CONSTRUCTING A 24 HOUR TIME-ENERGY BUDGET FOR AMERICAN BLACK DUCKS WINTERING IN COASTAL NEW JERSEY

by

Orrin E. Jones III

A thesis submitted to the Faculty of the University of Delaware in partial fulfillment of the requirements for the degree of Master of Science in Wildlife Ecology

Spring 2012

© 2012 Orrin E. Jones III
All Rights Reserved

CONSTRUCTING A 24 HOUR TIME-ENERGY BUDGET FOR

AMERICAN BLACK DUCKS WINTERING IN COASTAL NEW JERSEY

by

Orrin E. Jones III

Approved: _____
Christopher K. Williams, Ph.D.
Professor in charge of thesis on behalf of the Advisory Committee

Approved: _____
Douglas W. Tallamy, Ph.D.
Chair of the Department of Entomology and Wildlife Ecology

Approved: _____
Robin W. Morgan, Ph.D.
Dean of the College of Agriculture and Natural Resources

Approved: _____
Charles G. Riordan, Ph.D.
Vice Provost for Graduate and Professional Education

ACKNOWLEDGMENTS

I would like to thank the Black Duck Joint Venture for funding this project. I would also like to thank my graduate committee, Chris Williams, Paul Castelli, and Jake Bowman for giving me the opportunity to study black ducks and further my education at the University of Delaware. The New Jersey Division of Fish and Wildlife, particularly Paul Castelli and Ted Nichols, and Edwin B. Forsythe NWR were fantastic partners that made this collaborative research project a success.

The observers who braved long, cold, and dark observation shifts to gather this data have my utmost appreciation – Jaan Kolts, Matt Carney, Trevor Watts, Kurt Bond, Marissa Gnoinski, Andy Dinges, Ken Duren, Derek Brandt, Taylor Finger, Andrew Halbrunner, Linda Morschauser, and Tom Clifford. Dane Cramer was an integral component in the early stages of this project. Jeremiah Heise was an excellent colleague and friend throughout this long and often challenging process, whose assistance cannot be overstated.

I would like to thank my family and friends for their encouragement over the course of this project. My fellow graduate students have my utmost respect and gratitude for their friendship and advice over my time at the University. Finally, I would like to thank my mother for her continuous love and support and my father for instilling the wonder of whistling wings into a young boy.

TABLE OF CONTENTS

LIST OF TABLES v
LIST OF FIGURES vi
ABSTRACT vii

Chapter

1 AMERICAN BLACK DUCK BEHAVIOR ACROSS THE 24 HOUR PERIOD 1

Introduction 1
Study Area 3
Methods 5
Results 11
Discussion 16
Management Implications 21
References 22

2 INCORPORATING THE NOCTURNAL BEHAVIOR OF AMERICAN BLACK DUCKS INTO ESTIMATES OF DAILY ENERGY EXPENDITURE 38

Introduction 38
Study Area 40
Methods 42
Results 46
Discussion 48
Management Implications 52
References 53

Appendix

A CANDIDATE MODELS USED TO INVESTIGATE THE INFLUENCE OF 8 ENVIRONMENTAL VARIABLES ON THE BEHAVIOR OF AMERICAN BLACK DUCKS WINTERING IN COASTAL NEW JERSEY OCT.–FEB., 2009–2011 63

LIST OF TABLES

Table 1.1 Candidate models used to investigate the influence of 8 environmental variables on the behavior of wintering American black ducks in coastal New Jersey Oct.–Feb. 2009-2011.. 31

Table 1.2 Percent time ($\bar{x}$ ± SE) that American black ducks spent in different behaviors during four time periods while wintering in coastal New Jersey Oct-Feb, 2009–2011. 32

Table 1.3 Top models, within 2 ΔAIC units, used to investigate the influence of 8 environmental variables on the behavior of wintering American black ducks in coastal New Jersey Oct.–Feb. 2009–2011. 33

Table 1.4 Direction of significant relationships for 8 explanatory variables included in candidate models investigating the behavior of American black ducks wintering in coastal New Jersey, during four time periods within the 24 hr day. 35

Table 1.5 Disturbances of American black ducks wintering in coastal New Jersey Oct-Feb, 2009–2011. 37

Table 2.1 Hourly energy expenditure (*HEE*, kJ/bird/hr) by activity and period for American black ducks wintering in coastal New Jersey Oct-Feb, 2009-2011..... 59

Table 2.2 Average energy expenditure per period for wintering American black ducks in coastal New Jersey Oct-Feb, 2009–2011 61

LIST OF FIGURES

Figure 1.1 Study area consisting of estuarine habitats between Great Bay and Absecon Bay, of coastal New Jersey USA..... 30

Figure 1.2 Spatially and temporally distinct time budgets for American black ducks wintering in coastal New Jersey Oct-Feb, 2009–2011..... 36

Figure 2.1 Study area consisting of estuarine habitats between Great Bay and Absecon Bay, of coastal New Jersey USA..... 58

Figure 2.2 Average hourly energy expenditure (*HEE*) for American black ducks wintering in coastal New Jersey during four time periods..... 60

Figure 2.3 Weighted 24 hr energy budget for American black ducks wintering in coastal New Jersey, Oct-Feb, 2009–2011..... 62

ABSTRACT

American black ducks (*Anas rubripes*) have sustained a long-term population decline, as part of a larger effort to address this decline managers have sought to estimate the winter carrying capacity of black ducks. Carrying capacity can be estimated bioenergetically through a comparison of food availability and daily energy expenditure. Recently the food availability for black ducks wintering in the mid-Atlantic was estimated. Previous estimates of daily energy expenditure found a disparity between diurnal behavioral observations and predictive allometric equations. Black ducks have long been known to be active nocturnally, however their actual behavior has never been quantified. Therefore my objectives were to 1) quantify black duck behavior during diurnal, crepuscular, and nocturnal periods, 2) estimate the daily energy expenditure of black ducks, and 3) compare methodologies of estimating daily energy expenditure.

I conducted behavioral observations of black ducks wintering in coastal New Jersey from Oct–Feb 2009–2011. Black ducks were observed across all four time periods: morning crepuscular, diurnal, evening crepuscular, and nocturnal. Nocturnal observations were made using generation III night vision technology. I collected 11,542 observations of black ducks. Using these observations I constructed a time

budget for each period. Black ducks were found to exhibit all behavior states during all periods. However, black ducks exhibited reduced feeding during the morning crepuscular period and reduced flight during the nocturnal period. I modeled the effect of several environmental factors on behavior across all four time periods. Precipitation, temperature, and tide were found to influence black duck behavior across time periods. I investigated the effect of hunting on black duck behavior by comparing behavior across eight categories of spatial and temporal hunting designations. I observed increased feeding during diurnal and nocturnal periods on areas open to hunting when the duck hunting season was closed, while I observed increased resting on areas closed to hunting regardless of whether the hunting season was open.

I converted time budgets into estimates of energy expenditure. On an hourly basis, energy expenditure was lowest during the nocturnal period. I calculated a weighted 24 hr estimate of daily energy expenditure (DEE) by multiplying period specific hourly energy expenditures by the number of hours in each period. Averaged across months, black ducks expended 1,235.65 kJ/bird/day. Using only diurnal observations scaled to a 24 hr period, I estimated DEE to be 1,383.14 kJ/bird/day. I also used a predictive allometric equation which estimated DEE to be 1544.95 kJ/bird/day.

Differences in black duck energy expenditure between periods were driven by differences in flight between periods. Flight is the most energetically costly behavior, however it is also the most difficult behavior to quantify. My estimates of flight

during the morning crepuscular, diurnal, and evening crepuscular periods were higher than previous estimates, leading to a higher estimate of daily energy expenditure. I observed increased rates of disturbance during the morning crepuscular and diurnal periods, perhaps influencing behavior patterns. The nocturnal period appears to be a time of reduced flight and therefore reduced energy expenditure for black ducks. When estimating the DEE of free-living birds, researchers must carefully evaluate their methodology. I used four different methods of estimating DEE which resulted in three statistically different results. To further reduce the error associated with estimating DEE I recommend future research refine black duck specific resting metabolic rates and improve methodologies to quantify flight behavior.

Chapter 1

AMERICAN BLACK DUCK BEHAVIOR ACROSS THE 24-HOUR TIME PERIOD

Introduction

Wildlife behavioral research has historically focused on diurnal periods of activity. In a review of published habitat-use studies between 1970–1990, Beyer and Haufler (1994) found that only 33% of studies addressed nocturnal behavior in their design. Although the first successful nocturnal observation study of North American waterfowl was conducted in 1969 (Swanson and Sargeant 1972), and was followed by studies in the 1980's (Paulus 1984, Paulus 1988*a*, Bergan et al. 1989), subsequent nocturnal behavioral research has been limited due to a lack of methodology, technology, and initiative (Baldassare et al. 1988, Jorde and Owen 1988). Researchers have addressed these nocturnal constraints by limiting their results to 1) diurnal behavior (Hickey and Titman 1983, Johnson and Rohwer 2000), 2) assuming nocturnal behavior is similar to diurnal behavior (Cramer 2009, Ladin 2011), or 3) simply ignoring nocturnal behavior in their design and discussion (Turnbull and Baldasarre 1987, Conomy et al. 1998).

With limited technology and methodology, waterfowl have been shown to have widely variable nocturnal behavior. Previous researchers, forced to make

inferences based on observations hampered by limited technology and low sample sizes, have found waterfowl behavior to be similar during diurnal and nocturnal periods (Albright et al. 1983, Adair et al. 1996). While others have documented that waterfowl behavior is different nocturnally (Paulus 1984, Paulus 1988*a*, Bergan et al. 1989, Henson and Cooper 1994, Custer et al. 1996, Petrie and Petrie 1998, Green et al. 1999).

Three proximate factors may influence the amount of nocturnal activity. First, if a waterfowl species forages in tidal habitats, they may employ nocturnal foraging more when the tide stage is favorable (Albright 1983). Second, nocturnal foraging may represent a "thermodynamic advantage" for wintering waterfowl, promoting the most efficient use of daily energy (Tamisier 1976, Baldassarre et al. 1988, Jorde and Owen 1988, Thompson and Baldassarre 1991). Foraging may increase when thermal demands are the highest and resting and preening may increase when thermal demands are the lowest. This thermodynamic advantage may be especially important for black ducks (*Anas rubripes*) due to the increased effect of solar radiation on their dark plumage (Jorde 1986). Third, nocturnal foraging may be a response to avoid increased human disturbance such as waterfowl hunting (Owen and Williams 1976, Paulus 1984, Conroy et al. 1986, Madsen 1988, Morton et al. 1989*b*).

Although the American black duck is one of the more extensively studied waterfowl species, little is known about their nocturnal behavior. Studies of black duck movement using radio telemetry have reported activity (Albright et al. 1983, Hickey and Titman 1983, Conroy et al. 1986, Morton et al. 1989*a*, Cramer 2009)

and in some cases different habitat use patterns between diurnal and nocturnal periods (Conroy et al. 1986, Morton 2002). However, researchers have never quantified the actual behavior exhibited across all time periods.

Quantifying behavior allows researchers the ability to estimate daily energy expenditure. Due to the lack of information on the nocturnal behavior of black ducks, all prior estimates of winter daily energy expenditure (*DEE*) have been based on diurnal behavior (Hickey 1980, Albright et al. 1983, Morton 1989*b*, Cramer 2009). This is a questionable assumption considering the evidence that waterfowl behavior may be different at night (Paulus 1984, 1988*a*, Bergan et al. 1989, Henson and Cooper 1994, Custer et al. 1996, Petrie and Petrie 1998, Green et al. 1999) and that black ducks are known to be active and may use different habitats nocturnally (Conroy et al. 1986, Morton et al. 1989*a*). Therefore, I had three primary objectives: 1) to quantify the behavior of black ducks during four time periods: morning crepuscular, diurnal, evening crepuscular, and nocturnal, 2) to investigate the effects of environmental variables on behaviors across time periods, and 3) investigate the effects of spatial refuges on behaviors across time periods both within and outside the hunting season.

Study Area

I observed black duck behavior in coastal wetland habitat in Ocean and Atlantic counties, New Jersey, USA (Figure 1.1). I defined my study area as west of the Atlantic Ocean, north of New Jersey state route 30, east of New Jersey state route 9, and south of Little Egg Harbor. This area consistently has the highest counts of wintering black ducks in the Mid-winter Waterfowl Survey (MWS)

throughout the Atlantic Flyway and corresponds closely with MWS New Jersey flight segments 11, 13 and 14 (USFWS MBDC 2010). The major landscape features within the study area are the estuarine systems between Great Bay and Absecon Bay and the managed impoundments at Edwin B. Forsythe National Wildlife Refuge.

Habitat types that black ducks frequent within the study area consist of expansive areas of salt marsh: both high marsh and low marsh, mudflats, subtidal waters, and impounded freshwater and saline wetlands. These habitat types differ by tidal hydrology. High marsh habitat is located above the mean high tide line and is irregularly flooded. The high marsh is dominated by halophytic grasses with the most common being *Spartina patens* and *Distichlis spicata*. Quasi-tidal pools and pannes were occasional landscape features found in the high marsh. Low marsh habitat is located between the mean high tide and low tide line and is regularly flooded. The low marsh is dominated by tall form *Spartina alterniflora*. Mudflat habitat is exposed at low tide and was present in broad flats in bays or in narrow ribbons along the edges of tidal creeks and ditches. Vegetation is generally absent on mudflat habitat; however, occasional tussocks of *Spartina alterniflora* and submerged aquatic vegetation consisting of sea lettuce (*Ulva lactuca*) are present. Subtidal habitat is located below the mean low tide line and is rarely exposed. Subtidal habitat is generally absent of vegetation, with the exception of beds of submerged aquatic vegetation, the most common being *Ulva lactuca* (Tiner 1987, Collins and Anderson 1994). Also located within the study

area were 1,400 acres of freshwater and saline impoundments managed by Edwin B. Forsythe National Wildlife Refuge.

The historical mean temperature and precipitation of coastal New Jersey during months included in this study were 14.0°C and 8.4 cm in October, 8.3°C, and 8.1 cm in November, 2.94°C and 9.0 cm in December, 0.72°C and 8.9 cm in January, and 0.83°C and 8.3 cm in February (Office of the New Jersey State Climatologist 2010). The average tidal range of the study area was 0.978 meters and fluctuated on a approximately 12 hr and 25 minute cycle (NOAA 2012).

