	2732 (3)	6737 (2)
4911	2909 (6)	2472 (5)	5659 (5)
4962	8311 (2)	4539 (1)	9097 (1)
5011	6772 (6)	5993 (6)	10334 (6)
5210	6179 (7)	5054 (7)	10300 (7)
5351	8436 (7)	5838 (7)	13931 (7)
5390	11810 (7)	13222 (7)	22345 (7)
5592	3714 (3)	3235 (3)	5871 (3)
5630	3723 (8)	6349 (10)	9187 (8)
5861	3385 (3)	3141 (1)	6282 (1)
5871	2713 (7)	3748 (7)	5926 (7)

Table 16, Cont.

FREQ	MOVEMENT ¹ (m)		
	PM (n)	AM (n)	24 HOUR (n)
<u>Both Shores²</u>			
4041	6148 (4)	9653 (5)	12834 (4)
4141	4240 (5)	3255 (4)	6230 (4)
4212	1819 (4)	1784 (4)	3604 (4)
4563	14175 (3)	15785 (2)	31569 (2)
4683	**	11667 (1)	**
4692	8149 (2)	6463 (3)	16298 (2)
4790	12297 (8)	12894 (9)	26512 (8)
5311	6151 (4)	6151 (4)	12308 (4)

¹Movement data averaged from diurnal locations recorded on 2 consecutive days and 1 location recorded during the intervening night. PM=crepuscular day-to-night movement, AM=crepuscular night-to-day movement, 24 HOUR=average movement for a complete 24 hour cycle.

²Birds used both shores at some point during the winter.

Table 17. Mean movement estimates by season, hunting season and shore for juvenile female canvasbacks wintering on the upper Chesapeake Bay, Maryland, December 1988-March 1989.

	<u>MOVEMENT¹ (m)</u>					
	<u>PM</u>		<u>AM</u>		<u>24 HOUR</u>	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
<u>SEASON</u>						
Early	6515(12) ²	866.6	7420(12)	1455.9	16610(13)	4460.8
Mid	5305(26)	630.8	5622(25)	673.1	9043(30)	1078.5
Late	6106(26)	1104.2	5562(26)	814.8	12501(21)	1472.1
<u>HUNTING SEASON</u>						
Hunting	6515(12)	866.6	7420(12)	1455.9	16610(13)	4460.8
No Hunting	5705(52)	632.1	5592(51)	525.2	10467(51)	900.9
<u>SHORE</u>						
Western	5932(43)	705.3	5943(41)	631.0	12125(43)	1555.3
Eastern	4774(14)	795.0	4493(14)	800.8	8502(14)	1310.8
Both	7568(7)	1651.2	8456(8)	1721.7	15622(7)	3856.9

¹Movement data averaged from diurnal locations recorded on 2 consecutive days and 1 location recorded during the intervening night. PM = crepuscular day-to-night movement, AM = crepuscular night-to-day movement, 24 HOUR = average movement for a complete 24 hour cycle.

²Number in parentheses is sample size.

Table 18. Convex polygon and harmonic mean estimates of range and core area sizes (ha) for juvenile female canvasbacks wintering on the western and eastern shores of the Chesapeake Bay, Maryland.