Methods

I collected behavioral data between the third week in October and the third week in February 2009–2010 and 2010–2011. I quantified the morning crepuscular, diurnal, evening crepuscular, and nocturnal behavior of American black ducks during paired 6 hr observation sessions at the same location beginning 12 hr apart. Beginning observation sessions 12 hr apart allowed for a comparison between diurnal and nocturnal periods during similar tide cycles. I established 44 blind sites loosely grouped into sets of two or three for logistical access by observation teams. I randomly chose grouped blind sites for daily observations. I based blind site location on known concentrations of black ducks from field observations of black duck activity, local knowledge, and previous research. Access throughout the study period and the ability to minimize observer disturbance of black ducks was also considered when establishing locations. Each blind site was located a minimum of 400 m apart and had a predetermined field of view that did not overlap with that of other blinds.

I divided the 24-hr day into four observation periods; morning (03:00–09:00), diurnal (09:00–15:00), evening (15:00–21:00), and nocturnal (21:00–03:00). Each week was assigned a pair of time periods, either morning/evening or diurnal/nocturnal and weekly assignments alternated. Weekly observations began Tuesday morning and continued until Sunday.

A single observer arrived at a blind site ≥30 min before the designated observation period and either erected or entered an observation blind. Blinds were located in a position where they maximized viewing opportunity and minimized the potential of influencing waterfowl behavior. At the start of the observation period, observers scanned the surrounding area for waterfowl. Through a series of preseason tests of I identified 200 m as the maximum range that an observer could reliably determine behavior and species with the night vision equipment used in this study, similar ranges have been identified in recent studies using similar technology (Allison and Destefano 2006). Therefore, during diurnal observations only birds ≤200 m were included to ensure equal nocturnal and diurnal sampling coverage. Observers used 8x42 binoculars for diurnal observations and a generation 3, 6x night vision scope with an 8° field of view and a 64 lp/mm resolution (Morovision MV 760 Generation 3 Pinnacle) for nocturnal observations. Any waterfowl detected were identified to species and observed using the instantaneous scan sampling method (Altmann 1974). Species identification was possible during the nocturnal period using a variety of cues such as speculum color, head size and shape, bill color, and plumage color and pattern (light vs dark). The moment the observer detected the bird, they quietly

recorded behavior onto a micro-cassette tape or digital voice recorder. Behavior categories were: feeding, loafing, sleeping, comfort, swimming, alert, flying, walking, agonistic, and courtship. This was repeated every 10 min for the duration of the 6 hr observation period. Previous research has shown that black duck behavior becomes statistically independent with a time lag of 5 minutes between scans (Morton 1989*b*). Any disturbance event that altered the behavior of the birds while being scanned was identified and recorded.

Observers recorded environmental conditions (temperature, wind speed, cloud cover, and precipitation) on the hour. Temperature and wind speed were measured using a handheld anemometer (Kestrel 1000 series). Hourly precipitation rate (water equivalent) recorded at Atlantic City International Airport was incorporated into each observation (National Climatic Data Center 2011). The tidal stage (high, low, ebb, and flood) was recorded for each scan. Tide height was determined using tide height readings taken every 6 min by the New Jersey Tide Telemetry System (Hoppe 2007). The blind site, observer, presence of birds on arrival, hunting season designation (open vs. closed), sunrise/sunset times, and moon phase were also recorded.

I tested for correlation between covariates. I considered pairs of variables with a Pearson correlation coefficient >0.75 as collinear and removed them from further analysis. Wind-chill correlated with both wind and temperature and therefore was removed. The weather category was correlated with both cloud cover and precipitation rate and was removed. I further tested dependent and independent variables for normality, and as necessary transformed them using

either square root or log transformations. I detected a year effect across all behaviors except for walking. Due to a sample size of two years, yearly inferences would have been limited, therefore I blocked on year for all subsequent analyses.

Measuring Period Effects on Behavior

I compared the proportion of time spent in each behavioral state during morning crepuscular, diurnal, evening crepuscular, and nocturnal periods using a multiple analysis of variance (MANOVA, $\alpha = 0.05$) blocking on year. If different, I conducted a univariate analysis of variance (ANOVA, $\alpha = 0.05$) blocking on year, comparing each behavior across the 4 time periods. A Tukey's post-hoc pair-wise comparison was used to compare behavior between periods.

Measuring Environmental Effects on Behavior

Biological inferences have traditionally been drawn from null hypothesis testing and test statistics associated with a probability threshold. Over the last decade, ecology and evolutionary research has begun to use Information-Theoretic (IT) model selection based on likelihood theory (Hilborn and Mangel 1997, Anderson et al. 2000, Burnham and Anderson 2002). This approach has several advantages. First, researchers are no longer reliant upon a probability threshold to evaluate single models. Instead, using an IT approach, researchers can compare models with biological relevance for relative support based on their data (Johnson and Omland 2004, Garamszegi et al. 2009). Second, Speiss and Neumeyer (2010) recently suggested that when working with nonlinear and complex relationships the traditional use of R^2 in hypothesis testing may be a poor

measure of goodness of fit. Information-Theoretic approaches were found to be a more valid for this type of data (Spiess and Neumeyer 2010). Third, models can be ranked and weighted to provide a quantitative measure of relative support for each competing hypothesis. Fourth, in instances where models have similar levels of support, researchers can average top models to make parameter specific estimates and predictions. As a result of these advantages, there has recently been a call for greater use of IT modeling in the field of behavioral ecology (Garamszegi 2011) where multiple hypotheses may best describe a complex topic such as animal behavior. It is also well understood that black duck and waterfowl behavior is influenced by a wide range of environmental factors (Hickey and Titman 1982, Brodsky and Weatherhead 1984, Jorde et al. 1984, Paulus 1984, Paulus 1988*a*, and Gauthier et al. 1988); therefore, I used an IT approach to allow for multiple biological realities. This approach also allowed me the option of model averaging to better identify the direction and strength of parameter effects.

I used an Information-Theoretic approach to investigate the influence of 8 explanatory variables (precipitation rate, cloud cover, wind speed, temperature, tidal height, ice cover, moon size, and hunting season) on behaviors during each of the 4 time periods. I *apriori* constructed 16 candidate models including a null model, for behaviors during each of the 4 periods. I used Akaike's Information Criterion (AIC) (Burnham and Anderson 2002) to rank models for each behavior during each time period. I model averaged top models which I defined as those within 2 ΔAIC units (Appendix B). Within top model sets, I calculated a

weighted-average of beta (β) values of each explanatory variable based on the Akaike weight of each model in which that variable occurred. I further compared the variable's weighted parameter estimate with its weighted standard error to delineate its effect on behavior. If the weighted standard error did not cross zero when added or subtracted from the weighted parameter estimate, I considered the variable to have a significant relationship with that behavior (Hu 2007). I then reported the direction, positive or negative, of the relationship between the variable and the behavior during the given time period.

Spatial and Temporal Effects of Hunting on Behavior

Lastly, I investigated differences in behaviors between areas open to hunting and areas closed to hunting during both open and closed duck hunting season. I defined areas open to hunting as any area where hunting could legally occur, which primarily consisted of federal and state properties. I defined areas closed to hunting as areas where waterfowl hunting was illegal, this primarily consisted of portions of the Edwin B. Forsythe National Wildlife Refuge that were closed to public access (Figure 1.1). I divided diurnal and nocturnal observations into eight categories based on whether the duck hunting season was open or closed and 4 spatially or temporally distinct categories: 1) diurnal observations on areas open to hunting, 2) diurnal observations on non-hunting areas, 3) nocturnal observations on areas open to hunting, and 4) nocturnal observations on non-hunting areas. I also calculated the number of observations and the average flock size for each of these eight categories. I used an analysis of variance (ANOVA, $\alpha = 0.05$) to compare each behavior between eight categories

of observations. Tukey's post-hoc pair-wise comparison's were used to identify differences between each category.

Disturbance Events

Anytime the behavior of the birds under observation suddenly changed to alert, walking, swimming, or flying I considered the birds disturbed. Observers then attempted to determine the cause of the disturbance. I calculated a disturbance rate by dividing the number of disturbances in each time period by the number of ten-minute scans with black ducks present during that same time period.

Results

I conducted 742, 6 hr observation sessions over 160 day/night pairs. The waterfowl hunting season was open during 88 of the day/night pairs and closed during 72 pairs. Black ducks were observed in 11,542 10-min scans. Of those scans, 589 were during the morning crepuscular period, 4,456 were during the diurnal period, 708 were during the evening crepuscular period, and 5,863 were during the nocturnal period.

Period Effects on Behavior

I constructed a time budget for each period using observational data (Table 1.2). Behaviors differed across observation periods blocking on year (MANOVA, Hotelling's Trace statistic: $F_{24,\ 34,799} = 14.112$ $P < 0.001$). Feeding behavior varied across time periods blocking on year (ANOVA: $F_{3,\ 11,608} = 38.923$, $P < 0.001$). Pair-wise comparisons indicated that morning crepuscular and diurnal feeding behavior was significantly lower than feeding during the

evening crepuscular and nocturnal periods (Table 1.2). Resting behavior differed across time periods blocking on year ($F_{3, 11,608}$ =3.042, P = 0.028). Resting behavior was lower during the evening crepuscular period than during the nocturnal period (Table 1.2). Comfort behavior varied across time periods blocking on year ($F_{3, 11,608}$= 3.121, P = 0.025) and was highest during the diurnal period and lowest during the nocturnal period with no difference between crepuscular periods (Table 1.2).

Locomotion behaviors consist of swimming, walking and flying. Swimming behavior varied across time periods blocking on year ($F_{3, 11,608}$ = 7.158, P < 0.001). Swimming was highest during the morning crepuscular period and lowest during the evening crepuscular period (Table 1.2). Walking behavior did not differ across time periods blocking on year ($F_{3, 11,608}$ = 1.714, P = 0.162). Flying behavior varied across time periods blocking on year ($F_{3, 11,608}$ = 54.032, P < 0.001). Flying was significantly lower during the nocturnal period than morning crepuscular, diurnal, and evening crepuscular periods. Flying during the morning crepuscular period was significantly higher than flying during the diurnal or nocturnal periods (Table 1.2).

Alert behavior was not statistically different across time periods blocking on year ($F_{3, 11,608}$ = 0.618, P = 0.604). No statistically significant differences were found in agonistic ($F_{3, 11,608}$= 0.687, P = 0.560) and courtship ($F_{3, 11,608}$ = 0.234, P = 0.873) behavior across time periods blocking on year (Table 1.2).

To simplify statistical analyses and avoid misrepresenting uncommon behaviors, I removed behaviors that represented less than 5% of total behavior

from further analyses. These behaviors consisted of comfort (3.39%), alert (1.50%), walking (0.83%), agonistic (0.05%), and courtship (0.08%).

Environmental Effects on Behavior

All competing models of environmental variables affecting behaviors by time period are listed in Appendix A. During the morning crepuscular period, the top 2 models affecting feeding behavior were PRECIP+TEMP and PRECIP (Table 1.3). Feeding was negatively influenced by increasing temperature and positively influenced by increasing precipitation (Table 1.4). Resting was best predicted by the TEMP+CLOUD model (Table 1.3). Resting was negatively influenced by increasing temperature and positively influenced by increasing cloud cover. Swimming was predicted by four top models including: PRECIP, Null, TIDE, and PRECIP+TEMP (Table 1.3). Swimming was positively influenced by tidal height and negatively influenced by precipitation, while temperature did not have significant relationship (Table 1.4). Morning crepuscular flying was best predicted by the TIDE+TEMP model (Table 1.3). Flying was positively influenced by increasing temperature and tidal height (Table 1.4).

Diurnal feeding was negatively was best predicted by the TIDE+TEMP model (Table 1.3). Feeding was negatively influenced by tidal height and ice cover (Table 1.4). The TIDE+ICE and ICE COVER models best predicted diurnal resting (Table 1.3). Resting was positively influenced by increasing tidal height and ice cover (Table 1.4). Swimming was best predicted by the TEMP+CLOUD model (Table 1.3). Swimming was positively influenced by

increasing temperature and increasing cloud cover (Table 1.4). Diurnal flying was best predicted by the TIDE+TEMP and TIDE+ICE models (Table 1.3), flying was positively influenced by increasing temperature and tidal height but negatively influenced by ice cover (Table 1.4).

Evening crepuscular feeding was best predicted by the TIDE+MOON model (Table 1.3). Feeding was negatively influenced by increasing tidal height, and a larger moon phase. The WIND SPEED model best predicted resting (Table 1.3) with a positive relationship between resting and wind speed (Table 1.4). Swimming was best predicted by the TIDE+MOON and MOON PHASE models (Table 1.3). Swimming was positively influenced by increasing tidal height and a larger moon phase (Table 1.4). PRECIP+TEMP best predicted evening crepuscular flying (Table 1.4). Flying was positively influenced by increasing temperature and precipitation (Table 1.4).

Nocturnal feeding was best predicted by the TIDE+TEMP model (Table 1.3). Feeding was negatively influenced by increasing temperature and tidal height (Table 1.4). The TEMP+CLOUD model best predicted nocturnal resting (Table 1.3). Resting was positively influenced by increasing temperature and cloud cover (Table 1.4). Swimming was best predicted by 4 top models: TIDE+TEMP, TIDE, TIDE+MOON, and HUNT+TIDE (Table 1.3). Swimming was positively influenced by hunting season and increasing tidal height, but negatively influenced by increasing temperature and larger moon phase (Table 1.4). Nocturnal flying was best predicted by the TIDE+TEMP model (Table 1.3).

Flying was negatively positively influenced by increasing temperature and tidal height (Table 1.4).

Spatial and Temporal Effects of Hunting on Behavior

I collected the fewest observations during the diurnal period on areas open to hunting when the hunting season was closed. Conversely, I collected the most observations during the nocturnal period on areas closed to hunting when the hunting season was open. I observed similar flock sizes during diurnal and nocturnal periods on areas open to hunting. However, on non-hunting areas, I observed larger flock sizes during the diurnal period than during the nocturnal period (Figure 1.2).

Feeding behavior differed between the eight categories ($F_{7, 10,311} = 21.008$, $P < 0.001$). While nocturnal feeding was always higher than diurnal feeding in all spatial and temporal hunting categories, both diurnal and nocturnal feeding were highest on hunting areas when the hunting season was closed (Figure 1.2). Resting behavior differed between categories ($F_{7, 10,311} = 33.671$, $P < 0.001$). During both diurnal and nocturnal periods black ducks rested more on non-hunting areas than on hunting areas regardless of whether the hunting season was open. Swimming differed between categories ($F_{7, 10,311} = 26.498$, $P < 0.001$). During both diurnal and nocturnal periods swimming was highest on hunting areas during the hunting season. Lastly, flying differed between categories ($F_{7, 10,311} = 21.008$, $P < 0.001$) and was highest during the diurnal period and lowest during the nocturnal period (Figure 1.2).