FREQ	WEIGHTED HARMONIC MEANS ¹						UNWEIGHTED HARMONIC MEANS						CONVEX POLYGON		
	Range Area ²			Core Area			Range Area			Core Area					
	50%	95%	Area	No.	%area/%data ³	50%	95%	Area	No.	%area/%data	50%	95%		Area	No.
<u>Western Shore</u>															
4102 (31) ⁴	2534.0	31810.5	815.0	1	23.2/68.8	2957.0	24300.8	7293.6	1	24.4/67.2					
4161 (25)	970.1	20320.7	4823.8	1	17.2/65.6	1085.3	16387.4	2581.7	1	17.3/65.1					
4241 (29)	2620.2	20501.7	4422.3	3	19.4/65.3	2213.8	19203.8	3564.3	1	20.3/65.1					
4311 (27)	906.0	7035.2	1897.9	1	26.1/64.1	1069.3	8965.7	1936.3	1	25.0/66.1					
4332 (32)	1536.4	22592.9	4951.6	1	17.8/67.3	2037.3	32583.0	6803.2	1	17.6/69.0					
4391 (26)	3931.8	19650.8	5228.0	5	25.9/58.4	2903.3	18766.5	4572.8	4	24.1/57.6					
4432 (24)	2847.9	25665.8	7513.9	2	27.4/70.8	3172.5	20803.0	6340.9	3	27.7/67.3					
4462 (23)	2282.7	13667.4	4877.2	2	27.9/57.8	4367.7	19770.9	6098.6	3	30.0/62.9					
4471 (21)	3780.8	27156.6	7842.3	1	25.6/64.9	2818.4	21328.6	5835.6	2	23.4/60.4					
4491 (21)	2672.4	11953.1	3726.3	2	34.3/58.4	301.6	20115.2	7360.6	5	35.0/66.7					
4591 (30)	338.5	4079.1	8372.7	3	26.7/61.9	144.5	4134.4	1105.2	3	28.6/62.3					
4721 (22)	409.5	3694.0	**	**	**	536.6	4041.1	1359.2	2	42.9/61.8					
4830 (23)	862.4	6029.5	703.2	2	30.0/52.5	429.3	5220.8	525.6	3	35.3/54.1					
4881 (24)	3050.1	22808.0	8119.5	4	23.9/67.4	3324.2	23186.1	7126.9	2	25.7/65.0					
4981 (26)	2666.3	13497.1	339.4	4	33.3/58.7	2102.6	13726.2	3611.4	3	34.5/57.0					
5201 (27)	995.3	12978.9	3380.0	3	23.3/68.6	364.3	11967.1	2735.3	1	20.5/66.5					
5411 (28)	0.3	14054.6	**	0	20.0/49.3	30.1	11953.0	**	0	20.0/51.2					
5570 (26)	3305.6	35924.0	9266.3	3	20.2/66.6	3864.5	29399.8	7519.3	1	24.5/67.7					
5722 (25)	92.9	1217.7	**	0	16.7/37.6	47.7	1648.7	9.7	1	33.3/61.8					

Table 18, Cont.

FREQ	WEIGHTED HARMONIC MEANS				UNWEIGHTED HARMONIC MEANS				CONVEX POLYGON		
	Range Area		Core Area		Range Area		Core Area				
	50%	95%	Area	No. %area/%data	50%	95%	Area	No. %area/%data			
5831 (25)	69.9	2035.8	1348.2	1	33.3/61.8	25.3	1833.4	408.8	1	50.0/77.2	7557.5
5941 (25)	792.5	4878.8	1666.7	1	31.8/63.2	587.7	8736.6	2457.7	1	28.0/59.7	3368.7
5960 (20)	21.8	2978.0	206.8	3	36.4/57.2	821.4	5408.0	1875.3	3	35.3/59.2	1156.2
<u>Eastern Shore</u>											
4201 (24)	167.7	9116.4	2136.0	1	20.7/63.2	292.4	7516.3	2224.0	1	24.0/64.8	1499.6
4291 (26)	388.7	6063.0	1126.7	3	21.1/60.5	343.6	4574.2	1429.1	1	29.4/68.0	1069.1
4451 (27)	454.8	7863.3	965.4	1	14.8/59.8	508.3	12954.1	2505.1	3	18.7/63.0	7155.5
4911 (21)	271.4	2786.4	312.1	1	33.3/54.9	163.7	2065.8	480.1	1	37.5/58.6	1673.4
5011 (23)	1652.4	8245.8	2261.3	2	33.3/58.7	1778.1	14461.5	3569.3	1	34.3/64.8	3085.0
5210 (26)	587.2	11189.7	2359.4	1	19.4/64.0	628.9	16529.7	2668.2	3	14.8/63.0	3413.2
5351 (24)	4139.3	25732.9	7759.1	1	25.3/66.2	3365.1	21212.3	4343.5	4	20.9/61.4	9838.2
5390 (20)	5167.7	25119.8	7323.7	2	26.7/59.8	4610.1	25863.4	7932.3	2	24.1/58.3	15040.0
5630 (28)	3058.2	29889.4	7335.2	2	20.9/64.6	1864.5	23100.8	4373.2	1	17.8/62.9	14079.4
5671 (23)	945.7	13282.0	3212.1	4	22.7/67.7	615.1	10450.5	2303.3	3	19.4/64.3	2967.7
<u>Both Shores</u>											
4780 (27)	4599.0	33610.3	8033.9	2	22.0/58.8	5729.1	58298.5	13820.6	5	20.2464.1	121311.2

¹For weighted home ranges, nighttime locations were weighted twice as heavily as daytime locations because tracking regimes resulted in unequal sampling for day and night.