Disturbance

I observed 67 instances where black ducks were visibly disturbed during a scan. When disturbed black ducks would stop their prior behavior and exhibit alert, swimming, walking, or flying behaviors. I observed the most disturbances during the diurnal period (n = 46), followed by the nocturnal period (n = 10), the morning crepuscular period (n = 9), and the evening crepuscular period (n = 2) (Table 1.5). Disturbance during the diurnal and morning crepuscular periods was most commonly caused by human activity, followed by interspecific disturbances primarily from avian predators. During the nocturnal period mammalian predators were the most common cause of disturbance, followed by human activities (Table 1.3). I observed more instances of disturbance in non-hunting areas (52) than hunting areas (15) (Table 1.5).

Discussion

I observed black ducks to exhibit all behaviors nocturnally. While nocturnal activity has been reported through anecdotal descriptions (Mendall 1949, Hartman 1963, Morton et al. 1989*a*,*b*) and telemetry (Albright 1983, Conroy et al. 1986, Costanzo 1988, Morton et al. 1989*a*), the actual behavior black ducks exhibit nocturnally has never been adequately quantified. This study employed a novel approach to quantifying black duck behavior through the use of technologically advanced equipment and long observation sessions to quantify behavior during the diurnal, crepuscular, and nocturnal periods.

Nocturnal feeding of black ducks has been suggested as a behavioral response to diurnal disturbance (Mendall 1949, Hartman 1963, Conroy at al. 1986, Costanzo 1988, Morton et al. 1989*a,b*). Albright (1981, 1983) further

suggested that nocturnal foraging was important to the survival of overwintering black ducks in Maine due to increased food resources at low tide. My findings support these studies in several ways. I observed a higher proportion of black ducks feeding during the evening crepuscular and nocturnal periods than during the morning crepuscular and diurnal periods (Table 1.2). Temperature and tidal height had a negative relationship with feeding during three of the four periods (Table 1.4). These findings suggest that tide height and temperature have a greater influence on black duck feeding behavior than the time of day. Black ducks appear to use nocturnal feeding to take advantage optimal tide conditions and thermodynamically advantageous conditions to meet their energetic demands.

In one of the few studies to ever explicitly address the nocturnal resting of black ducks, Brodsky and Weatherhead (1985) reported that black ducks spent 100% of the nocturnal period resting. In contrast, I found black ducks to rest at similar rates during the morning crepuscular, diurnal, and nocturnal periods, with reduced resting during the evening crepuscular period. These findings support Paulus (1988) who did not find a difference between diurnal and nocturnal resting in mottled ducks. Interestingly, during the nocturnal period, black ducks rested more as the temperature increased. Further, during the morning crepuscular and nocturnal periods, resting increased with cloud cover, while diurnal resting increased with tide height and ice cover (Table 1.4). It may be most energetically efficient for black ducks to loaf and sleep during warm temperatures (cloudy nights, clear days) and forage in colder temperatures (clear nights and cloudy days). Jorde (1986) suggested that the dark plumage of black ducks would be

particularly advantageous for absorbing solar radiation and helping to offset thermodynamic costs. Albright (1983) found that black ducks wintering in Maine curtailed feeding and increased resting as temperatures fell below -10° to -20°C, thereby supporting Brodsky and Weatherhead's (1985) report of black ducks exclusively resting at night in Ontario. Low temperatures in my study rarely reached below -10°C, therefore my data may not reflect that behavioral response.

Flying was lowest during the nocturnal period. Paulus (1984, 1988) reported that gadwalls and mottled ducks flew less at night compared to the day. Link et al. (2011*a*) reported that radio-marked mallards were most active 20 to 90 minutes after sunset, but once they selected a nocturnal location they rarely flew until the morning crepuscular period (Link et al. 2011*b*). I detected fewer natural and anthropogenic disturbances during the nocturnal period as compared to the other three time periods, particularly during the morning crepuscular and diurnal periods. Black ducks may be disturbed less often at night and therefore fly less.

I acknowledge reduced flying during the nocturnal period could also be effected for by a methodological bias. Costanzo (1988), working with a sample of radio-marked black ducks in the same study area, reported that the daily movements of black ducks were not statistically different between day and night. However, he states, "nocturnal movements were generally smaller than diurnal movements" (Costanzo 1988). Detecting black ducks flying at night using night vision was probably more difficult than using binoculars during the day, therefore my nocturnal estimates of flight may be biased low.

My estimates of flight during the morning crepuscular, diurnal, and evening crepuscular periods were higher than all published values for black ducks (Hickey and Titman 1983, Morton 1989*b*, Cramer 2009). I estimated that black ducks would spend approximately 65 minutes in flight during a 24 hr period. My methodology of recording all birds within a 200 m radius circle differs from previous work and may have resulted in the observed increased rates of flight. Previous studies using instantaneous scan sampling targeted a single flock of birds (Morton 1989*b*) and may have missed birds flying that were not part of the flock under observation. Paulus (1988*b*) and Michot (2006) raise concerns about instantaneous scan sampling underrepresenting flight behavior as flying birds are quickly out of observation range and the duration of their flight is unknown; therefore my estimates may still be underestimates.

Conroy et al. (1986) and Costanzo (1988), with whom I share the study area, described a movement pattern of black ducks using the impoundments of Forsythe NWR as a diurnal refuge from waterfowl hunting. Nocturnally they found this pattern reversed, black ducks used the salt marsh to a much greater extent than the Refuge impoundments. Morton (1989*a*) reported a similar habitat use pattern of black ducks at Chincoteague NWR, where black ducks used Refuge impoundments during the day and salt marsh habitat at night. Costanzo (1988) further found that black ducks used salt marsh areas closed to hunting preferentially to salt marsh areas open to hunting. All three authors inferred that black ducks were feeding in the salt marsh at night and using the Refuge impoundments as diurnal roosts.

While my observations support the movement patterns described by Conroy, Costanzo, and Morton, my behavior data reveals some interesting differences. I also observed black ducks flying into Refuge impoundments during the morning crepuscular and diurnal periods and then leaving the Refuge impoundments during the evening crepuscular and nocturnal periods. Supporting this, I observed the largest flock size of black ducks diurnally on non-hunting areas (which includes Refuge impoundments). Nocturnally, the average flock size on non-hunting areas was substantially smaller, roughly half the size (Figure 1.2). Interestingly, this pattern was the same regardless of whether the hunting season was open or closed. On hunting areas I was much more likely to observe black ducks nocturnally although the flock size was roughly the same diurnally and nocturnally. When the hunting season was open black ducks fed at similar rates on areas open to hunting and non-hunting areas during both diurnal and nocturnal periods. Conversely, when the hunting season was closed black ducks fed more during both diurnal and nocturnal periods on hunting areas. Black ducks rested more on non-hunting areas regardless of whether the hunting season was open or closed. Black ducks flew more during diurnal periods on both hunting and non-hunting areas (Figure 1.2).

When viewed in conjunction with the previous radio-telemetry work my behavior observations provide a more complete understanding of the 24 hr behavior of wintering black ducks. Black ducks rest more on non-hunting areas regardless of the time of day or hunting season. Black ducks feed more on hunting areas when the hunting season is closed. I observed more black ducks on

non-hunting areas during diurnal periods then during nocturnal periods. These results suggest that wintering black ducks use non-hunting areas as spatial and temporal sanctuaries.

Management Implications

I echo previous authors (Costanzo 1988, Morton 1989*a*,*b*, Morton 2002, Cramer 2009) in documenting the use of non-hunting areas by wintering black ducks. Managers should also consider the effect of ice on black ducks. During severe cold the energetic demand of black ducks increases while the habitat available to them decreases. Non-hunting areas should include areas that provide open water and food resources during severe periods of ice. During severe ice cover Edwin B. Forsythe NWR provides black ducks with low disturbance resting and foraging habitat in the Little Beach and Holgate Beach units. These units are remote barrier beaches designated as wilderness areas.

References

Adair, S. E., J. L. Moore, and W. H. Kiel Jr. 1996. Wintering diving duck use of coastal ponds: an analysis of alternative hypotheses. Journal of Wildlife Management 60:83–93.

Albright, J. J. 1981. Behavioral and physiological responses of coastal wintering black ducks to changing weather in Maine. Thesis, University of Maine Orono, Maine, USA.

Albright, J. J. 1983. The effects of winter weather on the behavior and energy reserves of black ducks in Maine. Transactions of the Northeast Section of the Wildlife Society 40:118–128.

Allison, N. L., and S. Destefano. 2006. Equipment and techniques for nocturnal wildlife studies. Wildlife Society Bulletin 34:1036–1044.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–267.

Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64:912–923.

Baldassare, G. A., S. L. Paulus, A. Tamisier, and R. D. Titman. 1988. Workshop summary techniques for timing activity of wintering waterfowl. Pages

181–188 *in* M. W. Weller, editor. Waterfowl in winter. University of Minnesota Press, Minneapolis, USA.

Bergan, J. F., L. M. Smith, and J. M. Mayer. 1989. Time-activity budgets of diving ducks wintering in South Carolina. Journal of Wildlife Management 53:769–776.

Beyer, D. E. Jr., and J. B. Haufler. 1994. Diurnal versus 24-hour sampling of habitat use. Journal of Wildlife Management 58: 178–180.

Brodsky, L. M., and P. J. Weatherhead. 1984. Behavioral thermoregulation in wintering black ducks: roosting and resting. Canadian Journal of Zoology 62:1223–1226.

Brodsky, L. M., and P. J. Weatherhead. 1985. Variability in behavioral response of wintering black ducks to increased energy demands. Canadian Journal of Zoology 63:1657–1662.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information–theoretic approach. Springer–Verlag, New York, New York, USA.

Collins, B. R., and K. H. Anderson. 1994. Plant communities of New Jersey: a study in landscape diversity. Rutgers University Press, New Brunswick, New Jersey, USA.

Conomoy, J. T., J. A. Collazo, J. B. Dubovsky, and W. J. Fleming. 1998. Dabbling duck behavior and aircraft activity in coastal North Carolina. Journal of Wildlife Management 62:1127–1134.

Conroy, M. J., G. R. Costanzo, and D. B. Stotts. 1986. Winter movements of American black ducks in relation to natural and impounded wetlands in New Jersey. Pages 31–45 *in* Whitman, W. R., and W. H. Meredith, editors. Waterfowl and wetlands symposium: proceedings of a symposium on waterfowl and wetlands management in the coastal zone of the Atlantic flyway. Delaware Department of Natural Resources and Environmental Control, Dover, Delaware, USA.

Costanzo, G. R. 1988. Wintering ecology of black ducks along coastal New Jersey. Dissertation, Cornell University. Ithaca, New York, USA.

Cramer, D. M. 2009. Estimating habitat carrying capacity for American black ducks in wintering in Southern New Jersey. Thesis, University of Delaware. Newark, Delaware, USA.

Custer, C. M., T. W. Custer, and D. W. Sparks. 1996. Radio telemetry documents 24-hour feeding activity of wintering lesser scaup. Wilson Bulletin 108:556–566

Garamszegi, L. Z. S. Calhim, N. Dochtermann, G. Hegyi, P. L. Hurd, C. Jorgensen, N. Kutsukake, M. J. Lajeunesse, K. A. Pollard, H. Schielzeth, M. R. E. Symonds, and S. Nakagawa. 2009. Changing philosophies and tools for statistical inferences in behavioral ecology. Behavioral Ecology 20:1363–1375.

Garamszegi, L. Z. 2011. Information-theoretic approaches to statistical analysis in behavioural ecology: An introduction. Behavioral Ecology and Sociobiology 65:1–11.

Gauthier, G., Y. Bedard, and J. Bedard. 1988. Habitat use and activity budgets of greater snow geese in spring. Journal of Wildlife Management 52:191–201.

Green, A. J., A. D. Fox, B. Hughes, and G. M. Hilton. 1999. Time-activity budgets and site selection of White-headed Ducks *Oxyura leucocephala* at Burdur Lake, Turkey in late winter. Bird Study 46:62–73.

Hartman, F. E. 1963. Estuarine wintering habitat for black ducks. Journal of Wildlife Management 27:339–347.

Henson, P., and J. A. Cooper. 1994. Nocturnal behavior of breeding trumpeter swans. The Auk 111:1013–1018.

Hickey, T. E., and R. D. Titman. 1983. Diurnal activity budgets of Black Ducks during their annual cycle in Prince Edward Island. Canadian Journal of Zoology 61:743–749.

Hilborn, R., and M. Mangel. 1997. The Ecological Detective: Confronting models with data, Princeton University Press, New Jersey, USA.

Hoppe, H. L. 2007. New Jersey tide telemetry system. U.S. Geological Survey fact sheet 2007-3064. < http://pubs.usgs.gov/fs/2007/3064/> Accessed March 12th 2012.

Hu, S. 2007. Akaike's Information Criterion. Center for research in scientific computation, North Carolina State University, Raleigh, North Carolina USA.

Johnson, J. B., and K. S. Omland. 2004. Model selection in ecology and evolution. Trends in Ecology and Evolution 19:101–108.

Johnson, W. P. and F. C. Rohwer. 2000. Foraging behavior of green-winged teal and mallards on tidal mudflats in Louisiana. Wetlands 20:184–188.

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. The Condor 86:258–265.

Jorde, D. G. 1986. Nutritional and thermodynamic aspects of the ecology of black ducks wintering in Maine. Dissertation, University of Maine. Orono, Maine, USA.

Jorde, D. G., and R. B. Owen. 1988. The need for nocturnal activity and energy budgets of waterfowl. Pages 169–177 *in* M. W. Weller, editor. Waterfowl in winter. University of Minnesota Press, Minneapolis, USA.

Ladin, Z. S., P. M. Castelli, S. R. McWilliams, and C. K. Williams. 2011. Time energy budgets and food use of Atlantic brant across their wintering range. Journal of Wildlife Management 75:273–282.

Link, P. T., A. D. Afton, R. R. Cox Jr., and B. E. Davis. 2011*a*. Daily movements of female mallards wintering in southwestern Louisiana. Waterbirds 34:422–428.

Link, P. T., A. D. Afton, R. R. Cox Jr., and B. E. Davis. 2011*b*. Use of habitats by female mallards wintering in southwestern Louisiana. Waterbirds 34:429–438.

Madsen, J. 1988. Autumn feeding ecology of herbivorous wildfowl in the Danish Wadden Sea, and impact of food supplies and shooting on movements. Danish Review of Game Biology 13:1–32.

Mendall, H. L. 1949. Food habits in relation to black duck management Maine. Journal of Wildlife Management 13:64–101.