²Default grid size used for harmonic means estimation of 50% and 95% contours. Convex polygon estimates represent a 100% contour. Outliers were not excluded from harmonic means estimates because it was decided that due to the discrete patterns of use for canvasbacks statistical outliers were not always indicative of biological outliers.

³Statistical measure of importance of core area; estimate of the area (expressed as percent of total range area) that contains the clustered radio locations (expressed as percent of total number of locations). **Asterisk indicates no statistical core area identified.

⁴Number of radio locations used in range estimation (diurnal locations/nocturnal locations).

Table 19. Weighted convex polygon and harmonic mean estimates of diurnal and nocturnal ranges and core area sizes (ha) for juvenile female canvasbacks wintering on the western and eastern shores of the Chesapeake Bay, Maryland.

FREQ	DIURNAL RANGES'						NOCTURNAL RANGES					
	Range Area'			Core Area			Range Area			Core Area		
	50%	95%	Area	No.	%area/ %data	Convex Polygon	50%	95%	Area	No.	%area/ %data	Convex Polygon
<u>Western Shore</u>												
4102 (21/10)*	2110.9	19663.4	5399.6	5	24.6/63.7	4630.5	350.0	3390.5	**	**	**	607.2
4161 (16/9)	513.6	10045.5	2629.1	1	20.6/66.6	1361.9	169.5	1530.5	**	**	**	1978.9
4241 (21/8)	1309.0	12554.6	2739.7	1	19.0/64.1	7803.7	64.4	11.4	**	**	**	188.0
4311 (19/8)	564.5	4743.9	1319.9	1	22.2/65.2	433.4	456.0	40446.5	**	**	**	1697.7
4332 (22/10)	126.3	6047.4	1338.6	1	20.0/65.6	246.5	354.9	825.1	1676.9	1	19.2/65.3	2224.4
4391 (17/9)	1763.3	14631.8	2922.8	2	23.3/63.0	2427.9	1059.3	5207.0	**	**	**	2716.2
4432 (16/8)	2735.2	13602.9	4656.4	1	31.7/66.4	4162.9	**	603.0	**	**	**	127.4
4462 (16/7)	1027.6	10617.4	2693.9	2	28.1/61.1	8801.1	291.4	2467.2	**	**	**	34845.6
4471 (15/6)	1367.4	12536.9	2086.1	1	17.5/58.4	10311.2	**	514.9	**	**	**	47.5
4491 (16/5)	3913.4	17426.7	6154.7	1	34.0/66.6	8715.1	249.6	1414.5	**	**	**	6010.1
4591 (22/8)	62.6	2699.6	245.9	1	37.5/67.3	1026.5	0.7	1036.5	**	**	**	248.0
4721 (15/7)	1457.5	4874.5	1589.5	1	40.0/61.6	1704.6	269.4	2663.6	**	**	**	306.0
4830 (16/5)	151.0	3756.2	302.7	2	30.6/55.9	10436.7	**	**	**	**	**	35.7
4861 (16/8)	2248.6	17710.0	4294.1	2	25.5/60.6	5963.0	148.5	1439.0	**	**	**	392.5
4961 (17/9)	1213.1	5791.2	1729.0	1	31.2/55.7	10368.9	343.9	3614.7	**	**	**	8910.9
5201 (19/8)	581.0	9345.5	2061.4	1	21.9/70.4	282.7	30.0	2104.9	**	**	**	237.0
5411 (19/9)	5.6	793.8	**	0	33.0/67.1	950.0	43.4	35.3	**	**	**	109.7
5570 (16/10)	2271.0	17500.1	4272.5	3	22.2/60.9	3713.3	**	**	**	**	**	83.6
5722 (17/8)	**	900.7	**	0	33.3/59.0	1533.7	11.4	1413.4	**	**	**	160.4
5831 (18/7)	**	1222.4	**	0	33.3/65.7	1533.7	11.4	1413.4	**	**	**	160.4

Table 19, Cont.