Michot, T. C., M. C. Woodin, S. E. Adair, and E. B. Moser. 2006. Diurnal time-activity budgets of redheads (*Aythya americana*) wintering in seagrass beds and coastal ponds in Louisiana and Texas. Hydrobiologia 567:113–128.

Morton, J. M., R. L. Kirkpatrick, M. R. Vaughan, and D. F. Stauffer. 1989*a*. Habitat use and movements of American black ducks in winter. Journal of Wildlife Management 53:390–400.

Morton, J. M., A. C. Fowler, and R. L. Kirkpatrick. 1989*b*. Time and energy budgets of American black ducks in winter. Journal of Wildlife Management 53:401–410.

Morton, J. M. 2002. Effects of human disturbance on wintering American black ducks. Pages 11-16 *in* M. C. Perry, editor. Black ducks and their Chesapeake Bay habitats: proceedings of a symposium. U.S. Geological Survey, Biological Resources Discipline Information and Technology Report USGS/BRD/ITR–2002–0005, 44p.

National Climatic Data Center. 2011. Quality controlled local climatological data: Atlantic City International Airport, hourly precipitation. National Ocean and Atmospheric Administration. <http://cdo.ncdc.noaa.gov/qclcd/QCLCD> Accessed September 8th 2011.

National Ocean and Atmospheric Administration. 2012. Tidal station locations and ranges: main marsh thorofare.

<http://tidesandcurrents.noaa.gov/tides07/tab2ec2b.html#31> Accessed April 8th 2012.

Office of the New Jersey State Climatologist. 2010. Coastal New Jersey Monthly Temperature 1895–2010. <http://climate.rutgers.edu/stateclim_v1/data/index.html> Accessed April 6, 2010.

Owen, M., and G. Williams. 1976. Winter distribution and habitat requirements of wigeon in Britain. Wildfowl 27:83–90.

Paulus, S. L. 1984. Activity budgets of non-breeding gadwalls in Louisiana. Journal of Wildlife Management 48:371–380.

Paulus, S. L. 1988*a*. Time-activity budgets of mottled ducks in Louisiana in winter. Journal of Wildlife Management 52:711–718.

Paulus, S.L. 1988b. Time-activity budgets of nonbreeding Anatidae: a review. Pages 135–152 *in* M. W. Weller, editor, Waterfowl in winter. University of Minnesota Press. Minneapolis, USA.

Petrie, S. A., and V. A. Petrie. 1998. Activity budget of white-faced whistling ducks during winter and spring in northern Kwazulu-Natal, South Africa. Journal of Wildlife Management 62:1119–1126.

Spiess, A-N, and N. Neumeyer. 2010. An evaluation of R^2 as an adequate measure for nonlinear models in pharmacological and biochemical research: a Monte Carlo approach. BMC Pharmacology 10:6.

Swanson, G. A., and A. B. Sargeant. 1972. Observation of nighttime feeding behavior of ducks. Journal of Wildlife Management 36:959–961.

Tamisier, A. 1976. Diurnal activities of Green-winged teal and Pintail wintering in Louisiana. Wildfowl 27:19–32.

Tiner Jr., R. W. 1987. A field guide to coastal wetland plants of the northeastern United States. The University of Massachusetts Press, Amherst, USA.

Thompson, J. D., and G. A. Baldassarre. 1991. Activity patterns of neartic dabbling ducks wintering in Yucatan, Mexico. The Auk 108:934–941.

Turnbull, R. E., and G. A. Baldassarre. 1987. Activity budgets of mallards and American wigeon wintering in east-central Alabama. Wilson Bulletin 99:457–464.

United States Fish and Wildlife Service Migratory Bird Data Center [USFWS MBDC]. 2010. Midwinter waterfowl index database. . <https://migbirdapps.fws.gov/> Accessed 3/29/2010.

Figure 1.1. Study area consisting of estuarine habitats between Great Bay and Absecon Bay, of coastal New Jersey USA. Property owned by the U.S. Fish and Wildlife Service Edwin B. Forsythe NWR and the New Jersey Division of Fish and Wildlife is identified. Observation blind sites are identified with dots.

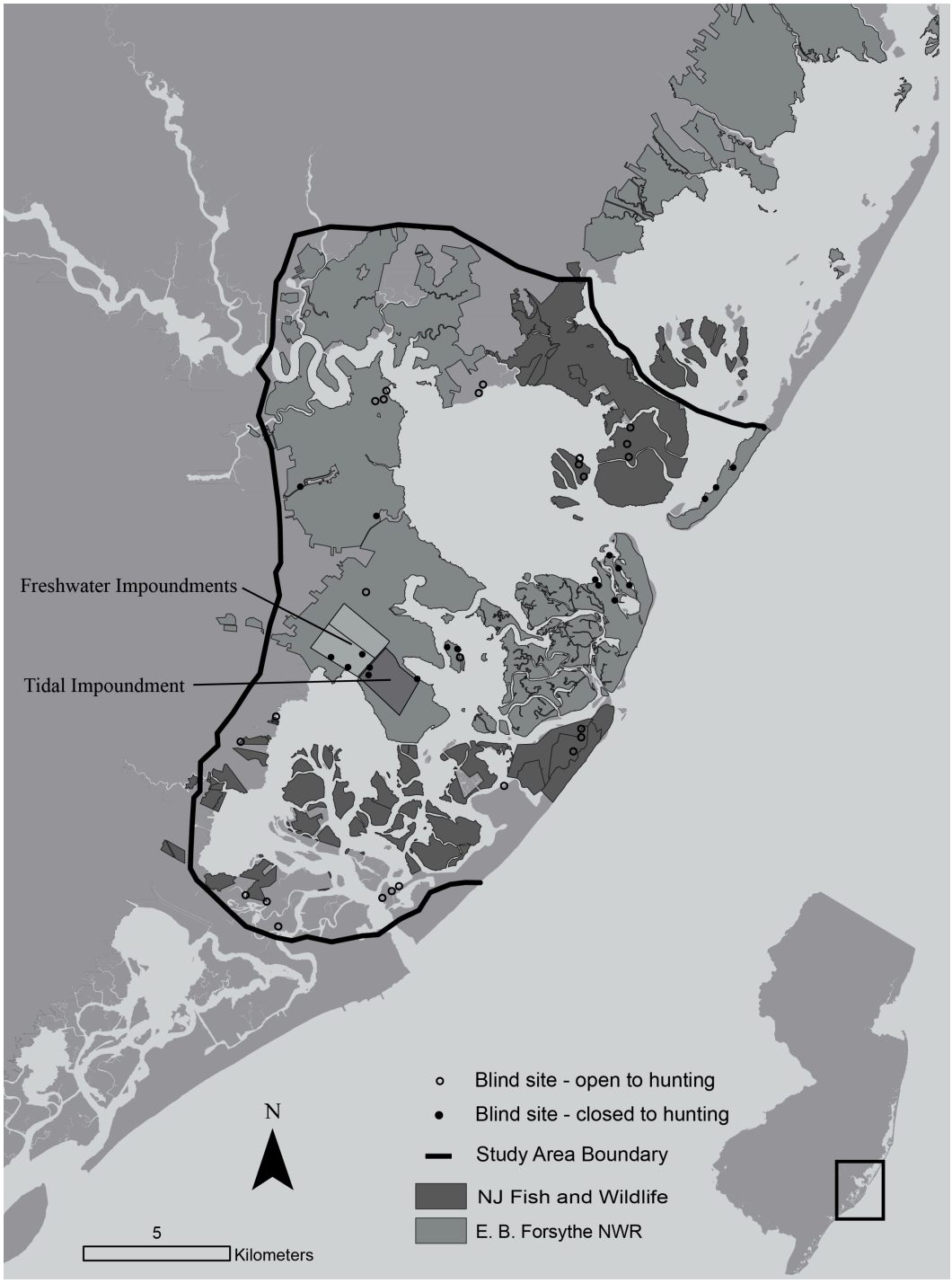


Table 1.1 Candidate models used to investigate the influence of 8 environmental variables on the behavior of wintering American black ducks in coastal New Jersey Oct.–Feb. 2009-2011.

Model	**K**	**N**
Null	1	11,542
Hunting Season (HUNT)	2	11,542
Moon Phase (MOON)	2	11,542
Cloud Cover (CLOUD)	2	11,542
Temperature (TEMP)	2	11,542
Precipitation (PRECIP)	2	11,542
Wind Speed (WIND)	2	11,542
Tide Height (TIDE)	2	11,542
Ice Cover (ICE)	2	11,542
TIDE+TEMP	3	11,542
TEMP+CLOUD	3	11,542
TIDE+MOON	3	11,542
PRECIP+TEMP	3	11,542
TIDE+ICE	3	11,542
HUNT+TIDE	3	11,542
HUNT+TEMP	3	11,542

Table 1.2. Percent time ($\bar{x}$ ± SE) that American black ducks spent in different behaviors during four time periods while wintering in coastal New Jersey Oct-Feb, 2009–2011.

	Percent time spent per behavior										
	Morning Crepuscular		Diurnal		Evening Crepuscular		Nocturnal		ANOVA results		
Behavior	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	*F*	df	P
Feed	24.35_{ab}	1.36	29.50_{cd}	0.53	39.70_{ac}	1.42	36.21_{bd}	0.51	38.923	3	< 0.00
Rest	26.46	1.41	26.45	0.51	22.23_{a}	1.21	27.48_{a}	0.49	3.042	3	0.03
Comfort	3.12	0.42	5.14_{a}	0.20	3.46	0.41	2.09_{a}	0.12	3.12	3	0.03
Swim	33.32_{ab}	1.45	28.78_{a}	0.51	24.87_{bc}	1.21	29.82_{c}	0.48	7.158	3	< 0.00
Walk	0.45	0.12	1.19	0.11	1.11	0.22	0.57	0.07	1.71	3	0.16
Fly	10.32_{ab}	1.10	7.20_{ac}	0.34	7.52_{d}	0.91	2.23_{bcd}	0.17	54.03	3	< 0.00
Alert	2.03	0.42	1.59	0.13	1.02	0.26	1.48	0.12	0.62	3	0.60
Agonistic	0.04	0.02	0.07	0.02	0.03	0.02	0.04	0.01	0.69	3	0.56
Courtship	0.02	0.02	0.08	0.03	0.09	0.03	0.09	0.03	0.23	3	0.87
N	589		4,456		708		5,863				

Table 1.3 Top models, within 2 ΔAIC units, used to investigate the influence of 8 environmental variables on the behavior of wintering American black ducks in coastal New Jersey Oct.–Feb. 2009–2011.

Period	Behavior	Model	K	N	AIC	ΔAIC
Morning Crepuscular	Feeding	PRECIP+TEMP	3	589	-1,052.93	0.00
		PRECIP	2	589	-1,052.43	0.49
	Resting	TEMP+CLOUD	3	589	-1,019.22	0.00
	Swimming	PRECIP	2	589	-965.58	0.00
		Null	1	589	-964.18	1.39
		TIDE	2	589	-964.04	1.54
		PRECIP+TEMP	3	589	-963.82	1.76
	Flying	TIDE+TEMP	3	589	-1,517.54	0.00

Period	Behavior	Model	K	N	AIC	ΔAIC
Diurnal	Feeding	TIDE+ICE	3	4,456	-7,380.03	0.00
	Resting	TIDE+ICE	3	4,456	-7,619.19	0.00
		ICE	2	4,456	-7,617.76	1.43
	Swimming	TEMP+CLOUD	3	4,456	-7,996.61	0.00
	Flying	TIDE+TEMP	3	4,456	-13,176.22	0.00
		TIDE+ICE	3	4,456	-13,175.80	0.42

Table 1.3 continued…

Period	Behavior	Model	K	N	AIC	ΔAIC
Evening Crepuscular	Feeding	TIDE+MOON	3	708	-1,058.80	0.00
	Resting	WIND	2	708	-1,322.43	0.00
	Swimming	TIDE+MOON	3	708	-1,374.40	0.00
		MOON	2	708	-1,373.89	0.50
	Flying	PRECIP+TEMP	3	708	-2,010.41	0.00

Period	Behavior	Model	K	N	AIC	ΔAIC
Nocturnal	Feeding	TIDE+TEMP	3	5,863	-9,042.71	0.00
	Resting	TEMP+COUD	3	5,863	-9,862.74	0.00
	Swimming	TIDE+TEMP	3	5,863	-10,263.49	0.00
		TIDE	2	5,863	-10,262.43	1.05
		TIDE+MOON	3	5,863	-10,262.31	1.18
		HUNT+TIDE	3	5,863	-10,261.84	1.65
	Flying	TIDE+TEMP	3	5,863	-23,827.48	0.00

Table 1.4 Direction of significant relationships for 8 explanatory variables included in candidate models investigating the behavior of American black ducks wintering in coastal New Jersey, during four time periods within the 24 hr day. Gray boxes indicate variables that were not included in top models (>2 ΔAIC units).

		Predictive variable							
Period	Behavior	Hunting Season	Temperature	Tidal Height	Precipitation	Cloud Cover	Wind Speed	Ice Cover	Moon Phase
Morning Crepuscular	Feeding		–		+				
	Resting		–			+			
	Swimming			+	–				
	Flying		+	+					
Diurnal	Feeding			–				–	
	Resting			+				+	
	Swimming		+			+			
	Flying		+	+				–	
Evening Crepuscular	Feeding			–					–
	Resting						+		
	Swimming			+					+
	Flying		+		+				
Nocturnal	Feeding		–	–					
	Resting		+			+			
	Swimming	+	–	+					–
	Flying		+	+					

Figure 1.2 Spatially and temporally distinct time budgets for American black ducks wintering in coastal New Jersey Oct-Feb, 2009–2011. Open season or closed season denotes the coastal duck hunting season. Hunting denotes the observations were collected on areas open to waterfowl hunting. Non-hunting denotes the observations were conducted in areas where waterfowl hunting is illegal.

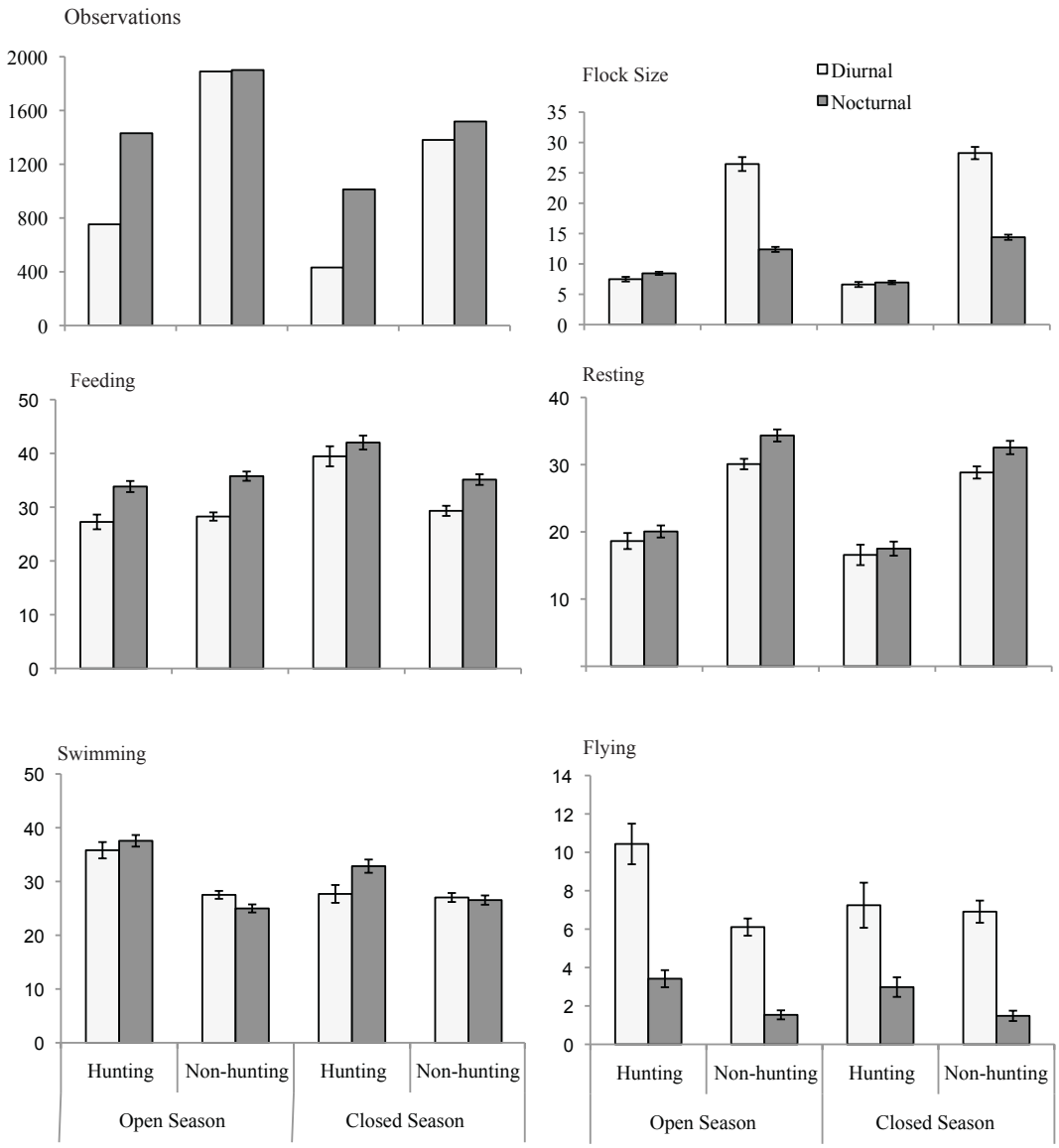


Table 1.5 Disturbances of American black ducks wintering in coastal New Jersey Oct-Feb, 2009–2011.

	Morning Crepuscular	Diurnal	Evening Crepuscular	Nocturnal	Total
Number of Disturbances	9	46	2	10	67
Disturbance Rate	0.015	0.01	0.003	0.002	0.006
Hunting boat		4		1	5
Commercial boat	2	2			4
Recreational boat		2			2
Fixed wing		3	1	2	6
Helicopter		2		1	3
Pedestrian	1	5			6
Vehicle	2	5			7
Gunshots	1	4			5
Avian predator	3	15	1		19
Mammalian predator				6	6
Unknown		4			4
Hunting Area	3	8		4	15
Non-hunting Area	6	38	2	6	52

Chapter 2

INCORPORATING THE NOCTURNAL BEHAVIOR OF AMERICAN BLACK DUCKS INTO ESTIMATES OF DAILY ENERGY EXPENDITURE

Introduction

The 1986 North American Waterfowl Management Plan (NAWMP) sought to address the decline of waterfowl by establishing population objectives and long-term management strategies. An important concept to restoring waterfowl populations as outlined in recent updates of NAWMP is a science-based linkage between population objectives and habitat conservation (NAWMP Plan Committee 2004, Runge et al. 2006). As a result, several joint ventures (JV; Arctic Goose JV, Central Valley Habitat JV, Mississippi Alluvial Valley JV, Gulf Coast JV) adopted a bioenergetic approach to quantify carrying capacities. A bioenergetic approach identifies the amount of foraging habitat required to meet population objectives, evaluates the extent to which these needs have been addressed on a regional scale, and identifies areas for priority action (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1986). In response to a long term decline in the Mid-winter Waterfowl Survey counts of wintering American black ducks (*Anas rubripes*) the Black Duck Joint Venture has identified its top

research priority as estimating regional nutritional carrying capacity (Black Duck Joint Venture Management Board 2008).

To assess bioenergetic estimates of carrying capacity, researchers must quantify the energy supply and demand. In the Atlantic Flyway, Plattner et al. (2010) and Cramer et al. (2012) recently estimated black duck food and energy supply in New York and New Jersey. However, little information is known about the associated energy demand, or daily energy expenditures (*DEE*). There are two methods to estimate *DEE*. Previous researchers have estimated *DEE* to be three times the resting metabolic rate (Purol 1975, Prince 1979, Heitmeyer 1989). Resting metabolic rate (*RMR*) for black ducks was historically estimated through a series of respirometry studies (Hartung 1967, Berger et al 1970, Wooley and Owen 1977, Bennett and Harvey 1987). Miller and Eadie (2006) recently proposed an allometric equation that predicted an average *RMR* for dabbling ducks based on a correlation with body mass and applied it to *DEE* (hereafter termed DEE_A). This method allows energetic demand for multiple species of waterfowl to be estimated with little labor investment (e.g., Bishop and Vrtiska 2008). However, it does not account for changes in behavior due to external variation (e.g., temperature, tide, time of day, month, latitude, harvest pressure, disturbance, etc.) that are known to influence both daily activities and *DEE* (Weathers 1979, Albright et al. 1983, Brodsky and Weatherhead 1985, Morton 1989*a*,*b*).

A second methodology of estimating *DEE*, using time-energy budgets, accounts for these external variations. This methodology relies on extensive

behavioral observations to determine the percentage of time free-living individuals spend in different behavioral states and then uses energetic equivalents to convert them into estimates of energy expenditure (Paulus 1988). Estimating *DEE* through time energy budgets is labor intensive, time consuming, assumes random observability, and is historically limited to diurnal observations (Jorde and Owen 1988, hereafter termed DEE_{TED} where the "TE" stands for time-energy budget and the "D" stands for time energy budget based on diurnal scans). However, there is concern as to whether this methodology is truly representative of 24-hour behavior. Due to both a lack of technology and initiative, the nocturnal behavior of wintering waterfowl has largely not been quantified (Jorde and Owen 1988, Paulus 1988).

Acknowledging the potential shortcomings of both DEE_A and DEE_{TED}, I had two objectives. First, I estimated the daily energy expenditure of wintering black ducks in coastal New Jersey calculated from 24-hour time-energy budgets inclusive of nocturnal and crepuscular behavior (hereafter DEE_{TE24}). Second, I evaluated whether estimates of *DEE* using the three methodologies differed. If the various estimates of *DEE* do not differ, managers can use DEE_A as a relatively simple and inexpensive way to estimate *DEE* and instead focus their efforts on quantifying energy supply to estimate bioenergetic carrying capacity.

Study Area

I observed black duck behavior in coastal wetland habitat in Ocean and Atlantic counties, New Jersey, USA (Figure 2.1). I defined my study area as west of the Atlantic Ocean, north of NJ state route 30, east of NJ state route 9, and

south of Little Egg Harbor. This area consistently has the highest counts of wintering black ducks in the Mid-winter Waterfowl Survey (MWS) throughout the Atlantic Flyway and corresponds closely with MWS New Jersey flight segments 11, 13 and 14. (USFWS MBDC 2010). The major landscape features within the study area are the estuarine systems between Great Bay and Absecon Bay and the managed impoundments at Edwin B. Forsythe NWR.

Habitat types that black ducks frequent within the study area consist of expansive areas of salt marsh, both high marsh and low marsh, as well as mudflats, subtidal waters, and impounded brackish and freshwater wetlands. These habitat types are differentiated by tidal hydrology. High marsh habitat is located above the mean high tide line and is irregularly flooded. The high marsh is dominated by halophytic grasses with the most common being *Spartina patens* and *Distichlis spicata*. Quasi-tidal pools and pannes were occasional landscape features found in the high marsh. Low marsh habitat is located between the mean high tide and low tide line and is regularly flooded. The low marsh is dominated by tall form *Spartina alterniflora*. Mudflat habitat was present in two forms, as broad flats in bays or in narrow ribbons along the edges of tidal creeks and ditches. Both forms are only exposed at low tide. Vegetation is generally absent on mudflat habitat however occasional tussocks of *Spartina alterniflora* and submerged aquatic vegetation consisting of sea lettuce (*Ulva lactuca*) are present. Subtidal habitat is located below the mean low tide line and is rarely exposed. Subtidal habitat is generally absent of vegetation, with the exception of beds of submerged aquatic vegetation, the most common being *Ulva lactuca* (Tiner 1987,

Collins and Anderson 1994). Also located within the study area were 1,400 acres of freshwater and saline impoundments managed by Edwin B. Forsythe National Wildlife Refuge.

The historical mean temperature and precipitation of coastal New Jersey during months included in this study were October 14.0°C, 8.4 cm, November 8.3°C, 8.1 cm, December 2.94°C, 9.0 cm, January 0.72°C, 8.9 cm, and February 0.83°C, 8.3 cm (Office of the New Jersey State Climatologist 2010).

Methods

To estimate DEE_{TE24}, I used a method similar to Albright et al. (1983) and Cramer (2009):

$$\mathrm{DEE_{TE}} = \sum_{hr=1}^{n}\sum_{i=1}^{n}\left[\left(\left(\mathrm{RMR} \times \mathrm{a_i}\right) + \mathrm{CT}\right) \times \mathrm{T_i}\right] \qquad (1)$$

where *RMR* = Resting Metabolic Rate (kJ/bird/hr), a_i = activity specific factorial increase in *RMR* for the ith behavioral activity, *CT* = cost of thermoregulation at a specified temperature (kJ/bird/hr), T_i = proportion of time engaged in the ith behavioral activity, and all values are summed across behaviors (*i*) and hours (*hr*) within the 24-hr cycle. I used an estimate of *RMR*, predicted by an allometric equation in Miller and Eadie (2006):

$$RMR = aMass^b \qquad (2)$$

where *a* = a mass proportionality coefficient, *Mass* = body mass (kg), and *b* = slope of the regression line on a log scale (Miller and Eadie 2006). I used the predicted *a* and *b* constants based on the allometric relationships reported for the group "dabbling ducks" (a = 457, b = 0.77; Miller and Eadie 2006). For the *Mass* term I used the same average weight (1.1678 kg) as Cramer (2009), which was

taken from a sample of black ducks (n = 140; 26 SY-M, 35 SY-F, 55 ASY-M, 25 ASY-F) trapped in southern New Jersey during the winter of 2009 (T. C. Nichols, New Jersey Division of Fish and Wildlife, unpublished data). This resulted in an estimated *RMR* of 514.98 kJ/bird/day. I used the values estimated by Wooley (1976) to derive the activity-specific factorial increase in *RMR* (a_i) which were: 1.7 for feeding, 1.2 for resting, 2.1 for comfort, 2.2 for swimming, 2.2 for alert, 12.5 for flying, 1.7 for walking, 2.4 for agonistic, and 2.4 for courtship. I calculated the cost of thermoregulation by:

$$m_c * \Delta T_{LCT-Ta} \quad (3)$$

where m_c is the slope of increasing metabolic energy above the lowest critical temperature (*LCT*) which I derived from Wooley (1977), and ΔT_{LCT-Ta} is the difference in ambient temperature from the lowest critical temperature.

I collected behavioral data, to inform T_i, between the third week in October and the third week in February 2009–2010 and 2010–2011. I quantified the morning crepuscular, diurnal, evening crepuscular, and nocturnal behavior of American black ducks during paired 6 hr observation sessions at the same location beginning 12 hr apart. Beginning observation sessions 12 hr apart allowed for a comparison between diurnal and nocturnal periods under similar tide cycles. I established 44 independent blind sites loosely grouped into sets of two or three for logistical access by observer teams. I randomly chose grouped blind sites for daily observations. I based observation locations on known concentrations of black ducks from field observations of black duck activity, local knowledge, and previous research. Access throughout the study period and the

ability to minimize observer disturbance of black ducks was also considered when establishing locations. Each blind site was located a minimum of 400 m apart and had a predetermined field of view that did not overlap with that of other blinds. I divided the 24-hr day into four observation periods; morning (03:00–09:00), diurnal (09:00–15:00), evening (15:00–21:00), and nocturnal (21:00–03:00). Each week was assigned a pair of time periods, either morning/evening or diurnal/nocturnal and weekly assignments alternated. Weekly observations began Tuesday morning and continued through Sunday.

A single observer arrived at a blind site ≥30 min before the designated observation period and either erected or entered an observation blind. Blinds were located in a position where they maximized viewing opportunity and minimized the potential of influencing waterfowl behavior. At the start of the observation period, observers scanned the surrounding area for waterfowl. Observers made diurnal observations with an 8x42 pair of binoculars and nocturnal observations with a generation 3, 6x night vision scope (Morovision MV 760 Generation 3 Pinnacle). Two hundred meters was identified as the maximum range that an observer could reliably determine behavior and species with the night vision equipment used in this study. Therefore, during diurnal observations, only birds ≤ 200 m were included to ensure equal nocturnal and diurnal sampling coverage. Any waterfowl detected were identified to species and observed using the instantaneous scan sampling method (Altmann 1974). The bird's behavior, the moment the observer detected the bird, was quietly recorded onto a micro-cassette tape or digital voice recorder. Behavior categories

were: feeding, loafing, sleeping, comfort, swimming, alert, flying, walking, agonistic, and courtship. This was repeated every 10 min for the duration of the 6 hr observation period. I then divided the number of birds exhibiting each activity by the total number of birds observed to calculate the proportion of birds in each activity.

Hourly Energy Expenditure

I multiplied each 10 min estimate of energy expenditure by 6 to calculate hourly energy expenditure (*HEE*). I used a one-way analysis of variance to compare hourly energy expenditure across all four periods (ANOVA, $\alpha = 0.05$). Tukey's post-hoc comparisons were used to detect pairwise differences.