FREQ	DIURNAL RANGES ¹						NOCTURNAL RANGES					
	Range Area ²			Core Area			Range Area			Core Area		
	50%	95%	Area	No.	%area/ ³ %data	Convex Polygon	50%	95%	Area	No.	%area/ %data	Convex Polygon
5941 (18/7)	63.7	1835.7	198.5	1	33.1/51.2	1919.2	387.2	2669.0	**	**	**	1087.7
5960 (13/7)	**	934.4	**	**	**	**	0.1	648.6	**	**	**	190.4
<u>Eastern Shore</u>												
4201 (14/24)	36.9	597.4	**	**	**	196.7	343.2	3908.3	987.6	1	38.5/75.6	1122.1
4291 (17/9)	92.3	318.5	706.8	1	30.8/71.3	565.2	11.6	88.2	**	**	**	292.0
4451 (18/9)	351.9	5948.9	1316.6	2	20.0/64.8	2298.7	195.6	2761.7	**	**	**	6546.7
4911 (14/7)	283.5	1090.9	**	**	**	670.2	217.4	897.9	**	**	**	503.1
5011 (13/10)	11.9	2752.3	**	0	10.0/47.9	0.0	80.7	5855.1	1181.8	1	22.2/55.7	2370.5
5210 (18/8)	414.2	7328.3	1676.3	1	24.0/70.1	0.0	141.4	2927.9	**	**	**	3410.7
5351 (14/10)	915.1	8960.6	2382.0	1	25.0/67.4	3777.0	242.6	3495.7	**	**	**	1651.2
5390 (13/7)	1821.4	15059.8	3144.6	2	24.4/63.5	8566.9	356.2	3572.8	**	**	**	3833.7
5630 (18/10)	774.8	13290.5	2208.3	1	16.3/66.8	3173.0	684.8	4890.1	**	**	**	3072.5
5871 (16/3)	55.3	6047.0	1316.0	1	19.0/65.3	642.0	594.7	2799.0	**	**	**	740.2
<u>Both Shores</u>												
4790 (18/9)	5077.9	12271.2	2549.7	3	19.5/66.1	53275.5	146.4	1454.3	**	**	**	3080.0

¹Traditional home ranges separated for diurnal and nocturnal locations. This was done because areas of day use were not contiguous with areas of use at night.

²Default grid size used for harmonic means estimation of 50% and 95% contours. Convex polygon estimates represent a 100% contour. Outliers were not excluded from harmonic means estimates because it was decided that due to the discrete patterns of use for canvasbacks statistical outliers were not always indicative of biological outliers.

³Statistical measure of importance of core area; estimate of the area (expressed as percent of total range area) that contains the clustered radio locations (expressed as percent of total number of locations). **Asterisk indicates no statistical area identified, or not calculated if fewer than 10 locations.

⁴Number of radio locations used in range estimation.

Table 20. Comparison of diurnal and nocturnal ranges with weighted home ranges of juvenile female canvasbacks wintering on the eastern and western shores of the upper Chesapeake Bay, Maryland, December 1988-March 1989.

	RANGE AREAS (ha)			Polygon (\bar{x})
	95% Contour (\bar{x})	50% Contour (\bar{x})	Core Area (\bar{x})	
Diurnal Ranges	7933.0(32) ¹	974.7(29)	2375.4(25)	3417.0(31)
Nocturnal Ranges	3717.0(30)	279.8(28)	1282.1(3)	2627.9(32)
Total	11650.0 ²	1254.5	3657.5	6044.9
Weighted Ranges	14286.6	1627.5	3641.1	7331.2
Percent ³	(81.5%)	(75.0%)	(100.5%)	(82.5%)

¹Sample size.

²Total represents the sum of diurnal + nocturnal ranges.

³Percent = (Weighted Range/Total) X 100.

Table 21. Comparison of range areas for juvenile female canvasbacks wintering on the eastern and western shores of the upper Chesapeake Bay, Maryland, December 1988-March 1989.

	<u>RANGE AREAS (ha)</u>											
	<u>95% Contour</u>			<u>50% Contour</u>			<u>Core Area</u>			<u>Convex Polygon</u>		
	$\bar{x}(n)$	SE	p-value	$\bar{x}(n)$	SE	p-value	$\bar{x}(n)$	SE	p-value	$\bar{x}(n)$	SE	p-value
<u>WEIGHTED RANGES</u>												
Western Shore	14449.1(22)	2327.1	0.92	1667.6(22)	280.9	0.98	3725.2(19)	680.4	0.91	7944.5(22)	1981.8	0.76
Eastern Shore	13928.9(10)	2991.7		1683.1(10)	570.4		3481.1(10)	909.3		5982.1(10)	1669.1	
<u>DIURNAL RANGES</u>												
Western Shore	8601.7(22)	1350.3	0.48	1237.2(19)	246.0	0.04	2590.8(18)	414.8	0.32	4097.1(21)	831.7	0.10
Eastern Shore	6462.0(10)	1547.6		475.7(10)	178.9		1821.5(7)	308.1		1989.0(10)	847.7	
<u>NOCTURNAL RANGES</u>												
Western Shore	4051.6(20)	1966.3	0.11	235.5(18)	60.6	0.22	1676.9(1)	**	0.54	2752.2(22)	1597.8	0.02
Eastern Shore	3119.7(10)	537.3		369.5(10)	81.0		1084.7(2)	97.1		2354.3(10)	611.9	