24 hr Energy Expenditure

I averaged the *HEE* by period for each month. To scale energy expenditure to a period level, I calculated the number of hours each period made up of each day. Each crepuscular period consisted of 1 hour, to account for the constantly changing length of the diurnal and nocturnal periods, I determined the number of respective hours between sunrise and sunset and subtracted by 1 hour to account for the crepuscular periods. I then multiplied the average *HEE* for each month by the average number of hours in each period of each month. This resulted in an estimate of energy expenditure for each period during each month. I summed the 4 periods to estimate *DEE* per month.

Comparison of Methodologies

To estimate DEE_{TED}, I multiplied my estimated diurnal *HEE* for each month by 24 thereby assuming that diurnal behavior was representative of all

hours within the 24 hr cycle. I used a paired t-test to compare the estimated DEE_{TED} and DEE_{TE24} for each month over the 2 years (n=10).

I then estimated two values of DEE_A with the following equation:

$$DEE_A = RMR \times 3 \tag{4}$$

where *RMR* was either the allometrically derived value (514.98 kJ/bird/day) from Miller and Eadie (2006) as used in equations 1 and 2, or a black duck specific *RMR* (414.75 kJ/bird/day) calculated by averaging the 4 published values of *RMR* for black ducks (Hartung 1967, Berger et al. 1970, Wooley and Owen 1977, and Bennett and Harvey 1987). The term "3" is the estimated increase of *RMR* used to account for external variation in the energetic costs of daily activities (Purol 1975, Prince 1979, Heitmeyer 1989). I used a one-sample t-test ($\alpha \leq 0.05$) to compare the estimated DEE_{TE24} against the single value of DEE_A.

Results

I collected 11,542 observations of black duck behavior. This consisted of 589 observations during the morning crepuscular period, 4,456 observations during the diurnal period, 708 during the evening crepuscular period, and 5,863 were during the nocturnal period. Across all behaviors, observation periods, and months, *HEE* averaged 51.32 ± SE 0.41 kJ/bird/hr. When scaled to a 24-hr day DEE_{TE24} was 1,231.78 ± SE 9.88 kJ/bird/day (Table 2.1).

Hourly Energy Expenditure

However, *HEE* was different between periods ($F_{3, 11,612} = 79.260$, $P < 0.001$): morning crepuscular 65.70 ± SE 2.53 kJ/bird/hr, diurnal 56.15 ± SE 0.78 kJ/bird/hr, evening crepuscular 55.88 ± SE 2.10 kJ/bird/hr, and nocturnal 45.43 ±

SE 0.41 kJ/bird/hr (Table 2.1 and Figure 2.2). Pair-wise comparisons indicated morning crepuscular *HEE* was higher than *HEE* during the diurnal, evening crepuscular, and nocturnal periods. Diurnal *HEE* was lower than morning crepuscular *HEE* and higher than nocturnal *HEE*. Nocturnal *HEE* was lower than all other periods (Figure 2.1).

24 hr Energy Expenditure

I further calculated a period-specific *HEE* for each month, multiplied this by the number of hours in each period, and then summed energy expenditure for the average period length per month (Table 2.2), thereby creating a weighted 24 hr energy budget (Figure 2.3). Across all periods, black ducks exhibited the highest energy expenditure in October-December (Oct: 1,281.28 ± SE 40.46, Nov: 1,259.24 ± SE 23.97, Dec: 1,269.05 ± SE 19.37), with a decreased energy expenditure in Jan-Feb (1,176.98 ± SE 14.76, 1,130.98 ± SE 19.23, respectively) (Table 2.2).

Comparison of Methodologies

To replicate previous research efforts I scaled the average monthly diurnal *HEE* to 24 hours. Using only diurnal observations the average daily energy expenditure (DEE_{TED}) over the entire winter was 1,349.01 ± SE 18.75 kJ/bird/day while the average *DEE* using observational data from all four periods summed to the 24 hr day, DEE_{TE24} was significantly lower at 1,235.65 ± SE 37.33 kJ/bird/day (paired t-test: $t_9 = 3.36$, $P < 0.001$). Additionally, my estimate of DEE_A produced a value of 1544.95 kJ/bird/day which was higher than DEE_{TE24} (one-sample t-test: $t_9 = -8.29$, $P < 0.001$). However, my estimate of DEE_A using a black duck

specific *RMR* produced a value of 1244.25 kJ/bird/day, which was not significantly different than DEE_{TE24} (one-sample t-test: $t_9 = -0.23$, $P = 0.82$).

Discussion

My estimate of daily energy expenditure using an extrapolated diurnal time-energy budget (DEE_{TED}) was higher than my 24-hr time-energy budget (DEE_{TE24}). However, my estimate of DEE_{TE24} was higher than all previous estimates of *DEE* even though prior estimates only included diurnal and limited crepuscular observations. Hickey (1980) estimated black duck winter DEE_{TED} as 929.07 kJ/bird/day for males and 887.22 kJ/bird/day for females. Albright et al. (1983) estimated DEE_{TED} between 665.42–1,000.22 kJ/bird/day dependent on temperature. Most recently Cramer (2009) estimated a DEE_{TED} of 1,187.3 kJ/bird/day.

My estimate of DEE_{TE24} (1,235.65 ± SE 37.33 kJ/bird/day) was similar to an estimate of *DEE* using a predictive equation with a black duck specific *RMR* (DEE_A, 1,244.25 kJ/bird/day), where *RMR* is simply multiplied by 3. To calculate this value of DEE_A I averaged the four published estimates of *RMR* for black ducks.

I believe the DEE_{TE24} I calculated is higher than previous estimates largely because of three factors. First, I recorded a higher percentage of flight behavior than other studies (Chapter 1). Flight is the most energetically expensive (12.5 × Resting Metabolic Rate, *RMR*) behavior, therefore the differences that I observed in flying between periods (Chapter 1) were magnified when I calculated the energetic cost of each behavior (Table 2.1). Flight comprised 43% of energy

expended during the morning crepuscular period, 35% of diurnal energy expenditure, 35% of evening crepuscular energy expenditure, but only 13% of nocturnal energy expenditure.

Second, I found energy expenditure to differ by time period. The crepuscular periods are short periods of increased energy expenditure due to high rates of flight, while the nocturnal period is a time of reduced flight and therefore reduced energy expenditure. Previous estimates, which relied solely on diurnal observations, would have missed these temporal variations thereby increasing the error in estimates of energy expenditure. Therefore, when using behavioral observations to quantify energy expenditure, researchers should make an effort to quantify behaviors across the 24 hr day to account for differences in diurnal, crepuscular, and nocturnal behavior. In this instance multiplying a black duck specific *RMR* by 3 resulted in a statistically similar estimate of *DEE*. If researchers are unable to conduct costly and labor-intensive 24 hr observations, the simple estimate of DEE_A using a species specific *RMR* may be a closer approximation than diurnal extrapolation methodology.

A third reason my estimates of DEE_{TE24} were high is that I used a higher estimate of *RMR* than earlier studies of black duck energetics. Following Cramer (2009) I used a value based on Miller and Eadie's (2006) allometric predictive equation for all dabblers (*RMR* = 514.98 kJ/bird/day). An alternative approach that I also used was to average the four historic published values of black duck *RMR* (Hartung 1967, Berger et al 1970, Wooley and Owen 1977, Bennett and Harvey 1987) which came out lower (*RMR* = 414.75 kJ/bird/day) than Miller and

Eadie's (2006) dabbler specific *RMR*, resulting in a lower estimate of DEE_A. I ultimately felt more confident with the higher estimate and larger sample size provided by Miller and Eadie's (2006) dabbler specific allometric prediction in comparison to the small sample size and wide range of the black duck specific values of *RMR*. I encourage future researchers to refine black duck specific *RMR* with modern technology to test the Miller and Eadie (2006) prediction. If black ducks do in fact have a lower *RMR* than would be predicted by the predictive allometric equation managers may be able to simply multiply this *RMR* value by 3 to get an estimate of *DEE*.

Managers and researchers using predictive allometric equations to estimate *DEE* often assume that the cost of free living is 3 times the *RMR* (King 1974, Prince 1979, Heitmeyer 1989, Miller and Eadie 2006). While this makes for a simple equation there appears to be little evidence supporting this assumption. My DEE_{TE24} of 1,244.25 kJ/bird/day was 2.4 times the dabbler specific *RMR* estimate I used. This disparity was the cause of the large difference between my DEE_{TE24} and DEE_A. Refining the factorial increase above *RMR* that comprises the cost of free living would make the predictive allometric estimate more accurate and realistic. Further research should investigate whether 3.0 accurately represents the cost of free living, in my study this would have been a 20% overestimate.

My study results in three consequences for black duck management. The Atlantic Flyway Council, the Black Duck Joint Venture, the Atlantic Coast Joint Venture, and the various state and federal agencies that comprise these

groups have long sought to estimate the carrying capacity for wintering black ducks (Black Duck Joint Venture Management Board 2008). This study takes one step closer to that objective by providing a refined estimate of *DEE* and comparing various methods of estimating *DEE*. Estimating winter carrying capacity for black ducks will allow managers to evaluate the hypothesis that a decline in the quantity and quality of winter habitat is related to the long-term decline of the black duck population.

Reinecke et al. (1982) estimated the energy reserves of wintering adult (4,185-4,605 kJ) and juvenile female black ducks (2,092-2,511 kJ/bird). Following Albright et al. (1983) and Cramer (2009) I used my DEE_{TE24} to estimate the number of days days and that female black ducks could survive without food. I estimated that adult female black ducks could survive 3.5 days and juvenile females could survive 1.9 days. This is lower than the estimate that Albright et al. (1983) produced, but within the range of Cramer 2009. However, it is likely that black ducks shift their behavior pattern to conserve energy and extend reserves during periods of extreme stress (Albright 1983, Jorde 1986).

Daily energy expenditure is driven by the amount of time black ducks spend in flight. A reduction in the amount of time black ducks spend in flight would result in a lower *DEE*. Managers can attempt to reduce flight by establishing refuge areas that provide for both the feeding and resting needs of wintering black ducks. Black ducks are sensitive to disturbance a common response to disturbance, especially human caused disturbance, is to fly (Morton 2002), thereby increasing energy expenditure. Managers should recognize that

disturbance likely increases *DEE* and therefore may reduce the number of duck-use-days available for black ducks. Disturbance can be limited through traditional management practices such as establishing areas closed to public access or limiting the ease of public access. However, managers should consider innovative methods such as modifying air traffic patterns, condensing boat traffic, and educational programs that highlight the sensitivity of black ducks to disturbance.

Management Implications

Care should be taken when estimating the energy expenditure of free-living birds. I used several different methods to estimate energy expenditure which resulted in different estimates of energy expenditure. These differences in methodologies will become magnified when scaled to a winter and population level. Managers should consider this variability when estimating landscape carrying capacity and use either our conservative DEE_{TE24} or the full range of values to create an approximate error around estimates.

References

Albright, J. J. 1983. The effects of winter weather on the behavior and energy reserves of black ducks in Maine. Transactions of the Northeast Section of the Wildlife Society 40:118–128.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behavior 49:227–267.

Bennett, P. M., and P. H. Harvey. 1987. Active and resting metabolism in birds: allometry, phylogeny, and ecology. Journal of Zoology, London 213:327–363.

Berger, M., J. S. Hart, and O. Z. Roy. 1970. Respiration, oxygen consumption, and heart rate in some birds during rest and flight. Zeitschrift fur Vergleichende Physiologie 66:201–214.

Bishop, A. A., and M. Vrtiska. 2008. Effects of the Wetlands Reserve Program on waterfowl carrying capacity in the Rainwater Basin Region of south-central Nebraska. Final report. Conservation Effects Assessment Project. Natural Resources Conservation Service. Washington D.C., USA.

Black Duck Joint Venture Management Board. 2008. Black Duck Joint Venture Strategic Plan 2008–2013. U.S. Fish and Wildlife Service, Laurel Maryland; Canadian Fish and Wildlife Service, Ottawa, Ontario.

Brodsky L. M., and P. J. Weatherhead. 1985. Variability in behavioral response of wintering black ducks to increased energy demands. Journal of Canadian Zoology 63:1657–1662.

Collins, B. R., and K. H. Anderson. 1994. Plant communities of New Jersey: a study in landscape diversity. Rutgers University Press, New Brunswick, New Jersey, USA.

Cramer, D. M. 2009. Estimating habitat carrying capacity for American black ducks in wintering in Southern New Jersey. Thesis, University of Delaware. Newark, Delaware, USA.

Cramer, D. M., P. M. Castelli, T. Yerkes, and C. K. Williams. 2012. Food resource availability for American black ducks wintering in southern New Jersey. Journal of Wildlife Management 76:214–219.

Hartung, R. 1967. Energy metabolism in oil-covered ducks. Journal of Wildlife Management 31:798–804.

Heitmeyer, M. E. 1989. Agriculture/wildlife enhancement in California: The Central Valley Habitat Joint Venture. Transactions of the 54th North American Wildlife and Natural Resources Conference 54:391–401.

Hickey, T. E., Jr. 1980. Activity budgets and movements of black ducks (*Anas rubripes*) in Prince Edward Island. M.S. Thesis, McGill University, Montreal, Canada.

Jorde, D. G. 1986. Nutritional and thermodynamic aspects of the ecology of black ducks wintering in Maine. Dissertation, University of Maine. Orono, USA.

Jorde, D. G., and R. B. Owen. 1988. The need for nocturnal activity and energy budgets of waterfowl. Pages 169–177 *in* M. W. Weller, editor. Waterfowl in winter. University of Minnesota Press, Minneapolis, USA.

King, J. R. 1974. Seasonal allocation of time and energy resources in birds. Pages 4–70 *in* R. A. Paynter, Jr., editor. Avian energetics. Nuttall Ornithologist Club Publication 15.

Miller, M. R., and J. McA. Eadie. 2006. The allometric relationship between resting metabolic rate and body mass in wild wintering waterfowl (Anatidae) and an application to estimation of winter habitat requirements. The Condor 108:166–177.

Morton, J. M., R. L. Kirkpatrick, M. R. Vaughan, and D. F. Stauffer. 1989*a*. Habitat use and movements of American black ducks in winter. Journal of Wildlife Management 53:390–400.

Morton, J. M., A. C. Fowler, and R. L. Kirkpatrick. 1989*b*. Time and energy budgets of American black ducks in winter. Journal of Wildlife Management 53:401–410.

Morton, J. M. 2002. Effects of human disturbance on wintering American black ducks. Pages 11-16 *in* M. C. Perry, editor. Black ducks and their Chesapeake Bay habitats: proceedings of a symposium. U.S. Geological Survey, Biological Resources Discipline Information and Technology Report USGS/BRD/ITR–2002–0005, 44p.