Conclusions and Management Recommendations

Canvasbacks were very inactive during the day and very active at night. Daily, they made crepuscular flights averaging over 11 km (round trip) to and from night-time foraging areas. Nocturnal feeding frequencies, as determined from telemetered birds, averaged nearly 40% compared to the amount of time spent foraging during the diurnal hours, which ranged from 1-6%. Total energy expenditure was estimated to be nearly twice as high during nocturnal periods as during diurnal periods. Sleeping was the predominant behavior in diurnal habitats. This pattern of nocturnal activity has been seen in canvasbacks during migration (Thornburg 1973, Takekawa 1987) and in the tufted duck during winter (Pedroli 1982).

Several hypotheses have been proposed to explain this nocturnal activity. The first hypothesis is that birds feed nocturnally because the benthic invertebrates they feed on are more active and/or are closer to the substrate surface at night. This theory seems unlikely for canvasbacks. Although canvasbacks presently do feed primarily on invertebrates in the Chesapeake Bay, they are traditionally much more vegetarian in food preference (Bent 1923, Cottam 1939, Munro and Perry 1981, Perry 1982, Perry and Uhler 1988). The second hypothesis is that disturbance by boaters and/or risk of predation cause the birds to feed nocturnally (Thornburg 1973, Pedroli 1982, Lovvern 1989b). There does seem to be some

evidence that boat traffic does limit access to feeding areas during the day (Thornburg 1973, Korschgen et al. 1985). This study showed that canvasbacks are extremely sensitive to disturbance by boats. Also, some disturbance from gulls and one osprey was noticed. The third hypothesis states that canvasbacks feed at night for energetic considerations (Pedroli 1982, Takekawa 1987). Canvasbacks roost during the diurnal hours allowing radiant energy to reduce thermoregulatory costs, and dive at night when activity helps keep them warm. Further evidence in support of this theory is that during the nesting season when thermoregulation is more likely to be concerned with heat stress, canvasbacks feed diurnally, even though avian predators are present. Another consideration is that canvasback courtship is highly visual. Nocturnal feeding would allow for more courtship and pairing activities during diurnal hours in late winter.

Perry (1986, 1987) argued that canvasbacks voluntarily reduce activity and food intake (and thereby body weight and BMR) during mid winter as a strategy for increasing survival during periods of winter stress. He believed that an endogenous rhythm was mechanistic in this approach. This study partially supports this hypothesis. Canvasbacks did show an increased incidence of sleeping and decreased feeding (diurnal and nocturnal) during the mid winter months. Also, 24 hour movements tended to be lower during January and February. Furthermore, this study provides weak evidence that this endogenous rhythm is triggered by photoperiod and not temperature. Finally, this study presents data showing that canvasbacks may be sufficiently plastic in their behaviors to take advantage of events such as unusually warm temperatures or increased food supplies to engage in more productive behaviors such as courtship and preening.

Strong evidence has been presented that distributional shifts of canvasback populations south to North Carolina are related to habitat degradation within the Bay, especially concerning the losses in submerged aquatic vegetation (SAV) (Perry and Uhler 1988, Lovvern 1989a). Similar relationships between waterfowl population numbers and food supplies have been noticed for

the shelduck (*Tadorna tadorna*) in Scotland (Buxton 1981) and for ducks in the lower Detroit River (Schloesser and Manny 1990). Van Eerden (1984) hypothesized that with changes in food availability one could expect: (1) shifts in bird numbers; (2) shifts in diets; (3) shifts in foraging speed, and; (4) increased competition. Apparently Chesapeake Bay canvasbacks have used options 1 and 2 above. Distributions of birds have shifted south, and canvasbacks remaining in the Bay rely much more on invertebrates now than in historical times. Perry (1986) indicated that canvasbacks may be unable to adjust intake rates to compensate for low energy diets. Further evidence for this relationship between habitat degradation and population shift is presented by Ketterson and Nolan (1983, p. 395.) when they state that "selection should stabilize at the frequency distribution of thresholds at which potential reproductive success is the same for all members of the population...". Essentially what this implies is that if the advantages in wintering farther north (through reduced migration costs and reduced risk of predation) are decreased, a new equilibrium will be established further south (increasing probability of overwinter survival).