North American Waterfowl Management Plan, Plan Committee. 2004. North American Waterfowl Management Plan 2004. Implementation Framework: Strengthening the Biological Foundation. Canadian Wildlife Service, U.S. Fish and Wildlife Service, Secretaria de Medio Ambiente y Recursos Naturales.

Office of the New Jersey State Climatologist. 2010. Coastal New Jersey Monthly Temperature 1895–2010. <http://climate.rutgers.edu/stateclim_v1/data/index.html> Accessed April 6, 2010.

Paulus, S.L. 1988. Time-activity budgets of nonbreeding Anatidae: a review. Pages 135–152 *in* M. W. Weller, editor. Waterfowl in winter. University of Minnesota Press. Minneapolis, USA.

Plattner, D. M., M. W. Eichholz, and T. Yerkes. 2010. Food resources for wintering and spring staging black ducks. Journal of Wildlife Management 74:1554–1558.

Prince, H. H. 1979. Bioenergetics of postbreeding dabbling ducks. Pages 103–117 *in* T. A. Bookhout, editor. Waterfowl and wetlands: An integrated review. The Wildlife Society, Betheseda, Maryland, USA.

Purol, D. A. 1975. Metabolizable energy of cellulose, three natural foods and three diets for mallards. M.S. Thesis. Michigan State University, Easting Lansing, USA.

Reinecke, K. J., T. L. Stone, and R. B. Owen Jr. 1982. Seasonal carcass composition and energy balance of female black ducks Maine. Condor 84:420–426.

Runge, M. C., F. A. Johnson, M. G. Anderson, M. D. Koneff, E. T. Reed, and S. E. Mott. 2006. The need for coherence between waterfowl harvest and habitat management. Wildlife Society Bulletin 34:1231–1237.

Tiner Jr., R. W. 1987. A field guide to coastal wetland plants of the northeastern United States. The University of Massachusetts Press, Amherst, USA.

United States Fish and Wildlife Service and Canadian Wildlife Service. 1986. North American Waterfowl Management Plan: a strategy for cooperation. U.S. Fish and Wildlife Service and Canadian Wildlife Service, Washington D.C. USA.

United States Fish and Wildlife Service Migratory Bird Data Center [USFWS MBDC]. 2010. Midwinter waterfowl index database. <https://migbirdapps.fws.gov/> Accessed 3/29/2010.

Weathers, W. W. 1979. Climatic adaptation in avian standard metabolic rate. Oceologia 42:81–89.

Wooley Jr., J. B. 1976. Energy expenditure of the black duck under controlled and free-living conditions. M.S. Thesis, University of Maine, Orono, USA.

Wooley Jr., J. B., and R. B. Owen. 1977. Metabolic rates and heart rate-metabolism relationships in the black duck (*Anas rubripes*). Journal of Comparative Biochemistry and Physiology 57:363–367.

Figure 2.1. Study area consisting of estuarine habitats between Great Bay and Absecon Bay, of coastal New Jersey USA. Property owned by the U.S. Fish and Wildlife Service Edwin B. Forsythe NWR and the New Jersey Division of Fish and Wildlife is identified. Observation blind sites are identified with dots

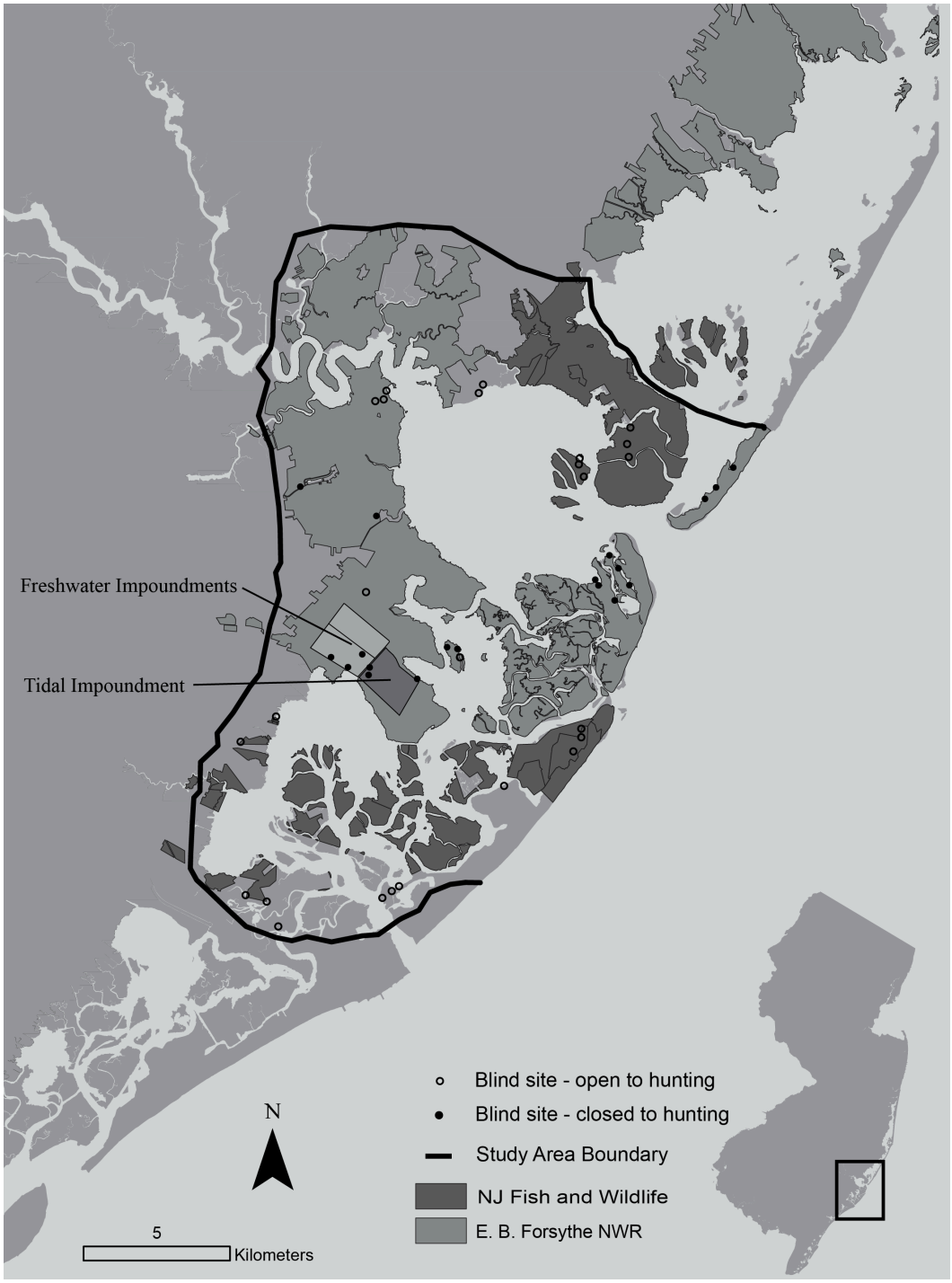


Table 2.1 Hourly energy expenditure (*HEE*, kJ/bird/hr) by activity and period for American black ducks wintering in coastal New Jersey Oct-Feb 2009–2011.

	Observation Period									
	Morning Crepuscular		Diurnal		Evening Crepuscular		Nocturnal		24 Hour[1]	
Behavior	x	SE	x	SE	x	SE	x	SE	x	SE
Feeding	9.85	0.55	11.42	0.21	15.67	0.56	14.37	0.20	13.09	0.14
Resting	8.08	0.44	7.44	0.14	6.32	0.34	7.95	0.14	7.66	0.10
Comfort	1.53	0.20	2.40	0.09	1.63	0.19	1.00	0.06	1.60	0.05
Swimming	17.09	0.74	14.20	0.25	12.52	0.61	15.05	0.24	14.67	0.16
Alert	1.01	0.20	0.77	0.06	0.50	0.13	0.73	0.06	0.75	0.04
Flying	27.94	2.98	19.44	0.91	20.31	2.45	6.04	0.47	13.16	0.48
Walking	0.18	0.05	0.46	0.04	0.44	0.09	0.22	0.03	0.32	0.02
Agonistic	0.02	0.01	0.04	0.01	0.01	0.01	0.02	0.01	0.03	0.01
Courtship	0.01	0.01	0.04	0.02	0.05	0.02	0.05	0.02	0.04	0.01
Total[2]	65.70	2.53	56.21	0.78	57.45	2.10	45.43	0.59	51.32	0.41

[1] Average *HEE* by behavior with observation periods combined

[2] Average *HEE* by observation period and all periods combined

Figure 2.2 Average hourly energy expenditure (*HEE*) for American black ducks wintering in coastal New Jersey during four time periods. Error bars report ± standard error (SE). Like letters denote statistical differences (Tukey's post-hoc comparison, $\alpha \leq 0.05$).

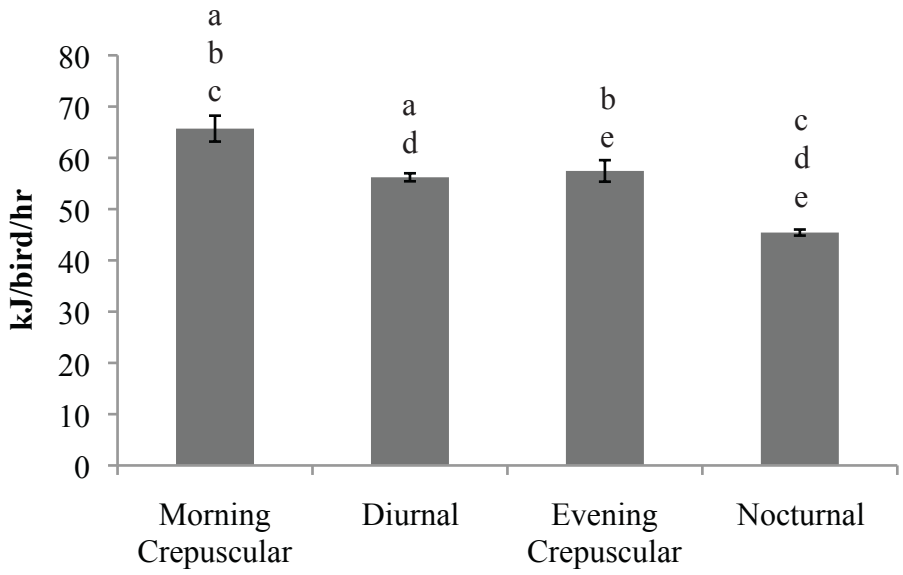
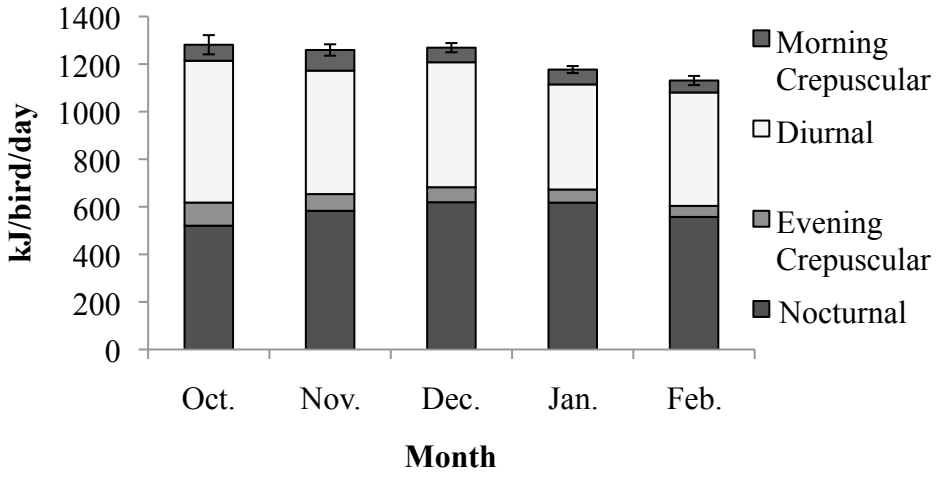


Table 2.2 Average energy expenditure per period for wintering American black ducks in coastal New Jersey Oct-Feb 2009–2011.

		October		November		December		January		February	
	Period	x	SE	x	SE	x	SE	x	SE	x	SE
kJ/hr	Morning Crepuscular	67.29	8.00	86.66	8.15	61.32	5.55	62.42	3.68	50.31	2.83
	Diurnal	60.92	2.97	59.19	1.91	62.03	1.73	50.47	1.17	49.99	1.50
	Evening Crepuscular	97.10	17.93	70.38	7.39	63.06	5.24	55.26	3.64	46.49	2.26
	Nocturnal	42.60	1.64	45.15	1.02	45.75	0.74	46.61	0.70	44.72	0.99
hr/period	Morning Crepuscular	1.00	-	1.00	-	1.00	-	1.00	-	1.00	-
	Diurnal	9.79	-	8.77	-	8.47	-	8.75	-	9.54	-
	Evening Crepuscular	1.00	-	1.00	-	1.00	-	1.00	-	1.00	-
	Nocturnal	12.22	-	12.91	-	13.53	-	13.25	-	12.46	-
kJ/period	Morning Crepuscular	67.29	8.00	86.66	8.15	61.32	5.55	62.42	3.68	50.31	2.83
	Diurnal	596.29	29.12	519.15	16.71	525.45	14.69	441.86	10.27	476.90	14.34
	Evening Crepuscular	97.10	17.93	70.38	7.39	63.06	5.24	55.26	3.64	46.49	2.26
	Nocturnal	520.60	20.10	583.05	13.21	619.22	10.07	617.44	9.25	557.27	12.29
	24 hr	1281.28	40.46	1259.24	23.97	1269.05	19.37	1176.97	14.76	1130.98	19.23

Figure 2.3 Weighted 24 hr energy budget for American black ducks wintering in coastal New Jersey, Oct-Feb, 2009–2011.



Appendix A: Candidate models investigating the behavior of American black ducks wintering in coastal New Jersey across four time periods Oct–Feb, 2009–2011.