Important management considerations should include measures to reduce disturbance to roosting canvasbacks. Laws, already in place, regarding the harassment of resting waterfowl should be enforced. The effect of disturbance on overall energy balance is still poorly understood, but is presumably significant, especially during a time when birds are apparently trying to reduce energy expenditure. Additionally, it is important to continue attempts to reverse the factors leading to the degradation of the Bay and to encourage the propagation of existing beds of SAV. It appears likely that artificial feeding plays an important role in maintaining current canvasback distributions and condition; however, more specific studies are needed to clarify this relationship.

LITERATURE CITED

- Bent, A. C. 1923. Life histories of North American wildfowl. Order: Anseres (Part 1). Bull. 126. U.S. Nat. Museum, Washington, D.C. 244pp.
- Buxton, N. E. 1981. The importance of food in the determination of the winter flock sites of the shelduck. *Wildfowl* 32:79-87.
- Cottam, C. 1939. Food habits of North American diving ducks. U.S. Dept. Agr. Tech. Bull. 643. 139pp.
- Ketterson and Nolan 1983. Evolution and migration?
- Korshgen, C. E., L. S. George and W. L. Green. 1985. Disturbance of diving ducks by boaters on a migrational staging area. *Wildl. Soc. Bull.* 13:290-296.
- Lovvorn, J. R. 1989a. Distributional responses of canvasback ducks to weather and habitat change. *J. App. Ecology* 26:113-130.
- _____. 1989b. Food defendability and antipredator tactics: implications for dominance and pairing in canvasbacks. *Condor* 91:826-836
- Munro, R. E. and M. C. Perry. 1981. Distribution and abundance of waterfowl and submerged aquatic vegetation in Chesapeake Bay. Final Report to FWS/OBS-78/D-X0391. 180pp.
- Pedroli, J. 1982. Activity and time budget of tufted ducks on Swiss lakes during winter. *Wildfowl* 105-112.
- Perry, M. C. 1982. Distribution and food habits of canvasbacks in the northeast. *Trans. N.E. Sect. Wildl. Soc.* 39:56-67.
- _____, W. J. Kuenzel, B. K. Williams and J. A. Serafin. 1986. Influence of nutrients on feed intake and condition of captive canvasbacks in winter. *J. Wildl. Manage.* 50:427-434.
- _____ and F. M. Uhler. 1988. Food habits and distribution of wintering canvasbacks, *Aythya valisineria* on Chesapeake Bay. *Estuaries* 11:57-67.
- _____, B. K. Williams and H. H. Obrecht III. 1989. Behaviour of captive canvasbacks *Aythya valisineria* fed different diets during winter. *Wildfowl* 40:80-87.

- Schloesser, D. W. and B. A. Manny. 1990. Decline of wildcelery buds in the lower Detroit River, 1950-85. *J. Wildl. Manage.* 54:72-76.
- Takekawa, J. Y. 1987. Energetics of canvasbacks staging on an Upper Mississippi River pool during fall migration. PhD. Diss. Iowa State University, Ames. 189pp.
- Thornburg, D. D. 1973. Diving duck movements on Keokuk Pool, Mississippi River. *J. Wildl. Manage.* 37:382-389.
- Van Eerden, M. R. 1984. Waterfowl movements in relation to food stocks. Pages 84-100 *in* P. R. Evan, J. D. Goss-Custard and W. G. Hale, eds. Coastal waders and waterfowl in winter. 331pp.

Vita

David W. Howerter received a Bachelor of Science degree in Wildlife Biology from the Colorado State University (CSU) in 1986. While attending CSU he worked as a temporary employee for the Colorado Cooperative Wildlife Research Unit and as a volunteer at the Alamosa-Monte Vista National Wildlife Refuge. In 1987, he became a candidate for a Master of Science degree in Wildlife Science from the Virginia Polytechnic Institute and State University.