Period	Behavior	Model	K	N	AIC	ΔAIC
Morning Crepuscular	Feeding	PRECIP+TEMP	3	589	-1052.93	0.00
		PRECIP	2	589	-1052.43	0.49
		WIND	2	589	-1046.28	6.65
		TIDE	2	589	-1042.77	10.16
		Null	1	589	-1041.37	11.55
		TIDE+TEMP	3	589	-1041.31	11.62
		TIDE+ICE	3	589	-1041.27	11.66
		HUNT+TIDE	3	589	-1041.00	11.92
		ICE	2	589	-1040.85	12.07
		TIDE+MOON	3	589	-1040.77	12.15
		TEMP	2	589	-1040.19	12.74
		CLOUD	2	589	-1039.54	13.38
		HUNT	2	589	-1039.46	13.46
		MOON	2	589	-1039.45	13.47
		TEMP+CLOUD	3	589	-1038.51	14.41
		HUNT+TEMP	3	589	-1038.44	14.48
	Resting	TEMP+CLOUD	3	589	-1019.22	0.00
		TIDE+TEMP	3	589	-1016.31	2.91
		PRECIP+TEMP	3	589	-1015.55	3.67
		TEMP	2	589	-1014.58	4.64
		HUNT+TEMP	3	589	-1013.32	5.90
		TIDE+ICE	3	589	-1012.85	6.37
		ICE	2	589	-1012.72	6.50
		TIDE+MOON	3	589	-1011.35	7.87
		HUNT	2	589	-1010.68	8.54
		PRECIP	2	589	-1009.98	9.24
		TIDE	2	589	-1009.88	9.33
		WIND	2	589	-1009.87	9.35
		MOON	2	589	-1009.49	9.72
		HUNT+TIDE	3	589	-1009.47	9.74
		CLOUD	2	589	-1009.06	10.15
		Null	1	589	-1007.03	12.18

Period	Behavior	Model	K	N	AIC	ΔAIC
Morning Crepuscular	Swimming	PRECIP	2	589	-965.58	0.00
		Null	1	589	-964.18	1.39
		TIDE	2	589	-964.04	1.54
		PRECIP+TEMP	3	589	-963.82	1.76
		CLOUD	2	589	-963.39	2.19
		ICE	2	589	-963.18	2.40
		HUNT+TIDE	3	589	-962.47	3.11
		HUNT	2	589	-962.46	3.11
		WIND	2	589	-962.44	3.14
		TIDE+ICE	3	589	-962.43	3.15
		TEMP	2	589	-962.21	3.37
		MOON	2	589	-962.19	3.39
		TIDE+MOON	3	589	-962.09	3.49
		TIDE+TEMP	3	589	-962.04	3.54
		TEMP+CLOUD	3	589	-961.50	4.07
		HUNT+TEMP	3	589	-960.53	5.04
	Flying	TIDE+TEMP	3	589	-1517.54	0.00
		TIDE+MOON	3	589	-1514.90	2.64
		TIDE+ICE	3	589	-1514.03	3.51
		TIDE	2	589	-1507.44	10.10
		ICE	2	589	-1506.26	11.28
		HUNT+TIDE	3	589	-1505.67	11.86
		TEMP	2	589	-1504.91	12.63
		HUNT+TEMP	3	589	-1503.70	13.84
		PRECIP+TEMP	3	589	-1503.05	14.49
		TEMP+CLOUD	3	589	-1502.91	14.63
		MOON	2	589	-1502.76	14.78
		Null	1	589	-1492.39	25.15
		CLOUD	2	589	-1490.77	26.77
		PRECIP	2	589	-1490.48	27.06
		WIND	2	589	-1490.44	27.09
		HUNT	2	589	-1490.41	27.13

Period	Behavior	Model	K	N	AIC	ΔAIC
Diurnal	Feeding	TIDE+ICE	3	4,456	-7380.03	0.00
		HUNT+TIDE	3	4,456	-7342.49	37.54
		TIDE+TEMP	3	4,456	-7339.83	40.21
		TIDE+MOON	3	4,456	-7337.71	42.32
		TIDE	2	4,456	-7327.60	52.43
		HUNT+TEMP	3	4,456	-7301.30	78.73
		TEMP+CLOUD	3	4,456	-7283.88	96.15
		ICE	2	4,456	-7281.30	98.73
		PRECIP+TEMP	3	4,456	-7273.65	106.38
		HUNT	2	4,456	-7273.65	106.38
		CLOUD	2	4,456	-7271.79	108.24
		TEMP	2	4,456	-7264.65	115.38
		PRECIP	2	4,456	-7259.13	120.90
		MOON	2	4,456	-7254.61	125.42
		Null	1	4,456	-7251.45	128.58
		WIND	2	4,456	-7251.32	128.71
	Resting	TIDE+ICE	3	4,456	-7619.19	0.00
		ICE	2	4,456	-7617.76	1.43
		TEMP+CLOUD	3	4,456	-7567.03	52.16
		CLOUD	2	4,456	-7553.74	65.45
		PRECIP+TEMP	3	4,456	-7552.85	66.34
		TEMP	2	4,456	-7550.65	68.54
		TIDE+TEMP	3	4,456	-7548.73	70.46
		HUNT+TEMP	3	4,456	-7548.68	70.51
		PRECIP	2	4,456	-7539.32	79.86
		WIND	2	4,456	-7539.11	80.08
		MOON	2	4,456	-7536.44	82.75
		Null	1	4,456	-7536.28	82.91
		HUNT	2	4,456	-7535.81	83.37
		TIDE+MOON	3	4,456	-7534.44	84.75
		TIDE	2	4,456	-7534.32	84.87
		HUNT+TIDE	3	4,456	-7533.82	85.37

Period	Behavior	Model	K	N	AIC	ΔAIC
Diurnal	Swimming	TEMP+CLOUD	3	4,456	-7996.61	0.00
		CLOUD	2	4,456	-7992.69	3.92
		HUNT+TEMP	3	4,456	-7976.34	20.28
		HUNT+TIDE	3	4,456	-7966.09	30.52
		PRECIP+TEMP	3	4,456	-7965.88	30.73
		HUNT	2	4,456	-7965.14	31.48
		WIND	2	4,456	-7963.93	32.68
		TIDE+TEMP	3	4,456	-7963.62	32.99
		TIDE+MOON	3	4,456	-7963.11	33.51
		TEMP	2	4,456	-7961.71	34.90
		PRECIP	2	4,456	-7960.32	36.29
		MOON	2	4,456	-7959.67	36.94
		TIDE	2	4,456	-7958.91	37.71
		TIDE+ICE	3	4,456	-7956.91	39.71
		Null	1	4,456	-7956.81	39.80
		ICE	2	4,456	-7954.90	41.71
	Flying	TIDE+TEMP	3	4,456	-13176.22	0.00
		TIDE+ICE	3	4,456	-13175.80	0.42
		TIDE	2	4,456	-13166.87	9.35
		HUNT+TIDE	3	4,456	-13165.47	10.76
		TIDE+MOON	3	4,456	-13164.89	11.33
		PRECIP+TEMP	3	4,456	-13122.28	53.94
		TEMP+CLOUD	3	4,456	-13118.70	57.52
		PRECIP	2	4,456	-13113.63	62.59
		WIND	2	4,456	-13111.93	64.30
		ICE	2	4,456	-13111.77	64.45
		CLOUD	2	4,456	-13109.42	66.80
		TEMP	2	4,456	-13101.25	74.97
		HUNT+TEMP	3	4,456	-13100.41	75.82
		Null	1	4,456	-13091.00	85.22
		MOON	2	4,456	-13089.98	86.24
		HUNT	2	4,456	-13089.02	87.21

Period	Behavior	Model	K	N	AIC	ΔAIC
Evening Crepuscular	Feeding	TIDE+MOON	3	708	-1058.80	0.00
		TIDE	2	708	-1053.56	5.25
		HUNT+TIDE	3	708	-1053.30	5.50
		TIDE+TEMP	3	708	-1051.83	6.98
		TIDE+ICE	3	708	-1051.80	7.01
		WIND	2	708	-1025.87	32.93
		HUNT+TEMP	3	708	-1023.20	35.60
		MOON	2	708	-1021.66	37.15
		PRECIP+TEMP	3	708	-1021.07	37.73
		HUNT	2	708	-1020.69	38.11
		TEMP	2	708	-1018.86	39.94
		PRECIP	2	708	-1018.52	40.28
		TEMP+CLOUD	3	708	-1017.40	41.41
		Null	1	708	-1015.66	43.14
		ICE	2	708	-1014.00	44.81
		CLOUD	2	708	-1013.99	44.81
	Resting	WIND	2	708	-1322.43	0.00
		TIDE+MOON	3	708	-1315.10	7.33
		TIDE+ICE	3	708	-1312.53	9.91
		TIDE	2	708	-1304.89	17.54
		HUNT+TIDE	3	708	-1304.47	17.97
		TIDE+TEMP	3	708	-1303.48	18.96
		MOON	2	708	-1303.11	19.32
		ICE	2	708	-1301.78	20.65
		PRECIP+TEMP	3	708	-1296.84	25.60
		PRECIP	2	708	-1296.22	26.21
		TEMP	2	708	-1295.06	27.38
		Null	1	708	-1293.97	28.46
		HUNT+TEMP	3	708	-1293.33	29.10
		TEMP+CLOUD	3	708	-1293.30	29.13
		CLOUD	2	708	-1292.34	30.09
		HUNT	2	708	-1292.14	30.30

Period	Behavior	Model	K	N	AIC	ΔAIC
Evening Crepuscular	Swimming	TIDE+MOON	3	708	-1374.40	0.00
		MOON	2	708	-1373.89	0.50
		WIND	2	708	-1363.84	10.56
		TIDE+ICE	3	708	-1359.87	14.53
		ICE	2	708	-1358.77	15.63
		HUNT	2	708	-1356.28	18.12
		HUNT+TIDE	3	708	-1356.01	18.39
		TIDE	2	708	-1355.43	18.97
		Null	1	708	-1354.49	19.90
		HUNT+TEMP	3	708	-1354.48	19.91
		TIDE+TEMP	3	708	-1354.16	20.24
		PRECIP	2	708	-1353.19	21.21
		TEMP	2	708	-1352.60	21.80
		CLOUD	2	708	-1352.57	21.82
		PRECIP+TEMP	3	708	-1351.26	23.14
		TEMP+CLOUD	3	708	-1350.66	23.73
	Flying	PRECIP+TEMP	3	708	-2010.41	0.00
		TIDE+TEMP	3	708	-2007.49	2.93
		TIDE+ICE	3	708	-2005.89	4.52
		WIND	2	708	-2005.39	5.02
		TIDE	2	708	-2003.98	6.44
		PRECIP	2	708	-2003.64	6.78
		TEMP	2	708	-2003.58	6.83
		HUNT+TEMP	3	708	-2003.19	7.23
		TIDE+MOON	3	708	-2002.54	7.88
		HUNT+TIDE	3	708	-2002.54	7.88
		TEMP+CLOUD	3	708	-2001.58	8.83
		ICE	2	708	-1997.66	12.75
		HUNT	2	708	-1995.70	14.71
		Null	1	708	-1995.58	14.83
		MOON	2	708	-1994.32	16.09
		CLOUD	2	708	-1993.63	16.78

Period	Behavior	Model	K	N	AIC	ΔAIC
Nocturnal	Feeding	TIDE+TEMP	3	5,863	-9042.71	0.00
		TIDE+MOON	3	5,863	-9019.55	23.16
		HUNT+TIDE	3	5,863	-9019.02	23.70
		TIDE	2	5,863	-9018.05	24.66
		TIDE+ICE	3	5,863	-9016.35	26.36
		TEMP+CLOUD	3	5,863	-8737.77	304.94
		CLOUD	2	5,863	-8728.39	314.32
		TEMO	2	5,863	-8703.43	339.29
		PRECIP+TEMP	3	5,863	-8702.28	340.43
		MOON	2	5,863	-8694.83	347.88
		WIND	2	5,863	-8690.49	352.22
		HUNT	2	5,863	-8690.39	352.32
		Null	1	5,863	-8684.14	358.57
		PRECIP	2	5,863	-8682.70	360.01
		ICE	2	5,863	-8682.64	360.07
		HUNT+TEMP	3	5,863	-8679.73	362.98
	Resting	TEMP+CLOUD	3	5,863	-9862.74	0.00
		CLOUD	2	5,863	-9859.17	3.57
		TIDE+TEMP	3	5,863	-9845.75	16.99
		TIDE+ICE	3	5,863	-9835.83	26.91
		TIDE+MOON	3	5,863	-9833.11	29.63
		TIDE	2	5,863	-9832.53	30.21
		HUNT+TIDE	3	5,863	-9831.18	31.56
		WIND	2	5,863	-9825.61	37.13
		HUNT+TEMP	3	5,863	-9820.88	41.86
		TEMP	2	5,863	-9816.07	46.67
		PRECIP+TEMP	3	5,863	-9814.44	48.29
		MOON	2	5,863	-9806.41	56.33
		ICE	2	5,863	-9805.52	57.22
		Null	1	5,863	-9803.87	58.87
		HUNT	2	5,863	-9803.23	59.51
		PRECIP	2	5,863	-9802.45	60.29

Period	Behavior	Model	K	N	AIC	ΔAIC
Nocturnal	Swimming	TIDE+TEMP	3	5,863	-10263.49	0.00
		TIDE	2	5,863	-10262.43	1.05
		TIDE+MOON	3	5,863	-10262.31	1.18
		HUNT+TIDE	3	5,863	-10261.84	1.65
		TIDE+ICE	3	5,863	-10261.12	2.37
		PRECIP+TEMP	3	5,863	-10129.55	133.93
		PRECIP	2	5,863	-10128.11	135.38
		WIND	2	5,863	-10123.25	140.23
		MOON	2	5,863	-10119.62	143.87
		TEMP	2	5,863	-10117.22	146.26
		HUNT	2	5,863	-10117.15	146.33
		HUNT+TEMP	3	5,863	-10117.13	146.36
		TEMP+CLOUD	3	5,863	-10116.76	146.72
		Null	1	5,863	-10115.24	148.25
		CLOUD	2	5,863	-10113.93	149.56
		ICE	2	5,863	-10113.24	150.25
	Flying	TIDE+TEMP	3	5,863	-23827.48	0.00
		TIDE+ICE	3	5,863	-23819.91	7.57
		TIDE	2	5,863	-23818.94	8.54
		TIDE+MOON	3	5,863	-23816.94	10.54
		HUNT+TIDE	3	5,863	-23816.94	10.54
		PRECIP+TEMP	3	5,863	-23813.92	13.56
		PRECIP	2	5,863	-23806.86	20.62
		TEMP+CLOUD	3	5,863	-23806.71	20.77
		HUNT+TEMP	3	5,863	-23806.25	21.23
		TEMP	2	5,863	-23806.16	21.32
		WIND	2	5,863	-23805.81	21.67
		ICE	2	5,863	-23800.48	27.00
		Null	1	5,863	-23798.30	29.18
		CLOUD	2	5,863	-23797.29	30.19
		MOON	2	5,863	-23796.59	30.89
		HUNT	2	5,863	-23796.42	31.06